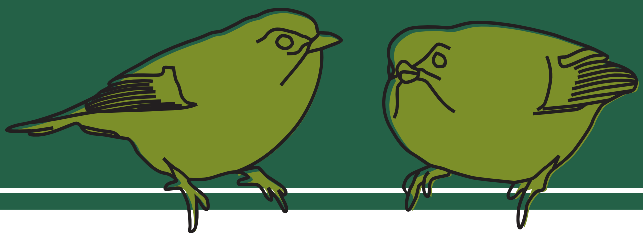


Miquel Vall-llosera Camps

Avian invasions: from basic to applied research

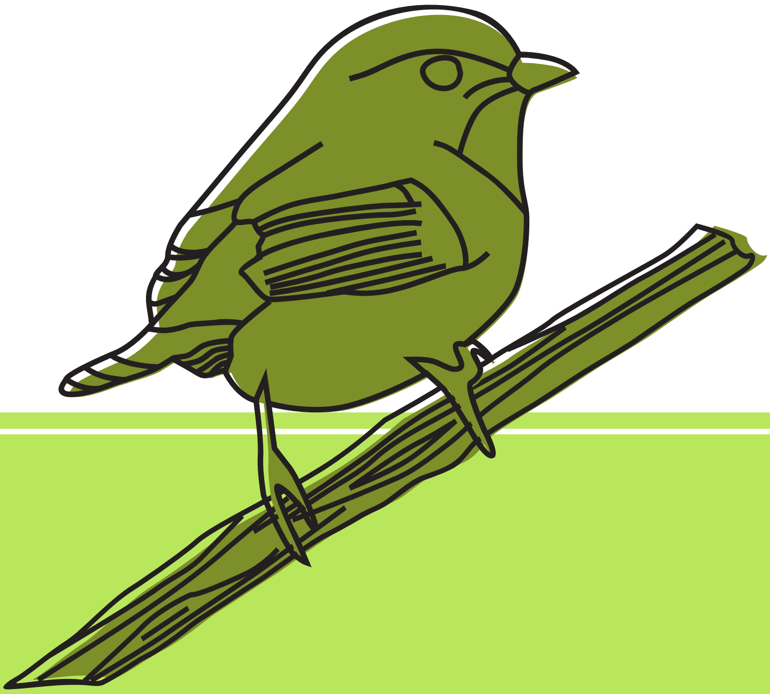
Ph.D. Thesis

Director: Dr. Daniel Sol Rueda

Centre de Recerca Ecològica i Aplicacions
Forestals

Universitat Autònoma Barcelona

Maig de 2012



Universitat Autònoma de Barcelona

CREAF

Avian invasions: from basic to applied research

Ph.D. Thesis

Miquel Vall-llosera Camps

Bellaterra, maig de 2012

Avian invasions: from basic to applied research

Memòria presentada per:

Miquel Vall-llosera Camps

per a optar al grau de Doctor

Amb el vist-i-plau de:

Director: Dr. Daniel Sol Rueda

Centre de Recerca Ecològicai Aplicacions Forestals

Centre d'Estudis Avançats de Blanes/

Centre Superior d'Investigacions Científiques

Programa de Doctorat en Diversitat i Funció d'Ecosistemes Mediterranis

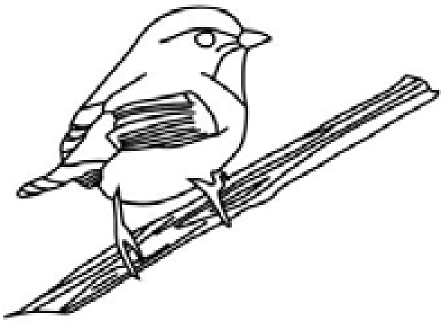
Centre de Recerca Ecologica i Aplicacions Forestals

Universitat Autònoma de Barcelona

Bellaterra, maig de 2012

I was just guessing at numbers and figures
Pulling the puzzles apart
Questions of science, science and progress
Could not speak as loud as my heart

(Coldplay, The scientist)



Cover design and illustrations by Marina Vall-llosera

Table of contents

Agraïments

La recerca científica no és mai una feina en solitari i la elaboració d'una tesi doctoral no n'és cap excepció. Aquest tesi és el resultat de la col·laboració de moltes persones a qui m'agradaria donar les gràcies en aquest moment. Espero no deixar-me a ningú.

En primer lloc m'agradaria donar les gràcies al meu director de tesi durant aquests llargs sis anys i pico, el Dr. Daniel Sol. Gràcies per confiar en mi per ser el seu primer estudiant de doctorat. Gràcies per tota l'ajuda, els consells i les correccions, per tot l'esforç invertit en mi, per la infinita paciència. Gràcies per haver ajudat a formar-me com a científic i també com a persona.

Igualment voldria donar les gràcies a les persones que formen i han format part del nostre petit grup d'investigació. Moltes gràcies a l'Anna, l'Oriol, el Gabriel, el Nacho, el César i el Joan. Moltes gràcies pels vostres comentaris i consells; no puc expressar amb prous paraules tot el que m'heu ajudat. I sobretot moltes gràcies per la vostra amistat.

Voldria donar les gràcies a coautors i col·laboradors per la seva ajuda i els seus consells, que han contribuït de manera molt important a la qualitat científica d'aquesta tesi. En especial vull donar les gràcies al Francesc, el Sergi i el Miquel.

Gràcies també als meus companys de despatx, per haver esdevingut no només companys de feina sinó també els meus amics. Moltes gràcies a la Marta, el Martín, el Shawn, i especialment, al Roger i la Rebeca. Com tampoc no em vull oblidar dels amics que he fet aquí durant tots aquests anys amb els que he compartit tantes bones estones. Moltes gràcies per la vostra companyia i amistat: Loles, Salva, Núria, Patricia, Jara, Belén, Helena, Laura, Irene, Elisa, Jose Luís, Corina, Gerard, Xavis, Bernat, Juancho, etc. Tampoc em voldria oblidar ni de l'Encarni ni de la Núria, gràcies per les rialles. Gràcies a tots per compartir amb mi els bons moments i per aguantar-me en els dolents. Estic molt content d'haver-vos conegut a tots.

És de justícia donar les gràcies al CREAF per acollir-me tant bé en les seves parets, i a totes les persones que fan d'aquest centre un lloc tan agradable per treballar, és quelcom que no es pot comptar amb diners. Gràcies al Javi per la part que li toca, i gràcies Cristina, Magda, Marta, Carreño i Franc per tenir solucions per tot i fer la vida una mica més fàcil.

També voldria donar les gràcies a totes les persones que he conegut al llarg d'aquest temps i que m'han acompanyat en els moments de desconnexió entre tanta tesi. Gràcies a tots el amics i companys de la UB (Raul, Oriol, Laura, Dario, Xènia, Palou, Carlota, Arnau, Neus, Mireia, les Maries, perdó però no us puc posar a tots). Gràcies a tots els bitxeros, als 'moritos', a l'Ignasi i la gent de Riet Vell i de la SEO; i també Joan, Xesco i companyia, la colla d'en Dani, de Veterinària, etc. Vosaltres també heu estat importants en aquest camí.

M'agradaria recordar també a les persones que sense elles arribar-s'ho a imaginar la seva aparició en la meva vida em va posar en la direcció que m'ha dut fins aquí. Així doncs, moltes gràcies Manel, Jaume, Jordi, Cristina i Esther.

I finalment m'agradaria donar les gràcies a tota la meva família, però especialment la meva mare i la meva germana, a vosaltres va dedicada aquesta tesi. Moltes gràcies pel vostre suport i la vostra generositat, per haver posat a la meva disposició tots els recursos que heu tingut, sense vosaltres al meu costat arribar fins aquí no hauria estat possible. I un record especial per a qui ja no hi és, m'hagués agradat tant.

Gràcies a tots per tot!!!

Aquesta tesi ha sigut finançada mitjançant una beca predoctoral per a la formació de personal investigador (FI) 2006FI 01245, concedida pel Departament d'Universitats, Recerca i Societat de la Informació; mitjançant els projectes de recerca CGL2007-66257/BOS i CGL2010-21838, finançats pel Ministerio de Educación y Ciencia; i mitjançant el projecte integrat del VI Programa Marc de la UE, ALARM GOCE-CT-2003-506675.

Abstract

Serious concern for environmental and economic problems caused by biological invasions has caused a huge interest in trying to understand the factors that influence the invasive process. This information is essential to prevent, assess, and mitigate the impacts of invasive species. In this context, this thesis has two main goals. The first is to ask what makes a species a successful invader, and second to investigate whether this information can be useful for preventing the impact of the invaders. This thesis explores these questions using birds as the object of study. To understand why exotic species, whose initial populations are generally small and genetically depleted, can sometimes succeed to establish themselves in environments to which they have had no opportunity to adapt it has often been invoked that successful invaders have adaptations that allow them to overcome these problems. Ecological theory suggests that life histories should be part of these adaptations. The characteristics of the species related to reproduction and survival should play an important role in reducing the risk of extinction by stochastic factors at the initial stages of the invasion process. The results indicate that successful invaders are characterized by prioritizing future over current reproduction, probably because a great success in reproducing in the future reduces the cost of reproductive failure under conditions of uncertainty and increases the opportunities to explore and respond to new environmental pressures. In addition, alien species should have adaptations to find an appropriate niche to survive in and prosper, to avoid extinction by negative population growth. This niche should include not only necessary resources, but also few competitors and enemies. Theory suggests two ways to achieve this niche: or invasive species are competitively superior and displace native species from their current niches, or invaders are opportunistic and have the ability to find unused ecological niches. In this thesis the relative importance of these two hypotheses has been contrasted trough the study of the invasion of the Red-billed Leiothrix (Leiothrix lutea) in the Collserola forest reserve. The invader established with relatively little resistance from the native species, reflecting its generalist and opportunistic nature and that its ecological requirements were underrepresented in the native community. However, there has been a decline of a native species ecologically similar to the invader during the period of expansion, presumably due to competitive displacement. These results show that both hypotheses are not mutually exclusive, but taken together can help to better understand of the establishment process. Finally, this thesis asks whether it is possible to use the species features proposed to be related to the invasive success to develop a methodology to detect potentially invasive species and, thus, to be able avoid future problems. The results show that invasive success can be predicted by the founder population size, habitat use, brain size, and the ability of species to prioritize future reproduction. Although there are few traits, the models predicted the probability of successful establishment for birds in Europe and Australia with high accuracy. Therefore, it is demonstrated that risk assessments based on characteristics related to the success of the establishment are difficult but feasible and provide a useful tool for guiding preventive polices aimed at mitigating the impact of invasive species. However, this thesis also shows that, to be fully effective, these methods have indeed to be applied in the environmental management policies if we really want to avoid a future dominated by invasive species.

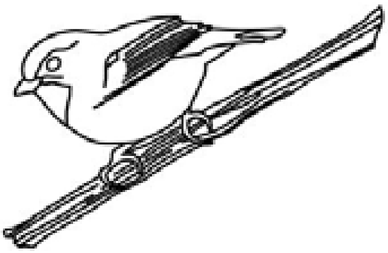
Resum

Invasions biològiques d'ocells: de la recerca bàsica a l'aplicada

La preocupació pels greus problemes ambientals i econòmics causats per les invasions biològiques ha provocat un enorme interès en tractar de comprendre els factors que influeixen en el procés invasiu. Aquesta informació és essencial per prevenir, avaluar i mitigar els impactes de les espècies invasores. En aquest context, aquesta tesi té dos objectius principals. El primer és descobrir què fa que una espècie tingui èxit en la invasió, i el segon investigar si aquests descobriments poden ser útils per prevenir l'impacte dels invasors. Aquesta tesi explora aquestes qüestions utilitzant les aus com a objecte d'estudi. Per entendre per què hi ha espècies exòtiques que, tot i començar amb poblacions sovint petites i genèticament empobrides, arriben a vegades a establir-se en ambients on no havien tingut oportunitat d'adaptar-se, sovint s'invoca que les espècies bones invasores tenen adaptacions que els permeten superar aquests problemes. La teoria ecològica proposa que una d'aquestes adaptacions haurien de ser les històries de vida. Les característiques de les espècies relacionades amb la reproducció i la supervivència haurien de jugar un paper destacat en disminuir el risc d'extinció per factors estocàstics just després de la introducció. Els resultats indiquen que els bons invasors es caracteritzen per donar prioritat a la reproducció futura en lloc de la actual, segurament perquè un gran èxit en la reproducció en el futur redueix els costos d'un fracàs reproductiu en condicions d'incertesa i augmenta les oportunitats per explorar i respondre a les pressions ambientals noves. A més, les espècies exòtiques haurien de tenir adaptacions que els permetin trobar un nínxol ecològic apropiat on sobreviure i prosperar, per evitar l'extinció per creixement poblacional negatiu. Aquest nínxol no només ha d'incloure els recursos necessaris, però també pocs competidors i enemics. La teoria suggereix dues formes de trobar aquest nínxol: o les espècies invasores són capaces de desplaçar competitivament les espècies natives dels seus nínxols, o bé els invasors són oportunistes i troben nínxols ecològics desaprofitats. En aquesta tesi la importància relativa d'aquestes dues hipòtesis s'ha contrastat mitjançant l'estudi de l'invasió del Rossinyol del Japó (Leiothrix lutea) a la serra de Collserola. L'invasor s'ha establit amb relativament poca resistència de les espècies natives, el que reflecteix la seva naturalesa oportunista i generalista i que els seus requeriments ecològics estaven poc representats en la comunitat nativa. No obstant, durant el període d'expansió de l'invasor s'ha detectat la disminució d'una espècie nativa ecològicament similar, presumiblement deguda a desplaçament competitiu. Aquests resultats mostren que les dues hipòtesis no són mútuament exclusives, sinó que conjuntament poden ajudar a millorar la comprensió de les invasions. Finalment, aquesta tesi planteja si és possible utilitzar les característiques proposades d'estar relacionades amb l'èxit invasor per desenvolupar una metodologia per detectar les espècies potencialment invasores i així poder evitar futurs problemes. Els resultats indiquen que l'èxit invasor pot ser predit per la mida de la població fundadora, l'ús de l'hàbitat, la mida del cervell i la capacitat de les espècies de prioritzar la reproducció futura. Tot i que són poques característiques, els models generats van predir la probabilitat d'èxit de l'establiment de les aus a Europa i Austràlia, amb una precisió molt alta. Així doncs, es demostra que fer avaluacions de risc basades en les característiques relacionades amb l'èxit de l'establiment és difícil, però possible, i proporcionen una eina útil per orientar les estratègies de prevenció destinades a mitigar l'impacte d'espècies invasores. Tot i així, aquesta tesi també demostra que per ser del tot efectives cal que aquestes metodologies siguin implementades realment en les polítiques de gestió ambiental si de debò volem evitar un futur dominat per les espècies invasores.

Chapter 1

General introduction



Biological invasions

Alien species are, by definition, taxa that are introduced outside their natural range either intentionally or unintentionally by human agency (IUCN 2000). Although humans have transported and traded plant and animal species for millennia, the frequency and extension of these artificial geographical expansions are increasing in recent times as a result of growing volumes of international trade and tourism (Levine and D'Antonio 2003, Meyerson and Mooney 2007, Hulme 2009). Nowadays, biological invasions are considered one of the most important global environmental change, contributing to current biodiversity loss and biotic homogenization (McKinney and Lockwood 1999, Mooney and Hobbs 2000, Rosenzweig 2001). The threats that biotic invasions pose to biodiversity and to ecosystem-level processes translate directly into economic consequences, such as losses in crops, forests, fisheries, and grazing capacity; and indirectly in terms of the costs of combating invasions (Mack et al. 2000, Pimentel et al. 2005). The concern over the impact of biological invasions has prompted an enormous interest in trying to understand the factors that influence the invasion process. Such information is essential to prevent, evaluate and mitigate the impact of invasive species (Byers et al. 2002, Andersen et al. 2004a).

The present thesis has two main goals. The first is to ask what makes a species a successful invader. Although there is a huge literature on this topic, the question remains largely unresolved. To try to fix this gap, I combine comparative analyses with field observations and experiments to address a number of unresolved issues of the invasion process (Chapters 2 to 4). The second goal is to explore whether the gained knowledge about the factors underpinning invasion success is useful to prevent the impact of invaders. To do so, I develop and test a risk analysis protocol for the establishment of alien species (Chapters 4 and 5). I address these two general issues using birds as subject of study. In the next sections, I discuss why I chose birds as study model and briefly describe the theoretical framework that is the basis of my thesis.

Why birds?

Birds are an ideal model for studying biological invasions. More than 400 species of birds have been introduced outside their native ranges over the years, many of which have become invasive in the new region. Invasive birds are responsible for ecological and economical damages as disease transmission, agricultural depredation, and regional biodiversity extinction (Long 1981). Furthermore there is a good historical record of worldwide bird introductions (Long 1981, Lever 1987, 2005) and high quality information is available for ecological and biological traits for most of the introduced species (Del Hoyo et al. 1992-2011). Thus, much of what we have learnt in the past on avian invasions come from the comparative analysis of historical introductions (Sol et al. 2008b). A substantial part of my thesis is based on such a comparative approach. Comparative studies are useful to understand the general patterns of biological invasions, however to investigate the mechanisms of invasion, research has to move to another level of approximation. Thus, I also use finer-scale observational and experimental approaches to analyses some of the questions. The integration of macro and micro ecological approaches is essential to obtain a complete understanding of the invasion process.

The invasion paradox

Ever since Elton (1958), invasive species have posed an interesting paradox to ecologists and evolutionary biologists (Sax and Brown 2000): why are exotic organisms, which come from distant locations and have had no opportunity to adapt to the local environment, able to become established and sometimes to displace native species? Solving the paradox of the invasions requires to understand two scientific problems (Sax and Brown 2000). The first is the fact that some species succeed to establish themselves despite that the founder population is very small. The second is the observation that successful alien species are able not only to become abundant and widespread, but often to become dominant in the community and displace native species. Both phenomena may be understood by invoking adaptations that allow species to overcome these two types of conflicts.

To identify the adaptations that make a species a successful invader, we must first consider the main causes of extinction of introduced populations. A main route toward extinction in natural populations is stochasticity in small populations. As frequently noted in the literature on exotic species, most human-driven introductions have failed to establish self-sustaining populations (Long 1981, Lever 1987). The explanation usually given is that introduced species are normally released in low numbers and so start with small founding populations. Small, isolated populations are at great risk of extinction from stochastic fluctuations owing to demographic, genetic, or environmental stochasticity (Pimm 1989). Then, why some introductions succeed where the vast majority of them fail to establish? A logical explanation is that these introductions involved the release of large number of individuals. Indeed, there is firm evidence that introductions that started with higher population sizes were more likely to be established successfully than those that started with smaller populations (Lockwood et al. 2005, Lockwood et al. 2009). Nevertheless, there are exceptions. There are many cases in the literature on bird invasions in which the introduction attempt ended in a failure despite being introduced in very high numbers (Long 1981, Lever 1987). On the contrary, there are introduction attempts involving very few individuals that have succeeded in establishing self-sustaining populations. Clearly, factors other than propagule pressure can be critical in determining the fate of introductions. In chapter 2, I argue that the varying response of introduced species to stochasticity is influenced by adaptive variation in life history.

Theory predicts that the life history strategy of a species should affect the vulnerability of small populations to stochastic factors (Legendre et al. 1999, Saether and Bakke 2000, Saether et al. 2004), but the analysis of historical introductions has failed to provide firm evidence for a link between life history and establishment success (Duncan et al. 2003, Blackburn et al. 2009b). Classical ecologic theory argues that establishment should be facilitated by life histories that promote rapid population growth, thus reducing the period during which the founder population remains small and highly vulnerable to stochastic extinctions (Lewontin 1965, Pimm et al. 1988, Pimm 1991). Although this "population growth" hypothesis has received a great deal of attention in the past, the hypothesis has been poorly supported. Surprisingly, little attempt has been made to formulate and test alternative hypotheses linking life history variation to establishment success. Theory for example predicts that prioritizing future reproduction should facilitate the response to uncertainties of novel environments. One reason is that species that prioritize future reproduction tend to distribute the reproductive effort in several attempts, thereby reducing the fitness cost of losing, delaying or skipping a reproductive event (Williams 1992, Wilbur and Rudolf 2006, Bokony et al. 2009). Further, prioritizing future over current reproduction should also facilitate establishment success because these species are more likely to develop adaptations that buffer them against environmental risks, reducing thus the likelihood that the population dies out (Legendre et al. 1999, Saether et al. 2004, Sol 2007). In chapter 2, I test the 'population growth' and the 'future returns' hypotheses with a global comparative analysis of successes and failures in past avian introductions.

The second problem I address in my thesis is the fact that some species not only become established in novel environments, but also become so abundant and widespread that they dominate certain communities and sometimes even displace native species. To resolve this issue, we need to refer to a second important cause of extinction in introduced populations: negative population growth. Theory argues that to escape extinction due to negative population growth, a invader must possess adaptations to find an appropriate ecological niche in the novel environment, which should include appropriate resources and suitable climatic conditions (Shea and Chesson 2002). Further, a species that has appropriate adaptations may still fail to establish due to the effect of competition or predation with native species (Shea and Chesson 2002, Ives and Helmus 2011), a process known as biotic resistance (Elton 1958). Consequently, to resolve the above paradox we need to understand how invaders are able to find appropriate ecological niches despite the resistance of the recipient community. Two observations suggest a possible explanation. The first is that most exotic species occur in environments that in some way have been altered by human activities, and that as a result contain fewer competitors and enemies. The second is that most exotic species rarely end up invading natural environments, which are expected to offer stronger biotic resistance. This suggests that the paradox may be resolved if we consider that the success of most invaders is related to adaptations that allow them occupying empty ecological niches derived from human activities that most native species are incapable to use (Sax and Brown 2000, Sol et al. 2011a).

Nevertheless, a selected number of species have had notable success invading natural habitats (Usher et al. 1992, Tennant 1994, Stohlgren et al. 1999, Hoffmann 2003, Macdonald and Harrington 2003). The reasons why these species are able to invade natural habitats remains largely unknown, despite that it is in these environments where ecological impacts on native biodiversity and ecosystems are expected to be greater (Mack et al. 2000). Ecological theory suggests two main hypotheses to explain the success of species in natural environments: competition and opportunism. The competition hypothesis argues that successful invaders are competitively superior over native species and can displace them from their current niches (Macarthur and Levins 1967, Schoener 1983, Tilman 1994). The opportunism hypothesis, instead, relates the success of invaders to their ability to find resource opportunities little used by native species (Sher and Hyatt 1999, Davis et al. 2000, Shea and Chesson 2002). In chapter 3, I address these hypotheses with an exhaustive analysis of the invasion success of a small passerine, the Red-billed Leiothrix *Leiothrix lutea* in the Collserola Park forest reserve (Barcelona), combining long-term monitoring results, field observations and experiments.

Assessing the risk of biological invasions

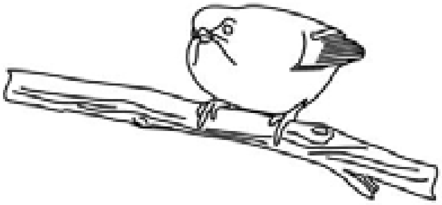
Given the apparently paradoxical nature of the biological invasions, a question arises: is it possible to accurately predict the risk that an alien species becomes successfully established in a new place? The ability to predict the success of invasions would be a basic tool to prevent ecological, economic and health of invasive species, since the eradication and control strategies have proved very costly and ineffective (Mack et al. 2000, Myers 2003). If we were able to know the real risk that a species will establish and create problems at the place of introduction, this information would be very valuable in the development of exotic species trade policies, the design of detection and early eradication strategies for particularly problematic species, and the critical role of informing the public opinion about the problems caused to own and release certain alien species.

Until recently, ecologists have been very skeptical about the possibility to predict the outcome of species introductions since chance is considered a main factor in the invasion process, as summarized by ecologist Paul Ehrlich (1989) when writing that "[while ecologists] can make general predictions about invasions, [they] are not able to accurately predict the result of a single invasion or introduction". However, the last two decades have seen enormous progress in our understanding of the invasion process. The most important discovery was the finding that, although random plays a major role in the invasions the possession of adaptations facilitates the persistence of successful invaders in novel environments. Since then, identifying the adaptations of successful invaders has been a central goal in biological invasions research. In birds, a large number of species-traits have been proposed to influence establishment success (Duncan et al. 2003, Cassey et al. 2004). However, despite all the efforts dedicated to identify traits associated with successful invaders very few of these features have been supported firmly by empirical evidence (Sol 2007, Blackburn et al. 2009b). This could indicate that only a few traits are relevant in determining the outcome of an introduction. The question that arises is whether we can use these traits to make predictions about the outcome of future introductions. In chapter 4, I analyze an extensive database on bird introductions with advanced statistical models and hierarchical decision systems to identify the traits of successful species and to develop a global risk assessment protocol for the establishment of alien bird species.

The goal of a risk assessment is to facilitate the decision-making process in invaders management strategies by identifying the fraction of introduced non-native species with a high risk to become established and generate impact in the new region (Pheloung et al. 1999, Kolar and Lodge 2002, Bomford 2003, Bomford et al. 2009). This methodologies have proven to be useful tools to guide and design environmental policies, potentially contributing to mitigate the impact of invaders (Keller et al. 2007). However, to be fully effective, prevention protocols must be implemented in the invasive species management plans. Otherwise, the effort inverted in mitigating biological invasions may be useless (Fowler et al. 2007, Smith et al. 2008). In chapter 5, I use the previously developed risk assessment to evaluate the invasive potential of alien bird species introduced in Catalonia, and I compare the resulting ranking with the Spanish national Catalogue of invasive species to predict the potential effectiveness of the recently approved legislation to prevent new biological invasions.

Chapter 2

Brood value, population growth and the life history of successful invaders[1]



---

[1] with Daniel Sol, Joan Maspons, Ignasi Bartomeus, Gabriel Garcia-Peña, Josep Piñol & Robert P. Freckleton. Submitted.

Resum

Valor de la posta, creixement poblacional i les estratègies de vida dels bons invasors

Tot i el considerable interès actual en les invasions biològiques, les característiques comunes de les històries de vida dels bons invasors continuen essent difícils d'identificar. La hipòtesi generalitzada que els bons invasors tenen altes taxes de reproducció ha rebut poc suport empíric, però, les possibilitats alternatives rarament han estat considerades. Combinant un anàlisi comparatiu global de les introduccions d'ocells (més de 2.500 esdeveniments) amb models demogràfics i mètodes basats en la filogènia, nosaltres hem trobat que si bé el creixement poblacional ràpid pot oferir avantatges durant les invasions en determinades circumstàncies, més sovint els bons invasors es caracteritzen per estratègies de vida en què que tendeixen a donar prioritat a la reproducció futura en lloc de la actual. Això era d'esperar perquè un gran èxit en la reproducció en el futur redueix els costos d'un fracàs reproductiu en condicions d'incertesa i augmenta les oportunitats per explorar i respondre a les pressions ambientals noves. Així doncs, les històries de vida sembla que influeixen en l'èxit de les invasions, però per mecanismes diferents dels habitualment considerats en la literatura.

Abstract

Despite considerable current interest in biological invasions, the common life history characteristics of successful invaders remain hard to identify. The widely-held hypothesis that successful invaders have high reproductive rates has received little empirical support, however alternative possibilities have rarely been considered. Combining a global comparative analysis of avian introductions (> 2,500 events) with demographic models and phylogenetic-based methods, we show here that although rapid population growth may offer advantages during invasions under certain circumstances, more generally successful invaders are characterized by breeding strategies in which they tend to give priority to future rather than current reproduction. This is to be expected because high expected future breeding success reduces the costs of a reproductive failure under uncertain conditions and increases the opportunities to explore and respond to novel environmental pressures. Life history thus seems to influence invasion success but by mechanisms different from those usually considered in the literature.

Introduction

Current concern over the impact of invaders on biodiversity and ecosystem functioning has generated enormous interest in understanding what determines the success of biological invasions (Kolar and Lodge 2001, Sakai et al. 2001, Blackburn et al. 2009b). Although there is now ample evidence that species differ in their invasion potential, controversy nevertheless exists regarding the nature of the features best describing successful and unsuccessful invaders (Kolar and Lodge 2001, Sol 2007). Life history, defined as the way organisms allocate time and energy over growth, reproduction, and survival (Stearns 1992, Ricklefs and Wikelski 2002), has long been in the core of the controversy. There are sounding theoretical arguments to expect that life history should influence invasion success (Lewontin 1965, Stearns 2000a, Saether et al. 2004), but confidence in these predictions is undermined by a perceived lack of empirical support (Kolar and Lodge 2001, Blackburn et al. 2009a). Here we attempt to clarify the role of life history in the invasion process by critically revisiting classical theory and by incorporating in the debate ideas previously ignored. We report evidence that life history does influence invasion success, but for reasons different from those generally invoked.

The most prominent theory relating life history with invasion success is the "population growth" hypothesis (Lewontin 1965, Pianka 1970). Proposed by Lewontin (1965) over 45 years ago, the hypothesis predicts that life histories enabling rapid population growth should promote establishment in novel regions by reducing the period during which the founder population remains at low numbers and susceptible to stochastic extinctions (Pimm 1991). Despite being rooted in classic demography (Pielou 1969), current empirical evidence for the hypothesis is inconclusive: some studies support a positive relationship between life history correlates of population growth and establishment success whereas others report a negative relationship or no relationship at all (Kolar and Lodge 2001, Blackburn et al. 2009a). While much previous effort has been directed at testing the "population growth" hypothesis, little attempt has been made to investigate alternative hypotheses linking life history variation to establishment success.

The lack of firm support for the "population growth" hypothesis has been interpreted by some as evidence of the overwhelming importance of chance in invasion success (Blackburn et al. 2009b). Yet the hypothesis has also been criticized because it does not acknowledge that a high reproductive effort incurs costs that may counterbalance the advantages of growing fast (Pimm 1991, Duncan et al. 2003). The most prominent cost of reproduction is in terms of future reproduction (Brown and Sibly 2006, Stahl and Oli 2006). The resulting trade-off is often simply characterized as the "fast-slow" continuum of life-history variation (Bielby et al. 2007), yet it may be more generally expressed as the extent to which species prioritize their current reproduction over future reproduction. There are theoretical reasons to think that a strategy of high expected future returns should afford some advantages in novel environments ('future returns' hypothesis, hereafter). Such a strategy relies on distributing reproductive effort across a number of events -whether by extending the reproductive life or by reproducing more continuously- and increases the value of adults over the value of offspring (Stearns 1980). This may have three major consequences for an species exposed to the uncertainties of a novel environment. First, it reduces the risk of putting ‘all eggs in one basket’ (Stearns 2000a, b). For an invaders that has just settled in a new environments, the lack of information on the enemies and other hazards may notably increase the probability of reproductive failure. Under such circumstances, it is better to spread the risk across a large number of reproductive events, whether in a same breeding season or in different ones, rather than on a few reproductive events (Stearns 2000a). Such a bet-hedging strategy reduces the likelihood of the population going extinct by bad luck and ultimately leads to an increase in the geometric mean lifetime reproductive success (Gillespie 1973), which may ensure the long-term persistence of the population.

The second consequence of a strategy of high expected future returns is the reduction in costs to fitness of skipping a breeding attempt. This should ensure that individuals engage in reproductive activities only when the chance of success is high and the costs and hazards are low (Williams 1966, Cubaynes et al. 2011). Time-lags in which the invader population remains at low numbers during some time before starting a rapid population increase are indeed common among invasive species (Sakai et al. 2001). Further, a lower urgency to reproduce should enable adults to allocate time and energy on tasks other than reproduction. This may for instance provide greater opportunities to explore the novel environment, thereby helping decisions about when and where to breed and increasing performance in avoiding predators and exploiting food sources (Sol 2007).

The final consequence of a strategy of high expected future returns is that the fitness gains are greater of investing in adult survivorship rather than in reproduction (Ricklefs and Wikelski 2002, Stahl and Oli 2006). It follows that selection should favor the evolution of adaptations that buffer individuals from extrinsic mortality sources (Ricklefs and Wikelski 2002), and that could also help them respond to novel ecological pressures. One of such adaptations classically considered in the literature is increased body size (Pimm 1991, Brown and Sibly 2006), which can provide competitive advantages and protection from enemies. However, evidence that bigger species are more successful invaders is contradictory (Sol et al. 2008a, Blackburn et al. 2009b). Stronger evidence is nonetheless available for a large brain, which is thought to assist animals in novel environments by enhancing their ability to construct behavioural responses to unusual or novel socioecological challenges (Sol 2009). In both birds and mammals, the taxonomic groups that contain the largest brains of any animal on Earth, species with larger brains are more likely to be successful when introduced in novel environments than are species with smaller brains (Sol et al. 2005, Sol et al. 2008a).

To elucidate the importance of life histories on invasion success, we present a global comparative analysis of avian introductions. Birds are particularly suited for such analyses because accurate information is available for many introduction events and life-history variation is well documented (Kolar and Lodge 2001). We analyze a dataset of more than 2,500 avian introductions using Generalized Linear Mixed Models (GLMM, hereafter), which allow us to take into account the non-random distribution of species across locations as well as the possibility of pseudoreplication resulting from some species being introduced to several locations, and most locations being subject to several introductions.

Methods

Introduction data

We used a previously compiled global database documenting recorded human-mediated introductions of terrestrial birds to new locations (Cassey et al. 2004, Sol et al. 2005, Blackburn et al. 2009b), updated with information from Lever (2005). In this database, the introduction of a species to a new location (an introduction event, hereafter) is defined as the release of individuals of a species to either an island or a governmental state within a continental mainland that is outside the species' native range. All introductions of a given species to the same place within a period of 10 years were considered as a sole introduction event. The outcome of each introduction was scored as 'established' if the species succeeded in developing a self-sustaining population in the new region, or 'extinct' if it did not. A self-sustaining population is defined as a population that persisted without declining for at least 20 years after release. We assembled information on 2,760 introduction events, comprising 428 species from 49 families, 1,292 of which were successful. Data on introduction effort, measured as the total number of individuals released, were available for 832 of these introduction events, 311 of which were successful.

Life history data

We collected information for a set of life history traits from published sources, including scientific journals, field guides and previously compiled datasets (see Appendix A). The traits were: (1) age at first breeding, in months; (2) clutch size, measured as the modal number of eggs per nest; (3) fecundity, computed as clutch size multiplied by the number of broods per year; (4) egg mass, in grams, (5) incubation period, in days; (6) fledgling period, as the number of days the young birds stay in the nest from hatching to leaving the nest; (7) reproductive lifespan, based on the oldest record of an individual age in years, substracting the period before its first breeding; (8) developmental mode, classified in four stages (altricial, semialtricial, semiprecocial and precocial) following Starck and

Ricklefs (Starck and Ricklefs 1998); and (9) adult survival, as the mean annual survival rate (Liker and Szekely 2005). These variables were used to estimate the fast-slow continuum, the intrinsic rate of population growth, the brood value and generation time, as explained below.

Following Bielby et al. (2007), we used a factor analysis to define variation in life history between species along the fast-slow continuum. The factor analysis was based on a correlation matrix of all these variables, including both species introduced and species that have never been introduced so as to mitigate possible biases in the estimates (N = 697 species). However, we found that the fast-slow continuum could be properly described with only four variables (correlation = 0.89; Appendix A: Fig. 1): fecundity, age of first breeding, egg size and length of the incubation period. These variables are easy to estimate and were available for many species, so we used this latter estimate to maximize the number of species included in the analyses. In any case, the conclusions hold regardless of the way the fast-slow continuum is quantified. Other methods exists to quantify the fast–slow continuum, like the logarithm of the ratio of fertility rate to age at first reproduction (F/α ratio) (Oli 2004). Due to the high correlation between the two measures (Appendix A: Fig. 2), we only present the results obtained with the first method.

We estimated the intrinsic rate of population increase (Rmax, hereafter) by solving Cole's (1954) equation. The variables included in the equation were fecundity, age at first breeding and lifespan (Cole 1954). We also used demographic models to estimate the deterministic growth rate (lambda), as detailed below, which allowed taking into account juvenile survival in the estimates. Due to the high correlation between the two measures (Appendix A: Fig. 2), and in order to maximize sample size, we only present the results obtained with the first method.

We expressed the value of current reproduction relative to the lifetime reproductive output of a species (henceforth, “brood value”) as log10(clutch size/[clutch size*broods per year*average reproductive lifespan]), following Bokony et al. (2009). Because clutch size appears in both the numerator and the denominator, this cancels to leave brood value equal to the logarithm of 1/total number of breeding attempts. Thus, the brood value can be a low number for a species that has a short lifespan and breeds several times per year, or for a species that has a long lifespan and breeds annually (see below for details on how we have dealt with it).

The analysis of population time series for bird species has revealed that the magnitude of environmental stochasticity, including transient fluctuations in age structure, increase with generation time (Saether et al. 2005). We consequently also took into account generation time as confounding factor in the analyses. Assuming a stable population, we calculated the generation time as $G = \alpha + s/(1 - s)$, where α is age at first reproduction and s is adult survival rate (Lande et al. 2003).

Confounding variables

We obtained information on the following confounding effects: (1) body mass, measured in grams; (2) brain mass, in grams (Sol et al. 2005, Sol et al. 2010a); (3) habitat generalism, quantified as the number of the following seven major habitat types included in a species' native range (Sol et al. 2005); (4) mating system (coded as polygamous vs. monogamous), (5) parental care (uniparental, biparental, cooperative); (6) coloniality (solitary, facultative, semi-colonial, colonial); (7) migratory behavior (resident vs. migratory); (8) latitude of the place of introduction; (9) climatic matching between the region of introduction and origin of the species; and (10) whether the place of introduction was in the mainland, on a continental island or on an oceanic island.

Previous work has shown that it is not brain size per se, but the extent to which the brain is either larger or smaller than that expected for a given body size which indicates adaptation for enhanced neural processing (Lefebvre et al. 2004). Two main methods have been proposed to remove the allometric effect of body size on brain size (Deaner et al. 2000): (1) estimate the residuals of a log–log least-square linear regression of brain mass against body mass, and (2) include absolute brain mass and body mass (both log-transformed) as covariates in a multivariate model. The two methods yielded qualitatively similar results, and for consistency with previous studies we report in the text the results obtained using the method of residuals.

To estimate climate matching, we obtained information on temperatures and precipitation in land from a public dataset of 12 mean values per month at a 30 arc second spatial resolution. We considered four climatic variables: temperature annual mean, precipitation annual mean, temperature annual variation, and precipitation annual variation (i.e. annual variation determined as the standard deviation of the monthly means values of temperature and precipitation within a year). To match the climatic information to the species breeding range, we used a public database were worldwide museum specimens are registered and the coordinates of collection are given (Global Biodiversity Information Facility, www.gbif.org), and considered the breeding range as the total area covered by all the breeding locations for the species in question. We found a total of 183,974 breeding locations for 142 species. To estimate climatic conditions in the place of introduction, we delimited a circular polygon of 5km radius around each location. Then we used map algebra to estimate four spatial statistics (mean, standard deviation, minimum and maximum values) for each climatic variable in the introduction area and the species breeding area. Climate matching was estimated as the Euclidean distance in a multidimensional space between the climatic variables at the introduction area and the climate at the species native breeding range.

Modeling establishment success

Variation in establishment success was modeled with GLMM with binomial error and logit link (Blackburn and Duncan 2001a), using Laplace approximations (Bolker et al. 2009) in the R-package lmer4 (Bates et al. 2011). The taxonomy (species, genus, family and order) and region of introduction (biome and country of introduction) were initially included as random factors. Differences in AICc were then used to define the optimal structure of the random component in models with all fixed effects (Zuur et al. 2009b), which invariably only retained in the model species and country of introduction. The effect of these random factors were quite large (see below), justifying the need to use a GLMM approach.

To identify the best structure of fixed effects, we used the function dredge in the package MuMin to perform automated model selection with subsets of all life history traits and confounding variables. The relative support for a model was assessed with the second order Akaike information criteria (AICc), which includes a correction for reduced sample sizes (Anderson and Burnham 2002). To avoid problems of co-linearity, we described all life history traits in two unique variables, the brood value and the fast-slow continuum (see above for justification). The importance of individual parameters was assessed with the sum of the weights of the models which comprise that factor. We then repeated the model selection again with the subset of variables with higher weights. This allowed us to remove uninformative variables for which sample size was reduced, thereby increasing the power to identify the importance of the rest of variables. In the text, we present the results of the best model, with significance of fixed effects evaluated with Wald t-tests (Bolker et al. 2009). This model did not show any symptom of overdispersion.

Tree regression

We used a conditional regression tree approach (Crawley 2002, Hothorn et al. 2006) to describe the brood value as a function of the number of broods and maximum lifespan. Conditional trees estimate a regression relationship by binary recursive partitioning (Hothorn et al. 2006), allowing to define homogeneous groups based on a set of predictors. In our case, the response variable was brood value and the predictors were number of broods per year, maximum lifespan, clutch size and the fast-slow continuum. We developed our classification tree with the option ctree available in the R package Party (Hothorn et al. 2006).

Phylogenetic-based analyses

We estimated the phylogenetic effects for single traits using two methods. First, we estimated Pagel's λ (Pagel 1999). The parameter λ measures the degree to which the variance/covariance matrix follows the Brownian model (Freckleton 2000a). Values close to zero indicate that the variable has low phylogenetic effects whereas values close to one indicate that the variable has high phylogenetic effects. We estimated λ for the studied traits using maximum likelihood techniques, and tested whether the value was different from zero with a log-likelihood ratio test (Freckleton 2000a). Second, we used the Moran's I statistic (Gittleman et al. 1996), as implemented in APE (Paradis et al. 2004). Positive values indicate that the variable at a particular taxonomic level is more similar than random, whereas negative values indicate that they are more different. We tested whether the Moran's I statistics were significantly greater than expected by chance by means of randomizations (Paradis et al. 2004). The justification of using the Moran's I is that it allows diagnosing positive and negative phylogenetic dependences, as well as phylogenetic effects stronger than predicted by a Brownian model.

The co-variation between life history traits among species was analyzed with a phylogenetic generalized least squares (PGLS) approach (Freckleton et al. 2002). We simultaneously estimated Pagel's λ and fitted GLS models, using the R-package Ape (Paradis 2006) and an R code developed by R. P. Freckleton (2002).

The phylogeny used in all the above analyses (Appendix A: Fig. 3) was extracted from the avian supertree developed by Katie Davis and Rod Page (University of Glasgow). The supertree assembles information from 748 published phylogenetic trees. The phylogeny and further details are available in Davis ([2008, http://theses.gla.ac.uk/178/]). Sensitivity analysis demonstrated that the results did not depend upon which branch lengths were used and in the text we report those based on a phylogeny with branch length set to 1.

Stochastic demographic model

Population trajectories were modeled by a life-cycle with as many stages as years until first breeding (from one to four). Only the female population was modeled and it was assumed that sex ratio at birth was 0.5 and that mortality was not sex-specific. The deterministic component of the model was based on the Lefkovitch matrix (Lefkovitch 1965, Case 2000) derived from the life-cycle graphs. From this matrix, we estimated the deterministic growth rate (lambda) as the dominant eigenvalue (Case 2000). Demographic stochasticity was added into deterministic models as follows. For survival parameters, the number of survivors was drawn at random from a binomial distribution with probability equal to the survival rate being examined. For fecundity rates, a Poisson distribution was used with mean and variance equal to the fecundity value multiplied by the number of adult females present at that time. We assumed that the invaders find an appropriate niche in the recipient community and hence strategies leading to lambdas lower than 1 were excluded from subsequent analyses. Simulations started with an initial adult population size (propagule size) from 2 to 100 individuals. For each set of demographic parameters and propagule size, we ran 5,000 simulations during 100 years producing different population trajectories and estimated the probability of establishment as the proportion of populations that persisted over the 100 years. As the probability of establishment rapidly converged to one when lambda was above 1.30, we present in the text the results of simulations with lambdas equal to 1.05, 1.15 and 1.30.

Results and discussion

We first use our large dataset to revisit the 'population growth' hypothesis. The analyses yield little empirical support for the hypothesis. Of the life history traits previously used to address the hypothesis, only clutch size is associated with establishment success when controlling for both taxonomic and regional effects (Table 2.1). Contrary to the hypothesis, however, species that lay larger clutches are worse (not better) invaders (Fig. 2.1a).

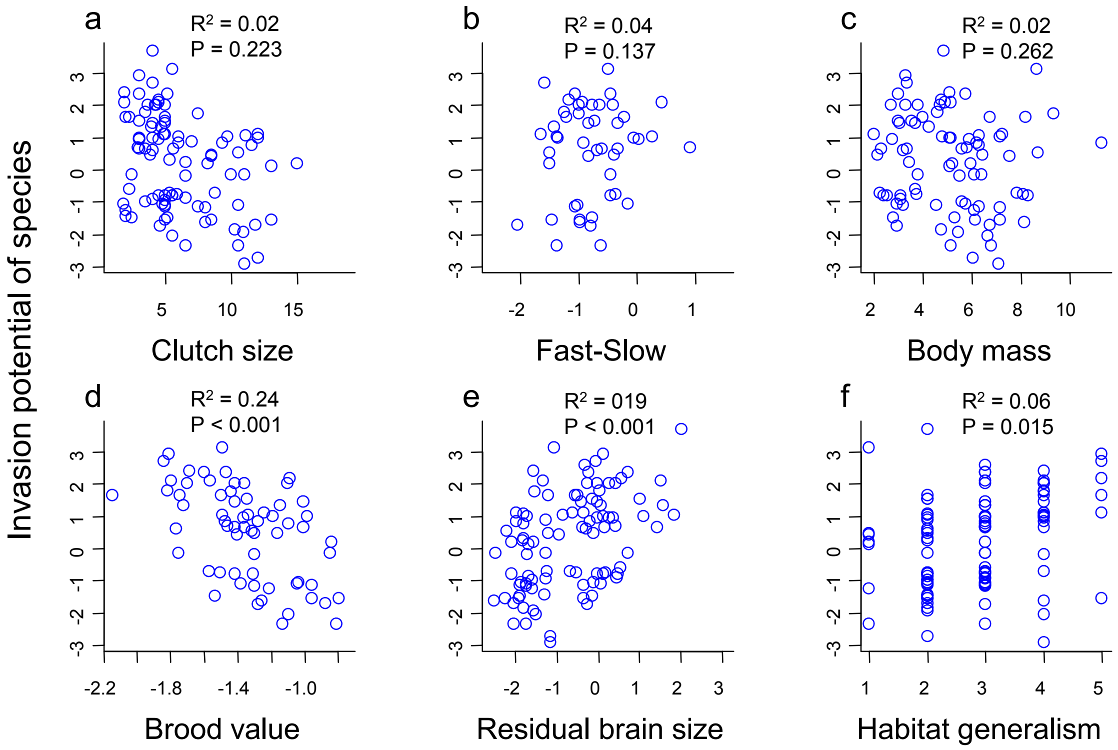
A stronger test of the "population growth" hypothesis is whether establishment success is correlated with direct measures of population growth rate, a possibility that has never been verified. To conduct such a test, we estimated the Rmax of each introduced species by solving Cole's (1954) equation. Although this approach has some limitations, it reliably captures variation among species in population growth and it is certainly more accurate that using life history surrogates. Contrary to expectation, there is no evidence that the likelihood of establishment is related to Rmax in birds (Table 2.1, Appendix A: Table1).

Table 2.1. Effects of life history traits and population growth rates on establishment success*.

Model	Estimate	SE	Z	P	N
Clutch size	-0.110	0.035	-3.12	0.002	2,593
Fecundity	0.018	0.038	0.39	0.696	2,138
Rmax	-0.283	0.198	-1.43	0.153	1,615
Fast-Slow	0.247	0.219	1.13	0.260	1,609
Clutch size + propagule	-0.253	0.067	-3.81	< 0. 0001	809
Fecundity + propagule	0.036	0.034	1.06	0.288	698
Rmax + propagule	-0.104	0.295	-0.35	0.725	568
Fast-Slow + propagule	0.233	0.363	0.64	0.520	567
Clutch size + propagule + brain residual	-0.097	0.071	-1.35	0.177	804
Fecundity + propagule + brain residual	0.057	0.059	0.96	0.335	698
Rmax + propagule + brain residual	0.133	0.268	0.49	0.619	568
Fast-Slow + propagule + brain residual	-0.729	0.395	-1.84	0.065	567

*In all models the response variable is success or failure of the introduction. Each predictor has been tested as fixed effect separately. For models with covariates (propagule size and relative brain size), these have been modeled as fixed effects. Although not presented, all models include species and country as random effects.

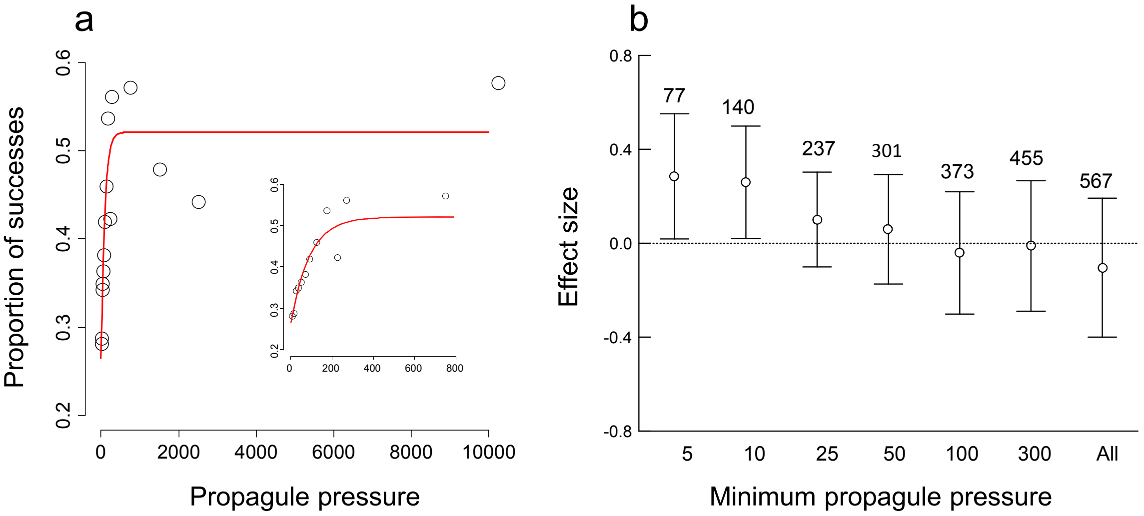
Figure 2.1. Species invasion potential as a function of life history traits. The invasion potential has been estimated as the random effect coefficients obtained from a generalized linear mixed model that included taxonomy and country of introduction as random factors and introduction effort as fixed effect, using only species with five or more introduction events. These coefficients provide a relative measure of the species ability to establish itself in a novel location having controlled for country and introduction effort effects. The P-values come from a PGLS that validates the effect of each variable on the invasion potential.



The 'population growth' hypothesis builds on the well-supported assumption that demographic stochasticity increases extinction in small populations (Pielou 1969). The likelihood of establishment is known to increase with 'propagule size' (defined in the literature as the number of introduced individuals) in a variety of organisms (Lockwood et al. 2005), consistent with the expectation that small populations should succumb more often to stochastic effects. Although in birds the number of individuals released correlates with several life history traits (Cassey et al. 2004), adding propagule size into the previous models does not change any of the above conclusions (Table 2.1).

However, models and empirical analyses indicate that the curve relating propagule size with establishment success typically has an effective threshold above which the release of more individuals does not increase establishment success (Lockwood et al. 2005). In the case of birds, this threshold is estimated to be over 300 individuals (Fig. 2.2a), implying that over 20% of introductions may be well beyond the influence of stochasticity. As we restrict the analyses to those introductions that involve a lower propagule size, the effect of Rmax on establishment success increases (Fig. 2.2b). Even when the

Figure 2.2. Establishment success and propagule size. (a) Relationship between propagule size and establishment success based on historical introductions. (Inset) Zoom on the interval of lowest propagule size. The curve has been fitted with the function nls from the MASS R-package. (b) Effect size (± standard error) of the relationship between establishment success and population growth rate when the analysis is restricted to introductions of respectively less than 5, 10, 25, 50, 100 and 300 individuals and when considering all introductions (“All”). The numbers above the bars are the sample size of introductions.

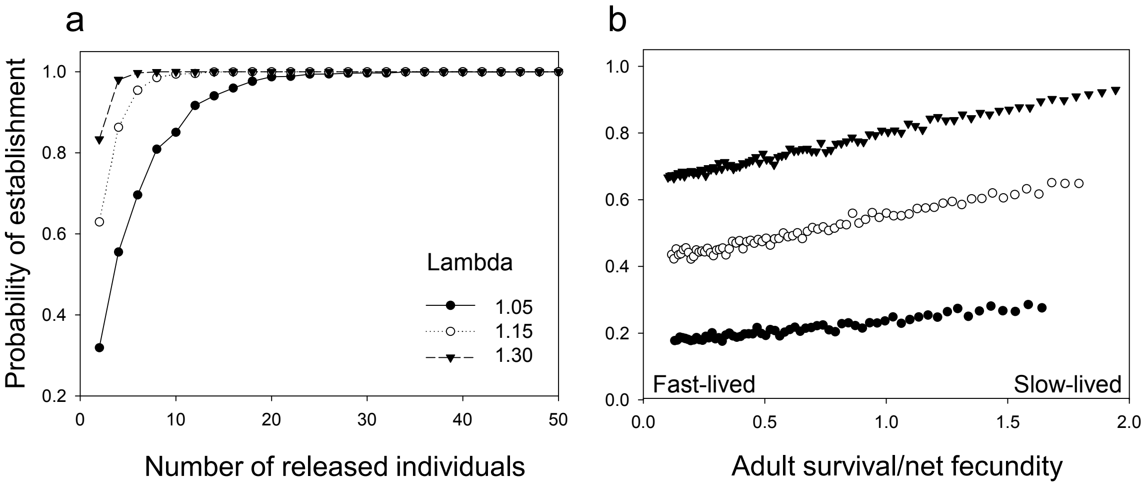


effect continues to be non-significant in all cases, this pattern points to the possibility that demographic stochasticity is most relevant when propagule size is extremely small (Grevstad 1999).

To further illustrate the above idea, we use a simple stochastic demographic model. Based on simulated trajectories during 100 years for 5,000 introduced populations, we estimated the probability of establishment as a function of the initial propagule size for different deterministic population growth rates. The simulations reveal that growing faster is advantageous to escape demographic stochasticity (Fig. 2.3a), as predicted by theory (Pielou 1969). However, the simulations also confirm that stochasticity is only an important cause of extinction when the number of individuals released is remarkably low (Grevstad 1999).

The ‘population growth’ hypothesis has been criticized for ignoring that a high reproductive effort may entail costs that counterbalance the advantages of fast population growth (Sakai et al. 2001, Sol 2007). The most prominent cost of reproduction is in terms of survival (Kolar and Lodge 2001, Blackburn et al. 2009b). The resulting trade-off defines a “fast-slow” continuum of life-history variation, ranging from high reproductive species with low survival prospects at one end to species that produce few offspring but survive well at the other (Appendix A: Fig. 4). Demographic models developed to project the routes toward extinction show that population fluctuations related to demographic stochasticity increase with the position of the species toward the fast end of this fast-slow continuum (Saether et al. 2004). It follows that for a same deterministic population growth rate, the probability of extinction when the population is small is higher for slow-lived species than it is for fast-lived ones (Fig. 2.3b, Appendix A: Fig. 4). Consequently, while populations of fast-lived species may increase faster, as reflected in the positive relationship between the fast-slow continuum and Rmax (PGLS: t = -23.83, P < 0.0001, Pagel's λ = 0.99, n = 135, R2adj = 0.81; Appendix A: Fig.5b), this initial advantage may be in part countered by an increased risk of extinction by population fluctuations, contributing to further obscure any effect of the fast-slow continuum on establishment success (Table 2.1).

Figure 2.3. Stochastic demographic model. (a) Probabilities of establishment as a function of propagule sizes for different population growth rates, derived from 5,000 populations simulated over 100 years. (b) Probabilities of establishment as a function of the fast-slow continuum, quantified as the ratio between annual adult survival and net fecundity (i.e. number of offsprings that survive until adulthood).



A critical issue is therefore whether fast-lived species may maintain high reproductive rates in niches to which they have had little opportunity to adapt. Theory predicts that fast-lived species should generally experience higher increases in mortality in a novel environment than slow-lived ones, as they are less likely to possess adaptations that may buffer individuals from extrinsic mortality (Pimm 1991, Brown and Sibly 2006). Our analyses yield no general evidence that body size is associated with establishment success (Binomial GLMM: P = 0.24 and 0.42, with and without control of propagule size; Fig. 2.1c). Stronger evidence is nonetheless available for another adaptation, a large brain (Table 2.1). A large brain, relative to body size (brain residual, hereafter), is associated with a higher likelihood of establishment, a possibility already supported by ample empirical evidence (Sol et al. 2005, Sol et al. 2008a). Because producing a relatively larger brain requires a longer development (Iwaniuk and Nelson 2003), only slow-lived species should be able to afford it (Appendix A: Fig. 6a). When brain residual is added in the GLMM, the effect of clutch size on establishment success becomes non-significant and the fast-slow continuum approaches significance in the direction predicted by the “population growth” hypothesis (Table 2.1).

Our results do not invalidate the “population growth” hypothesis but suggest that in birds the advantages of a fast-lived strategy for invaders will only be evident in very special cases, when the founder population is extremely small and when the challenges posed by the new environment do not substantially decrease the intrinsic rate of population growth (the latter may occur, for instance, when there is environmental matching between the regions of origin and introduction). It is also possible that reproductive effort exerts greater influence on establishment success in organisms with more limited capacity to respond to novel environmental challenges than birds.

The extent to which species prioritize their current reproduction over future reproduction is an alternative to the 'population growth' hypothesis. This axis of life history variation may be operationally described with the concept of brood value, which is expressed as log10(1/[broods per year*reproductive lifespan]) (Bokony et al. 2009). A high brood value means that all the reproductive effort is allocated into a few reproductive events, and hence that each brood has high fitness value, whereas a low brood value means that the effort is distributed into many attempts. Variation in brood value is not correlated with the fast-slow continuum (PGLS: R2adj = 0.008; Appendix A: Fig.5C) nor with Rmax (PGLS: R2adj = 0.015; Appendix A: Fig. 5d), indicating that it represents a somewhat different axis of life history variation (Appendix A: Figs. 4, 7).

The 'future returns' hypothesis is well supported by empirical data. As the hypothesis predicts, species with low brood values show a higher probability of establishment than those with a high brood value, when both taxonomic and regional effects are controlled for (Binomial GLMM: -2.313 ± 0.520, z = -4.44, P < 0.0001, n = 1,943 introduction events; Fig. 2.1d). From all the life history traits considered in our study, the brood value is the only one associated with establishment success (Fig. 2.1d, e, f; Appendix A: Tables 2, 3). The association holds when removing outliers (P < 0.0001), and when considering propagule pressure and all traits previously found to influence establishment success (Table 2, Appendix A: Table 3).

In birds, most variation in establishment success is found between species rather than at higher taxonomic levels such as genus and family. This suggests that characteristics typically shared by related species, including most life history traits, can explain only a small and non-significant amount of variation in global introduction success (Blackburn and Duncan 2001a). Nevertheless, the phylogenetic signal of the brood value is weak and, unlike clutch size and the fast-slow continuum, remarkably similar to that found for the invasion potential of species (Fig. 2.4, Appendix A: Fig. 8). Thus, the 'future returns' hypothesis offers a general explanation for the paradox that phylogenetically closely-related species often exhibit striking differences in their invasion potential.

However, it is worth noting that a low brood value may be achieved not only by having a long reproductive lifespan but also by laying several broods in a same year (Fig. 2.5). For the set of introduced birds, the lowest brood values are in fact found in species that combine several broods per year with a relatively long reproductive lifespan (Strategy 11), followed by species that lay a single clutch per year but have a very long reproductive lifespan (i.e. species that are at the slow extreme of the fast-slow continuum, Strategy 9) and finally by those that have a shorter lifespan but lay many broods per year (Strategy 5).

Table 2.2. Fixed-effect and random-effect parameters in the best model accounting for variation in establishment success*.

Fixed effects	Estimate	Std. Error	z value	P
Brood value	-2.078	0.771	-2.69	0.0071
Propagule size	0.452	0.062	7.28	< 0.0001
Brain residual	0.535	0.204	2.62	0.0092
Habitat generalism	0.750	0.199	3.77	< 0.0001

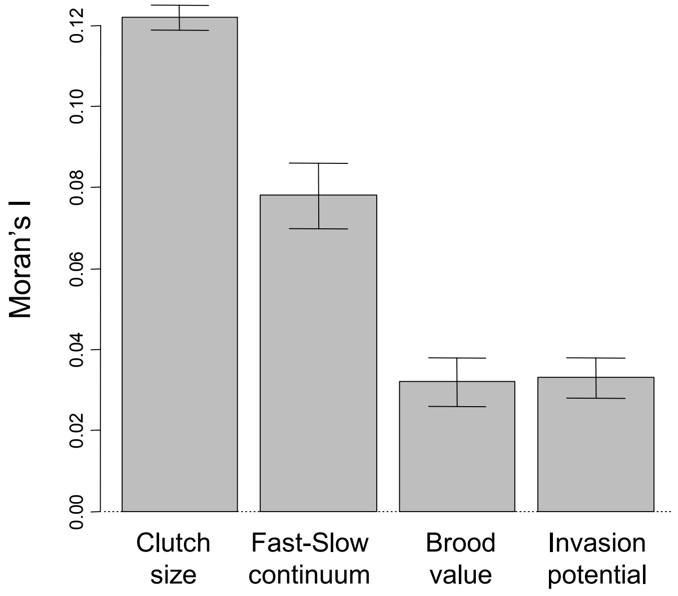
Random effects	Variance	Std. Dev.	Likelihood ratio test	P
Species	1.784	1.335	39.69	< 0.0001
Country	2.989	1.729	34.83	< 0.0001

*Based on 635 introductions**.**

The consequences of these strategies for invasion success are likely to differ, although it is difficult to anticipate how (see below). Our analyses reveal that only the species that combine several broods per year with a relatively long reproductive lifespan (strategy 11) and those that lay a single clutch per year but have a very long reproductive lifespan (strategy 9) are significantly more successful than species with high brood values (Binomial GLMM: $P < 0.05$ in all cases; see Appendix A: Table 4 and Appendix A: Fig. 9). This result suggests that the ability to distribute the reproductive effort among years (i.e. achieving a long reproductive life) is particularly relevant to succeed in novel environments, in line with previous suggestions that successful invaders should be at the slow extreme of the fast-slow continuum (Blackburn et al. 2009b). However, the above results also suggest that there is no single strategy to be a successful invader, which may explain the past difficulties in disentangling the life history of successful invaders.

There are two ways of thinking about the 'future returns' hypothesis. The first is in terms of the costs of giving too much fitness value to offspring, which contributes to explain why certain species repeatedly fail to establish themselves in a novel environment. Note that these costs are not only relevant when invaders are exposed to variable and/or heterogeneous environments, they are also relevant in any environment wherever there exist risks of reproductive failure and the organism cannot reduce the risk (Stearns 2000a). For an invader that has just settled in a new environment, the lack of information on the enemies and other hazards may for instance be a major factor of risk. Note also that the negative consequences of a reproductive failure should be more severe when the founder population is small, a situation that is common in biological invasions (see above).

Figure 2.4. Phylogenetic signal in life history traits and the invasion potential. The Moran's I (mean ± bootstraped standard deviation) describes the phylogenetic signal of each trait. All the estimates are significantly greater than expected by chance (P < 0.05), indicating positive autocorrelation.



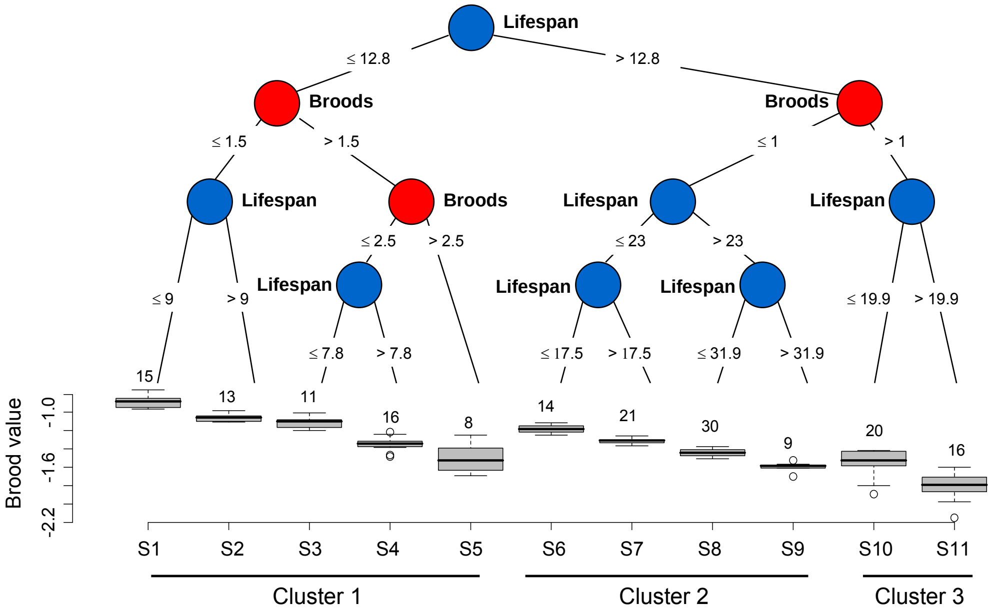
The second way of thinking about the hypothesis is in terms of benefits of increasing the value of adults over the value of offspring. In species with low brood value, the costs of reproductive failure are of course reduced. Yet in these species the benefits in terms of survival must also be considered because by adopting a strategy with high expected future returns, individuals should gain greater fitness benefits by improving adult survivorship rather than reproduction (Ricklefs and Wikelski 2002). In a novel environment, the ability to gather information on resource opportunities and hazards, and use the information to construct behavioural responses to new challenges may afford important advantages in terms of survival (Sol 2009). It is well-known that animals perform better and take better decisions with increased experience, but this takes time and may be constrained by cognitive limitations (Wunderle 1991). Nevertheless, these limitations are expected be less important in long-lived species. In these species, the fitness costs of delaying reproduction are lower, allowing more time and energy for acquiring information on the novel environment and improving performance on exploiting the resources and avoiding the enemies. In addition, they also often possess larger brains and enhanced capacity to use information and construct appropriate behavioural responses (Sol 2007). The propensity to construct behavioural responses is generally thought to be particularly advantageous in novel environments, which continually challenge the animal with problems and ecological opportunities (Sol 2007).

While the invasion success of long reproductive lifespan fits well with current theories proposed to explain the success of vertebrate invaders (Sol 2007, Blackburn et al. 2009b), the reasons why species that attain a low brood value by reproducing several times in a same season achieve similar success remain far less unclear. Their shorter lifespan should limit exploration and the construction of behavioural responses, but we found no evidence that they are worse invaders than species with longer reproductive lifespan. We speculate that one possible advantage of laying several clutches in a same season lies in allowing extending the breeding season and produce more offspring per year. This may compensate for a high offspring and adult mortality, expected for a species that has had little opportunity to adapt to the new environment. The extension of the breeding season has been related to the invasion success of dark-eyed juncos *Junco hyemalis* in a Mediterranean climate in coastal southern California (Yeh and Price 2004).

Conclusions

Disentangling the life history of successful has long been a major goal in invasions biology, but assembling empirical evidence to support theoretical expectations has proved challenging. Our results yield firm evidence for the long-standing yet poorly supported suggestion that life history does influence invasion success. However, the mechanisms seem to be complex and different from those generally considered in the invasion literature, which help explain why life history features of invaders have been hard to characterize. Thus, there is a variety of mechanisms that could potentially contribute to the relationship between brood value and invasion success; we anticipate that investigating the relative importance of these mechanisms will represent an important avenue for future research. While our results do not preclude that a high reproductive effort may offer advantages during the invasion process, they highlight that in terms of being a successful invader it can pay to possess life history traits that increases the value of adults over the value of offspring, even if this results in some reduction in arithmetic mean fitness.

Figure 2.5. Tree regression describing brood value as a function of the number of broods per year (blue dots) and the maximum lifespan (in years, red dots). The tree regression recursively partitions data into sets that maximize the explained variance of the response variable (i.e. brood value) as a function of a set of predictors using regression methods (21). The predictors are number of broods, lifespan, clutch size and the fast-slow continuum, although the later two traits are not retained in the final model. The λ of the overall model estimated with a PGLS approach is 0.08; this value is statistically non-different from zero (P = 0.163), and hence we do not use phylogenetic corrections in the analysis. The graphs in the bottom show the median and percentiles of the brood value for each strategy (from S1 to S11). Differences in brood value between strategies are all significant at P < 0.05 except for the pairs S4-S7, S5-S10 and S9-S10.

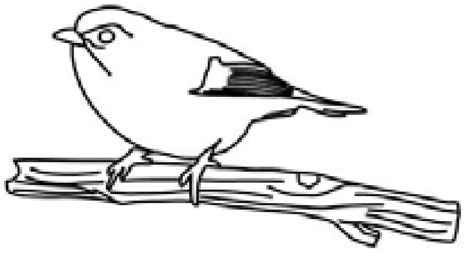


Acknowledgments

This research was supported by funds from Spanish Ministry of Education and Science (‘Proyecto de Investigación’ CGL2010-21838 and ‘Consolider-Ingenio Montes’ CSD2008- 00040) to DS. GEGP was funded by a CONACyT grant 121695 and RPF by a Royal Society University Research Fellowship. We thank Trevor Price, Veronika Bókony, Evan Marks and three anonymous referees for revising previous versions of the manuscript, Andras Liker for facilitating survival data, Katie Davis for making her avian supertree available, Louis Lefebvre, Veronika Bókony, Tamas Székely and Tim Blackburn for fruitful discussions, and Douglas Bates, Emmanuel Paradis and R-team for making available their R packages.

Chapter 3

Biotic resistance, niche opportunities and the invasion of natural habitats[2]



---

[2] with Daniel Sol, Francesc Llimona, Miquel de Cáceres & Sergi Sales. Submitted.

Resum

Resistència biòtica, oportunitats ecològiques i la invasió d'hàbitats naturals

Malgrat l'interès actual en els processos invasius, les raons per quals les espècies exòtiques s'estableixen en entorns als que han tingut poques oportunitats d'adaptar-se romanen poc compresos. Per a l'establiment és fonamental que l'invasor trobi un nínxol adequat en l'entorn nou, però, no és clar si això s'aconsegueix desplaçant les espècies autòctones dels seus nínxols i/o aprofitant les oportunitats ecològiques no monopolitzades per les espècies natives. En aquest treball, nosaltres hem contrastat la importància de les hipòtesis de la competència i de l'oportunitat com explicacions per l'èxit d'un passeriforme exòtic, el Rossinyol del Japó *Leiothrix lutea*, en un parc natural de la conca occidental de la Mediterrània. La invasió del Rossinyol del Japó proporciona una oportunitat única per avaluar la importància relativa de cada hipòtesi, perquè la informació sobre l'abundància d'aus natives per abans i després de la irrupció dels invasors està disponible. Els nostres resultats proporcionen evidències tant per la competència i les hipòtesis d'oportunitat. D'acord amb la hipòtesi de l'oportunitat, l'invasor s'ha establit amb relativament poca resistència o conseqüències per a les espècies natives, el que reflecteix la naturalesa oportunista i generalista de l'invasor i que els seus requeriments ecològics estaven escassament representats en la comunitat nativa. No obstant això, la irrupció dels invasors va coincidir amb el declivi d'una de les espècies natives amb la qual el nínxol ecològic es solapava més. Aquesta disminució no va ser causada per canvis ambientals, ja que no es van observar disminucions similars en els hàbitats on l'invasor era escàs. Més probablement, la disminució va ser deguda al desplaçament competitiu degut a l'invasor, el qual és més gran i s'alimenta en les grans estols. Per tant, els nostres resultats posen de manifest que les hipòtesis de la competència i de l'oportunitat no han de ser vistes com hipòtesis alternatives, sinó com explicacions que combinades poden contribuir a comprendre millor l'èxit de les espècies exòtiques en ambients naturals.

Abstract

Despite the current interest in the invasion process, the reasons why exotic species can establish in environments to which they have had little opportunity to adapt remain little understood. Fundamental to the establishment is that the invader finds an appropriate niche in the novel environment, yet it is unclear whether this is achieved by displacing native species from their niches and/or by exploiting niche opportunities that native species do not monopolize. In the present study, we contrasted the importance of the competition and opportunity hypotheses as explanations for the success of an exotic passerine, the Red-billed Leiothrix *Leiothrix lutea*, in a forest reserve from the Western Mediterranean basin. The invasion of Leiothrix provided a rare opportunity to assess the relative importance of each hypothesis because information on native bird abundance was available before and after the irruption of the invader. Our results yielded evidence for both the competition and opportunity hypotheses. In line with the opportunity hypothesis, the invader established with relatively little resistance or consequence for native species, reflecting the opportunist-generalist nature of the invader and that its niche requirements were poorly represented in the native community. Nevertheless, the irruption of the invader coincided with the decline of one of the native species with which resource niche overlapped to a greater extent. This decline was not caused by environmental changes, as no similar declines were observed in habitats where the invader was scarce. More likely, the decline resulted from competitive displacement by the invader, which was larger in body size and foraged in larger flocks. Thus, our results highlight that the competitive and the opportunity hypotheses should not be seen as alternative hypotheses but as explanations that combined may contribute to better understand the success of exotic species in natural environments.

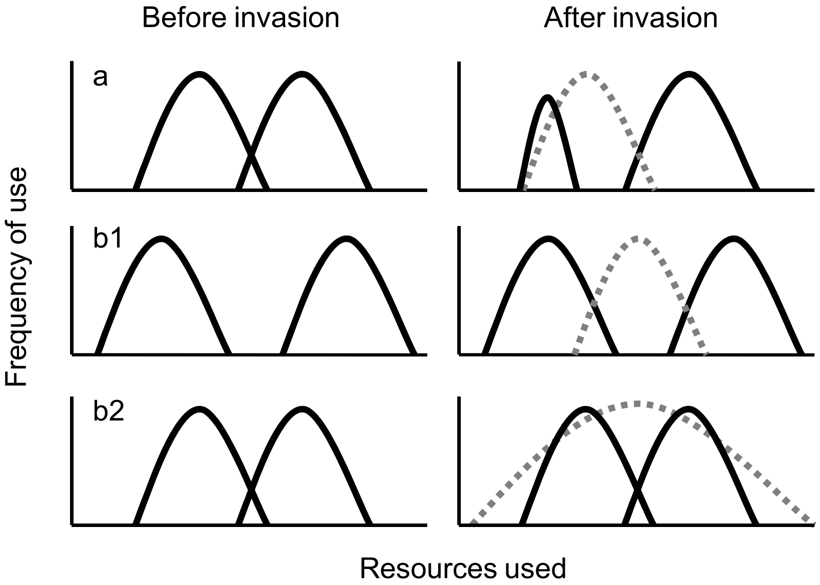
Introduction

Ever since Elton (1958), ecologists have sought to explain why alien species are able to invade novel environments to which they have had little opportunity to adapt, and even sometimes become more abundant than many native species (Sax and Brown 2000). As a way to resolve this paradox, it has been suggested that many successful invaders occupy empty ecological niches derived from human activities that most native species are incapable to use. While the use of human-made niches may account for the success of many invaders, perhaps most of them (Smallwood 1994, Case 1996, Sol et al. 2011a), not all successful invaders are restricted to disturbed environments. In fact, a selected number of species have had notable success in natural habitats (Usher et al. 1992, Tennant 1994, Stohlgren et al. 1999, Hoffmann 2003, Macdonald and Harrington 2003), posing a true paradox to ecologists and evolutionary biologists. Despite the current interest in the invasion process, the reasons why these species have been able to succeed in natural environments remain obscure. This is unfortunate because it is in these environments where the ecological impact of invaders is expected to be higher (Lowe et al. 2000, Clavero and Garcia-Berthou 2005). In this chapter, we study the invasion process of a bird native of subtropical South-east Asia -the Red-billed Leiothrix (*Leiothrix lutea*, Scopoli 1786)- that in the 1990s became successfully established in a forest reserve from the Western Mediterranean basin.

The success of an invader primarily depends on how it interacts with the resources and the native species (Shea and Chesson 2002, Ives and Helmus 2011). These interactions in turn depend on species specific-traits of the invader (Williamson and Fitter 1996, Kolar and Lodge 2002, Sol 2007, Pysek et al. 2009). Assuming that a species already established in a new region has found appropriate resources, the question of why the invader has succeeded turns on the question of how it has been able to exploit the novel resources. Ecological theory suggests two main explanations (Fig. 1): competition and opportunity. The competition hypothesis argues that successful invaders are competitively superior over native species and can displace them from their current niches (Macarthur and Levins 1967, Schoener 1983, Tilman 1994) (Fig. 3.1a). This hypothesis is related to the notion that native competitors offer resistance of the community against invaders, an idea that dates back to Elton (1958). Admittedly, an invader is unlikely to be superior in exploiting the resources than native species that have had more opportunities to adapt to the local environment. Nevertheless, an invader can displace native competitors when it possesses adaptations that confer advantages in contest competition, like aggressive behavior, large body size and high social behavior.

The opportunity hypothesis, on the other hand, relates the success of invaders to their ability to find resource opportunities little used by native species (Sher and Hyatt 1999, Davis et al. 2000, Shea and Chesson 2002) (Figs. 3.1b). This requires that the new environment offers resource opportunities not monopolized by native species and that the invader is able to use these opportunities. There are a number of situations that may generate resource opportunities. For example, species-depleted communities tend to offer more resource opportunities to invaders because the niches are less filled (Simberloff 1995, McKinney 2006) and some resource specialists have died out (Devictor et al. 2008, Helmus et al. 2010). Resource opportunities should in turn be more likely to be exploited by invaders if these possess adaptations that most native species lack (Fig. 3.1b1) and/or when the species show a broad ancestral niche (Fig. 3.1b2). For example, an ecological generalist is more likely to find appropriate resources in a novel environment, and hence reduce the intensity of competition with native species (Mayr 1954, Brown 1989, Vazquez 2005) (Fig. 3.1b3). A flexible generalist, which can respond to changing conditions by changing its behavior or morphology, may be able to do even better (Sol and Lefebvre 2000, Sol et al. 2005, Donaldson-Matasci 2008).

Figure 3.1. Mechanisms for the success of an invader in a one-dimensional resource niche (sensu MacArthur and Levins 1967). The invader (discontinuous lines) can succeed by displacing native species (solid lines) with too similar niches (a). Alternatively, the invader can succeed by exploiting niche opportunities little used by native species (b). This may be because the invader has adaptations that native species lack (b1) or because the invader's niche is broad and override competition with native species (b2). Adapted from Schoener (2009).



Recent attempts to contrast the competition and opportunity hypotheses have progressed in two distinct directions. The first focuses on measuring features to assess the degree of invasibility of the recipient community, such as biotic resistance (Baltz and Moyle 1993, Naeem et al. 2000, Hoffmann and Saul 2010) or availability of resources (Cleland et al. 2004, MacLeod et al. 2009). The second approach shifts the attention to examining whether the invader possesses key traits that may assist its establishment and population increase (Hill et al. 1993, Williams and Black 1994, Sol et al. 2011b).

Although both approaches are interesting in their own right, each of them is by itself insufficient to fully contrast the competition and opportunity hypotheses. This is because the success of an invader not only depends on species traits and features of the community, but also on the interaction between both. The importance of such interactions was already acknowledged by Darwin (1859), who argued that introduced species will be less likely to establish a self-sustaining wild population in places with congeneric native species because closely related species compete more strongly than species belonging to distantly related taxa (Darwin 1859, Duncan and Williams 2002).

A corollary is that to fully demonstrate the validity of the competition and opportunity hypotheses, we need information on how the invader and native species interact with each other over the resources. While these interactions have been measured in some studies of plants (Dyer and Rice 1999, Seabloom et al. 2003) and invertebrates (Le Breton et al. 2005), similar analyses are rarely conducted in vertebrates (but see Sol et al. 2011a). An obvious difficulty is that the interactions of the invader with the resources and the native species are expected to vary throughout the invasion process. For example, it is likely that the invader first settles in the most suitable habitats, and only start using less favorable environments when its density increases (Fretwell and Lucas 1969). Thus, the habitats currently used by the invader may not necessarily reflect the conditions that facilitated the initial establishment of the species. Likewise, the importance of competition is notoriously difficult to quantify because interactions measured today have been shaped by interactions in the past (Bruno et al. 2005). For example, if the effects of competition are not assessed in the initial stages of the invasion process, these effects may be later obscured as competitors become displaced.

The invasion of Leiothrix offers a rare opportunity to assess the relative importance of the competition and opportunity hypotheses because the avian community of the forest reserve has been systematically monitored for the last 23 years, and hence information on bird abundance is available before and after the irruption of the invader. Moreover, this information is available for all major habitats of the invaded location; making it possible to examine how the species selected the habitats where to settle and what were the consequences of such sorting process. Based on the above information, we contrasted the competition and the opportunity hypotheses by addressing key predictions regarding species adaptations, niche use and population dynamics of both the invader and the avian species from the native community.

Predictions

We tested the validity of the competition and the opportunity hypotheses as follows. First, we indirectly measured biotic resistance of the community during the period of establishment of Leiothrix using a phylogenetic-community analysis. The competition hypothesis predicts that the invader should settle in habitats even when these offer biotic resistance, while the opportunity hypothesis predicts that the invader should settle in habitats that offer little biotic resistance. Differences in biotic resistance across habitats are commonly measured in terms of species diversity (Kennedy et al. 2002), but it may nonetheless be better inferred from the analysis of the phylogenetic structure of the native community (Webb et al. 2002). Assuming that closely related species compete more strongly than species belonging to distantly related taxa, an overdispersed phylogenetic distribution of taxa would reflect that closely related taxa with the most similar niche-use are being locally excluded, such that there is minimum niche overlap of coexisting species. On the contrary, neutral and clustered distribution of taxa would indicate that competition plays a less important role in organizing the community. Biotic resistance may be also indirectly measured by quantifying the degree of habitat specialization among members of the native community (Devictor et al. 2008). The competition hypothesis predicts that the invader should establish itself despite the presence of native habitat specialists, assuming that specialists are better competitors than generalists; on the other hand, the opportunity hypothesis expects that the invader settles in habitats with low presence of specialists, where competition is expected to be less intense.

Second, we conducted field observations to evaluate the frequency of contest interactions between the exotic and native species as well as the extent to which the niche of the invader overlaps with that of native species. The competitive hypothesis suggests that the invader should behave aggressively against native species, particularly against those with which niche overlap was greater. However, as already discussed, competition in the past may have lead to niche displacement and competitor avoidance. One alternative in this case is to examine traits such as body size or flocking behavior (see below), which in birds are known to influence the success in interspecific contest competition (Jonart et al. 2007). The opportunity hypothesis, on the other hand, suggests that the establishment of the exotic species should be facilitated when the degree of niche overlap with native species is low or when the foraging niche of the invader is broader than that of native species. The opportunism of the invader may be indirectly measured with the relative size of the brain. In birds, species with larger brains, relative to their body size, tend to show a greater propensity to adopt novel feeding opportunities and to develop new foraging techniques (Lefebvre et al. 1997), abilities that should facilitate success in novel environments (Sol et al. 2005). Thus, according to this hypothesis, the invader should have a brain larger than most natives. As a more direct way to quantify foraging opportunity, we performed a field experiment to simulate the apparition of punctual, novel and non-predictable trophic resources, available to all species of the community.

Finally, we analyzed the population trends of Leiothrix and native species over the 23 years of study to examine the prediction of the competition hypothesis that, once well established, the invader should negatively affect the abundance of those native species with which resource niche overlap is greatest; the opportunity hypothesis predicts no effect at all. As body size and gregariousness are an important determinant of competition success (Jonart et al. 2007), we also examined the prediction that the most affected native species would be those with large niche overlap but smaller size and less gregarious tendencies than Leiothrix.

Methods

Study area

The study area was located in the Collserola Park (41º 25' N, 2º 7' E), a forested area of over 8500-ha close to the city of Barcelona (NE Spain) protected since 1987. Censuses were conducted all over the park whereas experiments and field observations were carried out in two study sites located 2 km apart: the Can Balasc Biological Station forests and the Vil·la Joana Park Information Center surroundings. Bird banding was conducted in Can Balasc Biological Station.

The invader

The Leiothrix is a medium sized babbler, belonging to the Leiothrichidae family (Clements et al. 2011). Native from China, Myanmar, Vietnam, west to Himalayas of India, Bhutan, and Nepal, the species has been introduced to several regions of the world mostly through accidental releases (Long 1981). In Collserola Park, the Leiothrix was first detected in 1998, and its current population is estimated to be about 200-500 breeding pairs (Llimona 2004).

Bird censuses

Between 1987 and 2010, standardized censuses of the bird populations were performed in seven habitats of the Park: orchards, dry grasslands, abandoned arable land, maquis shrubland, conifer woodland, Holm oak forest and riparian forest. The censuses were used to estimate population trends and habitats preferences of both Leiothrix and native species (Llimona and Prodon 2000). Within each habitat, two lineal transects (between 1.5 and 2 km long) were conducted per year by a same observer, one during the winter and another during the spring. In spring, the lineal data corresponded to visual or auditory contacts in a band size of 25 m wide from the progression line of the observer; in winter, because of the scarce territoriality and major mobility of birds, the total number of contacts inside and outside of the band was counted (Colin et al. 1992). Although information on bird abundance was available for almost the entire 1987-2010 period, censuses in the dry grassland habitat started a bit later (in 1991) and censuses could not be conducted for the winters of 1992, 1999 and 2009, as for the springs of 1989 and 1993. Thus, our analyses are based on 129 censuses for the winter and 139 for the spring, in which a total of 67 and 83 bird species were detected, respectively.

Bird banding

For the period 2003-2009, we trapped birds with mist nets following a Constant Banding Effort Site Scheme (ICO 2011). The captures allowed us to obtain information on recapture rates, morphology and body condition of the species in the community. Captures were carried out during two periods of each year, 5 sessions during wintering period (December to March) and 10 sessions during the breeding period (May to August), from dawn to 6 h later. We used 10 nets 12 m long and 2.5 m high, distributed with a density of 1 or 2 nets per ha. A total of 1723 individuals of 21 species were captured. For each bird trapped, we identified the species and obtained information of two morphometric measures (third primary feather length in mm, and body mass in g; Svensson 1992). Length measurements were taken to the nearest half mm using the appropriate rulers, and weights were obtained with a 0.1-g precision digital balance. Body condition was measured based on two different methods: estimating visually (1) the size of subcutaneous fat deposits (according to nine-value scale; Kaiser 1993), and (2) amount of pectoral muscle (Bairlein 1995). The age and sex of the individuals (EURING code) was determined following Svensson (1992). All measurements were carried out by the same researcher. Once measured, the bird was banded with a numbered aluminum ring and released in the same place of capture.

Morphological data

In addition of the measures taken during bird banding sessions, we completed morphometric data for the forest species not captured with information from Cramp (1994). We obtained measures of brain endocasts from A. Iwaniuk.

Foraging observations

In 2009 and 2010, we carried out transects in Can Balasc and Vil·la Joana study sites to record detailed information of foraging behavior of Leiothrix and the coexisting native species. This information was used to estimate key foraging niche components (see below). The observations were restricted to the set of native species that were more abundant in the sites, and hence were more likely to interact with Leiothrix: Great Tit *Parus major*, Blue Tit *Cyanistes caeruleus*, Crested Tit *Lophophanes cristatus*, Long-tailed Tit *Aegithalos caudatus*, European Robin *Erithacus rubecula*, Eurasian Blackcap *Sylvia atricapilla*, Common Blackbird *Turdus merula* and Common Firecrest *Regulus ignicapilla*.

Transects were carried out from 08:00 h to 12:30 h. When a bird was found foraging, we recorded the time of the day, group size, foraging substrate (foliage, branches, trunk, undergrowth, air or ground), foraging location (conifer, evergreen-broadleaved tree, deciduous-broadleaved tree, undergrowth or ground), and foraging technique (glean, jump, hang, hover, hawk, and peck); if the foraging substrate was vegetation, we also measured the height (in meters) at which the birds foraged and the height of bush or tree, using a laser rangefinder (Laser 550A s, Nikon, Japan). When a group of conspecifics was observed, we recorded the behavior of only one individual, chosen at random. All observations were carried out by a same observer. The analyses were based on 661 focal observations, 313 of which were during the non-breeding season.

Feeding experiment

To test whether Leiothrix is opportunistic in its feeding habits, we designed a field experiment. We placed bird feeders (RSPB, Sandy, Bedforshire, UK) in the forest, and we subsequently registered the presence and behavior of the birds attracted to the feeders with trail cameras activated automatically by infrared sensors (Trail Scout 5.0, Bushnell, Overland Park, Kansas, USA). In this way, we simulated the apparition of punctual, novel and non-predictable trophic resources, available to all species. The utilization of artificial feeding sources to study the relations of the species of a community is a methodology that has been demonstrated very effective, since it allows maintaining the birds in their natural environment and subject to their natural motivations (Brown 1988, Shochat et al. 2004).

The feeders consisted in metallic mesh rectangular open trays wide enough to allow more than one individual feeding together. These trays were held by a metallic stake sunk into the forest floor, which placed them at 1.70 m from the floor. We filled the feeders with approximately 200 g of commercial mixture for omnivorous birds (KIKI, Alicante, Spain) in order to increase the range of species potentially attracted. Cameras and feeders were placed inside the forest, under the canopy and far away from any path to avoid human disturbances.

The test started once the camera and the feeder were installed, and lasted until there was no food on the feeder or after three weeks, time that we considered sufficient for the birds to have found the feeder. Two tests were conducted at the same time in different places (a minimum of 200 m apart) of the study area. We conducted 15 of such tests (one of the tests was crippled by wild boars). For each test we registered the latency of each species to visit the feeder, in daytime hours after the feeder was set, as well as inter- and intra-specific interactions among the birds visiting the feeder.

As the species that visited the feeders could simply be those that are more abundant in the habitat and not those with a more explorative behavior, we also conducted 20 min point counts in the area around while the feeders were activated to estimate the abundance of the species, following (Gibbons and Gregory 2006). Each point count was visited three times (morning, noon and afternoon) in a same day, and the average number of individuals recorded was used to control for the species abundance in the analyses.

Data analyses

Body condition.— To compare body condition of Leiothrix with that of native species, we used General Linear Mixed models to fit, separately, fat and breast muscle indices for the banded birds as a function of the species identity (fixed factor), with the third primary feather and age included as fixed covariates and taxonomic family and banding season as random factors. Analysis were conducted with the function lmer of the lme4 R-package (Bates et al. 2011).

Community diversity measures.— To test whether Leiothrix was established in habitats with lowest biotic resistance, we characterized the native avian community of each habitat and season (spring and winter) with a variety of metrics defining species diversity, phylogenetic structure and degree of habitat specialization. We restricted these analyses to the 1995-2001 period, which corresponds to the period of introduction and establishment of the Leiothrix in Collserola Park. Each metric was estimated for each year separately and averaged to obtain a unique estimate for the whole period. The first metric we calculated was the Simpson’s Index of Diversity (Simpson 1949). We estimated this index with all the species present in the community, as well as with only the species morphologically closer to Leiothrix, assuming that morphology reflects ecology (Miles and Ricklefs 1984). To assess which species were closer to Leiothrix, we used length of the wing, tail, bill, tarsus, and body mass (all log-transformed and standardized) to calculate the Euclidean distance matrix for the species of the community within each habitat. Those species situated within the first quartile in the distance matrix from Leiothrix were considered to be morphologically similar.

Phylogenetic structure of the community.— We used a phylogenetic framework as implemented in the picante R-package (Kembel et al. 2010). First, we calculated the phylogenetic diversity (Faith 1992). Unlike the Simpson’s Index, the phylogenetic diversity (PD) is a measures of biodiversity that incorporates phylogenetic differences between species, assessed as the total branch length spanned by the tree including all species in the community (Kembel et al. 2010). The likelihood of finding a competitor should be generally higher in communities with high PD than in those with low PD. We also estimated phylogenetic distances between Leiothrix and the native species to assess whether the invader tended to settle in habitats with more distant close-relatives (Strauss et al. 2006). Finally, we estimated the mean pairwise distance (MPD) between the native species to examine the phylogenetic structure of the community (Kembel et al. 2010). A MPD higher than expected by chance may indicate that closely-related species are being locally excluded whereas a MPD lower than expected can reflect niche conservation. To formally distinguish between both possibilities, we compared the observed MPD values of each community with that of null communities generated randomly by shuffling tip labels across the tips of the phylogeny. We calculated all the measures of phylogenetic relatedness for each habitat of the park for the period of introduction and establishment. We focused the analysis on native passerines, as these are the species more likely to compete with Leiothrix. Our passerine phylogeny was extracted from the avian supertree developed by Katie Davis and Rod Page (University of Glasgow) (Sol et al. 2010b), modified with Treplin (2006) and Thomas (2008).

Community specialization.— We used Juillard et al. (2006) approach to quantify an specialization index for each habitat of the park for the period of introduction (1995-2001), to describe the changes in community specialization for Leiothrix’s breeding habitat during the entire invasion process (1989-2010), and to compare the current degree of specialization of Leiothrix with that of native species of the same foraging guild (period 2008-2010). These authors used the coefficient of variation (standard deviation/average) of the species density across habitats as a measure to quantify species habitat specialization. The community specialization index was calculated as the weighted average of the species specialization index of all species detected in each habitat (Devictor et al. 2008).

Habitat preference.— We used the function multipatt of the indicspecies package (De Caceres and Legendre 2009, De Caceres et al. 2011) to determine the habitat or combination of habitats preferred by Leiothrix at different stages of the invasion process. This function calculates the strength of association between the species and each combination of habitats, and retains the combination corresponding to a maximum association value. A permutation test using the maximum association value as the test statistic is performed to assess significance of the association between the target species and the best matching habitat combination. We used the ‘Indicator Value’ index (IndVal, Dufrene and Legendre 1997) as measure of association between the species and each combination of habitats (De Caceres et al. 2011).

Brain size.— Larger species tend to have larger brains, and this allometric effect needs to be accounted for before any comparison can properly be made (Bennett and Harvey 1985). Similarly to the precious analysis, we modeled brain size as a function of the species identity (fixed factor), with body mass included as fixed covariate and taxonomic family as random factor. For graphical representations we used the relative size of the brain, computed as the residuals of a log-log least-squares linear regression of brain mass against body mass (Sol et al. 2005).

Foraging niche components.— The foraging niche components used in our study were foraging height, tree height, group size, foraging location, foraging substrate and foraging technique. We compared the foraging niche components of Leiothrix respect to that of native species by modeling each component as a function of the species identity (fixed factor) with the functions lmer of the lme4 R-package (Bates et al. 2011). To assess whether Leiothrix differed in the niche relative to native species, each niche component was used as response variable and modeled as a function of the species identity, which was coded as fixed factor. Hour of the observation was also included as fixed covariate whereas taxonomic family and transect were coded as random factors. We used models with Gaussian error in all cases except for foraging location, substrate and feeding technique, which were instead modeled with a Poisson distribution and log link to fit log-lineal models.

Breadth and overlap in foraging niche components.— The resniche R-package (De Caceres et al. 2011) was used to calculate niche breadth and niche overlap between Leiothrix and native species. Niche breadth was calculated as the variance of the resources used by each species. Niche overlap was computed as the cosine of the angle between the two vectors of relative resources use (Pianka 1974); niche overlap ranged from 0 (no overlap) to 1 (complete overlap). For the niche analyses, we assumed equal resource resemblance.

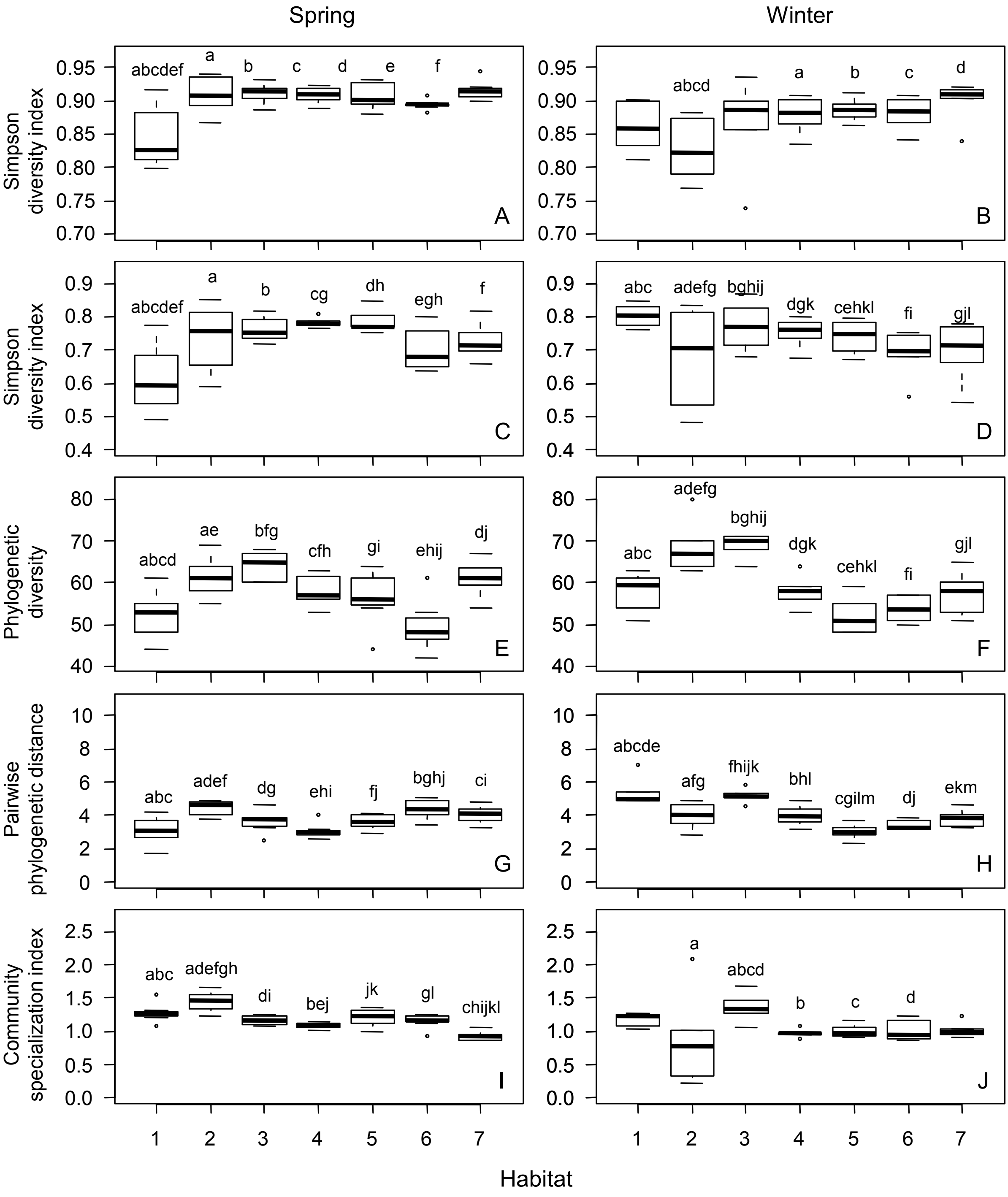
Population trends.— We investigated the population trends of native resident birds after (1998-2010) and before (1987-1997) the arrival of Leiothrix to assess the impact of the invader on the community. Using seasonal kilometric abundance indices (see above), we analyzed species trends for the habitats for which Leiothrix showed a clear preference. To take into account the possible auto-correlation in the time series data, we used auto-regressive moving average (ARMA) serial correlation structures (Zuur et al. 2009a). For each species and habitat, we compared models with different auto-regressive residual ARMA structure of order, and used AIC to assess which model best fitted the data. The models were fitted with the gamm function of the mgcv R-package (Wood 2004), using a Gaussian distribution and identity link.

Results

The success of Leiothrix in Collserola Park

Although Leiothrix was one of the most abundant species in the park, present almost in all habitats in all seasons (Appendix B: Fig. 1), the analysis of capture-recaptures of banded individuals revealed a low recapture rate among years (Appendix B: Fig. 2). This may reflect high mobility and/or mortality, typical of species poorly adapted to their environment. However, leiothrixs were not in worse body condition than native species (Appendix B: Table 2), indicating that somehow the invader had found an

Figure 2. Signatures of biotic resistance in each habitat during the early stages of invasion of Leiothrix (1995-2001): (A, B) total species diversity; (C, D) morphological-similar species diversity; (E, F, G, H) phylognetic structure; and (I, J) habitat specialization. Lowercase letters indicate significant differences (P<0.005) between each pair of habitats as determined with separated GLMM models. The habitats are ordered from less to more preferred by Leiothrix, according to the order of appearance and abundance of the species in each habitat (see Appendix B: Fig. 1). Abbreviations are: 1, dry grasslands; 2, orchards; 3, abandoned arable land; 4, maquis shrubland; 5, conifer woodland; 6, Holm oak forest; and 7, riparian forest.

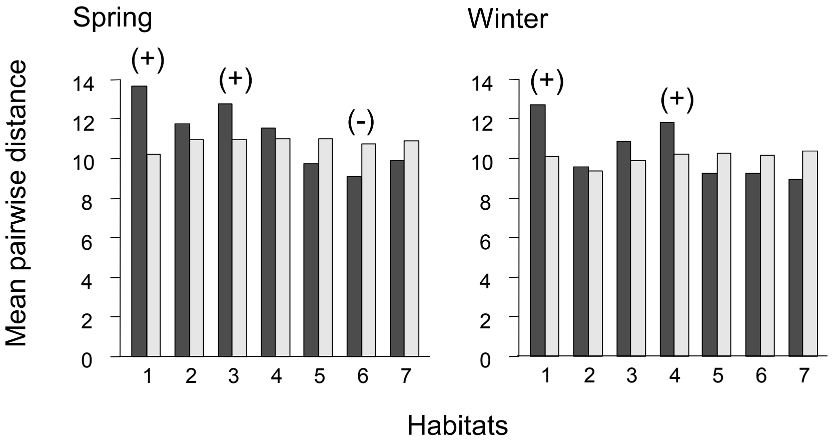


appropriate foraging niche in the recipient region. The fact that practically there were not captures of leiothrixs during the winter (Appendix B: Fig. 3) indicates the possibility that the invader moves outside their breeding territories during this period.

Habitat selection and biotic resistance

Leiothrix neither preferred to settle in the habitats with less avian phylogenetic diversity nor in those where species were more distantly related to it (Fig. 3.2). Nevertheless, there were no clear signatures of biotic resistance in the habitats invaded. First, there was little evidence of phylogenetic overdispersion among the species of the native community. Rather, co-occurring native species were often more closely related to each other than expected from the regional species pool, indicative that habitat selectivity predominates over competition in the organization of the avian community (Fig. 3.3, Appendix B: Figs. 4, 5, Table 3). Second, Leiothrix first settled in the habitat with a comparatively larger number of habitat generalists (Fig. 3.2).

Figure 3.3. Observed (solid bars) and random (open bars) phylogenetic mean pairwise distance between species within habitats for the period 1995-2001. Positive signs denote habitats with greater phylogenetic distance among co-occurring species than expected, while minus signs denote lesser phylogenetic distance than expected (see Appendix B: Table 3). Abbreviations and habitat order are as in Fig. 3.2.



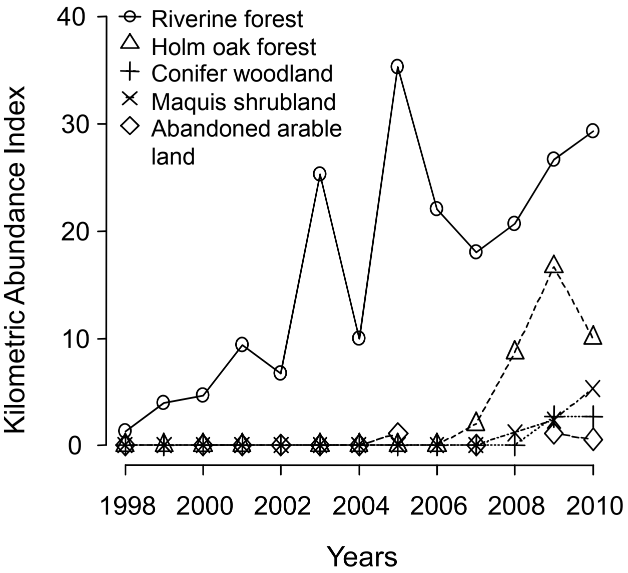
Habitat generalism

Leiothrix behaved as a forest specialist (Fig. 3.4). In the early stages of the invasion process, the species was mostly associated with the riparian forest (maximum IndVal = 0.987 for a single habitat, P = 0.001). However, when the population increased in numbers, individuals started invading three other habitats (maximum IndVal = 0.979 for a combination of four habitats, P = 0.009). Despite this habitat expansion, Leiothrix still exhibited a higher degree of habitat specialization than that of most native species more than a decade after the introduction (Fig. 3.5b, Appendix B: Table 4).

Foraging niche use

Leiothrixs foraged mainly among the foliage of evergreen broadleaved trees, although they also used deciduous trees and undergrowth in a proportion that increased during the winter (Appendix B: Fig. 6, Appendix B: Tables 5, 6). Individuals tended to forage in vegetation about 6.5m ± 4 tall, both in spring and winter, exploiting mostly the parts around 4 m ± 2.75. The major foraging technique was gleaning, both during the breeding and the wintering season, but in spring jumping was also used frequently.

Figure 3.4. Population growth of Leiothrix in different habitats in Collserola for the period 1998-2010. Gaps in the series points represent years without data.



Behavioral opportunism

Leiothrix had a brain larger than expected for their size, and clearly larger than that of most native species belonging to the same foraging guild (Fig. 3.6, Appendix B: Fig. 7, Table 7). The opportunistic character of Leiothrix was also apparent in the field experiment. During the experimental tests, only six species of the forest avian community visited the feeders: the Robin, Great and Coal Tit, Jay, Blackbird and Wren (Appendix B: Fig. 8). Leiothrix visited the experiments in two different trials, although it was not the fastest to arrive and used the feeder less often than predicted by its abundance (Appendix B: Fig. 8).

Figure 3.5. (a) Variation in Leiothrix specialization index since the beginning of the invasion. A LOESS smoother with a span width of 0.75 was added to aid visual interpretation. (b) Comparison of species specialization index between Leiothrix and native forest species for the period 2008-2010. Asterisks indicate a significant difference respect to Leiothrix (see Appendix B: Table 3 for statistics). Abbreviations are: RBL, Red-billed Leiothrix; LTT, Long-tailed Tit; ROB, Eurasian Robin; BLT, Blue Tit; CRT, Crested Tit; GRT, Great Tit; FIR, Common Firecrest; BLK, Eurasian Blackcap; and BLB, Common Blackbird.

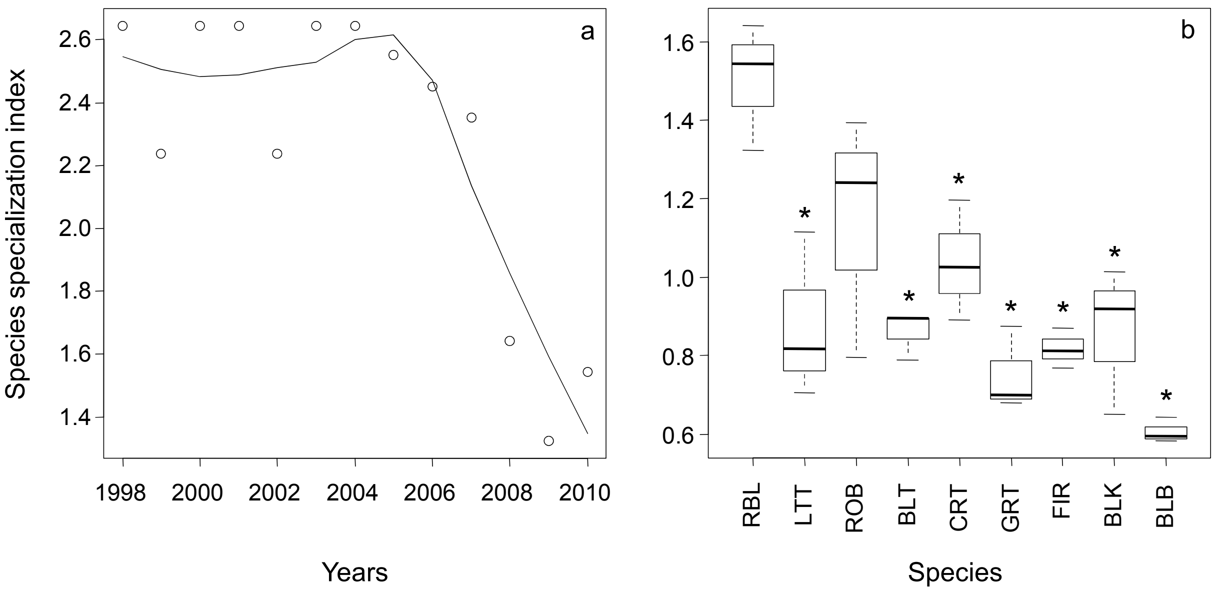
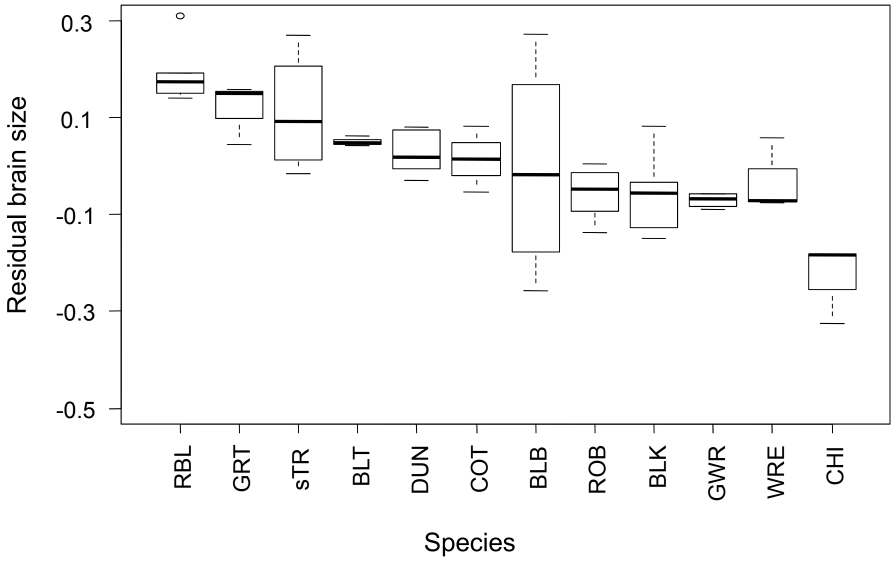


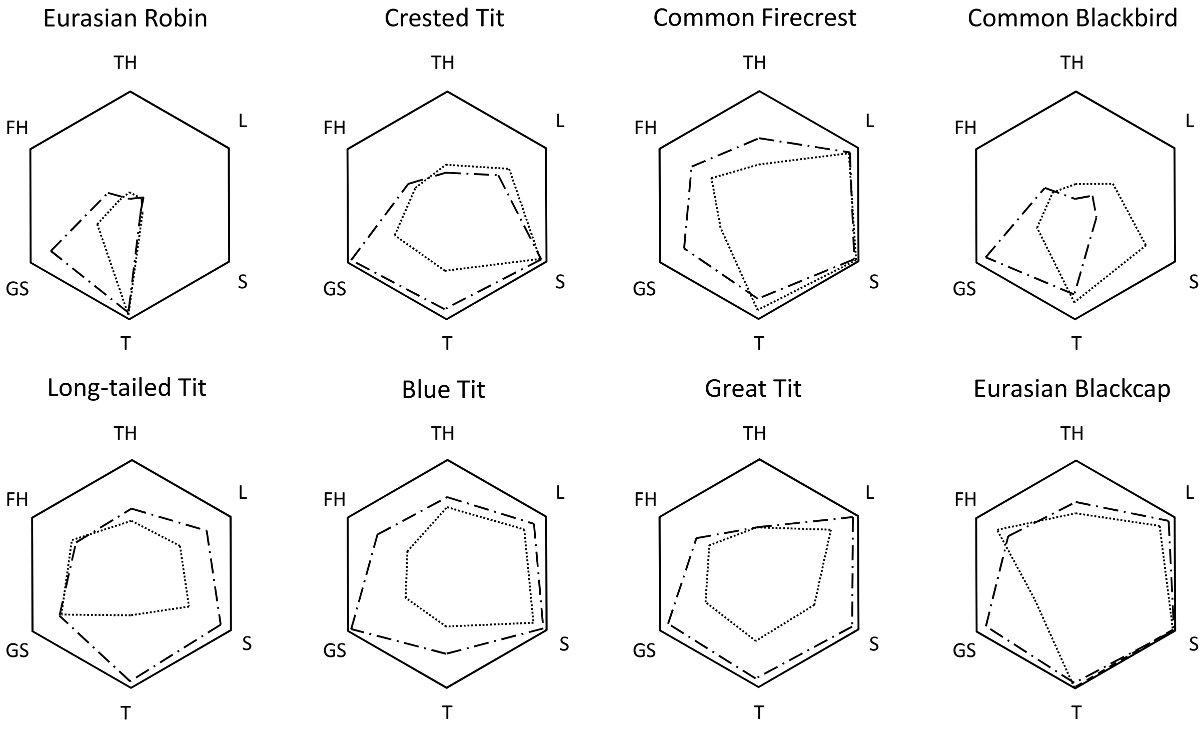
Figure 3.6. Comparison of residual brain size between Leiothrix and native forest species of similar size. We only used native species for which brain information was available for several specimens (sample size shown beside each species box). See Appendix B: Table 1 for full species names, Table 6 for statistics and Fig. 9 for a similar comparison with the rest of species.



Foraging niche overlap

In the native community, there was a number of species with foraging niches that overlapped at some extent with that of Leiothrix; however, none overlapped entirely (Fig. 3.7). The only species that overlaps importantly with Leiothrix was the Blackcap and, in a minor degree, the Firecrest during the breeding season. Leiothrix's social behavior was quite unique within the Collserola Park forest avian community (Fig. 3.7). Among native species the only group-forager was the Long-tailed Tit, but this species showed little niche overlap with Leiothrix in the other niche components. The foraging niche components of Leiothrix were not generally broader than that observed in native species (Fig. 3.8), contradicting model b2 in Figure 3.1.

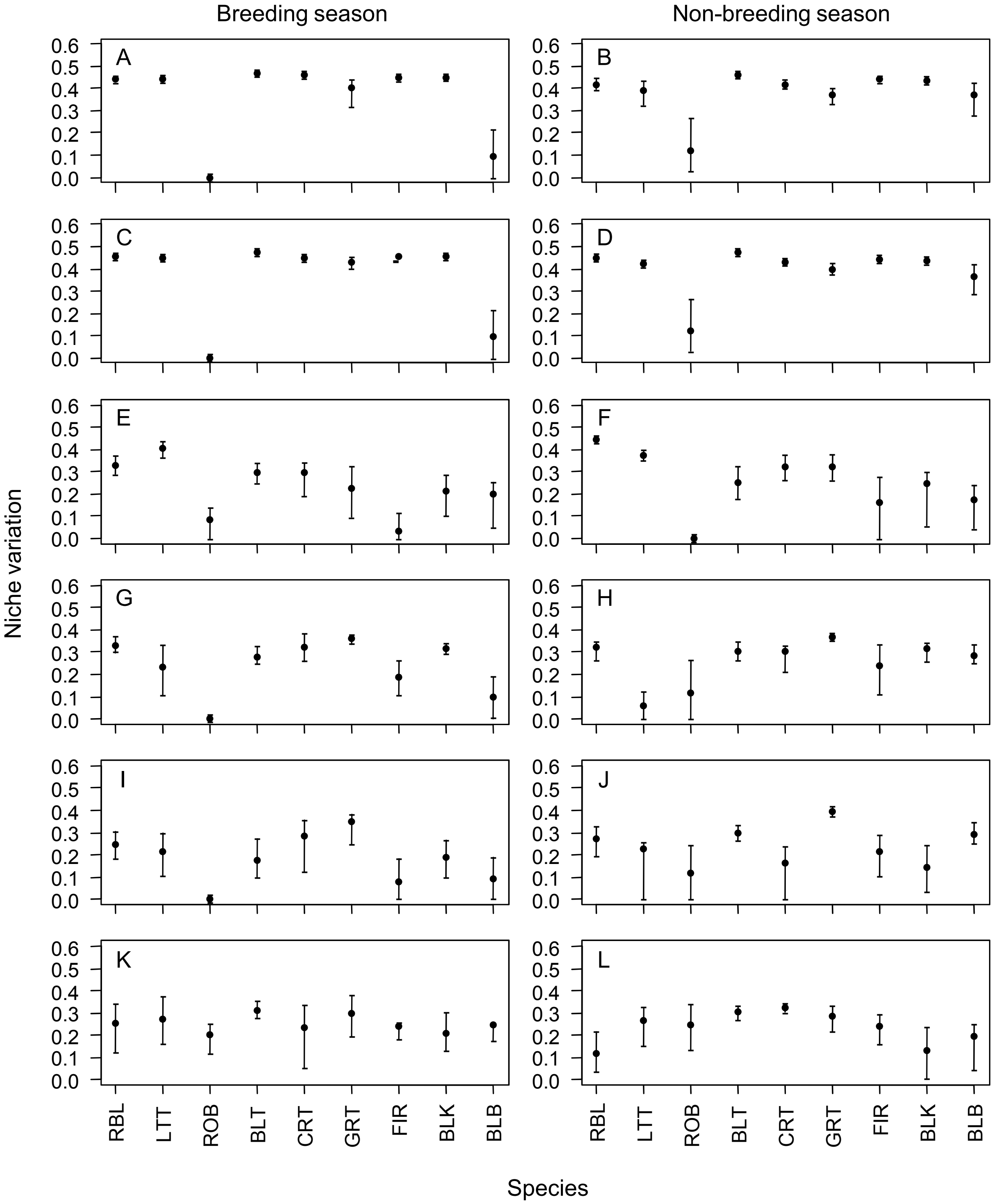
Figure 3.7. Native species niche overlap versus Leiothrix for six components of the foraging niche. Abbreviations are: FH, foraging height; TH, tree height; L, foraging location; S, foraging substrate; T, foraging technique; and GS, group size. Lines: Exterior, total niche overlap; dotdashed, breeding season overlap; and dotted, non-breeding season overlap.



Social dominance

Our behavioral observations yielded little evidence that Leiothrix behaved aggressively against native species. Of 117 foraging behavior observations, either alone or in group, in four occasions the Leiothrix was feeding close to a Blue Tit, in four was close to a Blackcap, in three close to a Great Tit, and in only one close to a Robin. In none of these cases there was any aggression or supplanting attack.

Figure 3.8. Foraging niche breadth (mean ± 95% confidence interval): (A, B) foraging height, (C, D) tree height; (E, F) group size; (G, H) foraging location; (I, J) foraging substrate; and (K, L) foraging technique. The minimum niche breadth is 0, obtained when all resources used are equal or when a single resource is used. Abbreviations are as in Fig. 3.5.



Likewise, during the experiments most interactions involving Leiothrix were against conspecifics, and only in one occasion we observed Leiothrix displacing a Robin from the feeder, a species otherwise dominated by the rest of species.

Leiothrix was not the largest species when compared with native species occurring in the same habitat in the same season (Appendix B: Fig.9). Nine native species in the community were larger than Leiothrix and two had similar size (Appendix B: Table 8). However, 20 native species were significantly smaller than Leiothrix (Appendix B: Table 8). When compared with species that share at least one component of the niche, Leiothrix was only the fifth larger species in the community, just below the Jay, the Blackbird, the Song Thrush and the Golden Oriole.

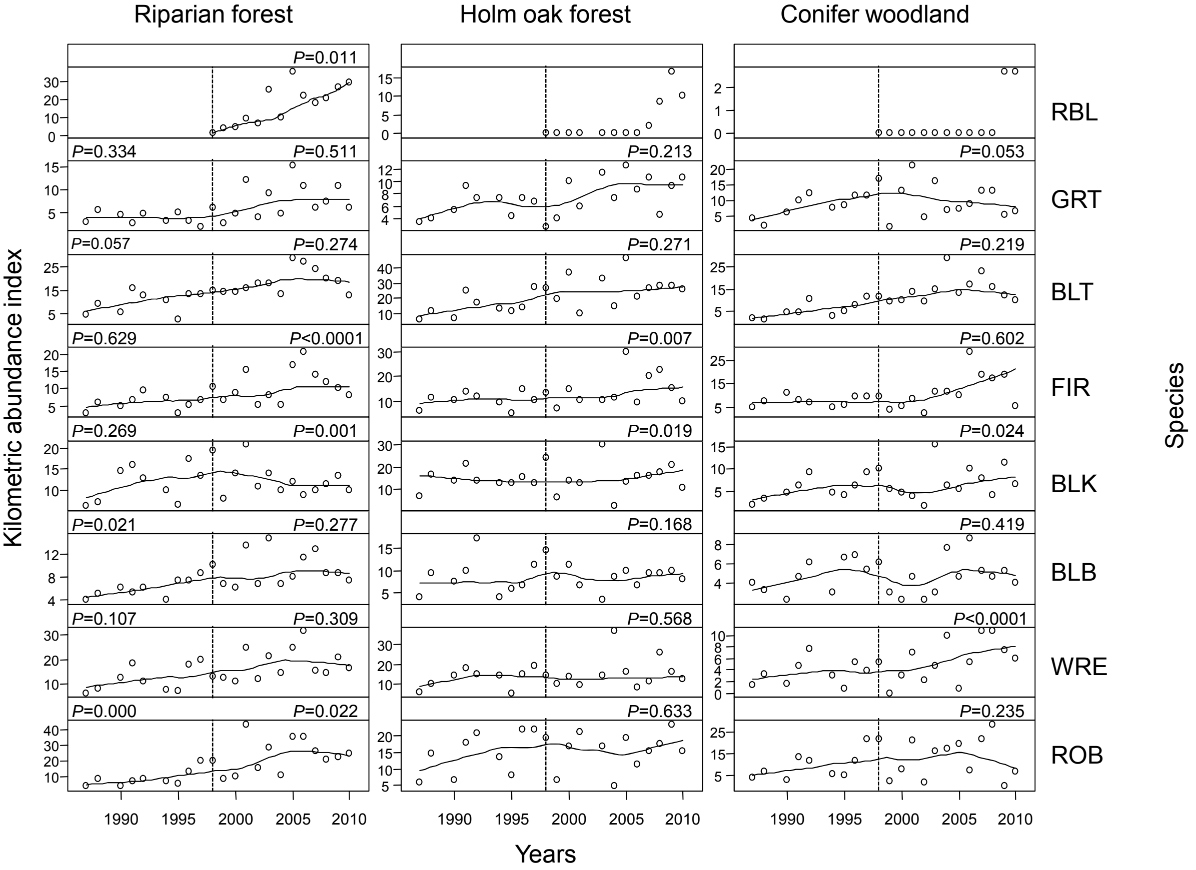
Population effects of Leiothrix on native avian community

Since the Leiothrix was first observed in the riparian forest, the Blackcap showed a significant decline in number in this habitat. Instead, the population trend for the Blackcap was positive in the Holm oak forest and conifer woodland, two habitats only recently invaded by the species (Fig. 3.9). This reinforces the view that the decline of the Blackcap was associated with the invasion of the Leiothrix rather than to changes in environmental conditions. Indeed, when the abundance of Leiothrix was included in the model that evaluated how the Blackcap changed in abundance over the years, the negative trend found in the previous analyses (Appendix B: Table 9) turned out non-significant ($t = -0.543$, $df = 10$, $P = 0.599$). The Leiothrix is larger than the Blackcap (almost 23% larger), and tend to flock in large groups, which should make it superior in contest competition. For the rest of native species, the population trends did not vary across habitats, except for the Long-tailed Tit. In this species, the population in both the Holm oak forest and conifer woodland experienced an increase, but in the riparian forest where Leiothrix was more abundant the species did not exhibit such an increase (Appendix B: Table 9).

Discussion

Introduced species are confronted with environmental conditions that differ in many aspects from their ancestral environments, and to which they have had little opportunity to adapt, which should severely limit their survival and reproduction. It is not surprising then that most human-mediated past introductions of plants and animals have failed to establish self-sustaining populations (Williamson and Fitter 1996). Nevertheless, some species -like the Leiothrix in Spain and Japan- seem to have attained great success in their new environments, attaining densities that rival those of the most abundant native species. The question is why. Our comprehensive analysis sheds new light on this question, suggesting

Figure 3.9. Population trends based on a kilometric abundance index of Leiothrix and native species for the forested habitats 1987-2010 spring censuses. A LOESS smoother with a span width of 0.5 was added to aid visual interpretation. P-values correspond respectively to the slope of the trend for the time series before and after the arrival of Leiothrix to Collserola for riparian forest, and after its arrival for Holm oak forest and conifer woodland. Date of first appearance of Leiothrix (1998) marked with a vertical dotted line. Trends could not be calculated for Leiothrix for Holm oak forest and conifer woodland because the data were too scarce, included only for comparison purposes. Only the most abundant native species are included. See Appendix B: Table 1 for full species names and Table 8 for the complete population trend analysis.



that both the opportunity and the competition hypotheses may contribute to explain the success of Leiothrix in Mediterranean forests.

The opportunity hypothesis

The opportunity hypothesis is favored by three lines of evidence. First, the recipient communities seemed to offer little resistance against the invader, as suggests the lack of phylogenetic overdispersion and the predominance of generalist species. The absence of phylogenetic overdispersion in a community may be an indicator that the benefits in occupying a suitable habitat outweigh the potential increased cost of competing with close congeners, and hence that competitive exclusion is not the main factor organizing species composition (Webb et al. 2002, Davies 2006). A predominance of generalist species, on the other hand, it is expected to reduce the strength of competition, as in a evolved community generalists should generally show less proficiency in using the resources than specialists. This should in turn facilitate species coexistence (Lovette and Hochachka 2006) and the establishment of invaders. It is worth noting that the study area is close the city of Barcelona and hence it has not been free from human disturbances. The absence of foraging specialists in the avian communities may be a consequence of these disturbances. Thus, it is possible that biotic resistance plays a greater role in more pristine environments.

Second, the invader behaved both as a generalist and opportunist. These features are reflected in the way the species used the habitats and adopted novel feeding opportunities, as well as in their large brain relative to their body (Sol et al. 2005). As most native species were also generalists, it seems that this strategy was particularly useful to persist in the environment. A broad niche strategy may facilitate that the invader finds appropriate resources in the new environment and allows the coexistence with species with which overlaps to a great extent in the niche. The ability of the Leiothrix to adjust their behavior to new environments, which should be facilitated by its relatively large brain (Lefebvre et al. 1997, Overington et al. 2009), is also revealed when comparing the foraging behavior in Collserola Park respect to Japan. In Japan, Leiothrix used jumping with almost the same frequency as gleaning, and in a higher proportion than in Collserola Park, where gleaning is the usual foraging technique. Jumping allows chasing aerial insects above the understorey in the lower layer of the forest, a foraging space not used by Japanese native species. Thus, in Japan Leiothrix seems to have adjusted its behavior to exploit an ecological niche where the native guild is poor (Amano and Eguchi 2002a). However, it is worth noting that in Collserola Leiothrix was neither the species with the broadest resource niche nor the one with more opportunistic feeding habits, reinforcing the view that other factors are also important in the invasion success of the species.

Third, the resource niche of the invader generally exhibited little overlap with respect to that of most native species. Leiothrix‘s social behavior was quite unique within the Collserola avian community. Among native species, the only group-forager was the Long-tailed Tit, but this species showed little niche overlap with Leiothrix in the other niche components. Social foraging should be particularly useful when confronted to a novel environment, as the ability to rapidly gathering information about resources and enemies may make a life or death difference (Liker and Bokony 2009, Rodriguez et al. 2010). A high mobility in winter, reflected in our low recapture rates as well as in previous observations of erratic movements (Herrando et al. 2011), may be another distinctive strategy of Leiothrix. Unlike Leiothrix, most native species remained in their breeding grounds during the winter, some even defending feeding territories (Telleria et al. 1999, Senar and Borras 2004). In average winters, such a strategy may be advantageous (Perez-Tris and Telleria 2002a), but during particularly harsh winters a high mobility may facilitate tracking changes of the resources when in short supply (Perez-Tris and Telleria 2002b). In their native range, the foothills of the Himalayan Mountains, the species perform annual altitudinal winter migrations (Ali 1977), as they also do in their invasive range in Japan (Eguchi and Masuda 1994, Tojo and Nakamura 2004), where the species breeds over the 800 m and the climate is much colder than in the Mediterranean basin.

The competitive hypothesis

Despite the central importance of niche opportunities, the competitive ability could also play a role in the success of Leiothrix in Collserola. The arrival of Leiothrix in the community coincided with a decline of the native species with which overlaps in the niche to a greatest extent, the Blackcap. The decline of Blackcaps did not seem to be caused by environmental changes, as no similar declines were observed in habitats where the invader was absent. The alternative is that the Blackcap suffered from competition with the invader, a possibility that receives credence from the great niche overlap between both species. Indeed, Leiothrix has suggested to have caused similar declines of native species in other regions where the species is invading natural habitats (Sato 2006). Although we found no evidence of agonistic encounters between Leiothrixs and Blackcaps, this does not exclude a role for contest competition. This is because contest competition may lead to avoidance behaviors, which may reduce the frequency of encounters. Leiothrix was larger in size and flocked in larger groups than blackcaps, which would have given some competitive advantages. Other mechanisms are also possible, however. One is exploitation competition. Although in general one would expect that native species are better adapted to exploit the local resources than an exotic species, as the former have had more opportunity to adapt locally, this is not necessarily true for generalists. Moreover, as already mentioned, social foraging may help overcome the lack of proficiency in foraging under novel contexts through social learning and skill-pool effects (Liker and Bokony 2009, Rodriguez et al. 2010).

While no one questions the importance of niche opportunities in the success of invaders, the role of competition is more controversial (Duncan et al. 2003, Levine et al. 2004, Gilbert and Lechowicz 2005, Perelman et al. 2007). Recent evidence suggests that invasions generally do not cause extinctions of native species, and hence their impact on biodiversity is generally additive rather than substitutive (Bruno et al. 2005). Biotic resistance may certainly reduce the establishment of individual exotic plants, yet ecological interactions rarely enable communities to resist invasion but instead constrain the abundance of exotic species once they have successfully established (reviewed in Levine et al. 2004). Nevertheless, most previous field studies have been carried out in disturbed environments, where most invaders have proliferated. In disturbed environments, competition regimes may have been altered by a variety of factors, such as an increase in extinction risk of native species, creating new niche opportunities for newcomers and generating environmental heterogeneity that may allow resource partitioning (see Bartomeus et al. 2011 and reference therein). In less altered environments, competition between invaders and native species is expected to be more important. Although the only noticeable effect of Leiothrix was on a single native species and the effect was mostly in terms of abundance reduction rather than local extinction, the potential risk of the species on native biodiversity should not be under-appreciated considering that the species is still spreading (Clarabuch 2011) and that their potential range could be 36 times greater than the present one (Herrando et al. 2010).

Conclusions

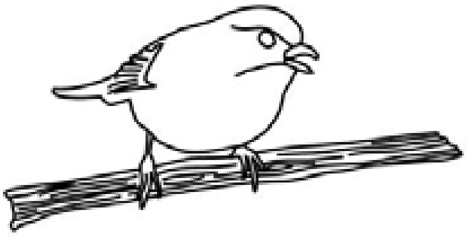
Our study highlights the complexity of the invasion process, and the need to see alternative hypotheses as complementary explanations rather than as mutually exclusive. This complexity makes it necessary to study the invasion process with an integrative approach that combines a variety of analytical approaches, from classical ecological approaches to more modern phylogenetically-based methods. Moreover, it also requires information on the native community before and after the arrival of the invader, which in the case of the Red-billed Leiothrix in the Collserola Park proved critical to validate key predictions of the competition and opportunity hypotheses. Admittedly, there are still numerous issues to be resolved to fully understand the success of Leiothrix in Collserola. Despite these uncertainties, our study represents one of the few examples in the literature that has pinpointed some of the key factors influencing the success of an invasive species in a natural environment.

Acknowledgements

We thank Andrew Iwaniuk for facilitating brain data, Gabriel Garcia-Peña, Oriol Lapiedra, César Gonzalez and Joan Maspons for useful comments on the manuscript, and Xavier Espadaler for providing references. This research was supported by a DURSI scholarship of the Generalitat de Catalunya and the European Social Fund 2005SGR00090 to MV, and by funds from the Spanish Ministry of Education and Science (‘Proyecto de Investigación’ CGL2010-21838 and ‘Consolider-Ingenio Montes’ CSD2008- 00040) to DS.

Chapter 4

A global risk assessment for the success of bird introductions[3]



---

[3] with Daniel Sol. Published as: Vall-llosera, M., Sol. D (2009) A global risk assessment for the success of bird introductions. Journal of Applied Ecology 46:787-795.

Resum

Una avaluació de riscos global per a l'èxit de les introduccions d'ocells

La preocupació per l'impacte de les espècies invasores ha portat al desenvolupament de metodologies d'avaluació de risc per identificar els possibles invasors i prevenir futurs problemes ecològics i econòmics. No obstant això, el desenvolupament d'un protocol d'avaluació de riscos és un repte a causa de les dificultats de predir amb exactitud el resultat de la introducció d'espècies. En aquest capítol, nosaltres hem desenvolupat una avaluació global de riscos per a les aus. Nosaltres hem integrat dos aproximacions, models lineals generalitzats mixtos (GLMM) i models d'arbres jeràrquics, per poder identificar les introduccions amb el risc més alt d'èxit de l'establiment. Treballs anteriors han demostrat que el nombre d'individus alliberats és el factor que més influeix en l'èxit de l'establiment en els animals, una conclusió que va ser recolzada pels nostres anàlisis. L'èxit en l'establiment també va ser superior per les espècies amb nínxols ecològics més amplis i amb cervells més grans en relació amb la mida del cos. Aquestes característiques haurien d'augmentar la probabilitat de trobar un nínxol adequat a la regió d'introducció. El GLMM i model en arbre van predir la probabilitat d'èxit de l'establiment de les aus a Europa i Austràlia, amb una precisió alta (més del 80% de les introduccions van ser correctament classificades). Això posa en relleu que el risc d'establiment pot ser avaluat raonablement amb la informació sobre l'ús de l'hàbitat, la mida del cervell i la mida de la població fundadora. Quan el comparem amb una mètode d'avaluació de riscos alternatiu basat en un sistema de classificació qualitatiu, el mètode quantitatiu aconsegueix una major precisió amb menys informació. Creiem que fer avaluacions de risc quantitatives basades en les característiques relacionades amb l'èxit de l'establiment és difícil, però possible, i proporcionen una eina útil per orientar les polítiques de prevenció destinades a mitigar l'impacte d'espècies invasores.

Abstract

Concern over the impact of invasive species has led to the development of risk assessment methodologies to identify potential invaders and prevent future ecological and economic problems. However, developing a risk assessment tool is challenging because of the difficulties of accurately predicting the outcome of species introductions. In this chapter, we develop a global risk assessment for birds. We integrate two approaches, generalized linear mixed models (GLMM) and hierarchical tree models, to help identify those introductions with the highest risk of establishment success. Past work has shown that the number of individuals released is the main factor influencing establishment success in animals, a conclusion that was supported in our analyses. Establishment success was also higher for species with broader ecological niches and larger brains relative to body size. These features should increase the likelihood of finding an appropriate niche in the region of introduction. The GLMM and tree model predicted the probability of establishment success of birds in Europe and Australia with high accuracy (over 80% of introductions correctly classified). This highlights that establishment risk can be reasonably assessed with information on general habitat use, brain size and the size of the founder population. When compared with an alternative risk assessment tool based on a qualitative ranking, our quantitative approaches achieved higher accuracy with less information. We believe that quantitative risk assessments based on traits related to establishment success are difficult but feasible, and provide a useful tool for guiding preventive polices aimed at mitigating the impact of invasive species.

Introduction

Concern over the impact of invasive species on biodiversity loss and homogenization has spurred governments worldwide to increase investment in prevention and control measures (Leung et al. 2005). Once a non-indigenous species is established in a new region it is extremely difficult and costly to eradicate or control (Bergman et al. 2000, Fagerstone 2003). Recent attention has therefore switched to developing systems for preventing the establishment or the spread of the invasive species (Hulme et al. 2008). One possible strategy is to develop risk assessment protocols that identify high-risk situations for species that may become established and have a negative impact in a new region. Risk assessments for alien species seek to simplify the decision making process by identifying those characteristics that are linked to invasion success and using them to make predictions about the outcome of future introductions (Kolar and Lodge 2002). An effective risk assessment method would be highly valuable in guiding and designing environmental policies; for instance, it can inform decisions about the planned introduction of alien species, and help establish priorities in eradication and control programmes. The goal of our study is to develop a global risk assessment for birds, a group of organisms that has become a model for the study of invasion biology (Duncan et al. 2003).

Recent attempts to develop risk assessment protocols have progressed in two distinct directions. The first uses a ranking approach that converts responses to questions related to species invasiveness and expected impacts to a score whose value determines the overall risk posed by the invader (hereafter, ranking systems). These are non-statistical, qualitative methods based on expert knowledge, and they require a large amount of information in order to answer the questions. Moreover, the nature of the questions and their weight on the final score are arbitrary and not always based on rigorous scientific knowledge. The second approach uses advanced statistical techniques to predict the probability that a species can establish itself or spread based on their intrinsic features (hereafter, quantitative systems). The work reported here utilises the statistical approach, which *a priori* should be more powerful than qualitative methods.

We built two types of quantitative risk assessment, one based on generalized linear mixed models (hereafter GLMMs) and the other on Hierachical decision trees. The GLMM approach is an extension of Generalized Linear Models that has been used previously to identify the predictors of establishment success. It allows problems associated with phylogenetic and spatial non-independence among introductions to be corrected (Blackburn and Duncan 2001a, Sol et al. 2008b). GLMMs can also be useful in making predictions, but to date there have been no attempts to use this methodology as a risk assessment tool for biological invasions. Hierarchical decision trees, on the other hand, use a likelihood approach to split a response variable (e.g. success or failure in an introduction) into increasingly homogenous subsets by binary recursive partitioning on a set of predictor variables (Clark and Pregibon 1992). Our risk assessment was based on a particular type of Hierarchical decision trees called regression trees. They allow quantitative estimations of the risks, are able to handle complex interactions between variables, and present the results in a graphical format that is easy to understand even for non-experts. A similar approach has been used successfully to predict invasive potential of freshwater fish (Kolar and Lodge 2002), and this provides the foundation of our second approach.

Developing risk assessment protocols is not an easy task. Because the invasion process is generally seen as highly idiosyncratic, there is a widespread perception that it is impossible to predict which species will invade in any given situation (Ehrlich 1989, Kolar and Lodge 2001). In birds, for example, a large number of species-traits have been proposed to influence establishment success (Newsome and Noble 1986, Blackburn and Duncan 2001a, Cassey 2001b, Kolar and Lodge 2001, Cassey et al. 2004, Jeschke and Strayer 2006) (see Table 4.1), but very few of these features have been supported firmly by empirical evidence (Duncan et al. 2003). This could indicate that only a few traits are relevant in determining the outcome of an introduction. If so, we can ask whether these few traits are sufficient to produce reliable risk assessment tools. Alternatively, the lack of success in identifying the features of successful invaders could reflect the low power of the tests used due to insufficient sample sizes or the failure to deal with biases and confounding effects associated with historical introductions (Blackburn and Duncan 2001a, Sol et al. 2008b). In this case, the solution is to re-analyse whether these features influence establishment success with a larger sample of introductions and using approaches that allow controlling for possible biases and confounding effects. To develop our quantitative risk assessments, we employ a global database documenting the outcome of 832 introductions of 202 avian species to new locations, 311 of which were successful. With this information, we test the predictive power of 17 traits that have been either demonstrated or suggested to be associated with establishment success (Table 4.1), using both the GLMM and tree regression approaches. We validate our risk assessment models with the subset of species introduced to Europe and North America. Finally, we compare the performance of both methods with a ranking system proposed for vertebrates in Australia (Bomford 2003).

Methods

Introduction data

The information on avian introductions comes from a compiled global database (Sol et al. 2005), reported mainly in Long (1981) and Lever (1987), which we updated with information from Lever (2005). An introduction event was defined as the human-driven accidental or deliberate release of a species to a new location, outside its area of natural distribution. All introductions of a given species to the same place within a period of 10 years were considered as a sole introduction event (Cassey et al.

2004). From this global database, we restricted the analyses to introduction events that included information on propagule size, as this is a major determinant of introduction success in birds (Lockwood et al. 2005). Data on introduction effort were available for 832 introduction events (i.e. 25% of all introduction events reported in the literature), comprising 202 species from 36 families, 311 of which were successful (Appendix C: Table 1). The outcome of each introduction was scored as 'established' if the species succeeded in establishing itself in the new region, or 'extinct' if it did not. A species was considered established when it had developed a self-sustaining population, defined as a population that persisted without declining for at least 20 years after release. Consequently, introductions carried out after 1987 were excluded from the analysis. We also excluded recorded introductions with unknown or uncertain outcome, failures associated with human eradication and natural colonisations.

Explanatory and confounding variables

Those characteristics hypothesized to influence establishment can be grouped into three categories (Duncan et al. 2003, Sol 2007): (a) traits that pre-adapt species to the new environment, (b) traits that favour population increase from a low level, and (c) traits that constrain establishment success (Table 4.1). We extracted data from the literature (see Appendix C: Supplementary references) for all major traits that have been hypothesized to influence establishment success in birds (Table 4.1).

In addition, we quantified several factors that could inflate or obscure the predicted link between species-level traits and establishment success: (1) propagule size, measured as the minimum number of individuals released (log-transformed) (Cassey et al. 2004); (2) locations where species were introduced, assigned to the six biomes (Australasia, Ethiopian, Nearctic, Neotropical, Oriental and Palaearctic) (Blackburn and Duncan 2001a, Cox 2001, Cassey 2003); (3) latitudinal difference, measured as the difference between the latitudinal mid-point of the native range of the species and the latitude of introduction calculated without reference to the hemisphere (Blackburn and Duncan 2001a); (4) island/mainland location, whether the introduction was to a mainland or island location, and in that case which type of island (continental or oceanic) (Cassey 2003); and (5) intra-/inter-regional location, whether the introduction site and the native range were in the same biome, noted as 'intra-regional', or in different biomes, noted as 'inter-regional'(Blackburn and Duncan 2001a).

Data analyses

Following previous studies (Blackburn and Duncan 2001a, Cassey et al. 2004, Sol et al. 2005), we used GLMM to identify the traits related with establishment success. GLMMs allow taxonomic and regional variables to be specified as random factors in the model, effectively dealing with the fact that

Table 4.1. Hypotheses proposed relating species-level traits with establishment success. Adapted from Sol (2007).

Hypothesis	Definition	Supporting evidence	Species traits	Categories
Pre-adaptations				
Niche breadth	Generalist species should be better invaders than specialists, because they are more likely to find appropriate resources in a new environment (Mayr 1965, Brown 1989)	McLain et al. (1999), Cassey et al. (2001c, 2001b, 2004), Duncan et al. (2001), Sol et al. (2005)	Habitat generalism	Mixed lowland forest Alpine scrub and forest Grassland Mixed scrub Marsh and wetland Cultivated and farm land Urban environs
			Diet generalism	Grasses and herbs Seeds and grains, Fruits and berries Pollen and nectar Vegetative material Invertebrate prey Vertebrate prey Carrion
			Latitudinal range (Cassey et al. 2004)	
Human comensalism	Human commensalists should be better invaders than non-commensalists, because introductions are generally carried out in huma-modified habitats (Mayr 1965, Moulton and Pimm 1986)	Sax and Brown (2000), Sol et al. (2002)	Use of human-disturbed habitats	Infrequent Frequent
Novel weapons	Successful invaders have traits to which native species have no-counter strategy, e.g. tropical species from high diversity environments may outcompete native species.	Blackburn & Duncan (2001b)	Biome of origin	Australasia Ethiopian Nearctic Neotropical Oriental Palaearctic Holarctic New World Multi-regional
Behavioural flexibility	Species with higher behavioural flexibility should be better invaders than less flexible ones, because they should adapt more	Sol et al. (2002, 2005)	Relative brain size* (Sol and Lefebvre 2000)	

	easi;y to the new environment (Mayr 1965, Sol and Lefebvre 2000)			
Constraints of establishment				
Migratory behaviour	Species that are migratory within their native range are less likely to establish in a new area than non-migratory species (Thompson 1922, Veltman et al. 1996)	Veltman et al. (1996), Cassey (2002), but see Duncan et al. (2001), Cassey et al. (2004)	Migratory tendency	Sedentary Nomadic Local movements Partial migrant Total migrant
Sexual selection	Sexually selected species may be more vulnerable to extinction risks and therefore have lower introduction success when compared to non-sexually selected species (Sorci et al. 1998, McLain et al. 1999)	Sorci et al. (1998), McLain et al. (1999), Cassey (2002), but see Duncan et al. (2001), Cassey et al. (2004)	Sexual dichromatism	Monochromatic Dichromatic
			Mating system (Sorci et al. 1998)	Monogamous Polygamous
Nesting site	Ground nesters should have a lower probability of establishing in a new environment compared to canopy, shrubs or hole nesters (McLain et al. 1999, Reed 1999)	McLain et al. (1999), but see Sol et al. (2002)	Nesting site	Ground-nesters Canopy/shrub-nesters Non-excavatory hole nesters
Traits that help avoid stochastic extinction				
Life history traits	Species with life histories that increase population survival are expected to have a higher chance of invasion success because these species may attain a large population size faster (Moulton and Pimm 1986)	Sorci et al. (1998), McLain et al. (1999), Cassey (2001a, 2001c), but see Veltman et al. (1996), Duncan et al. (2001)	Body size (Cassey 2001a) Clutch size Annual fecundity Incubation period Age at first reproduction Parental care (Liker and Szekely 2005)	
			Chick development mode (Nice 1986)	Precocial-1 Precocial-2 Precocial-3 Precocial-4 Semiprecocial Semialtricial-1 Semialtricial-2 Altricial

* Information on relative brain size was available for 157 of the 202 introduced species (77.7%) that were considered; for the remaining species, brain residuals were estimated by using the average brain residual of the genus, which predicts 91% of the variance at the species level (Sol et al. 2002).

the species introduced and the regions of introduction are a non-random sample of all species and regions available (Blackburn and Duncan 2001b). The inclusion of taxonomy and region as random effects in the model also deals with pseudoreplication that arises from introductions of the same species in different regions or different species in a same region. Because the taxonomy was incorporated in the model with a hierarchical structure (i.e. species nested within genera, genera nested within families and families nested within orders), the model also helps correct for the phylogenetic effects described between these taxonomic categories. The models we used assume a common positive correlation between introduction outcomes within the same taxa or region, but a zero correlation between outcomes involving different taxa or regions.

The GLMMs were fit using the GLIMMIX procedure (Littell et al. 1996) in SAS (SAS Institute, Cary, NC). The outcome of each introduction (success or failure) was modelled by specifying a binomial error distribution and a logit link function (Blackburn and Duncan 2001b, Sol et al. 2005), with the explanatory variables coded as fixed effects and region, species and higher taxonomic levels coded as random effects. The minimum adequate model (MAM, hereafter) was obtained by removing from the full model those fixed effect variables that did not lead to an improvement. At each step, the less significant variable was removed until the model retained only significant predictors. We investigated the significance of alternative models by adding the previous variable removed from the model. The MAM was the one that only retained variables with significant effect on establishment success. Standardized coefficients of the fixed effects (Kramer 2005) are reported to help assess the relative importance of each explanatory variable.

The MAM was used to produce predictive risk assessment models with GLMMs with the OUTPUT statement of the GLIMMIX procedure. To assess the accuracy of our models in predicting the success of introductions, we used a cross-validation approach, partitioning our sample of introductions into subsets such that the analysis was initially performed on a single subset that generate the predictions, while the other subsets were used in confirming the model (observed values). We ran a series of 50 10-fold cross-validations to assess the accuracy of our GLMM risk assessment. The overall predictive accuracy of the model was evaluated comparing the predicted and observed values. As the GLMM model delivered specific predicted probabilities for each introduction event, we estimated the predicted values as follows. First, we classified each predicted value in ten probability categories (0-10%, 10-20%, 20-30%, and so on). Then, we calculated the expected outcomes for each category as the product of the total observed outcomes and the respective probability of establishment. Finally, we compared the predicted values with the observed outcomes of the introduction events to obtain the overall predictive accuracy.

Tree regressions were performed with the statistical package R 2.4.1 (R Development Core Team 2010). The library mvpart (MultiVariate PARTitioning), developed by Therneau et al. (2007), was used to perform the regression tree. Trees are modelling techniques that aim to explain variation of a single response variable by one or more explanatory variables. The tree is constructed by repeatedly splitting the data so that at any node, the split which maximally distinguishes the response variable in the left and the right branches is selected. Then the splitting is applied to each group separately and the procedure continues until nodes are homogenous or the data are too sparse (Crawley 2002). To determine the robustness and the number of variables to be included in the model, we ran a series of 50 10-fold cross-validations and selected the most frequently occurring tree size using the 1-SE rule (De'ath and Fabricius 2000). Agglomeration of nodes was considered appropriate if some node did not have biological meaning and the change did not decrease the power of the model.

To demonstrate the practical utility of the GLMM and Tree regression approaches, we developed separate models for Europe and Australia based on information from all the introduction events of our database but excluding those introductions that took place in their respective continent. The overall predictive accuracy of these models were then evaluated using the observed introduction outcomes of a subset of introductions carried out in the particular continent compared to those predicted by the models.

We also compared the performances of our quantitative models in predicting the outcome of introductions to Europe and Australia with the performance of an alternative ranking system model, the risk assessment developed by Bomford (2003) for Australian vertebrates. Bomford’s risk assessment also includes questions about the impact of invaders, not considered in our study; consequently, to facilitate the comparison among approaches, we only used those questions that were related to establishment success (see Appendix C). As our models classify introduction events according to the probability of establishment success while the Bomford’s system classifies the introduced species in categories of risk, we had to adapt our data in order to make the models comparable. From our global database we selected those introduction events that had been carried out to Europe or Australia. For the evaluation we compiled all same species introduction events in a single entry and, as outcome, we recorded the final result of all their introductions to the region. We then used the information already collected in our database to answer the questionnaire according to Bomford’s system criteria. We used the information on climate matching published in Bomford’s paper (Bomford 2003), but for Europe that information was not available. Following Bomford’s criteria, when the required data was unavailable, the maximum score was given to that question. Then we calculated the establishment risk score and used it to assign the species to a risk category of establishing a wild population (Bomford 2003). After classifying the species we compared the predictions with the known outcome of the introductions to both regions. To be able to calculate the overall predictive accuracy of this ranking system, we assigned an establishment probability to each risk category as follows: low risk, 0.25, moderate risk, 0.50; high risk, 0.75, extreme risk, 1.00.

Results

GLMM approach

As in previous analyses (Blackburn and Duncan 2001a, Sol et al. 2002), the GLMM approach revealed that most variation in establishment success is found at the species level (see Appendix C: Table 2 for the complete set of random effect solutions). This suggests low phylogenetic autocorrelation in establishment success. The MAM retained four variables: habitat generalism, propagule size (log-transformed), relative brain size and island/mainland introduction location (Table 4.2). Establishment success was higher for species that occupy a higher diversity of habitats in their native ranges, have bigger brains in relation to their body size, are introduced in higher numbers, and are released onto islands. The standardized coefficients indicated that propagule size has the most influence on the probability of establishment, followed by relative brain size and habitat generalism, while island/mainland introduction location is the least important factor. This model showed high consistency: a 10-fold cross validation estimated 91.50% of overall predictive accuracy.

Table 4.2. Fixed and random effects in a minimum adequate generalized linear mixed model explaining variation in bird establishment success while controlling for biome of introduction and taxonomic levels.

Effect	Std. estimate	SE	Type III, F	*P*
Fixed				
Propagule size	-23.6594	3.4322	47.52	<0.0001
Island/mainland location	-14.544 to -6.6150	2.8387 to 3.0901	11.45	<0.0002
Relative brain size	19.6348	5.1210	14.7	0.0001
Habitat generalism	14.8543	4.1232	12.98	0.0003
Random				
Orders	0.1724	0.2079		
Families within orders	1.29E-18	-		
Genus within families	9.46E-19	-		
Species within genus	13.222	0.3464		
Biome of introduction	0	-		

Regression tree approach

The resulting regression tree had four terminal nodes, and only included three variables: habitat generalism, relative brain size and propagule size (Fig. 4.1). Big-brained species with generalist habits had higher probabilities of establishment (predicted probability of establishment: 0.63) than specialist species (0.235). Within the generalist species with smaller brains, the probability of establishment was associated with propagule pressure: species released in larger numbers had a higher probability of success (0.595) than those released in smaller numbers (0.276). As in the GLMM model, the consistency of the regression tree model was high: a 10 fold-cross validation estimated 91.50% of overall predictive accuracy.

Comparing risk assessment approaches

Do our risk assessment tools accurately predict the establishment of birds introduced into Europe and Australia? To answer this question, we developed separate models for Europe and Australia based on information from all the introduction events of our database but excluding those introductions that took place in their respective continent. For Europe, we used the models to classify the 62 introduction events belonging to 29 species. The tree model classified the introductions with 80.65% accuracy: only 12 of 62 introductions were misclassified (seven false negatives and five false positives). The GLMM predictive model classified the same subset of introductions with 74.19% accuracy, only failing to classify correctly 16 events (seven false positives and nine false negatives). For Australia, we analysed 80 introductions events belonging to 36 species. The tree model classified the introduction with 100% accuracy, while the GLMM applied to the same subset predicted the outcome of these introductions with 87.5% accuracy, only yielding 4 false negatives and 6 false positives.

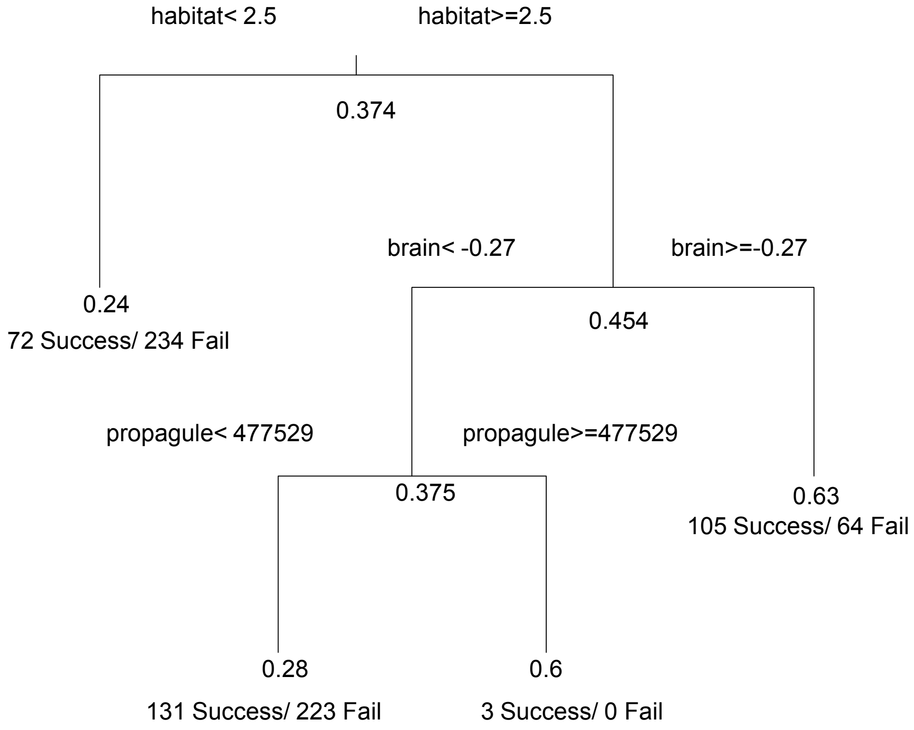
Finally, we asked whether our quantitative risk assessments have a higher predictive power than Bomford’s (2003) ranking system, when applied to Europe and Australia. The ranking system correctly classified 87.07% of introductions carried out in Europe, with only 4 of 29 species misclassified. However, the ranking system applied to the Australian species subset correctly classified the introduced birds with only 67.93% of accuracy: 28 of 29 species were classified by the model as ‘Extreme’ or ‘High’ risk, while in fact 12 of these high risk potential species did not become established in Australia.

Discussion

A common belief among students of invasion biology is that risk assessment tools are of little use given the idiosyncratic nature of the invasion process, which makes it difficult to accurately predict the outcome of introductions (Ehrlich 1989, Kolar and Lodge 2001). At first sight, our results appear to confirm this perception. Despite analysing more than 800 introduction events, the largest data set ever used in any recent analysis of bird introductions, and many traits reported as affecting establishment success, we found that only four out of the twenty-one variables considered were significantly associated with establishment success. Of these variables, only two were species-level traits. These were habitat generalism and relative brain size, traits that previous analyses have related to the ability of the introduced species to find an appropriate ecological niche in the region of introduction (Cassey et al.

2004, Sol et al. 2005). The other two variables significantly associated with establishment success were propagule pressure, an event-level factor that has been previously considered as the most important predictor of establishment success (Green 1997, Forsyth and Duncan 2001, Cassey et al. 2004, Lockwood et al. 2005), and whether the introduction was on an island or on the mainland. Islands are species-poor and are traditionally perceived as easy to invade (Williamson 1996, Sax and Brown 2000).

Figure. 4.1. Regression tree analysis of establishment success in bird introductions. The partitioning variable and its value are presented adjacent to, and the predicted probability of establishment is presented beneath each split. The number of known successful and failed introduction events categorized into each node are given below. Abbreviations are: habitat (habitat generalism), brain (relative brain size) and propagule (propagule size). The vertical lengths are proportional to the deviance explained by each split.



The limited success in identifying traits that pre-adapt species to novel environments is not surprising because we should expect that adaptations that have arisen under certain environmental circumstances do not generally function so well when the circumstances change (see Sol 2007). More surprising is the lack of success in identifying traits that constraint establishment or life history traits that influence population dynamics (see Duncan et al. 2003, Sol 2007). If the vast majority of species' traits are not useful as a tool to predict the outcome of bird introductions, can we still assess the risk of establishment with enough accuracy to be used for guiding conservation policies? Previous work suggests that it is possible to build reliable risk assessment protocols with only a few variables. The regression tree based risk assessment developed by Kolar and Lodge (2001) used four predictors (minimum temperature threshold, diet breadth and two measures of relative growth) to predict establishment success for alien fishes introduced in US Great Lakes with 94% accuracy. Likewise, the regression tree developed by Caley and Cuhnert (2006) based on the Australian Weed Risk Assessment (Pheloung et al. 1999) used only four questions, all them surrogates of introduction effort, to classify the species according to the probability of being a weed; this predictive model correctly classified the species with a 93.6% accuracy. Our results confirm that risk assessment tools able to predict the outcome of new introductions with high accuracy can be produced with just a few predictors. The risk assessments based on GLMM and tree regression approaches only used four and three variables, respectively, but correctly classified the outcome of a high fraction (more than 80%) of birds introduced into Europe and Australia.

A main advantage of tree models over other approaches to invasive species risk assessment is that it delivers the results in a graph that is easy to understand even for non-experts. In addition, the regression tree organizes the predictors in a hierarchical way, giving different weight according to their power to classify introductions, and is able to deal with missing information for the factors through the use of surrogate variables. Tree models also have some limitations, however. For example, the approach assumes that introduction events are statistically independent, but this is unlikely to be true (Duncan et al. 2003, Sol et al. 2008b). Introduction outcomes are likely to be correlated because the same species were introduced to many locations, and because most locations were subject to several introductions (Blackburn and Duncan 2001a). Moreover, there is evidence that the identity of the species introduced by humans is non-random. In birds, most of the species chosen for introduction come from temperate regions, and hence it is expected that traits characteristic of the taxa in these regions are over-represented (Duncan et al. 2003). Without taking into account these issues, it is difficult to draw firm conclusions about the species' traits that facilitate or limit establishment success. The GLMM approach overcomes these problems by implementing as random effects variables that code for the clustering of introduction events within species, higher taxa and biogeographic region of introduction (Blackburn and Duncan 2001a). Thus, the GLMM approach is more robust in identifying the factors that actually affect the success of introductions. Despite the differences between the tree model and GLMM approaches, both produced risk assessments with similar accuracy levels. When comparing the pool of misclassified species, we found few differences in the misclassified introductions between the two approaches. We suggest that the best strategy when developing risk assessment tools would be to exploit the respective strengths of both methodologies and combine them to identify potentially risky species with higher exactitude.

Risk assessments based on tree models and GLMMs can be criticized on the grounds that they assign equal costs to false positives and false negatives (Caley and Kuhnert 2006). This issue is particularly relevant because the risks of importing a pest are higher than the risks of excluding an innocuous species (Smith et al. 1999). In the present study unsuccessful introductions were predicted by the tree model better than successful introductions. The implication is that at least for some species (i.e. those characterized by being habitat specialists and small-brained), we have some certainty that they are unlikely to become established when introduced. These species should be the ones for which international trade can be allowed, while the species for which the predictions are less reliable merit a cautionary approach, i.e. prohibiting any importation and release of these species, and, where a release has already taken place, carrying out monitoring and eradication programmes to avoid increases in numbers and the spread of the invader.

A comparison between our quantitative risk assessments and the alternative semi-quantitative ranking system of Bomford (2003), found that quantitative models performed better when all the required information was available to answer the ranking system's questionnaire (the Autralian case), while the ranking system was better for the European subset when one question was overscored due to lack of key data. Semi-qualitative ranking systems are more arbitrary than quantitative approaches, but also require more information and are sensitive to a lack of key information. This is because the ranking system handles missing data by scoring them with the highest value of the ranking. This decision is justified from a conservation point of view, yet the consequence is that the method overestimates the total risk of the species. Thus, an advantage of quantitative risk assessments is that they deal with missing data through the use of surrogate factors when the information for a determinate split is unknown. Despite the advantages of quantitative risk assessments, ranking systems can also achieve an acceptable level of accuracy and can still be a useful tool for some organisms for which quantitative predictive models are unreliable.

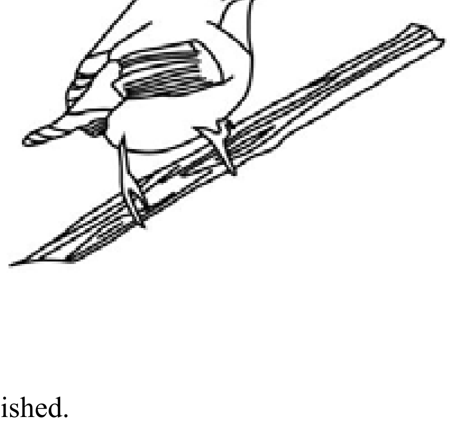
Much of the focus of current research in invasion biology is on the development of screening methodologies to limit the introduction of noxious species. Recent studies have shown that the implementation of risk assessments with 80% accuracy, such as the one presented here, is economically beneficial for planning medium term policies (Keller et al. 2007). In fact, recently developed risk assessments for exotic species importation are, at present, producing net economic benefits in those regions where they are implemented (World Trade Organization 2005). The use of risk assessments as preventive tools to guide future environmental policies provide a means to reduce the damage caused by invasive species thereby contributing to the conservation of biodiversity and ecosystem function.

Acknowledgements

We thank to Montse Vilà, Sven Bacher, Richard Duncan, Dan Blumstein, Mark Cadotte, Esteban Fernandez-Juricic, Gillian Kerby, Francisco Lloret, Josep Piñol, Bernat Claramunt and two anonymous referees for statistical advice and/or useful comments on early versions of the manuscript. MV was supported by a scholarship of the General Direction of Research of the Department of Universities, Innovation and Enterprise of the Generalitat de Catalunya and the European Social Fund (2005SGR00090). The project was funded by a “Proyecto de Investigación” (ref. CGL2007-66257/BOS) to DS, a project Consolider (CSD 2008-00040) and European 6th integrated project ALARM grant (GOCE-CT-2003-506675).

Chapter 5

From journals to plans: the importance of using scientific advice in invasive species management[4]



---

[4] Unpublished.

Resum

De les revistes als plans: la importància de la utilització de criteris científics en la gestió d'espècies invasores

La importació d’animals és una important font d'ingressos a tot el món, però pot arribar a ser una gran amenaça per als ecosistemes i la infraestructura humana si s'escapen o són alliberats en el medi natural. El desenvolupament de metodologies d'avaluació de riscos ha de ser una eina important per a filtrar la importació d'espècies potencialment perilloses, no obstant això, per tenir èxit en el maneig de les invasions d'espècies exòtiques és fonamental la integració efectiva dels avanços científics en els plans de protecció del medi ambient. En aquest treball he avaluat en primer lloc el potencial invasor de les espècies d'aus exòtiques introduïdes a Catalunya amb un protocol d'avaluació del risc global per a la creació d'envair les aus, i, en segon lloc, he comparat els resultats obtinguts amb la legislació espanyola sobre espècies invasores recentment aprovada per comprovar el potencial d'aquesta nova eina per resoldre el problema de les invasions biològiques. En l'actualitat, s'han trobat 158 espècies no natives d'aus vivint en llibertat, la majoria dels quals pertanyen a ocells de gàbia alliberats accidentalment (lloros i passeriformes). La majoria es va observar només en ocasions, però una petita proporció ja s'ha establert. Els resultats de l'anàlisi de risc va mostrar que hi ha 49 espècies que tenen un alt potencial invasor, dels quals tres ja han fundat poblacions estables. La comparació entre els resultats de l'avaluació i la recent legislació revela deficiències importants en la regulació de les espècies invasores. Només tres de les espècies classificades d'alt risc s'inclouen en la llista d'aus considerades legalment els invasores, mentre que 14 espècies d'alt risc s'inclouen només com a possibles invasors, pel que la seva importació continuarà essent permesa. La resta de les espècies potencialment invasores han sigut excloses de la llista. Per tant, encara que l'eficàcia de la nova legislació per mitigar el problema de les espècies invasores s'ha d'avaluar en el futur, les deficiències detectades que ofereix la legislació actual no ens permeten preveure un escenari esperançador.

Abstract

Imported animals are an important source of revenue worldwide, but can become a major threat for ecosystems and human infrastructure if they escape or are released into the wild. The development of risk assessment methodologies should be a major tool to filter the importation of potentially dangerous species. However, to succeed in managing invasions of exotic species is critical the effective integration of scientific advances in environmental protection plans. In this paper I first evaluated the invasive potential of alien bird species introduced in Catalonia with a global risk assessment protocol for the establishment of invading birds, and, second, I compared the results with the recently approved Spanish legislation on invasive species to check the potential of this new tool to solve the problem of biological invasions. At present, 158 non-native bird species were found living in the wild, most of which belong to accidentally released cage birds (parrots and passerines). The majority was only observed occasionally, but a small proportion has already been established. The results of the risk analysis showed that there are 49 species that have a high invasive potential, of which three already have founded stable populations. The comparison between the results of the assessment and the recent legislation reveals major flaws in the regulation of invasive species. Only three of the species classified as high risk are included in the list of birds legally considered invaders, while fourteen high-risk species are included in the list of potential invaders, so their import would be still permitted. The remaining potential invasive species were excluded. Therefore, although the effectiveness of the new legislation to mitigate the problem of invasive species must be evaluated in the future, the detected deficiencies presented by the actual legislation cannot allow us to foresee a hopeful scenario.

Introduction

Concern has grown all over the Word to address the threat posed by biological invasions (Mack et al. 2000), which has led to the development of systems for preventing the establishment or the spread of the invasive species (Cory and Myers 2000, Myers et al. 2000, Sharov 2004, Perrings et al. 2005). Eradication and control are two strategies that have proven too often to be expensive and ineffective (Manchester and Bullock 2000, Myers 2003, Simberloff 2009), the alternative has been to implement risk analysis procedures to identify potentially high-risk species (Ruesink et al. 1995, Kaiser 1999). However these tools are not useful if they are not employed for the stakeholders to guide environmental management policies (Lodge et al. 2006). In this chapter I demonstrate the importance of using scientific criteria in the design of invasive species management plans by comparing the evaluation of the list of invasive birds in Catalonia (Spain) with the Catalogue and List of invasive species legally recognized in Spain.

Biological invasions are consequence of globalization that is increasing in recent times as a result of the intensification of the international trade of people and goods (Levine and D'Antonio 2003, Meyerson and Mooney 2007). Invaders are recognized a major threat to global biodiversity (Vitousek et al. 1996, Clavero and Garcia-Berthou 2005) and human economic interests (Bergman et al. 2000, Vila et al. 2010). Mainly driven by this last type of impacts, administrations have shown interest in promote strategies to address biological invasions (Pheloung et al. 1999, Andersen et al. 2004b, Baker et al. 2008, Bomford 2008, Essl et al. 2011). However, policy makers are faced with two major problems to implement sustainable management practices to mitigate the impact of alien species. First, preventing the introduction of invasive species by stopping the importation of all species is not a reasonable measure because exotic species trade is a major economic activity worldwide (Ewel et al. 1999, Padilla and Williams 2004, Knowler and Barbier 2005) and is protected by transnational free trade agreements (Jenkins 1996, Cooper and Rosser 2002). Second, environmental managers have to deal with the invasive species already present in the territory. Mitigating the damage caused by invasive species and/or control their population represents is costly to the responsible administrations (Pimentel et al. 2005, Vila et al. 2010). Budgets are always limited so is not a feasible strategy to act against all exotic species present in the region.

Since it is impossible to stop all trade of invasive species or control all invasive species, the solution has been developing systems to set priorities (Pheloung et al. 1999, Kolar and Lodge 2002, Bomford 2003, Bomford et al. 2009). The risk assessment protocols are useful tools that simplify the decision making process by evaluating the likelihood of adverse ecological effects derived of human related activities (Sutter II 1993, Hope 2006). Risk assessments for alien species look for facilitating the decision-making process in invaders management strategies by identifying those species traits related with invasion success and then using them to predict the outcome of future introductions (Rejmanek and Richardson 1996, Blackburn and Duncan 2001a, Moyle and Marchetti 2006, Hayes and Barry 2008). The protocols can be used either preventively to identify potentially invasive species before the introduction, either to identify species with more potential to establish if the species are already introduced; in order to prioritize control or eradication actions to prevent introduction, establishment or spread.

However, to effectively prevent new invasions risk assessments must be used by policy makers to design the legislation on invasion species regulation. Although risk assessments have demonstrated their capacity to produce economic benefits (Keller et al. 2007), too often administrations are still reluctant to be guided by scientific criteria when taking decisions and rely much on the opinion of the commercial sectors (Justo-Hanani et al. 2010). Ignoring the scientific advice or applying partially the protocols can turn into ineffective the efforts to deal with the invasive species (Fowler et al. 2007, Smith et al. 2008).

In this chapter I evaluated the invasive potential of alien bird species introduced in Catalonia with a global risk assessment protocol for the establishment of invading birds and then I compared the results with the recently approved national Royal Decree of invasive species. First I updated the global risk assessment for the establishment of exotic birds with newly discovered possible predictors of invasion success. Second I used the risk assessment to classify the exotic species present in Catalonia in different risk categories according to their probability of establishment. Third I evaluated the ability of the protocol to correctly identify the establishment potential with the species that are already established. Fourth, I identified the probability of establishment for those species not established. Fifth, I compared the classification with the list of species collected in the Royal Decree in order to check whether has included all potentially bird invasive species identified by the protocol. Finally I give some recommendations for the management of the different risk categories of the species evaluated.

Methods

Risk assessment description

In Chapter 4 I presented a global risk assessment protocol for the establishment of invasive birds (Vall-llosera and Sol 2009). From the literature on biological invasions in birds up to 22 possible predictors were identified among all the major traits hypothesized to influence establishment success. Next, it was analyzed the relationship between these variables and establishment success for 832 bird introductions around the world involving 202 different species, for which quality information was available.

In the present chapter I updated the previously published global risk assessment developed for bird introductions. Since its publication, we discovered other traits related to bird invasion success and for this chapter I incorporated them to the model to improve the risk assessment prediction capacity. In Chapter 1 (Sol et al. in prep.) we demonstrated that brood value was an establishment success predictor for bird invasions. Consequently, I recalculated the regression tree decision model incorporating brood value as a variable, along with the previously identified predictors of establishment success.

I performed hierarchical classification trees to build the risk assessment protocol. These are quantitative methods, which operate by splitting the response variable in to increasingly homogenous subsets by binary recursive partitioning on a set of predictor variables (De'ath and Fabricius 2000). They have the advantage of being non-parametric, so can use both categorical and continuous predictors, and deliver the results in dendrograms easy to understand even for non experts. Tree regressions were performed with library mvpart (Therneau et al. 2007) with the statistical package R 2.11.0 (R Development Core Team 2010). To determine the robustness and the number of variables to be included in the model, I ran a series of 50 10-fold cross-validations and selected the most frequently occurring tree size using the 1-SE rule (De'ath and Fabricius 2000).

To facilitate the interpretation of the results of the evaluation and the decision-taking process, I created three risk categories for classifying species based on the probability of establishment: species with a probability less than 30% are within the low risk category, the species with probabilities between 30 and 60% in the medium risk category, and the species with 60% probabilities of establishment or more in the category high risk.

Catalan alien bird species list

The list included all the species of exotic birds that have been observed in the wild in the Catalan territory (Appendix D: Table 1). Catalonia is an autonomous community in northeastern Spain and covers an area of 32,114 km^2. It borders France to the north and the Mediterranean Sea to the east (580 km coastline). The presence of these species in the territory should have a no-natural origin, so I also taked into account observations of individuals of artificial origin for species with wild native populations. Species had to be cited at least once and had accurate documented references of their presence. Data on bird presence was obtained from the Catalog of the birds of the Catalan Territories (Clavell 2002) and the Catalan Breeding Bird Atlas (Estrada et al. 2004), and was complemented with the databases of the Catalan Institute of Ornithology, the Spain the Exotic Birds Group (GAE) and the Biodiversity data bank of Catalonia.

Bird species were classified according to the category system recommended by the Association of European Rarities Committees (AERC 2001). This system classifies the species according if their origin is natural (the bird arrives or is found in the region on their own) or facilitated by human (accidental or deliberate introductions) (Table 5.1). A unique category is indicated for each species; in the case that a species could be included in a more than one category, priority was given to C to E. For each category only the subcategory indicating higher degree of establishment is noted, although it could exist other populations that deserve a lower subcategory. The distinction between the categories C and E depends on each particular species. To be include in the category C, it has to be verified that the species is regularly breeding in the wild, that the reproduction leads to a population increase that is not the result of new introductions, and that the interval during which reproduction has been observed is longer than the species lifespan.

Table 5.1. Exotic species category classification according to AERC criteria (AERC 2001).

Category	Subcategory	Definition
A		Species that have been cited in an apparently natural state at least once since January 1, 1950.
B		Species that had been cited in an apparently natural state at least once until the December 31, 1949, but subsequently have not been cited.
C		Species, which having been introduced or re-introduced by humans deliberately or accidentally in the region, have established breeding populations without further introductions or re-introductions.
	C1	Exotic species. Species present as a result of an introduction.
	C2	Introduced native species. Species with established populations resulting from introduction by man, but also cited in an apparently natural state.
	C3	Reintroduced species. Species with populations successfully re-introduced by man in areas where they were extinct.
	C4	Feral species. Domestic species (ie artificially selected) with populations established free.
	C5*	Naturalized species in neighboring areas. Species with naturalized populations established in other countries within the same region.
D		Species that should appear in categories A or B, but there are reasonable doubts that have ever been observed naturally.
E		Species, which having been introduced or re-introduced by humans deliberately or accidentally in the region, have not established self-sustained breeding populations.
	E1	Species for which reproduction has been verified on a regular basis and are suspected that may become established.
	E2	Species for which reproduction has been verified occasionally, and without any indication that they are in process of establishment.
	E3	Species observed only occasionally, without having been found breeding.

*For the assessment of the risk of establishment, I considered category C5 species as not established species, because they did not have stable populations in Catalonia.

Spanish invasive alien species Royal Decree

The Royal Decree 1628/2011, adopted on November 14, 2012, regulate the Spanish national Catalogue and List of invasive alien species. The objective was to regulate the procedure and criteria for the inclusion of invasive alien species on the Catalogue and List, and to establish the action measures necessary to prevent their introduction into the wild and for their control and possible eradication, to promote the development of management strategies and control of invasive alien species, and implement them effectively and coordinated throughout the Spanish territory. The Catalogue and List have administrative and state level so is the current legislative framework for Catalan alien species.

The Catalogue included exotic species for which there was information that constituted a serious threat to native biodiversity and/or economic resources associated with the use of natural heritage. The List included exotic species capable of becoming a serious threat by competing with native wildlife, altering their genetic purity or disturbing the ecosystems, and those potentially invasive alien species, especially those that have proven that potential in other countries or regions in order to be proposes to be included in the Catalogue. Also, are included in the list those invasive alien species considered in national, European or international regulations.

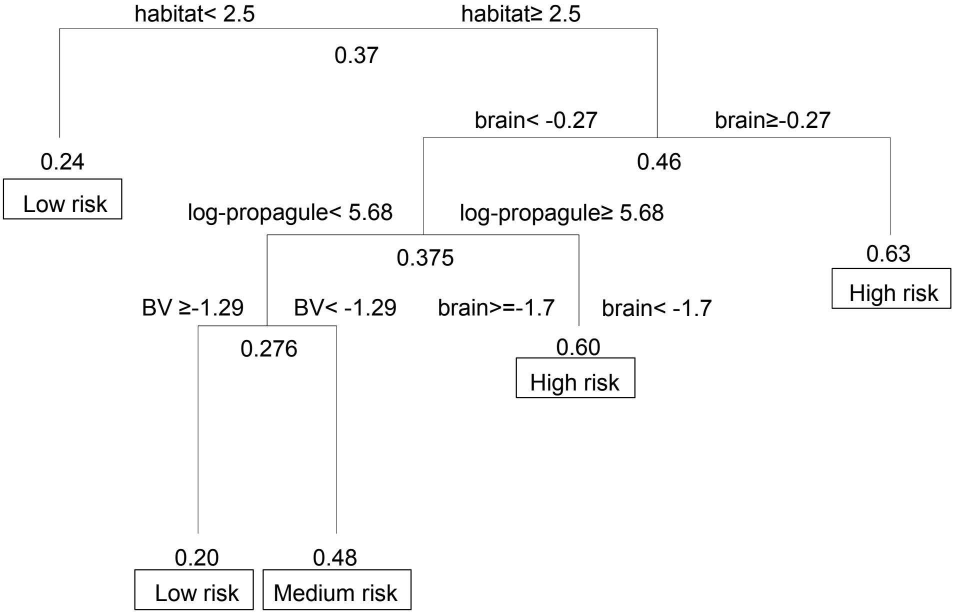
The inclusion of a species in the Catalogue and List implied the prohibition of introduction into the wild, throughout the national territory. Also, the inclusion of a species in the Catalogue involved generic prohibition of possession, transportation and trade. Likewise, specimens of species included in the Catalogue captured from nature cannot be returned to the wild; and under no circumstances will be considered actions or behaviors for the promotion of the species included in the List and Catalogue.

Results

Regression tree approach

The new regression included four variables: habitat generalism, relative brain size, propagule size and brood value, respect to the original, while excluded island/mainland introduction location (Fig. 5.1). Habitat generalist species with big brains had higher probabilities of establishment (predicted probability of establishment: 0.63) than specialist species (0.24). Generalist species with smaller brains released in large numbers had more chance of success (0.6) than those released in smaller numbers (0.28). Finally, generalists species with small brains released in low numbers and with low brood values are more likely to establish (0.48) than species with higher brood value (0.2).

Figure 5.1. Regression tree analysis of establishment success in bird introductions. Abbreviations are: habitat (habitat generalism), brain (relative brain size), log-propagule (propagule size, log-transformed), and BV (brood value). Updated from Vall-llosera and Sol (2009).



Characteristics of exotic bird species

The Catalan list of exotic species of birds included 158 species, from all these species, the taxonomic order that had the highest number of species were Passeriformes. The family of Passeriformes most represented were Passeridae (67%), followed by Sturnidae and Fringillidae (15.5% and 13.5%, respectively) and finally by Timalidae and Pycnonotidae (2% each). The second order most represented in the list were Psittaciformes, followed by Anseriformes, Galliformes, Ciconiformes, Columbiformes, Strutioniformes, the two groups of raptors, Accipitriformes and Falconiformes, and finally Strigiformes (Fig. 5.2).

The vast majority of exotic bird species in Catalonia had origins outside of Europe. Africa was the main donor region of potentially invasive species, followed by Asia, Central and South America, Oceania, North America and Europe. The remaining species had a cosmopolitan origin, i.e., their original area included two or more of the above regions. The only entirely European native species was *Branta leucopsis*, which is native from Europe but its natural range did not include Catalonia. There were other 14 species classified as cosmopolitan which part of their original distribution included European ground (Fig. 5.3).

Figure 5.2. Taxonomic classification of alien bird species for Catalonia.

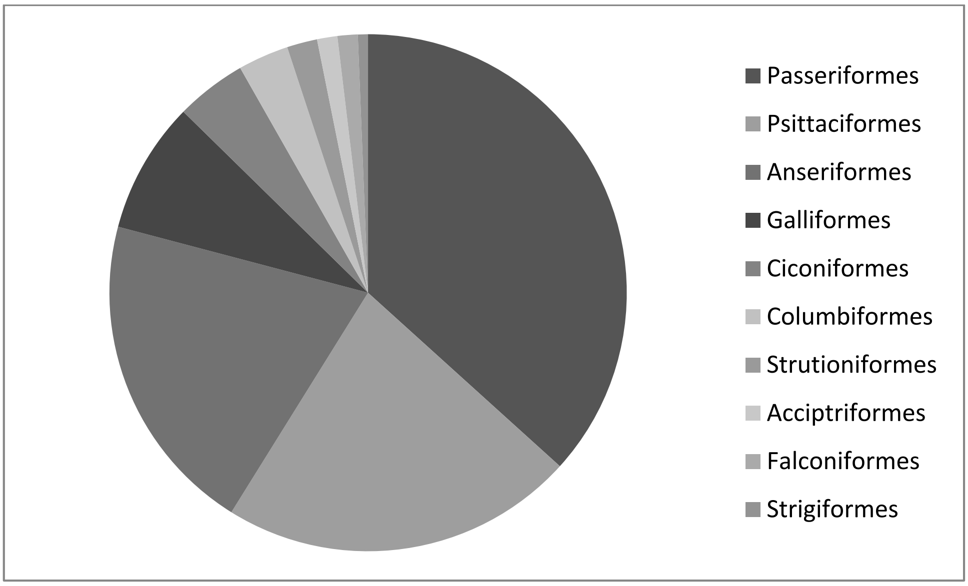
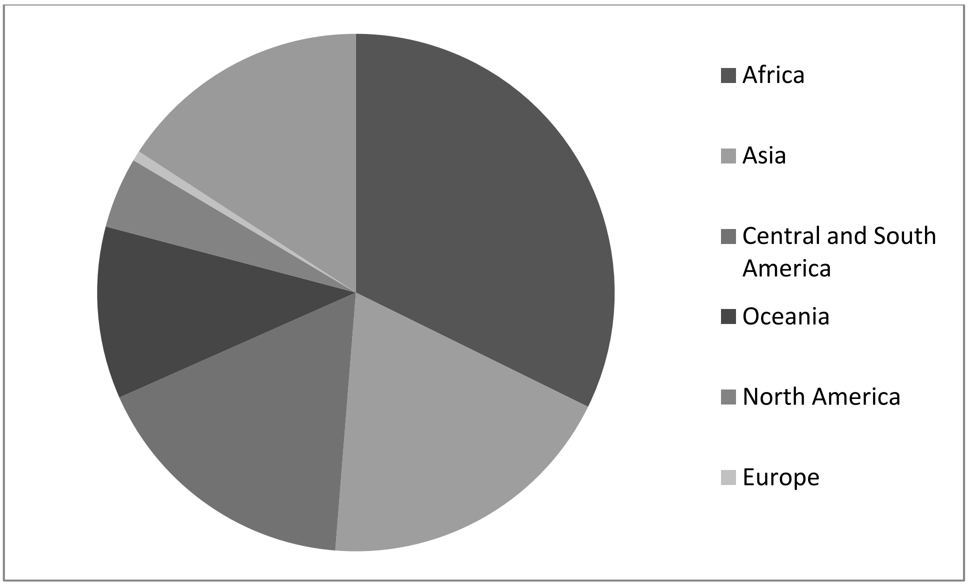
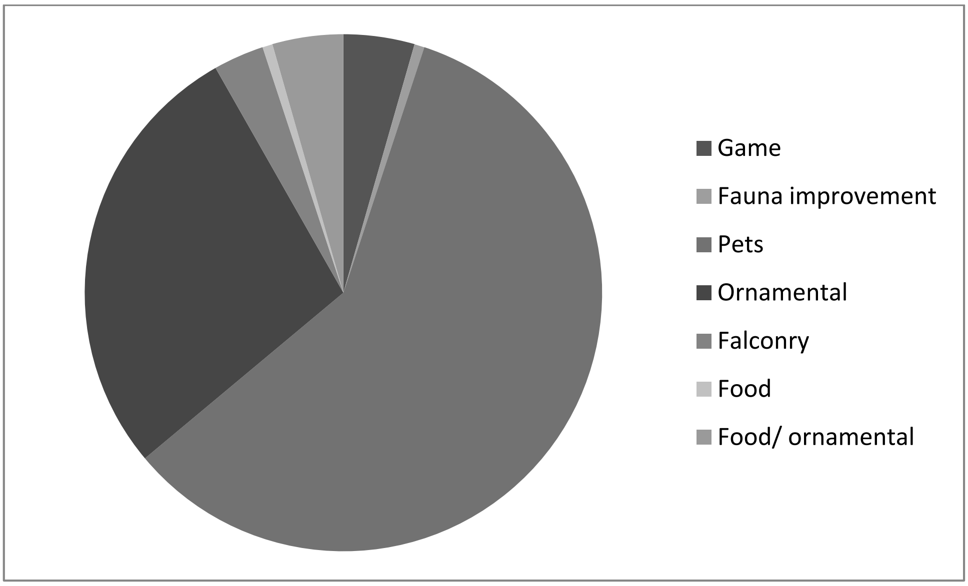


Figure 5.3. Geographical region of origin of alien bird species for Catalonia.



From the list of exotic birds present in Catalonia, only a minority were released intentionally (Fig. 5.3), most of them as game birds. The majority of birds were species kept in captivity and accidentally released into the environment. The vast majority were cage birds, followed by species kept in captivity for ornamental or aesthetic purposes. The rest were species used for falconry, as a food source, and birds that served both as ornaments or for food.

Figure 5.4. Primary sources of alien bird species for Catalonia.



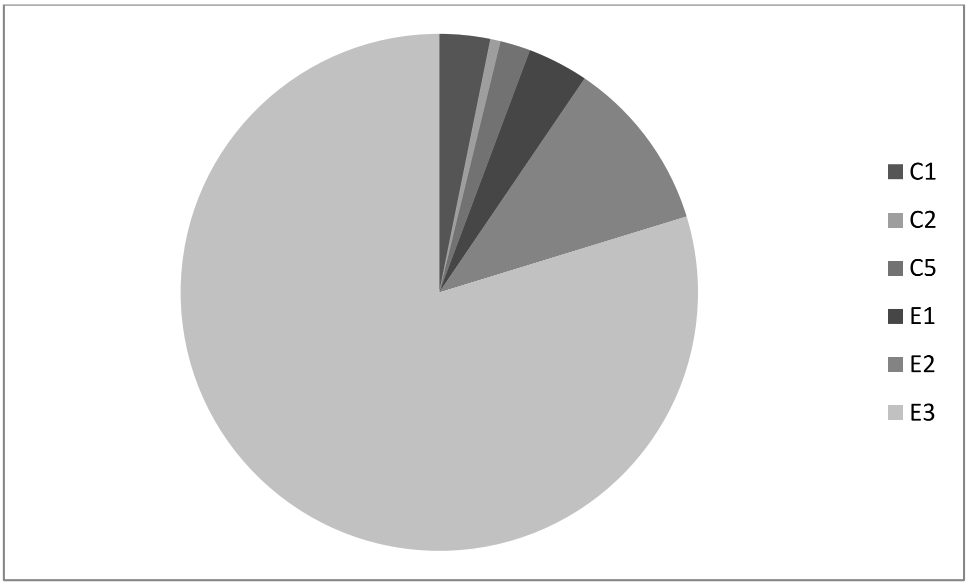
From the 158 species of exotic birds that had been detected living free in Catalonia until today, according to the AERC criteria for classification of alien species (AERC 2001), there were six established species, 5 in category C1, that is, species with self-sustained populations, and one species in category C2, naturalized but also with native populations. The remaining 151 species can be considered not yet established, three species were in category C5, that is, species that come from neighboring countries where they are established; six species in category E1 and 17 in E2, species that have reproduced in the wild but, although do not have yet stable populations, could rise to category C1 in the future. Finally, there are 125 species in category E3, those that only have been seen in the wild occasionally (Fig. 5.5).

Ranking and description of the potential invaders

The risk assessment for establishment of exotic bird species present in Catalonia had determined that currently there were 49 species (31%) in the high-risk category of establishment, that is, species that have more than 60% chances of establishment. Of these there were three that are already established (category C1). The remaining 46 were in different categories of non-established: two species were classified as E1, five as E2 and 39 as E3. Likewise there were nine species (5.7%) in the medium-risk category, with a probability of establishment of almost 50%: one species in category C1 one in category C2, one in category C5, one in category E1 and the remaining five in category E3. Finally, there were 100 species (63.3%) classified with low risk of establishment, with a probability below 30%; of these, only one had established (category C11), two came from neighboring countries, 13 had reproduced occasionally (three in the category E1 and 12 in E3) and 82 species in category E3, that are only observed sporadically (Table 5.2).

The Catalan list had five species classified in category C1 and one in category C2, that is, species considered already established in Catalonia (Fig. 5.5). Of these, the risk assessment classified three in category of maximum risk, two in the medium risk category and one in the low risk category. The risk assessment identified three of the already established species as species with a high risk of establishment, while there were two also established species that the risk assessment classified with a lower risk of establishment. The risk assessment was able to identify the species with most potential to establish reasonably well given the small set of such species. It must have taken into account that even those species with fewer probabilities can get established if they have enough opportunities, either because they are introduced in high numbers or because they are given enough time.

Figure 5.5. Classification of the of alien bird species for Catalonia according to AERC criteria.



The three species with the higher risk of establishment were *Myopsitta monachus*, *Psittacula kramer* and *Leiothrix lutea*. All these species were imported deliberately to be sold as pets and escaped to the wild resulting from accidental releases. Two are species of Psittaciformes (*Myopsitta monachus* and *Psittacula krameri*). The parrots are a group of birds that have more representatives among the invasive species around the world (Long 1981, Lever 2005). The invasive potential of parrots can be related to their higher relative brain size (Iwaniuk et al. 2005), a feature that is related to flexibility in behavior (Lefebvre et al. 1997), and therefore to a great ability to adjust to the conditions of the new places where are introduced (Sol and Lefebvre 2000). *Myopsitta monachus* is a species of parakeet, native from South America, that was introduced in Barcelona in the 70's and since then has invaded the main urban centers, mainly on the coast (Domenech and Senar 2004). It is a colonial species and cause important damage to infrastructure and urban gardening (Domenech and Senar 2004). *Psittacula* *krameri* is another species of parakeet, native mainly from Africa, which established in Barcelona during the eighties (Clavell et al. 2004). This species also has been established in countries in northern Europe where it has been demonstrated that compete with native hole-nester birds (Strubbe and Matthysen 2009). The other established high-risk species, *Leiothrix lutea*, is an insectivorous bird, original from Asia, belonging to the family Timalidae, that was introduced in Catalonia in mid 90's, and has established in the forests around Barcelona (Llimona 2004). The success of the invasion seems to be related to its general character and opportunistic, as well as a higher competitive ability (Vall-llosera et al. in prep.).

Table 5.2. Risk assessment of the exotic bird species present in Catalonia.

Category of risk	Probability of establishment	Established species	Not-established species
High	>60%	C1 3	E1 2
			E2 5
			E3 39
Medium	~50%	C1 1	C51
		C2 1	E1 5
			E3 5
Low	<30%	C1 1	C52
			E1 3
			E1 3
			E2 12
			E3 82

There are three species that despite being classified with a lower risk have managed to establish. *Pashianus colchicus* is a category C1 species classified with medium risk. Native from Asia, thousands of individuals are released every year as game birds (Mañosa 2004). *Estrilda astrid* is a granivorous bird that was ranked as low-risk, original from Africa and very popular as a cage bird, is released to the wild through accidental escapes and has been established in rural surroundings and river banks (Jensen and Fernández-Ordóñez 2004). *Columba livia* is the only species classified as C2, and was identified with medium risk. This bird is one of the commonest in the cities and has its origins in domestic pigeons escaped from captivity (Sol 2004).

There were 152 bird species observed living in the wild but not yet been established (categories C5 to E3). 46 were classified with a higher risk of invasion. Seven of these high risk species are classified in categories E1 and E2. Three are *Aratinga* species, three are weavers and the other one is *Threskiornis aethiopicus*. *Aratinga* is a genus of parakeets, natives from South America, introduced in Barcelona during the 80' and reproducing in the wild since the 90's. There are currently restricted to urban gardens but have the same invader potential as the other two established parrots (Estrada et al. 2004). Weavers are African granivorous passerines of the genus *Ploceus* and *Euplectes*, among others.

Several species are imported as cage birds and reach the environment through accidental escapes. Weavers are colonial and they colonize aquatic habitats shores (Estrada et al. 2004). *Threskiornis aethiopicus* is an African ibis which its naturalized populations come from escaped birds kept in semi captivity in zoos. This species has been established in France where they learned to feed at garbage dumps and cause damage to colonies of native waterbirds (Kumschick and Nentwig 2010). There were other 39 species with high potential invader that had been observed occasionally living in the wild. 19 were species of passerines, 17 were parrots, and three were raptors. Both passerines and parrots arrived with the pet trade, while the raptor species are used for falconry. All are introduced by accident, mainly escaped from captivity (Estrada et al. 2004).

Regarding the rest of not established species, there were seven species classified with medium risk of establishment. *Branta canadensis* is a species of goose, native from North America and established in northern Europe, mainly Scandinavia and the British Isles, which occasionally arrives naturally to Spain from its naturalized area (category C5 species) (Hagemeijer and Blair 1997). *Quelea quelea* is another weaver species that founded a population in Catalonia that lasted several years but that ended up failing (category E1) (Clavell and Fernández-Ordóñez 2004). The other five species (category E3) are *Streptopelia senegalensis*, a dove species which comes from escaped domestic individuals; *Ciconia abdimi*, with origins in zoological collections; and five species of small cage birds (Estrada et al. 2004). Of the 98 not established species with low risk of establishment, two are species of ducks in category C5 species (*Aix galericulata* and *Oxyura jamaicensis*), 15 are species that have been found breeding from time to time (categories E1 and E2), and 82 were only observed in the wild occasionally (category E3). These latter species are basically game species, escaped ornamental or cage birds and falconry raptors (Clavell 2002, Estrada et al. 2004).

Comparison with the Spanish national Catalogue and List

The Royal Decree that regulates the listing and catalog of invasive alien species in Spain includes 75 species of invasive exotic birds, within its two sections (Catalogue and List). 11 species are considered invasive and are include in the Catalogue, while the remaining 64 are relegated to the List of potentially invasive species. Of these 75 species, 58 species are present in Catalonia and have been evaluated. The Royal Decree did not include all the potentially invasive species in Catalonia. Only 17 of the 49 species that the risk assessment identified with high risk of establishment were included: three in the Catalogue and 14 in the List. The remaining 32 high-risk species are not legally recognized as potentially invasive.

In the Catalogue there are 11 species legally considered invasive in Spain, all of them also present in Catalonia. Among these, three species are already established (category C1) and nine are still not established, one is in category C5, three in E1, two in E2 and two in E3. According to the risk assessment, three species on this list have maximum risk category. Of these two are already established in Catalonia (*Myopsitta monachus* and *Psittacula krameri*) while the other has been found already reproducing (*Euplectes afer*).

This work revealed flaws on the recent approved Royal Decree that legislates on invasive species in Spain. The Catalogue of invasive species excluded species that the risk protocol identified as high potential invaders, these species will continue being imported and marketed without restrictions. The Catalogue excluded species already established for reasons other than scientific criteria, for example *Phasianus colchicus* is a game bird, and *Columba livia* is a domestic bird with many uses, especially flying tippler. Instead the Catalogue included eight species with medium or low probability of establishment. Although among them there is a species that is already established (*Estrilda astrid*), the inclusion of these species means that efforts and financial resources will be used to pursue species that have high probability of not established stable populations in the long term. In contrast, were included in the Catalogue some species with low invasive potential but that are already causing impacts on native biodiversity. *Oxyura jamaicensis* and *Coturnix japonica* are alien species that hybridize with its native relative and threaten their populations (Green and Hughes 1996, Puigcerver et al. 2007); in fact, currently *Oxyura jamaicensis* has a specific program to eradicate their populations in Europe (Smith et al. 2005).

The List contained 64 species considered potentially invasive in Spain. 47 species on this list are present in Catalonia. None of these species is established, two species are in the category C5, three in the E1, 12 in the E2 and 30 in the E3. The risk assessment ranked 14 species of the List with high risk of establishment, two with medium risk and the remaining 31 with low risk. The 14 species with high risk will continue being traded without restriction and only monitoring their populations is planned. Even so, six of the species with high risk are classified as E1 and E2, which means that they have found reproducing in the wild and could be promoted to the category C in a near future.

Discussion

Given the large number of species traded annually across the world that arrive to our borders, a scientific-based assessment to filter the arrival of potentially invasive species should be very well received by policy makers, because it should be a very useful tool to help them to design better strategies to stop further invasions (Panel 1). Instead it seems that such tools are mostly ignored by legislators when deciding the rules for controlling these species (Fowler et al. 2007, Smith et al. 2008, Justo-Hanani et al. 2010).

Successful prevention not only requires the designment of accurate screening tools, but also the ability to authorize and implement control measures on the importation, the only phase of the invasion process that the legislation could effectively interrupt (Fowler et al. 2007). A regulatory framework at national-level can be a powerful tool for controlling invasions, preventing the transport of species from other countries. Thus, the approval of a new Royal Decree appeared as a great advance in the effort to mitigate the impacts of invasive species because is the first provision protecting Spanish biodiversity against introduction and spread of invasive species. However, as this new regulatory system was not based on coherent scientific assessments, the lack of an efficient application of the risk assessment procedures undermined the effectiveness of this provision to control the importation.

The success of the efforts dedicated to address biodiversity threats depends to a large degree on how well scientific knowledge is translated into policy (Rohlf 1991). Perhaps the problem remains on lack of transference between science and management (Nature 2007). On the part of the science, it might exist a lack of knowledge about how to transfer the obtained information into tools useful for managers, and also a lack in the spreading of the information beyond the areas of scientific discussion (Hulme 2003). On the other hand, it could exist by the part of the administration a lack of interest or ignorance about research advances (Hulme 2011). Transference is not favored by the production of complicated qualitative risk assessment protocols based on large questionnaires that require either extensive information on invasive species or must be answered by experts on the subject. To facilitate transference, would be more useful developing quantitative protocols, which require a lower volume of information and do not need to be answered by an expert (Vall-llosera and Sol 2009).

The lack of confidence in the use of quantitative scientific tools for the design of invasive species management plans may be due to a perceived lack of precision in forecasting which invasive species will establish and spread by stakeholders (Hulme 2003). I agree that a degree of uncertainty is inherent, because the context-dependent nature of biological invasions produces difficulties in predicting species invasive potential. However, in recent years much has been achieved in the understanding of what factors influence the establishment success of invasive species (Duncan et al. 2003, Blackburn et al. 2009b). This knowledge has been used to develop the risk assessment protocols that, even though, are unable to say with absolute certainty whether a particular species will become invasive or not, they are able identify with a high level of accuracy situations where there is high risk that species will become established, with enough accuracy to generate economic benefits (Keller et al. 2007).

The deficit of cohesion between scientific research and policy makers inhibits the development and application of management practices, particularly when economic and ecological conflict arises. It seems that the decision making system is heavily influenced by pressure groups from the commercial sector, that do not necessarily have interests in protecting the environment or the welfare of society in general. Benefits of the introduction of non-native species are clearly evident (Gozlan and Newton 2009), however the profits are received only for one group of stakeholders whereas the costs are paid by the entire society (Hulme et al. 2009).

To overcome these problems, integration between scientists and policy makers is essential to generate plans for sustainable protection of native biodiversity and effective prioritization of both research and policy developments (Stokes et al. 2006). Although prevention is considered the most desirable approach to managing invasions, this strategy is hampered by the lack of implementation of quantitative risk analysis on legislation. As better policies are sought for controlling new invasions, scientific-based regulation should be the key element into developing future environmental conservation policies.

Acknowledgments

I want to thank Jara Andreu for providing the Catalan list of invasive species. This research was supported by a DURSI scholarship of the Generalitat de Catalunya and the European Social Fund 2005SGR00090 to MV, and by funds from the Spanish Ministry of Education and Science (‘Proyecto de Investigación’ CGL2010-21838 and ‘Consolider-Ingenio Montes’ CSD2008- 00040) to DS.

Panel 1. Advice for the management.

The main objective of the risk assessment protocols is to provide accurate information to managers to facilitate the decision-taking process. Here, I'd like to propose some advice for the invasive species management according to the situation of each species (Table 5.3).

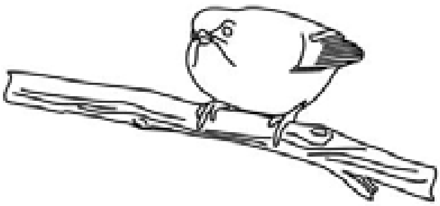
Table 5.3. Recommendations for the management of the exotic bird species present in Catalonia.

Category of risk	Probability of establishment	Established species	Not-established species
High	>60%	Import control Population control	Import control Eradication
Medium	~50%	Import control Eradication	Import control Eradication
Low	<30%	Monitoring Eradication	Eradication (C5) Monitoring (E)

For high-risk species that are already established, if they are causing damage, the suggestion is that control is the recommended actuation, but at the same time the arrival of new individuals has to prevented because that could undermine the control efforts. This could be achieved through controls on the species importation and awareness campaigns designed to prevent consumers to want high-risk species. If the high-risk species are not yet established it has to be avoid, for these species must also be prevented the arrival of new individuals to the wild and the individuals already in freedom must be removed. For species that represent a medium risk of establishment, by the principle of precaution, the measures that we recommend must be taken are the same as for high-risk species. But given limited resources, the priority is the first on the latter. Finally, for species with low risk of establishment, if they are already established the main advice is to monitor their population and if cause damage try to eradicate them, if their population can be decreased below the threshold of extinction is possible that can be eliminated. For the species non-established then minor concern, in any case we recommend monitoring the species to detect any possible establishment, and if the species is category C5, to try to eradicate them, because the species are already established elsewhere. In any case monitoring is a measure advised by any species that happens to E2 or E1 to E3.

Chapter 6

General Discussion



Resolving the invasion paradox

Biological invasions pose a challenging paradox to ecologists: Why invasive species, whose initial populations are generally small and genetically impoverished, are able to thrive and sometimes even displace native species in environments to which they have had little opportunity to adapt? The paradox, as Sax and Brown refer to this scientific problem, it is less paradoxical if we consider that only a small part of the large number of species that have been introduced around the world have successfully established wild populations (Long 1981, Lever 1987). However, a fraction of organisms has managed to succeed where most have failed, so obviously these species have been able to overcome the obstacles that led other introductions to fail. Theory suggests two main routes toward extinction in introduced populations (Saether et al. 2004, Sol 2007): first, extinction by stochastic factors associated with small founder populations (Pimm 1989); and second, extinction by negative population growth associated with the failure to find a suitable niche in the new environment (Shea and Chesson 2002). The chance of escaping stochastic risk of extinction and finding a favorable niche is expected to depend on adaptations to survive environmental fluctuations, to exploit new resources and to escape enemies in the new environment (Duncan et al. 2003). In the following sections I discuss these adaptations in the light of the more relevant results of the present thesis.

Adaptations to survive to the founder event

The phase between the introduction and the establishment is the most critical period of the process of invasion. As exposed in Chapter 1, ecological theory suggest that, at that point, extinction by stochastic factors should explain most of introductions failures for species introduced in small numbers (Pimm 1989, Lockwood et al. 2005). However, there are many cases in the literature of species that have only established themselves after multiple failed events and, on the contrary, species that established themselves despite being introduced in small numbers. Further, there exists evidence that some species repeatedly failed to become introduced whereas others succeeded almost everywhere where they were released. Taken together, these observations suggest that the establishment success depends on other factors in addition to the size of the founding population. Evolutionary theory suggests that life history strategies should be key adaptations in the success in novel environments (Stearns 1992, Ricklefs and Wikelski 2002, Saether et al. 2004), although these expectations have received little empirical support. In Chapter 2, I explore two alternative explanations suggested to explain the survival of alien species founding populations through the link between life-histories and the invasion success: the ‘population growth’ and ‘future returns’ hypotheses.

The ‘population growth’ hypothesis represents the classical view of how life history should influence invasion success. It predicts that the life history of successful invaders should be characterized by traits enabling a rapid population growth, so as to reduce the period which the founder population remain at low numbers and highly vulnerable to stochastic extinctions (Saether 1988). However, I find little evidence in favor of this hypothesis. One reason is that the effect of demographic stochasticity seems to be only relevant for introduction success when propagule size is extremely low. In these cases, it is reasonable to think that the ability to grow rapidly in numbers would give certain advantages to the species that invest more in reproduction rather than in survival. However, that invest more in reproduction are also more vulnerable to suffer dramatic stochastic population fluctuations, and therefore more likely that their populations fall below a threshold at which the recovery is not possible. Thus the species that invest in growth should have advantage only in those events in which the species were introduced in very low numbers, and released in an environment that does not put the founder population into many difficulties, for example, in environments that show reduced fluctuations or that are very similar to those found in their original region.

The alternative 'future returns' hypothesis, on the contrary, argues that species that have a strategy based on prioritizing future over current reproduction are the ones most likely to establish. In Chapter 2, I present the first evidence that species that have a strategy based on high expected future returns are more likely to succeed than the species that mostly rely on current reproduction effort. Using the brood value, i.e. the relative fitness value of current reproduction relative to lifespan reproduction, as an operational measure of the variation of the species along the life history axis of reproduction prioritization, the results indicate that species with low brood values have more likely to establish in novel regions than those with high brood values. However, the results also show that a low brood value can be achieved either by distributing the reproductive effort over many breeding seasons or by reproducing many times during a few breeding seasons, so there are two alternative strategies through which the species may be successfully established. The first strategy is based on investing in survival and extending lifespan. The species that have a long lifespan may distribute the reproduction effort over many breeding seasons, and hence can withstand to lose the clutch some season or to postpone the reproduction until the conditions are more favorable, so the costs of reproductive failure by stochastic factors is much lower. Investing in a long life has additional advantageous consequences, as it allows investing in adaptations such as enhanced cognitive abilities that buffer adult against ecological challenges and that may thus enable them to overcome the difficulties inherent in living in unfamiliar environments. The second strategy is not based in survival but in investing in different reproduction events within a same season, which allows extending the breeding season. This strategy could thus be useful to compensate the high juvenile and adult mortalities, expected for a species introduced into a new location in which has no previous experience. In conclusion, the species that have adaptations to avoid or offset the mortality during the early stages of invasion, either through having a long life, and surviving until environmental conditions allow for successful reproduction, or extending the breeding seasons, are those most likely to survive the founder event and successfully establish in the new place.

Although the presented evidence highlights the importance of possessing appropriate life histories to avoid extinction during the early phases of the invasion process, adaptations for surviving the founder event are insufficient to ensure establishment. In Chapter 5, it is revealed that the brood value is not the major predictor of establishment success; instead, the results indicate that the ability to have future returns is only relevant for less flexible generalist species introduced in low numbers. In this case the species that invest more in future reproduction are more likely to establish that those who invest more in current reproduction, but still are less likely to establish than the most flexible alien species or than those species introduced in greater numbers. Thus, these results show that to be successful in establishment is critical to possess adaptations to find the necessary resources and to deal with possible resistance of the native community.

Adaptations to find an appropriate niche

To succeed in a new environment, the invader population has to grow in numbers through a positive balance between births and deaths, and this is only possible if individuals find an appropriate ecological niche. The results presented here indicate that the species that are successful are those that have features that facilitate that individuals encounter appropriate niches in the new environment.

One of the most important adaptations that enhance the chances of a newly introduced species to find a suitable niche in a new environment is ecological generalism (Mayr 1965, Vazquez 2005). The results presented here confirm the classic hypothesis that the species with broader niche are more likely to find a suitable niche in the regions of invasion than species with narrower niches (Mayr 1965, Brown 1989, Ehrlich 1989). Supporting evidence that habitat generalism is a main predictor of establishment success is found in Chapters 4 and 5. Using coarse measures of ecological generalism, the analyses show that species that are able to live in a greater number of habitats in their native areas are also more likely to establish in the new region than more specialized species, confirming and generalizing previous studies (Cassey et al. 2004, Sol et al. 2005) The importance of this adaptation is highlighted when, added in a same predicting model along with the rest of the factors hypothesized to be related with establishment success, habitat breadth appears as the main variable to distinguish between species that are likely to be successful from species that have virtually no chance. One advantage of macroecological studies, like the one just discussed, is that allow drawing general conclusions. However, the previous analyses are based on macroecological measures of niche breadth, which may be considered too coarse for some. In Chapter 3, I provide finer evidence of the importance of niche breadth during the invasion success when examining the establishment of the Red-billed Leiothrix in Collserola. Thus, I find evidence that one of the reasons for the success of the species is their capacity to use a wide array of forested habitats, despite showing clear preferences for some over others.

Likewise, within the habitat, the species is able to use different types of foraging substrates and locations.

Another important adaptation that enables alien species to find their own niche in the native community is behavioral flexibility. Recently arrived species are faced with a new environment which have not had a chance to adapt, consequently those that can compensate for such poor fit by adjusting their behavior may be more successful in the invasion that the more conservative species (Mayr 1965) . A more flexible behavior can aid establishment by helping individuals to find new food resources, or to avoid novel enemies. This is because flexible species tend to be more exploratory and ecologically generalists, and have a higher ability to construct behavioral responses to new ecological challenges (Lefebvre et al. 1997). Thus, flexible species should have higher chances to find appropriate habitats and resources appropriate in the region of introduction (Sol 2007), and hence should be more buffered against novel environmental challenges (Sol 2009). The hypothesis that behavioral flexibility favors establishment has been supported by the evidence that the successful species tend to have larger brains relative to their body size and to show more innovative behaviors (Sol and Lefebvre 2000, Sol et al. 2002). The influence of behavioral flexibility on the success in the establishment has received support in the present thesis. In Chapters 2, 4 and 5, relative brain size is found to be related significantly to the success in establishing, and in Chapters 4 and 5 appears as the second most important predictor of establishment, only behind ecological generalism. In fact, generalist species with more flexible behavior are those with more chances to become established when introduced. The importance of behavioral adjustments to deal with novel ecological problems is also supported by experimental evidence (Sol et al. 2011b). Behavioral flexibility as a mechanism of alien species to establish in a new region also receives support from the analyses presented in Chapter 3. Leiothrix behaved both as a generalist and opportunist, features that were reflected in the way the species used the habitats and adopted novel feeding opportunities as well as in their large brain relative to their body. The ability of the Leiothrix to adjust their behavior to new environments was also revealed by its behavior in other regions, where the invader displays a different array of behaviors according to the particularities of each place (Male et al. 1998, Amano and Eguchi 2002a, b, Basly 2007).

Behavioral flexibility and ecological generalism are the two most important adaptations that facilitate finding a niche where to establish to alien species. However, as shown in Chapter 3, there are other species traits that may have helped species to find a niche unused by native species. In the case of Leiothrix, these include social behavior, high mobility during the unfavorable period and larger body than that of native species of the same functional group. These adaptations may have been key in allowing the invader finding a niche little overlapped with native species. In this vein, social foraging should be useful to rapidly gathering information about resources and enemies in the new location (Liker and Bokony 2009, Rodriguez et al. 2010) and a high mobility in winter may be advantageous during harsh winters when this strategy may facilitate tracking changes of the resources when become scarce (Perez-Tris and Telleria 2002b). A larger body, on the other hand, should help to win competitive encounters with similar native species (Jonart et al. 2007), and hence it could have provided competitive superiority in the few cases where the overlap (i.e. the potential for competition) was high. Obviously such adaptations that explain how species find place in the recipient community can be useful only in certain species for certain contexts, as it depends on the nature of the native community and/or the physical environment of the introduction location. Indeed, social behavior or migration ability have received little or no evidence in general comparative studies, as for example in Chapters 4 and 5.

Others factors associated with establishment success

Aside from the adaptations of introduced species, this thesis have highlighted the relative importance of two other types of factors that have been suggested to influence the success of invaders: factors associated with circumstances unique to each introduction event, such as the number of individuals released; and features of the introduction location, such as the structure of the native community and the degree of insularity (Duncan et al. 2003). In the following section, I discuss these factors to better understand the successful establishment of invasive species.

Introduction effort (e.g. number of individuals released or number of introduction attempts) is the most widely accepted predictor of establishment success in both plants and animals (Lockwood et al. 2009). As discussed in Chapter 1, there is ample evidence that introduced species that start with small founder populations are at higher risk of extinction by stochastic factors than those that start with large populations. However, there also are many cases of species that have been successful despite being introduced in low numbers. In Chapter 2 evidence is provided to explain this apparent paradox. According to the results, propagule size is only relevant when the species are introduced in very low numbers, because these are introductions that are more exposed to suffer stochastic fluctuations. Thus, above a threshold value of 300 individuals, the introduction effort is no longer relevant in explaining the success of invasions. This result could explain that although the propagule size appears as one of the main explanatory variables related to invasion success, is not, however, the main predictor of establishment. In Chapter 4 and 5 the propagule size appears as the third predictor of establishment success in the hierarchical decision tree model, being only relevant to enhance the chances of establishment for introductions made with less flexible generalist species. Hence, the introduction of these species in large quantities could be compensating for their limitations to find a suitable niche.

The other factors that influence invasions are related to the site of introduction. As commented in Chapter 1, the success of an introduction depends on whether or not the species finds an appropriate niche with the necessary resources and favorable physical environment and enemies pressures (Shea and Chesson 2002). The biotic resistance hypothesis (Elton 1958) suggest that finding an appropriate niche should be easier in species-poor than in species-rich environments. Species richness is commonly used as a surrogate for the number of enemies, competitors or vacant niches. In this context, there are some types of environments that have been traditionally viewed as more vulnerable to invasion. Islands, for example, are often perceived as more vulnerable to invasion due to their lower species richness, lack of certain functional groups and reduced competitive ability of island species. Contrarily to previous studies (Sol 2000, Blackburn and Duncan 2001a), and probably as a result of the extended dataset used in the analyses, in Chapter 4 I do find support for the greater vulnerability of islands to invasions. Thus, my results show that species introduced on oceanic islands are most likely to succeed than those introduced in continental islands or mainland. However, the insularity of the place of introduction is a factor of less importance than propagule pressure and species adaptations to explain the success in new environments. In fact, in the analysis of Chapter 4 and 5, when taken together with the other predictors, insularity does not appear in the hierarchical decision tree model.

Nevertheless, it remains unclear whether the vulnerability of islands to invaders result from an intrinsic lack of native species caused by the insularity or, alternatively, is an artifact from the combination of a higher introduction effort and the effect of human disturbance on the island’s natural habitats. As mentioned in Chapter 1, human disturbance is major cause of biodiversity loss (Devictor et al. 2008), implying that humanized habitats contain less native species and hence fewer competitors than natural habitats. According to the biotic resistance hypothesis, disturbed habitats should generally be highly vulnerable to invasions whereas the natural habitats should exhibit more resistance (Mack et al. 2000, Sax and Brown 2000). Given that most introductions tend to occur in disturbed environments (Case 1996), disturbance may thus be viewed as an additional explanation for the invasion paradox. Thus, the paradox may be resolved if we consider that the success of most invaders is related to adaptations that allow them occupying empty ecological niches derived from human activities that most native species are incapable to use. But, paradoxically, there have been some exotic species, like Leiothrix in Collserola, that have succeeded to invade natural habitats. The invasion of the Leiothrix shows that a little disturbed community can also be vulnerable to biological invasions when biotic resistance is low. In Chapter 3, low biotic resistance appears as a factor that may have favored the invasion of Red-billed Leiothrix, as suggests the lack of phylogenetic overdispersion in the native community and the predominance of generalist species.

Predicting invasion success

The solution to the paradox of invasion involves the participation of only a few adaptations of the species: the ecological generalism, behavioral flexibility and investment in future reproduction

(Chapter 5). This should not come as a surprise because adaptations evolve as a response to certain ecological pressures, and are unlikely to be useful when the ecological pressures change (Sol 2007). In addition, the results show that the success of invaders does not only depend on species adaptations, but also on certain characteristics of the location of introduction and the effect of the introduction effort. Then, if there are so few species traits that affect the establishment success and the stochastic factors seem to have an effect as important, can we still use the information obtained to assess the risk of future introductions? Previous work suggests that it is possible to build reliable risk assessment protocols with only a few variables (Kolar and Lodge 2001, Sol 2007). The results of the Chapter 4 and 5 confirm that with just a few predictors, it is possible to predict the outcome of new introductions with sufficient accuracy. The produced models were able to predict the success or failure of bird introductions to Europe and Australia with high accuracy (more than 80%) with only four of the variables described above. My models were able to predict the outcome of introductions more accurately and with less information than the previous protocols for risk assessment, based on long questionnaires to classify species into different risk groups according to the score obtained. Thus, although it is not possible to predict the result of a particular introduction with a 100% accuracy, the analyses indicate that it is possible at least to identify situations where the risk is high that a species establishes itself with sufficient accuracy for the method to be useful.

Given the scarce success of strategies of control and eradication as tools for combating biological invasions (Mack et al. 2000, Myers 2003), the implementation of risk assessment protocols in environmental protection policies seems critical to mitigate the impact of invasive birds species and contribute to the preservation of biodiversity and ecosystem functionality. Previous studies show that the use of risk assessment protocols can produce benefit when used to filter out harmful invasive species (Keller et al. 2007), while also show the danger of the limited application or no application of this methodologies (Fowler et al. 2007, Smith et al. 2008, Justo-Hanani et al. 2010) In Chapter 5, it is shown that the recently approved Spanish legal framework excludes a significant percentage of potentially dangerous species from the list of species for which the import will be banned. The failure to correctly identify potentially invasive species makes ineffective the management strategy against invasive species, creating doubts that it is really useful to mitigate the problem of biological invasions in the near future. Scientific research, so far, has proven to be able to generate tools useful for the improvement of the environment quality; the last step is whether stakeholders will be willing to implement these tools in active policies. Although political decisions may be based on a variety of legitimate arguments, including the social and economic impact of the exotic marked-trade, we cannot develop environmental management plans ignoring scientific criteria if we really want to avoid a future dominated by invasive species.

Conclusions

Resolving the invasion paradox

I. To establish successfully in a new environment, alien species must have, first, adaptations to find a suitable niche in the regions of invasion, and second, adaptations to overcome the risk of extinction by stochastic factors after the founder event.

Surviving the founder the founder event

II. As predicted by ecological theory, life history influences invasion success; however the mechanisms are complex and different from those classically considered in the literature, which may explain the past difficulties in disentangling the life history of successful invaders.

III. Successful invaders are characterized by life history traits that tend to prioritize future rather than current reproduction. This strategy reduces the costs of the offspring and increases the value of adults over the value of offspring.

IV. Rapid population growth strategy is only advantageous to escape earlier extinction when the founder population is quite small and when the challenges posed by the new environment do not substantially decrease the intrinsic population growth rate. Nevertheless, this situation is still valid for the majority of new introduction events.

Finding an appropriate niche

V. Ecological generalism and behavioral flexibility are the two main adaptations that facilitate alien species to find an apropiate niche in the new locations. Species that could use a major numbers of habitats and with higher cognitive capacity are those with more chances to establish

VI. To be successful in invading new environments it is important that the invader has a generalist and opportunistic behavior, and that its ecological niche exhibits little overlap with that of native species. Although the local community could offer little biotic resistance to the invader, is also important of being competitively superior to the natives.

VII. The proposal that finding an appropriate niche had to be explained by either alternative hypothesis must be revised. Therefore, different hypotheses hypotheses are not mutually exclusive, but combine to explain the establishment process of the invader. For this reason, for a correct understanding of the complexity underlying the invasion process is important to consider integrative approaches combining a variety of analytical approaches.

Invasions in natural habitats

VIII. Natural habitats are apparently less disturbed by human activity but this does not directly mean that they have more biotic resistance against invasions. Native communities dominated by generalist species may be vulnerable to biological invasions because there are many opportunities in the form of unexploited ecological niches.

IX. Although often go unnoticed, it is important to pay attention to invasions occurring in habitats less humanized because invaders can have negative effects on native biodiversity and generate significant impacts on ecosystems.

Predicting invading species

X. The models predict that more flexible generalist species have the highest chances to establish. On the other hand, habitat specialists are the species less likely to get established, regardless others factors. High propagule size and low brood value can increase the probabilities of establishment for species with limitations to find a new niche.

XI. Although it is not possible to predict the future of an introduction with absolute certainty, it is possible to identify situations in which there is high probability that a species will get established or that the invasion will fail, with enough precision to be useful to identify potential invaders.

XII. Risk assessments based on quantitative methods are more efficient than qualitative ones, because are less subjective, require less information and not have to be answered by experts.

XIII. Even though the risk assessment protocols are formidable tools to help mitigate the damage caused by alien species, to be truly useful must be effectively implemented in invasive species management plans.

XIV. Basic ecological research is very important to discover the patterns and mechanisms that rule biological invasions, and this will allow improve the strategies to deal with invasive species. Applied research is necessary for transfering the gained information into tools beneficial to the society. But especially, coordination between scientific research and conservation management is essential to properly address the problems caused by invasive species.

References

AERC. 2001. Minutes. *in* 6th Conference of European Rarities Committees, Hel Peninsula, Poland.

Ali, S. 1977. Field Guide to the Birds of the Eastern Himalayas. Oxford University Press, London, UK.

Amano, H. E., and K. Eguchi. 2002a. Foraging niches of introduced Red-billed Leiothrix and native species in Japan. Ornithological Science **1**:123-131.

Amano, H. E., and K. Eguchi. 2002b. Nest-site selection of the Red-billed Leiothrix and Japanese Bush Warbler. Ornithological Science **1**:101-110.

Andersen, M. C., H. Adams, B. Hope, and M. Powell. 2004a. Risk analysis for invasive species: General framework and research needs. Risk Analysis **24**:893-900.

Andersen, M. C., H. Adams, B. Hope, and M. Powell. 2004b. Risk assessment for invasive species. Risk Analysis **24**:787-793.

Anderson, D. R., and K. P. Burnham. 2002. Avoiding pitfalls when using information-theoretic methods. Journal of Wildlife Management **66**:912-918.

Bairlein, F. 1995. Manual of Field Works. European-African Songbird Migration Networks. Institut fur Vogelkunde, Wilhelmshaven, Germany.

Baker, R. H. A., R. Black, G. H. Copp, K. A. Haysom, P. E. Hulme, M. B. Thomas, A. Brown, M. Brown, R. J. C. Cannon, J. Ellis, M. Ellis, R. Ferris, P. Glaves, R. E. Gozlan, J. Holt, L. Howe, J. D. Knight, A. MacLeod, N. P. Moore, J. D. Mumford, S. T. Murphy, D. Parrott, C. E. Sansford, G. C. Smith, S. St-Hilaire, and N. L. Ward. 2008. The UK risk assessment scheme for all non-native species. Pages 46-57 *in* Biological Invasions – from Ecology to Conservation. NEOBIOTA, Berlin, Germany.

Baltz, D. M., and P. B. Moyle. 1993. Invasion Resistance to Introduced Species by a Native Assemblage of California Stream Fishes. Ecological Applications **3**:246-255.

Bartomeus, I., D. Sol, P. J., P. Vicente, and X. Font. 2011. Deconstructing the native-exotic richness relationship in plants. Global Ecology and Biogeography **In press**.

Basly, J. P. 2007. Le Léiothrix jaune Leiothrix lutea en Béarn: répartition, effectifs et comportement. Ornithos **14**:370-375.

Bates, D., M. Maechler, and B. Bolker. 2011. lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-39.

Bennett, P. M., and P. H. Harvey. 1985. Relative Brain Size and Ecology in Birds. Journal of Zoology **207**:151-169.

Bergman, D. L., M. D. Chandler, and A. Locklear. 2000. The Economic Impacts of Invasive Species to Wildlife Services' Cooperators.

USDA/APHIS/WS, National Wildlife Research Center, Fort Collins, CO, USA.

Bielby, J., G. M. Mace, O. R. P. Bininda-Emonds, M. Cardillo, J. L. Gittleman, K. E. Jones, C. D. L. Orme, and A. Purvis. 2007. The fast-slow continuum in mammalian life history: An empirical reevaluation. American Naturalist **169**:748-757.

Blackburn, T. M., P. Cassey, and J. L. Lockwood. 2009a. The role of species traits in the establishment success of exotic birds. Global Change Biology **15**:2852-2860.

Blackburn, T. M., and R. P. Duncan. 2001a. Determinants of establishment success in introduced birds. Nature **414**:195-197.

Blackburn, T. M., and R. P. Duncan. 2001b. Establishment patterns of exotic birds are constrained by non-random patterns in introduction. Journal of Biogeography **28**:927-939.

Blackburn, T. M., J. L. Lockwood, and P. Cassey. 2009b. Avian Invasions. The Ecology & Evolution of Exotic Birds. Oxford University Press, Oxford, UK.

Bokony, V., A. Z. Lendvai, A. Liker, F. Angelier, J. C. Wingfield, and O. Chastel. 2009. Stress Response and the Value of Reproduction: Are Birds Prudent Parents? American Naturalist **173**:589-598.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J. S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution **24**:127-135.

Bomford, M. 2003. Risk Assessment for the Import and Keeping of Exotic Vertebrates in Australia. Bureau of Rural Science, Canberra, Australia.

Bomford, M. 2008. Risk Assessment Models for Establishment of Exotic Vertebrates in Australia and New Zealand. Invasive Animals Cooperative Research Centre, Canberra, Australia.

Bomford, M., F. Kraus, S. C. Barry, and E. Lawrence. 2009. Predicting establishment success for alien reptiles and amphibians: a role for climate matching. Biological Invasions **11**:713-724.

Brown, J. H. 1989. Patterns, modes and extents of invasions by vertebrates. . Pages 89-109 *in* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological invasions: a global perspective John Wiley & Sons, New York, USA.

Brown, J. H., and R. M. Sibly. 2006. Life-history evolution under a production constraint. Proceedings of the National Academy of Sciences of the United States of America **103**:17595-17599.

Brown, J. S. 1988. Patch Use as an Indicator of Habitat Preference, Predation Risk, and Competition. Behavioral Ecology and Sociobiology **22**:37-47.

Bruno, J. F., J. D. Fridley, K. Bromberg, and M. D. Bertness. 2005. Insights into biotic interactions from studies of species invasions. Pages 13-40 *in* D. F. Sax, S. D. Gaines, and J. J. Stachowicz, editors. Species Invasions: Insights into Ecology, Evolution and Biogeography. Sinauer, Sunderland, MA, USA.

Byers, J. E., S. Reichard, J. M. Randall, I. M. Parker, C. S. Smith, W. M. Lonsdale, I. A. E. Atkinson, T. R. Seastedt, M. Williamson, E. Chornesky, and D. Hayes. 2002. Directing research to reduce the impacts of nonindigenous species. Conservation Biology **16**:630-640.

Caley, P., and P. M. Kuhnert. 2006. Application and evaluation of classification trees for screening unwanted plants. Austral Ecology **31**:647-655.

Case, T. J. 1996. Global patterns in the establishment and distribution of exotic birds. Biological Conservation **78**:69-96.

Case, T. J. 2000. An illustrated guide to theoretical ecology. Oxford University Press, Oxford, UK.

Cassey, P. 2001a. Are there body size implications for the success of globally introduced land birds? Ecography **24**:413-420.

Cassey, P. 2001b. Comparative analyses of establishment among introduced land bird. Griffin University, Queensland, Australia.

Cassey, P. 2001c. Determining variation in the success of New Zealand land birds. Global Ecology and Biogeography **10**:161-172.

Cassey, P. 2002. Life history and ecology influences establishment success of introduced land birds. Biological Journal of the Linnean Society **76**:465-480.

Cassey, P. 2003. A comparative analysis of the relative success of introduced land birds on islands. Evolutionary Ecology Research **5**:1011-1021.

Cassey, P., T. M. Blackburn, S. Sol, R. P. Duncan, and J. L. Lockwood. 2004. Global patterns of introduction effort and establishment success in birds. Proceedings of the Royal Society of London Series B-Biological Sciences **271**:S405-S408.

Clarabuch, O. 2011. Anuari d'Ornitologia de Catalunya. 2009. Institut Català d'Ornitologia, Barcelona.

Clark, L. A., and D. Pregibon. 1992. Tree based models. *in* J. M. Chambers and T. J. Hastie, editors. Statisticals Methods Wadsworth & Brooks/ Cole Advanced

Books and Software, Pacific Grove, CA, USA.

Clavell, J. 2002. Catàleg dels ocells dels Països Catalans (Catalunya, País Valencià, Illes Balears, Catalunya Nord. Lynx Editions, Bellaterra, Spain.

Clavell, J., and J. C. Fernández-Ordóñez. 2004. Teixidor de bec vermell Quelea quelea. Pages 512-513 *in* J. Estrada, V. Pedrocchi, L. Brotons, and S. Herrando, editors. Atles dels ocells nidificants de Catalunya 1999-2002. Institut Català d'Ornitologia (ICO) / Lynx Edicions, Barcelona, Spain.

Clavell, J., D. Sol, and X. Batllori. 2004. Cotorra de Kramer Psittacula krameri. Pages 270-271 *in* J. Estrada, V. Pedrocchi, L. Brotons, and S. Herrando, editors. Atles dels ocells nidificants de Catalunya 1999-2002. Institut Català d'Ornitologia (ICO) / Lynx Edicions, Barcelona, Spain.

Clavero, M., and E. Garcia-Berthou. 2005. Invasive species are a leading cause of animal extinctions. Trends in Ecology & Evolution **20**:110-110.

Cleland, E. E., M. D. Smith, S. J. Andelman, C. Bowles, K. M. Carney, M. C. Horner-Devine, J. M. Drake, S. M. Emery, J. M. Gramling, and D. B. Vandermast. 2004. Invasion in space and time: non-native species richness and relative abundance respond to interannual variation in productivity and diversity. Ecology Letters **7**:947-957.

Clements, J. F., T. S. Schulenberg, M. J. Iliff, B. L. Sullivan, C. L. Wood, and D. Roberson. 2011. The Clements Checklist of Birds of the World: Version 6.6.

Cole, L. C. 1954. The Population Consequences of Life History Phenomena. Quarterly Review of Biology **29**:103-137.

Colin, J. B., N. D. Burgess, D. A. Hill, and S. Mustoe. 1992. Bird Census Techniques. BTO-RSPB Academic Press, London, UK.

Cooper, M. E., and A. M. Rosser. 2002. International regulation of wildlife trade: relevant legislation and organisations. Revue Scientifique Et Technique De L Office International Des Epizooties **21**:103-123.

Cory, J. S., and J. H. Myers. 2000. Direct and indirect ecological effects of biological control. Trends in Ecology & Evolution **15**:137-139.

Cox, C. B. 2001. The biogeographic regions reconsidered. Journal of Biogeography **28**:511-523.

Cramp, S. 1994. The Birds of the Western Palearctic. Handbook of the Birds of Europe, the Middle East, and North Africa. Oxford University Press, Oxford, UK.

Crawley, M. J. 2002. Statistical Computing. An Introduction to Data Analysis using S-

Plus. John Wiley & Sons Ltd., Chichester, UK.

Cubaynes, S., P. F. Doherty, E. A. Schreiber, and O. Gimenez. 2011. To breed or not to breed: a seabird's response to extreme climatic events. Biology Letters **7**:303-306.

Darwin, C. 1859. On the Origin of Species. Murray, London, UK.

Davies, T. J. 2006. Evolutionary ecology: When relatives cannot live together. Current Biology **16**:R645-R647.

Davis, K. E. 2008. Reweaving the tapestry: a supertree of birds. University of Glasgow, Glasgow, Scotland.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology **88**:528-534.

De'ath, G., and K. E. Fabricius. 2000. Classification and regression trees: A powerful yet simple technique for ecological data analysis. Ecology **81**:3178-3192.

De Caceres, M., and P. Legendre. 2009. Associations between species and groups of sites: indices and statistical inference. Ecology **90**:3566-3574.

De Caceres, M., D. Sol, O. Lapiedra, and P. Legendre. 2011. A framework for estimating niche metrics using the resemblance between qualitative resources. Oikos **120**:1341-1350.

Deaner, R. O., C. L. Nunn, and C. P. van Schaik. 2000. Comparative tests of primate cognition: Different scaling methods produce different results. Brain Behavior and Evolution **55**:44-52.

Del Hoyo, J., A. Elliott, J. Sargatal, and D. A. Christie. 1992-2011. Handbook of the Birds of the World. Lynx Editions, Barcelona, Spain.

Devictor, V., R. Julliard, J. Clavel, F. Jiguet, A. Lee, and D. Couvet. 2008. Functional biotic homogenization of bird communities in disturbed landscapes. Global Ecology and Biogeography **17**:252-261.

Domenech, J., and J. C. Senar. 2004. Cotorreta de pit gris Myopsitta monachus. Pages 272-273 *in* J. Estrada, V. Pedrocchi, L. Brotons, and S. Herrando, editors. Atles dels ocells nidificants de Catalunya 1999-2002. Institut Català d'Ornitologia (ICO) / Lynx Edicions, Barcelona, Spain.

Donaldson-Matasci, M. C. 2008. Adaptation in a changing environment: Phenotypic diversity in response to environmental uncertainty and information. University of Washington, Washington, USA.

Dufrene, M., and P. Legendre. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecological Monographs **67**:345-366.

Duncan, R. P., T. M. Blackburn, and D. Sol. 2003. The ecology of bird introductions. Annual Review of Ecology Evolution and Systematics **34**:71-98.

Duncan, R. P., M. Bomford, D. M. Forsyth, and L. Conibear. 2001. High predictability in introduction outcomes and the geographical range size of introduced Australian birds: A role for climate. Journal of Animal Ecology **70**:621-632.

Duncan, R. P., and P. A. Williams. 2002. Ecology - Darwin's naturalization hypothesis challenged. Nature **417**:608-609.

Dyer, A. R., and K. J. Rice. 1999. Effects of competition on resource availability and growth of a California bunchgrass. Ecology **80**:2697-2710.

Eguchi, K., and T. Masuda. 1994. A report on the habitats of Peking Robin Leiothrix lutea in Kyushu. Japanese Journal of Ornithology **43**:91-100.

Ehrlich, P. R. 1989. Attributes of invaders and the invading processes: vertebrates. Pages 315-328 *in* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, and F. G. Kruger, editors. Biological Invasions: a Global Perspective. John Wiley & Sons Ltd., Chichester, UK.

Elton, C. S. 1958. The Ecology of Invasions by Animals and Plants. Methuen, London, UK.

Essl, F., S. Nehring, F. Klingenstein, N. Milasowszky, C. Nowack, and W. Rabitsch. 2011. Review of risk assessment systems of IAS in Europe and introducing the German-Austrian Black List Information System (GABLIS). Journal for Nature Conservation **19**:339-350.

Estrada, J., V. Pedrocchi, L. Brotons, and S. Herrando. 2004. Atles dels ocells nidificants de Catalunya 1999-2002. Institut Català d'Ornitologia (ICO) / Lynx Edicions, Barcelona.

Ewel, J. J., D. J. O'Dowd, J. Bergelson, C. C. Daehler, C. M. D'Antonio, L. D. Gomez, D. R. Gordon, R. J. Hobbs, A. Holt, K. R. Hopper, C. E. Hughes, M. LaHart, R. R. B. Leakey, W. G. Lee, L. L. Loope, D. H. Lorence, S. M. Louda, A. E. Lugo, P. B. McEvoy, D. M. Richardson, and P. M. Vitousek. 1999. Deliberate introductions of species: Research needs - Benefits can be reaped, but risks are high. Bioscience **49**:619-630.

Fagerstone, K. A. 2003. Mitigating Impacts of Terrestrial Invasive Species. Pages 347-352 *in* D. Pimentel, editor. Encyclopedia of Pest Management. Volume II. Taylor and Francis.

Faith, D. P. 1992. Conservation Evaluation and Phylogenetic Diversity. Biological Conservation **61**:1-10.

Forsyth, D. M., and R. P. Duncan. 2001. Propagule size and the relative success of exotic ungulate and bird introductions to New Zealand. American Naturalist **157**:583-595.

Fowler, A. J., D. M. Lodge, and J. F. Hsia. 2007. Failure of the Lacey Act to protect US ecosystems against animal invasions. Frontiers in Ecology and the Environment **5**:353-359.

Freckleton, R. P. 2000a. Phylogenetic tests of ecological and evolutionary hypotheses: checking for phylogenetic independence. Functional Ecology **14**:129-134.

Freckleton, R. P. 2000b. Phylogenetic tests of ecological and evolutionary hypotheses: checking for phylogenetic independence. Functional Ecology **14**:129-134.

Freckleton, R. P., P. H. Harvey, and M. Pagel. 2002. Phylogenetic analysis and comparative data: A test and review of evidence. American Naturalist **160**:712-726.

Fretwell, S. D., and H. L. J. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Part I. Theoretical Development. Acta Biotheoretica **19**:16-36.

Gibbons, D. W., and R. D. Gregory. 2006. Birds. Pages 308-350 *in* W. J. Sutherland, editor. Ecological Census Techniques. A Handbook. Cambridge University Press, Cambridge, UK.

Gilbert, B., and M. J. Lechowicz. 2005. Invasibility and abiotic gradients: The positive correlation between native and exotic plant diversity. Ecology **86**:1848-1855.

Gillespie, J. H. 1973. Natural-Selection with Varying Selection Coefficients - Haploid Model. Genetical Research **21**:115-120.

Gittleman, J. L., C. G. Anderson, M. Kot, and H.-K. Luh. 1996. Comparative tests of evolutionary lability and rates using molecular phylogenies. Pages 289-307 *in* P. H. Harvey, A. J. L. Brown, J. Maynard-Smith, and S. Nee, editors. New uses for a new phylogenies. Oxford University Press, Oxford, UK.

Gozlan, R. E., and A. C. Newton. 2009. Biological Invasions: Benefits versus Risks. Science **324**:1015-1015.

Green, A. J., and B. Hughes. 1996. Action plan for the White-headed Duck Oxyura leucocephala. Pages 119–146 *in* B. Heredia, L. Rose, and M. Painter, editors. Globally Threatened Birds in Europe. Council of Europe, Strasbourg, France.

Green, R. E. 1997. The influence of numbers released on the outcome of attempts to introduce exotic bird species to New Zealand. Journal of Animal Ecology **66**:25-35.

Grevstad, F. S. 1999. Factors influencing the chance of population establishment: Implications for release strategies in biocontrol. Ecological Applications **9**:1439-1447.

Hagemeijer, E. J. M., and M. J. Blair. 1997. The EBCC Atlas of European Breeding Birds: Their Distributions and Abundance. T & AD Poyser, London, UK.

Hayes, K. R., and S. C. Barry. 2008. Are there any consistent predictors of invasion success? Biological Invasions **10**:483-506.

Helmus, M. R., W. Keller, M. J. Paterson, N. D. Yan, C. H. Cannon, and J. A. Rusak. 2010. Communities contain closely related species during ecosystem disturbance. Ecology Letters **13**:162-174.

Herrando, S., L. Brotons, J. Estrada, S. Guallar, and M. Anton. 2011. Atles dels ocells de Catalunya a l'hivern 2006-2009. Institut Català d'Ornitologia (ICO) / Lynx Edicions, Barcelona.

Herrando, S., F. Llimona, L. Brotons, and J. Quesada. 2010. A new exotic bird in Europe: recent spread and potential range of Red-billed Leiothrix Leiothrix lutea in Catalonia (northeast Iberian Peninsula). Bird Study **57**:226-235.

Hill, A. M., D. M. Sinars, and D. M. Lodge. 1993. Invasion of an Occupied Niche by the Crayfish Orconectes-Rusticus - Potential Importance of Growth and Mortality. Oecologia **94**:303-306.

Hoffmann, B. D. 2003. An assessment of the status and possible eradication of yellow crazy ants in north-eastern Arnhem Land. CSIRO, Darwin, Australia.

Hoffmann, B. D., and W. C. Saul. 2010. Yellow crazy ant (Anoplolepis gracilipes) invasions within undisturbed mainland Australian habitats: no support for biotic resistance hypothesis. Biological Invasions **12**:3093-3108.

Hope, B. K. 2006. An examination of ecological risk assessment and management practices. Environment International **32**:983-995.

Hothorn, T., K. Hornik, and A. Zeileis. 2006. Unbiased recursive partitioning: A conditional inference framework. Journal of Computational and Graphical Statistics **15**:651-674.

Hulme, P. E. 2003. Biological invasions: winning the science battles but losing the conservation war? Oryx **37**:178-193.

Hulme, P. E. 2009. Trade, transport and trouble: managing invasive species pathways in an era of globalization. Journal of Applied Ecology **46**:10-18.

Hulme, P. E. 2011. Practitioner's perspectives: introducing a different voice in applied ecology. Journal of Applied Ecology **48**:1-2.

Hulme, P. E., S. Bacher, M. Kenis, S. Klotz, I. Kuhn, D. Minchin, W. Nentwig, S. Olenin, V. Panov, J. Pergl, P. Pysek, A. Roques, D. Sol, W. Solarz, and M. Vila. 2008. Grasping at the routes of biological invasions: a framework for integrating pathways into policy. Journal of Applied Ecology **45**:403-414.

Hulme, P. E., W. Nentwig, P. Pysek, and M. Vila. 2009. Biological Invasions: Benefits versus Risks Response. Science **324**:1015-1016.

ICO. 2011. SYLVIA Project. Constant effort ringing stations in Catalonia. Barcelona, Spain.

IUCN. 2000. Guidelines for the Prevention of biodiversity Loss Caused by Alien Invasive Species. International Union for the Conservation of Nature, Gland, Switzerland.

Ives, A. R., and M. R. Helmus. 2011. Generalized linear mixed models for phylogenetic analyses of community structure. Ecological Monographs **81**:511-525.

Iwaniuk, A. N., K. M. Dean, and J. E. Nelson. 2005. Interspecific allometry of the brain and brain regions in parrots (psittaciformes): Comparisons with other birds and primates. Brain Behavior and Evolution **65**:40-59.

Iwaniuk, A. N., and J. E. Nelson. 2003. Developmental differences are correlated with relative brain size in birds: a comparative analysis. Canadian Journal of Zoology-Revue Canadienne De Zoologie **81**:1913-1928.

Jenkins, P. T. 1996. Free trade and exotic species introductions. Conservation Biology **10**:300-302.

Jensen, C., and J. C. Fernández-Ordóñez. 2004. Bec de corall senegalès. Pages 514-515 *in* J. Estrada, V. Pedrocchi, L. Brotons, and S. Herrando, editors. Atles dels ocells nidificants de Catalunya 1999-2002. Institut Català d'Ornitologia (ICO) / Lynx Edicions, Barcelona, Spain.

Jeschke, J. M., and D. L. Strayer. 2006. Determinants of vertebrate invasion success in Europe and North America. Global Change Biology **12**:1608-1619.

Jonart, L. M., G. E. Hill, and A. V. Badyaev. 2007. Fighting ability and motivation: determinants of dominance and contest strategies in females of a passerine bird. Animal Behaviour **74**:1675-1681

Julliard, R., J. Clavel, V. Devictor, F. Jiguet, and D. Couvet. 2006. Spatial segregation of specialists and generalists in bird communities. Ecology Letters **9**:1237-1244.

Justo-Hanani, R., T. Dayan, and A. Tal. 2010. The role of regulatory decision-making on non-indigenous species introductions. Biological Invasions **12**:2815-2824.

Kaiser, A. 1993. A new multi-category classification of subcutaneous fat deposits of songbirds. journal of Field Ornithology **64**:38-46.

Kaiser, J. 1999. Fighting back: Stemming the tide of invading species. Science **285**:1836-+.

Keller, R. P., D. M. Lodge, and D. C. Finnoff. 2007. Risk assessment for invasive species produces net bioeconomic benefits. Proceedings of the National Academy of Sciences of the United States of America **104**:203-207.

Kembel, S. W., P. D. Cowan, M. R. Helmus, C. W. K., H. Morlon, D. D. Ackerly, S. P. Blomberg, and C. O. Webb. 2010. Picante: {R} tools for integrating phylogenies and ecology. Bioinformatics **26**:1463-1464.

Kennedy, T. A., S. Naeem, K. M. Howe, J. M. H. Knops, D. Tilman, and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. Nature **417**:636-638.

Knowler, D., and E. Barbier. 2005. Importing exotic plants and the risk of invasion: are market-based instruments adequate? Ecological Economics **52**:341-354.

Kolar, C. S., and D. M. Lodge. 2001. Progress in invasion biology: predicting invaders. Trends in Ecology & Evolution **16**:199-204.

Kolar, C. S., and D. M. Lodge. 2002. Ecological predictions and risk assessment for alien fishes in North America. Science **298**:1233-1236.

Kramer, M. 2005. R2 statistics for mixed models. *in* 17th Annual Kansas University Conference on Applied Statistics in Agriculture, Manhattan, KS, USA.

Kumschick, S., and W. Nentwig. 2010. Some alien birds have as severe an impact as the most effectual alien mammals in Europe. Biological Conservation **143**:2757-2762.

Lande, R., S. Engen, and B. E. Saether. 2003. Stochastic population dynamics in ecology and conservation. Oxford University Press, Oxford, UK.

Le Breton, J., H. Jourdan, J. Chazeau, J. Orivel, and A. Dejean. 2005. Niche opportunity and ant invasion: the case of Wasmannia auropunctata in a New Caledonian rain forest. Journal of Tropical Ecology **21**:93-98.

Lefebvre, L., S. M. Reader, and D. Sol. 2004. Brains, innovations and evolution in birds and primates. Brain Behavior and Evolution **63**:233-246.

Lefebvre, L., P. Whittle, E. Lascaris, and A. Finkelstein. 1997. Feeding innovations and forebrain size in birds. Animal Behaviour **53**:549-560.

Lefkovitch, L. 1965. Study of Population Growth in Organisms Grouped by Stages. Biometrics **21**:1-&.

Legendre, S., J. Clobert, A. P. Moller, and G. Sorci. 1999. Demographic stochasticity and social mating system in the process of extinction of small populations: The case of passerines introduced to New Zealand. American Naturalist **153**:449-463.

Leung, B., D. Finnoff, J. F. Shogren, and D. Lodge. 2005. Managing invasive species: Rules of thumb for rapid assessment. Ecological Economics **55**:24-36.

Lever, C. 1987. Naturalised Birds of the World. Longman Sc & Tech, Harlow, Essex, UK.

Lever, C. 2005. Naturalised Birds of the World. T. & A. D. Poyser, London, UK.

Levine, J. M., P. B. Adler, and S. G. Yelenik. 2004. A meta-analysis of biotic resistance to exotic plant invasions. Ecology Letters **7**:975-989.

Levine, J. M., and C. M. D'Antonio. 2003. Forecasting biological invasions with increasing international trade. Conservation Biology **17**:322-326.

Lewontin, R. C. 1965. Selection for colonizing ability. *in* H. G. Baker and G. L. Stebbins Jr, editors. The Genetics of Colonizing Species. Academic Press, New York, NY, USA.

Liker, A., and V. Bokony. 2009. Larger groups are more successful in innovative problem solving in house sparrows. Proceedings of the National Academy of Sciences of the United States of America **106**:7893-7898.

Liker, A., and T. Szekely. 2005. Mortality costs of sexual selection and parental care in natural populations of birds. Evolution **59**:890-897.

Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS system for mixed models. SAS Inst. Inc., Cary, NC, USA.

Lockwood, J. L., P. Cassey, and T. Blackburn. 2005. The role of propagule pressure in explaining species invasions. Trends in Ecology & Evolution **20**:223-228.

Lockwood, J. L., P. Cassey, and T. M. Blackburn. 2009. The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. Diversity and Distributions **15**:904-910.

Lodge, D. M., S. Williams, H. J. MacIsaac, K. R. Hayes, B. Leung, S. Reichard, R. N. Mack, P. B. Moyle, M. Smith, D. A. Andow, J. T. Carlton, and A. McMichael. 2006. Biological invasions: Recommendations for US policy and management. Ecological Applications **16**:2035-2054.

Long, J. L. 1981. Introduced Birds of the World. David & Charles, London, UK.

Lovette, I. J., and W. M. Hochachka. 2006. Simultaneous effects of phylogenetic niche conservatism and competition on avian community structure. Ecology **87**:S14-S28.

Lowe, S., M. Browne, S. Boudjelas, and M. De Poorter. 2000. 100 of the World's Worst Invasive Alien Species. A selection from the Global Invasive Database. Aliens **12**:12.

Llimona, F. 2004. Rossinyol del Japó Leiothrix lutea. Pages 448-449 *in* J. Estrada, V. Pedrocchi, L. Brotons, and S. Herrando, editors. Atles dels ocells nidificants de Catalunya 1999-2002. Institut Català d'Ornitologia (ICO) / Lynx Edicions, Barcelona, Spain.

Llimona, F., and R. Prodon. 2000. Canvis avifaunístics globals al parc de collserola en una sèrie de 10 anys de seguiment. Pages 292 *in* F. Llimona, J. M. Espelta, J. C. Guix, E. Mateos, and J. D. Rodriguez-Teijeiro, editors. I Jornades sobre la Recerca en els sistemes naturals de Collserola: aplicacions a la gestió del Parc. Patronat del Parc de Collserola, Barcelona, Spain.

Macarthur, R. H., and R. Levins. 1967. Limiting Similarity Convergence and Divergence of Coexisting Species. American Naturalist **101**:377-&.

Macdonald, D. W., and L. A. Harrington. 2003. The American mink: the triumph and tragedy of adaptation out of context. New Zealand Journal of Zoology **30**:421-441.

Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. Ecological Applications **10**:689-710.

MacLeod, C. J., S. E. Newson, G. Blackwell, and R. P. Duncan. 2009. Enhanced niche opportunities: can they explain the success of New Zealand's introduced bird species? Diversity and Distributions **15**:41-49.

Male, T. D., S. G. Fancy, and C. J. Ralph. 1998. Red- billed Leiothrix (Leiothrix lutea). *in* A. Poole and F. Gill, editors. The Birds of North America. The Birds of North America, Inc., Philadelphia, PA.

Manchester, S. J., and J. M. Bullock. 2000. The impacts of non-native species on UK biodiversity and the effectiveness of control. Journal of Applied Ecology **37**:845-864.

Mañosa, S. 2004. Faisà Phasianus colchicus. Pages 114-115 *in* J. Estrada, V. Pedrocchi, L. Brotons, and S. Herrando, editors. Atles dels ocells nidificants de Catalunya 1999-2002. Institut Català d'Ornitologia (ICO) / Lynx Edicions, Barcelona, Spain.

Mayr, E. 1954. Change of genetic environment and evolution. Pages 157-180 *in* J. Huxley, A. C. Hardy, and E. B. Ford, editors. Evolution as a Process. Allen & Unwin, London, UK.

Mayr, E. 1965. The nature of colonizing birds. *in* H. G. Baker and G. L. Stebbins, editors. The genetics of colonizing species Academic Press, New York, NY, USA.

McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. Biological Conservation **127**:247-260.

McKinney, M. L., and J. L. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in Ecology & Evolution **14**:450-453.

McLain, D. K., M. P. Moulton, and J. G. Sanderson. 1999. Sexual selection and extinction: The fate of plumage-dimorphic and plumage-monomorphic birds introduced onto islands. Evolutionary Ecology Research **1**:549-565.

Meyerson, L. A., and H. A. Mooney. 2007. Invasive alien species in an era of globalization. Frontiers in Ecology and the Environment **5**:199-208.

Miles, D. B., and R. E. Ricklefs. 1984. The Correlation between Ecology and Morphology in Deciduous Forest Passerine Birds. Ecology **65**:1629-1640.

Mooney, H. A., and R. J. Hobbs. 2000. Invasive Species in a Changing World. Island Press, Washington, D.C., USA.

Moulton, M. P., and S. L. Pimm. 1986. Species introductions to Hawaii. Pages 231-249 *in* J. A. Drake and H. A. Mooney, editors. Ecology of biological invasions in North America and Hawaii. Springer-Verlag, New York, NY, USA.

Moyle, P. B., and M. P. Marchetti. 2006. Predicting invasion success: Freshwater fishes in California as a model. Bioscience **56**:515-524.

Myers, J. H. 2003. Eradication: Is it ecologically, financially, environmentally, and realistically possible? . Pages 533-539 *in* D. J. Rapport, W. L. Lasley, D. E. Rolston, N. O. Nielsen, C. O. Qualset, and A. B. Damania, editors. Managing for Healthy Ecosystems. Lewis Publishers, Boca Raton, FL, USA.

Myers, J. H., D. Simberloff, A. M. Kuris, and J. R. Carey. 2000. Eradication revisited: dealing with exotic species. Trends in Ecology & Evolution **15**:316-320.

Naeem, S., J. M. H. Knops, D. Tilman, K. M. Howe, T. Kennedy, and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. Oikos **91**:97-108.

Nature. 2007. The great divide. Nature **450**:135-136.

Newsome, A. E., and I. R. Noble. 1986. Ecological and physiological characters of invading species. Pages 1-20 *in* R. H. Groves and J. J. Burdon, editors.

Biological Invasions. Cambridge University Press Cambridge, UK.

Nice, M. M. 1986. Development of behavior in precocial birds. Transactions of the Linnaean Society of New York **8**:1-211.

Oli, M. K. 2004. The fast-slow continuum and mammalian life-history patterns: an empirical evaluation. Basic and Applied Ecology **5**:449-463.

Overington, S. E., J. Morand-Ferron, N. J. Boogert, and L. Lefebvre. 2009. Technical innovations drive the relationship between innovativeness and residual brain size in birds. Animal Behaviour **78**:1001-1010.

Padilla, D. K., and S. L. Williams. 2004. Beyond ballast water: aquarium and ornamental trades as sources of invasive species in aquatic ecosystems. Frontiers in Ecology and the Environment **2**:131-138.

Pagel, M. 1999. Inferring the historical patterns of biological evolution. Nature **401**:877-884.

Paradis, E. 2006. Analysis of Phylogenetics and Evolution with R. Springer, New york, NY, USA.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: Analyses of Phylogenetics and Evolution in R language. Bioinformatics **20**:289-290.

Perelman, S. B., E. J. Chaneton, W. B. Batista, S. E. Burkart, and R. J. C. Leon. 2007. Habitat stress, species pool size and biotic resistance influence exotic plant richness in the Flooding Pampa grasslands. Journal of Ecology **95**:662-673.

Perez-Tris, J., and J. L. Telleria. 2002a. Migratory and sedentary blackcaps in sympatric non-breeding grounds: implications for the evolution of avian migration. Journal of Animal Ecology **71**:211-224.

Perez-Tris, J., and J. L. Telleria. 2002b. Regional variation in seasonality affects migratory behaviour and life-history traits of two Mediterranean passerines. Acta Oecologica-International Journal of Ecology **23**:13-21.

Perrings, C., K. Dehnen-Schmutz, J. Touza, and M. Williamson. 2005. How to manage biological invasions under globalization. Trends in Ecology & Evolution **20**:212-215.

Pheloung, P. C., P. A. Williams, and S. R. Halloy. 1999. A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. Journal of Environmental Management **57**:239-251.

Pianka, E. R. 1970. R-Selection and K-Selection. American Naturalist **104**:592-&.

Pianka, E. R. 1974. Niche Overlap and Diffuse Competition. Proceedings of the National Academy of Sciences of the

United States of America **71**:2141-2145.

Pielou, E. C. 1969. An introduction to mathematical ecology. John Wiley & Sons, New York, NY, USA.

Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics **52**:273-288.

Pimm, S. L. 1989. Theories of predicting success and impact of introduced species. Pages 351-367 *in* J. M. Drake, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson, editors. Biological Invasions: a Global Perspective. John Wiley & Sons Ltd., Chichester, UK.

Pimm, S. L. 1991. The balance of nature? Ecological issues in the conservation of species and communities. University of Chicago Press, Chicago, IL, USA.

Pimm, S. L., H. L. Jones, and J. Diamond. 1988. On the Risk of Extinction. American Naturalist **132**:757-785.

Puigcerver, M., D. Vinyoles, and J. D. Rodriguez-Teijeiro. 2007. Does restocking with Japanese quail or hybrids affect native populations of common quail Coturnix coturnix? Biological Conservation **136**:628-635.

Pysek, P., M. Krivanek, and V. Jarosik. 2009. Planting intensity, residence time, and species traits determine invasion success of alien woody species. Ecology **90**:2734-2744.

R Development Core Team. 2010. R: A Language and Environment for Statistical Computing.

Reed, J. M. 1999. The role of behavior in recent avian extinctions and endangerments. Conservation Biology **13**:232-241.

Rejmanek, M., and D. M. Richardson. 1996. What attributes make some plant species more invasive? Ecology **77**:1655-1661.

Ricklefs, R. E., and M. Wikelski. 2002. The physiology/life-history nexus. Trends in Ecology & Evolution **17**:462-468.

Rodriguez, A., M. Hausberger, and P. Clergeau. 2010. Flexibility in European starlings' use of social information: experiments with decoys in different populations. Animal Behaviour **80**:965-973.

Rohlf, D. J. 1991. 6 Biological Reasons Why the Endangered Species Act Doesnt Work - and What to Do About It. Conservation Biology **5**:273-282.

Rosenzweig, M. L. 2001. The four questions: What does the introduction of exotic species do to diversity? Evolutionary Ecology Research **3**:361-367.

Ruesink, J. L., I. M. Parker, M. J. Groom, and P. M. Kareiva. 1995. Reducing the Risks of Nonindigenous Species Introductions - Guilty until Proven Innocent. Bioscience **45**:465-477.

Saether, B. E. 1988. Pattern of Covariation between Life-History Traits of European Birds. Nature **331**:616-617.

Saether, B. E., and O. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology **81**:642-653.

Saether, B. E., S. Engen, A. P. Moller, H. Weimerskirch, M. E. Visser, W. Fiedler, E. Matthysen, M. M. Lambrechts, A. Badyaev, P. H. Becker, J. E. Brommer, D. Bukacinski, M. Bukacinska, H. Christensen, J. Dickinson, C. du Feu, F. R. Gehlbach, D. Heg, H. Hotker, J. Merila, J. T. Nielsen, W. Rendell, R. J. Robertson, D. L. Thomson, J. Torok, and P. Van Hecke. 2004. Life-history variation predicts the effects of demographic stochasticity on avian population dynamics. American Naturalist **164**:793-802.

Saether, B. E., R. Lande, S. Engen, H. Weimerskirch, M. Lillegard, R. Altwegg, P. H. Becker, T. Bregnballe, J. E. Brommer, R. H. McCleery, J. Merila, E. Nyholm, W. Rendell, R. R. Robertson, P. Tryjanowski, and M. E. Visser. 2005. Generation time and temporal scaling of bird population dynamics. Nature **436**:99-102.

Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, N. C. Ellstrand, D. E. McCauley, P. O'Neil, I. M. Parker, J. N. Thompson, and S. G. Weller. 2001. The population biology of invasive species. Annual Review of Ecology and Systematics **32**:305-332.

Sato, S. 2006. Influence of the invasion of Leiothrix lutea on a native avifauna in a natural beech forest on Mt. Karimata, Kyushu. Bulletin of the Forestry and Forest Products Research Institute **5**:243-247.

Sax, D. F., and J. H. Brown. 2000. The paradox of invasion. Global Ecology and Biogeography **9**:363-371.

Schoener, T. W. 1983. Field Experiments on Interspecific Competition. American Naturalist **122**:240-285.

Schoener, T. W. 2009. Ecological Niche. *in* S. A. Levin, editor. The Princeton Guide to Ecology. Princeton University Press, New Jersey, USA.

Seabloom, E. W., W. S. Harpole, O. J. Reichman, and D. Tilman. 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. Proceedings of the National Academy of Sciences of the United States of America **100**:13384-13389.

Senar, J. C., and A. Borras. 2004. Surviving to winter: Strategies of wintering birds in the Iberian Peninsula. Ardeola **51**:133-168.

Sharov, A. A. 2004. Bioeconomics of managing the spread of exotic pest species with barrier zones. Risk Analysis **24**:879-892.

Shea, K., and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. Trends in Ecology & Evolution **17**:170-176.

Sher, A. A., and L. A. Hyatt. 1999. The Disturbed Resource-Flux Invasion Matrix: A New Framework for Patterns of Plant Invasion. Biological Invasions **1**:107-114.

Shochat, E., S. B. Lerman, M. Katti, and D. B. Lewis. 2004. Linking optimal foraging behavior to bird community structure in an urban-desert landscape: Field experiments with artificial food patches. American Naturalist **164**:232-243.

Sibley, C. G., and B. L. Monroe Jr. 1993. A World Checklist of Birds Yale University Press New Haven, CT, USA.

Simberloff, D. 1995. Why do introduced species appear to devastate islands more than mainland areas? Pacific Science **49**:87-97.

Simberloff, D. 2009. We can eliminate invasions or live with them. Successful management projects. Biological Invasions **11**:149-157.

Simpson, E. H. 1949. Measurement of Diversity. Nature **163**:688-688.

Smallwood, K. S. 1994. Site Invasibility by Exotic Birds and Mammals. Biological Conservation **69**:251-259.

Smith, C. S., W. M. Lonsdale, and J. Fortune. 1999. When to ignore advice: predictions and decisions theory. Biological Invasions **1**:89-96.

Smith, G. C., I. S. Henderson, and P. A. Robertson. 2005. A model of ruddy duck Oxyura jamaicensis eradication for the UK. Journal of Applied Ecology **42**:546-555.

Smith, K. F., M. D. Behrens, L. M. Max, and P. Daszak. 2008. US drowning in unidentified fishes: Scope, implications, and regulation of live fish import. Conservation Letters **1**:103-109.

Sol, D. 2000. Are islands more susceptible to be invaded than continents? Birds say no. Ecography **23**:687-692.

Sol, D. 2004. Colom roquer Columba livia. Pages 260-261 *in* J. Estrada, V. Pedrocchi, L. Brotons, and S. Herrando, editors. Atles dels ocells nidificants de Catalunya 1999-2002. Institut Català d'Ornitologia (ICO) / Lynx Edicions, Barcelona, Spain.

Sol, D. 2007. Do Successful Invaders Exist? Pre-Adaptations to Novel Environments in Terrestrial Vertebrates. Pages 127-141 *in* W. Nentwig, editor. Biological Invasions. Springer, Heidelberg, Germany.

Sol, D. 2009. The Cognitive-Buffer Hypothesis for the Evolution of Large Brains. Pages 111-134 *in* R. Dukas and R. R. M., editors. Cognitive Ecology II.

Sol, D., S. Bacher, S. M. Reader, and L. Lefebvre. 2008a. Brain size predicts the success of mammal species introduced into novel environments. American Naturalist **172**:S63-S71.

Sol, D., I. Bartomeus, and A. Griffin. 2011a. The paradox of invasion in birds: Competitive superiority or ecological opportunism? Oecologia **In press**.

Sol, D., R. P. Duncan, T. M. Blackburn, P. Cassey, and L. Lefebvre. 2005. Big brains, enhanced cognition, and response of birds to novel environments. Proceedings of the National Academy of Sciences of the United States of America **102**:5460-5465.

Sol, D., N. Garcia, A. Iwaniuk, K. Davis, A. Meade, W. A. Boyle, and T. Szekely. 2010a. Evolutionary Divergence in Brain Size between Migratory and Resident Birds. Plos One **5**.

Sol, D., N. Garcia, A. Iwaniuk, K. Davis, A. Meade, W. A. Boyle, and T. Szekely. 2010b. Evolutionary Divergence in Brain Size between Migratory and Resident Birds. Plos One **5**:e9617.

Sol, D., A. S. Griffin, I. Bartomeus, and H. Boyce. 2011b. Exploring or Avoiding Novel Food Resources? The Novelty Conflict in an Invasive Bird. Plos One **6**.

Sol, D., and L. Lefebvre. 2000. Behavioural flexibility predicts invasion success in birds introduced to New Zealand. Oikos **90**:599-605.

Sol, D., J. Maspons, M. Vall-llosera, I. Bartomeus, G. E. Garcia-Peña, J. Piñol, and R. P. Freckleton. in prep. Brood value, population growth and the life history of successful invaders.

Sol, D., S. Timmermans, and L. Lefebvre. 2002. Behavioural flexibility and invasion success in birds. Animal Behaviour **63**:495-502.

Sol, D., M. Vila, and I. Kuhn. 2008b. The comparative analysis of historical alien introductions. Biological Invasions **10**:1119-1129.

Sorci, G., A. P. Moller, and J. Clobert. 1998. Plumage dichromatism of birds predicts introduction success in New Zealand. Journal of Animal Ecology **67**:263-269.

Stahl, J. T., and M. K. Oli. 2006. Relative importance of avian life-history variables to population growth rate. Ecological Modelling **198**:23-39.

Starck, J. M., and R. E. Ricklefs. 1998. Patterns of Development: The Altricial-Precocial Spectrum. Pages 3-30 *in* J. M. Starck and R. E. Ricklefs, editors. Avian Growth and Development. Evolution within the altricial precocial spectrum. Oxford University Press, Oxford, UK.

Stearns, S. C. 1980. A New View of Life-History Evolution. Oikos **35**:266-281.

Stearns, S. C. 1992. The Evolution of Life Histories. Oxford University Press, Oxford, UK.

Stearns, S. C. 2000a. Daniel Bernoulli (1738): evolution and economics under risk. Journal of Biosciences **25**:221-228.

Stearns, S. C. 2000b. Life history evolution: successes, limitations, and prospects. Naturwissenschaften **87**:476-486.

Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. Ecological Monographs **69**:25-46.

Stokes, K. E., K. P. O'Neill, W. I. Montgomery, J. T. A. Dick, C. A. Maggs, and R. A. McDonald. 2006. The importance of stakeholder engagement in invasive species management: A cross-jurisdictional perspective in Ireland. Biodiversity and Conservation **15**:2829-2852.

Strauss, S. Y., C. O. Webb, and N. Salamin. 2006. Exotic taxa less related to native species are more invasive. Proceedings of the National Academy of Sciences of the United States of America **103**:5841-5845.

Strubbe, D., and E. Matthysen. 2009. Experimental evidence for nest-site competition between invasive ring-necked parakeets (Psittacula krameri) and native nuthatches (Sitta europaea). Biological Conservation **142**:1588-1594.

Sutter II, G. W. 1993. Ecological risk assesment. Lewis Publishers, Boca Raton, FL, USA.

Svensson, L. 1992. Identification Guide to European Passerines, Stockholm, Sweden.

Telleria, J. L., B. Asensio, and M. Díaz. 1999. Aves Ibéricas. II. Passeriformes. J. M. Reyero Editor, Madrid, Spain.

Tennant, L. E. 1994. The Ecology of Wasmannia-Auropunctata in Primary Tropical Rain-Forest in Costa-Rica and Panama. Pages 80-90 *in* D. F. Williams, editor. Exotic Ants: Biology, Impact, and Control of Introduced Species. Westview Press, Boulder, CO, USA.

Therneau, T. M., B. Atkinson, B. Ripley, J. Oksanen, and G. De'ath. 2007. mvpart: Multivariate Partitioning. R package version 1.2-6.

Thomas, G. H. 2008. Phylogenetic distributions of British birds of conservation concern. Proceedings of the Royal Society B-Biological Sciences **275**:2077-2083.

Thompson, G. M. 1922. The naturalization plants and animals in New Zealand. Cambridge University Press, Cambridge, UK.

Tilman, D. 1994. Competition and Biodiversity in Spatially Structured Habitats. Ecology **75**:2-16.

Tojo, H., and S. Nakamura. 2004. Breeding density of exotic Red-billed Leiothrix and native bird species on Mt. Tsukuba, central Japan Ornithological Science **3**:23-32.

Treplin, S. 2006. Inference of phylogenetic relationships in passerine birds (Aves: Passeriformes) using new molecular markers. University of Potsdam, Potsdam, Germany.

Usher, M. B., T. J. Crawford, and J. L. Banwell. 1992. An American Invasion of Great-Britain - the Case of the Native and Alien Squirrel (Sciurus) Species. Conservation Biology **6**:108-115.

Vall-llosera, M., and D. Sol. 2009. A global risk assessment for the success of bird introductions. Journal of Applied Ecology **46**:787-795.

Vall-llosera, M., D. Sol, F. Llimona, M. de Cáceres, and S. Sales. in prep. Biotic resistance, niche opportunities and the invasion of natural habitats.

Vazquez, D. P. 2005. Exploring the relationship between niche breadth and invasion success. Pages 317-332 *in* M. W. Cadotte, S. M. McMahon, and T. Fukami, editors. Conceptual ecology and invasion biology: reciprocal approaches to nature. Springer, The Netherlands.

Veltman, C. J., S. Nee, and M. J. Crawley. 1996. Correlates of introduction success in exotic New Zealand birds. American Naturalist **147**:542-557.

Vila, M., C. Basnou, P. Pysek, M. Josefsson, P. Genovesi, S. Gollasch, W. Nentwig, S. Olenin, A. Roques, D. Roy, P. E. Hulme, P. Andriopoulos, M. Arianoutsou, S. Augustin, S. Bacher, I. Bazos, F. Bretagnolle, F. Chiron, P. Clergeau, P. O. Cochard, C. Cocquempot, A. Coeur dAcier, M. David, P. Delipetrou, M. L. Desprez-Loustau, V. Didziulis, F. Dorkeld, F. Essl, B. S. Galil, J. Gasquez, K. Georghiou, M. Hejda, V. Jarosik, S. Kark, I. Kokkoris, I. Kuhn, P. W. Lambdon, C. Lopez-Vaamonde, A. Marcer, A. Migeon, M. McLoughlin, D. Minchin, M. Navajas, V. E. Panov, M. Pascal, J. Pergl, I. Perglova, J. Pino, K. Poboljsaj, W. Rabitsch, J. Y. Rasplus, D. Sauvard, R. Scalera, O. Sedlacek, S. Shirley, M. Winter, A. Yannitsaros, A. Yart, P. Zagatti, A. Zikos, and D. Partners. 2010. How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. Frontiers in Ecology and the Environment **8**:135-144.

Vitousek, P. M., C. M. DAntonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. American Scientist **84**:468-478.

Webb, C. O., D. D. Ackerly, M. A. McPeek, and M. J. Donoghue. 2002. Phylogenies and community ecology. Annual Review of Ecology and Systematics **33**:475-505.

Wilbur, H. M., and V. H. W. Rudolf. 2006. Life-history evolution in uncertain environments: Bet hedging in time. American Naturalist **168**:398-411.

Williams, D. G., and R. A. Black. 1994. Drought Response of a Native and Introduced Hawaiian Grass. Oecologia **97**:512-519.

Williams, G. C. 1966. Adaptation and natural selection. Oxford University Press, Oxford, UK.

Williams, G. C. 1992. Adaptation and natural selection. Oxford University Press, Oxford, UK.

Williamson, M. 1996. Biological Invasions. Chapman & Hal, London, UK.

Williamson, M. H., and A. Fitter. 1996. The characters of successful invaders. Biological Conservation **78**:163-170.

Wood, S. N. 2004. Stable and efficient multiple smoothing parameter estimation for generalized additive models. Journal of the American Statistical Association **99**:673-686.

World Trade Organization. 2005. Sanitary and Phytosanitary Agreement. World Trade Organization, Geneva, Switzerland.

Wunderle, J. M. 1991. Age-Specific Foraging Proficiency in Birds. Current Ornithology, Vol 8 **8**:273-324.

Yeh, P. J., and T. D. Price. 2004. Adaptive phenotypic plasticity and the successful colonization of a novel environment. American Naturalist **164**:531-542.

Zuur, A. F., C. Barbraud, E. N. Leno, G. M. Weimerskirsch, G. M. Smith, and N. J. Walker. 2009a. Estimating Trends for Antarctic Birds in Relation to Climate Change. Pages 343-361 *in* A. F. Zuur, E. N. Leno, N. J. Walker, A. A. Saveliev, and G. M. Smith, editors. Mixed Effects Models and Extensions in Ecology with R. Springer, New York, USA.

Zuur, A. F., E. N. Leno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009b. Mixed Effects Models and Extensions in Ecology with R. Springer, New york, NY, USA.

Appendices

Appendix A

Chapter 2. Brood value, population growth and the life history of successful invaders

Table 1. Effects of deterministic growth rate (lambda) on establishment success*.

Univariate fixed effects	Estimate	SE	Z	P	N
Lambda	0.471	0.578	0.82	0.415	818
Lambda + propagule size	1.243	0.830	1.49	0.134	327
Lambda + propagule + brain residual	1.229	0.775	1.59	0.113	327

*In all models the response variable is success or failure of the introduction. For models with covariates (propagule size and relative brain size), these have been modelled as fixed effects. Propagule size is the number of individuals released, log-transformed. Although not presented, all models include species and country as random effects (see Materials and Methods for justification).

Table 2. Comparison of candidate models of establishment success levels based on ΔAIC_c and relative Akaike weights (ω). Only the best models ($\Delta AIC_c < 2$) and the variables (fixed effects) appearing in at least one of these models are presented. Akaike weights estimate the probability that a given model is actually the best model in the model set. Variables included in the model selection process were all those described in the Methods. The structure of random factors is shown in Table 2.2. The models are based on 465 introduction events.

Climate matching	Island/ continent	Residual brain	Brood value	Body mass	Habitat generalism	Migratory behaviour	Propagule pressure	df	AICc	ΔAICc	weight
	+	+	+		+		+	9.00	492.43	0.00	0.05
	+	+	+		+	+	+	10.00	492.54	0.11	0.05
	+		+		+		+	8.00	492.55	0.11	0.05
			+		+		+	6.00	492.83	0.40	0.04
	+	+	+	+	+		+	10.00	493.09	0.66	0.04
		+	+		+		+	7.00	493.37	0.94	0.03
	+		+		+	+	+	9.00	493.49	1.05	0.03
		+	+	+	+		+	8.00	493.63	1.20	0.03
	+	+	+	+	+	+	+	11.00	493.72	1.29	0.03
+			+		+		+	7.00	493.72	1.29	0.03
+	+		+		+		+	9.00	494.24	1.80	0.02
+	+	+	+		+	+	+	11.00	494.29	1.86	0.02
			+		+	+	+	7.00	494.33	1.90	0.02
+	+	+	+		+		+	10.00	494.34	1.91	0.02
		+	+		+	+	+	8.00	494.34	1.91	0.02

Table 3. Effects of life history traits on establishment success when accommodated in the best model including brood value, propagule size, relative brain size and habitat generalism (see Table 2.2)*.

Predictor	Estimate	SE	Z	P	N
Clutch size	0.088	0.089	0.991	0.321	635
Fecundity	-0.011	0.063	-0.188	0.851	635
Incubation period	0.561	0.566	0.99	0.321	629
Fledgling period	0.466	0.393	1.18	0.235	402
Age of first breeding	0.817	0.454	1.79	0.072	568
Reproductive lifespan	0.035	0.032	1.09	0.275	635
Developmental mode	0.164	0.222	0.73	0.459	621
Adult survival	2.256	1.935	1.16	0.243	327
Rmax	-0.193	0.261	-0.73	0.460	568
Fast-Slow	-0.217	0.392	-0.55	0.579	567
Generation time	0.533	0.476	1.12	0.262	327

*In all models the response variable is success or failure of the introduction. Each predictor has been tested as fixed effect separately from the others. Although not presented, all models include species and country as random effects (see Table 2.2 in the main text).

Table 4. Establishment success as a function of brood value (decomposed in its different components), while accounting for the confounding factors and random-effect parameters from the best model*.

Fixed effects	Estimate	Std. Error	z value	P	P‡
Propagule size	0.461	0.062	7.36	< 0.0001	-
Brood value strategy					
S1	0.000	-			
S2	0.961	0.813	1.18	0.2371	0.3677
S3	2.323	0.978	2.37	0.0175	0.0170
S4	0.808	0.885	0.91	0.3612	0.0871
S5	0.677	1.240	0.54	0.5846	0.0431
S6	0.531	0.959	0.55	0.5795	0.0714
S7	0.807	0.833	0.96	0.3327	0.0071
S8	2.303	0.767	3.00	0.0027	0.0423
S9	3.776	1.896	1.99	0.0464	< 0.0001
S10	1.263	0.856	1.47	0.1401	0.0093
S11	2.200	0.865	2.54	0.0110	< 0.0001
Brain residual	0.432	0.210	2.04	0.0405	-
Habitat generalism	0.822	0.200	4.09	< 0.0001	-

Random effects	Variance	Std. Dev.	Likelihood ratio test	P	
Species	1.306	1.142	24.50	< 0.0001	< 0.0001
Country	2.960	1.720	34.02	< 0.0001	< 0.0001

*The response variable of the model is success or failure of the introduction. Each predictor has been tested as fixed effect in the model (see Table 2.2) separately from the others. Although not presented, all models include species and country as random effects. For categorical variables, one level is set to zero and used as reference for comparison with the others (Crawley 2002). The model is based on 635 introductions. ‡Probability of the model with no confounding fixed effects, based on 1,935 introductions.

Figure 1. Relationship between the fast-slow variable estimated with a factor analysis using all the life history traits and that estimated using only the four most relevant traits.

Figure 2. Validation of the Rmax and the fast-slow continuum with estimates of lambda and the fecundity/age of first reproduction ratio (Oli 2004).

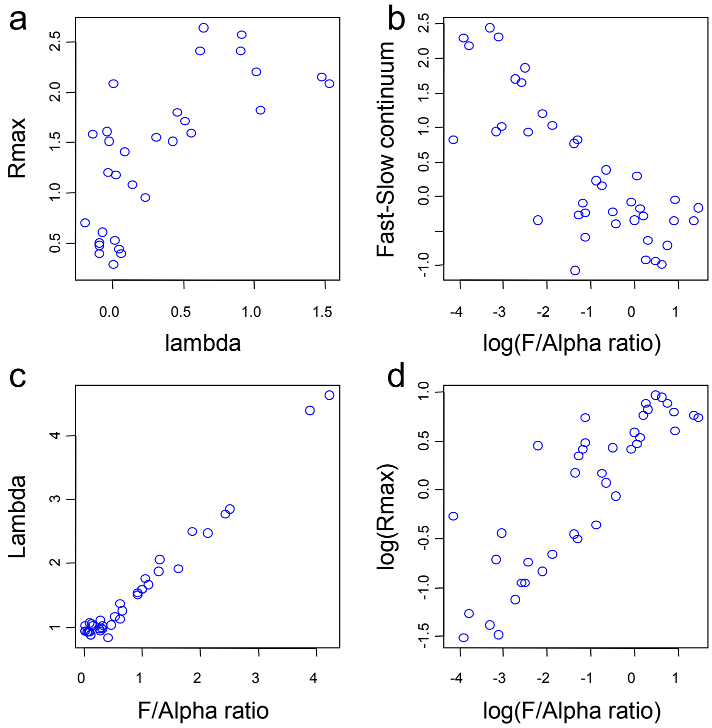


Figure 3. Phylogenetic hypothesis used for interspecific comparisons.

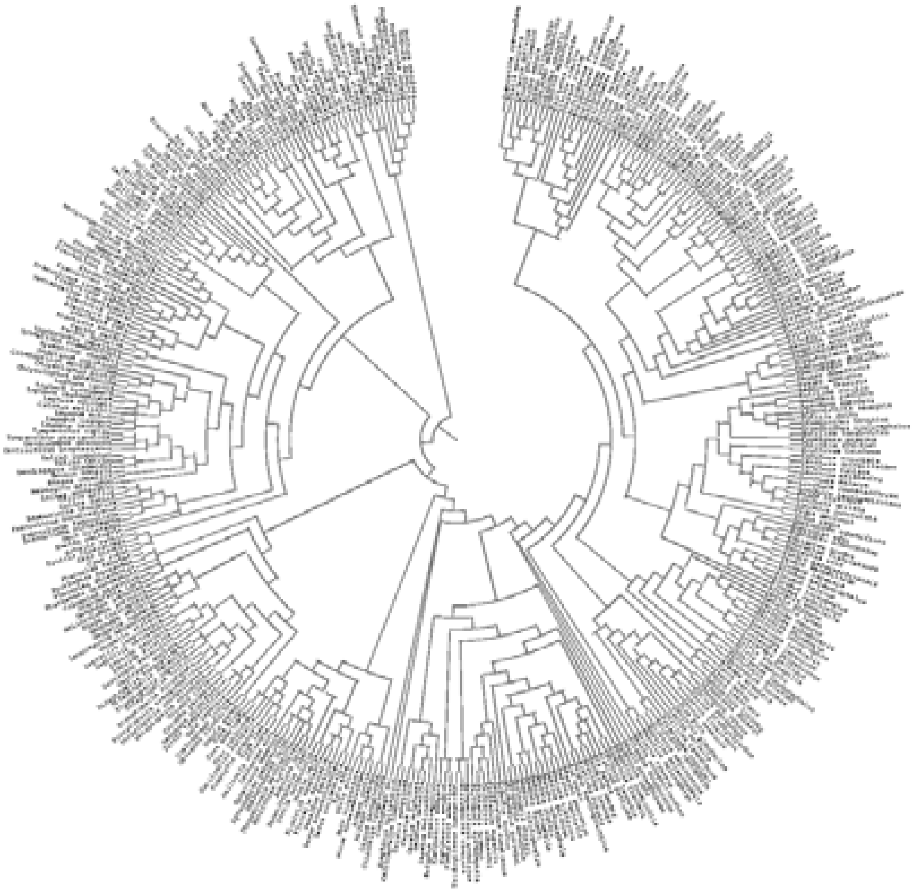


Figure 4. Main life history descriptors of the fast-slow continuum and brood value.

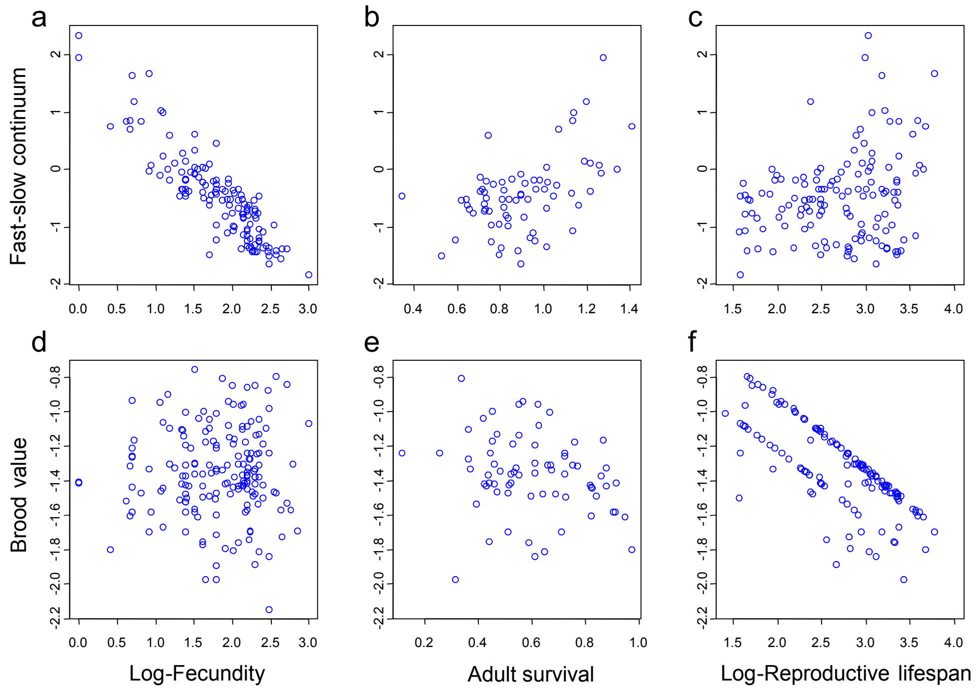


Figure 5. Relationships between Rmax, clutch size, the fast-slow continuum and brood value.

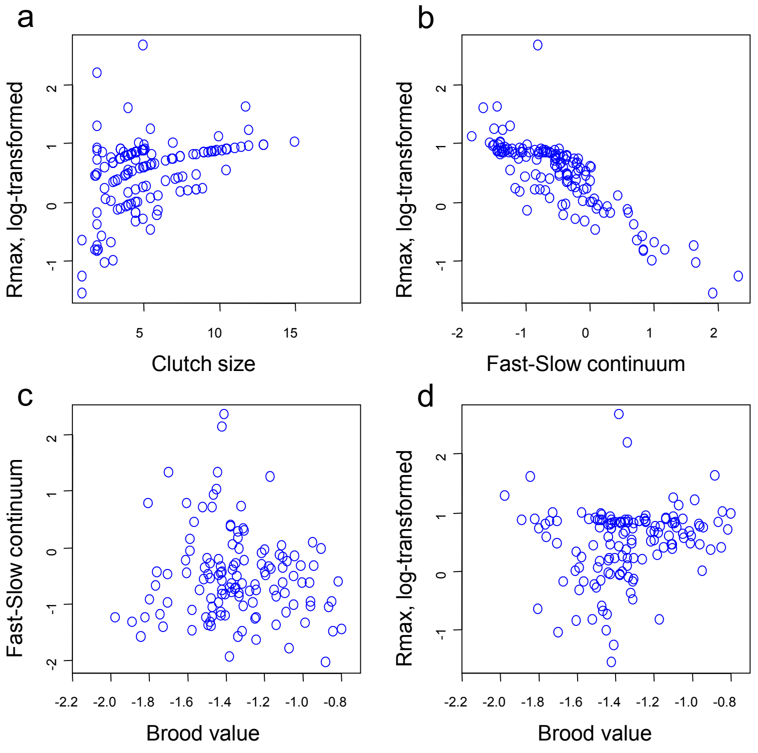


Figure 6. Relationship of the relative size of the brain with the fast-slow continuum (a) and the brood value (b).

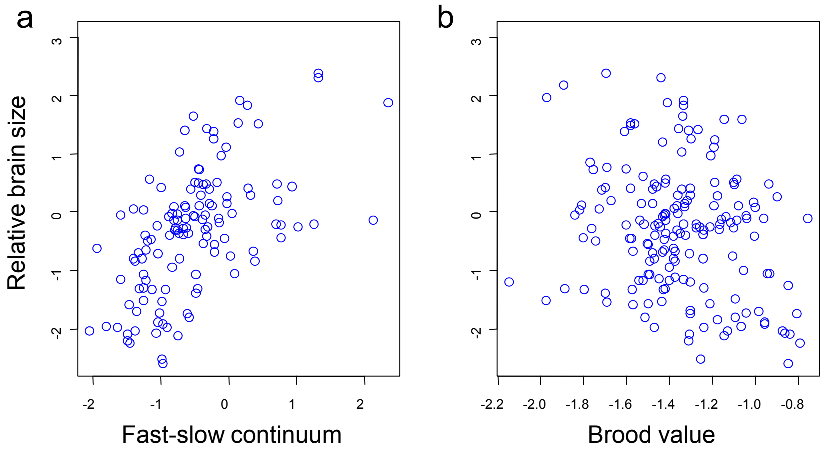


Figure 7. Differences (median and percentiles) among avian families in (a) brood value and (b) the fast-slow continuum.

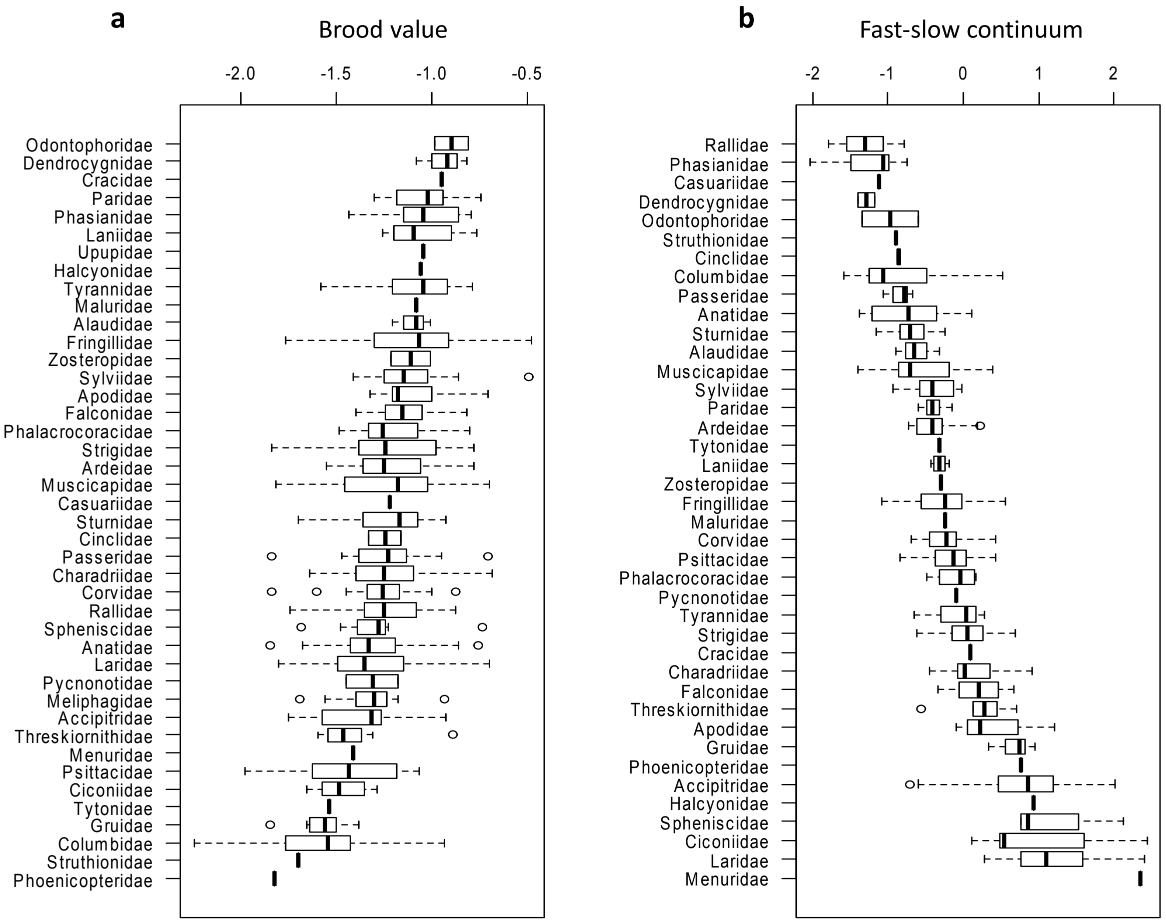


Figure 8. Likelihoods for different values of Pagel's λ (Freckleton 2000b) for clutch size, fast-slow continuum, brood value and invasion potential (n = 95 species).

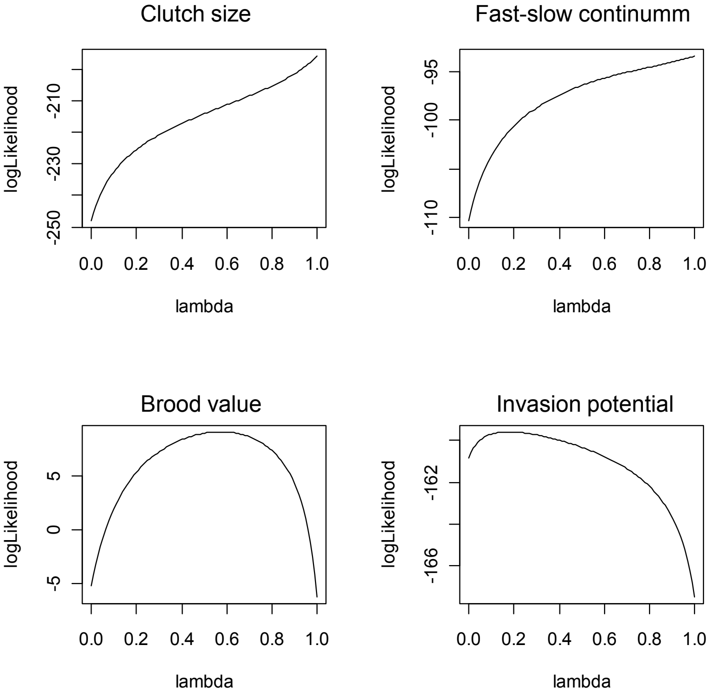
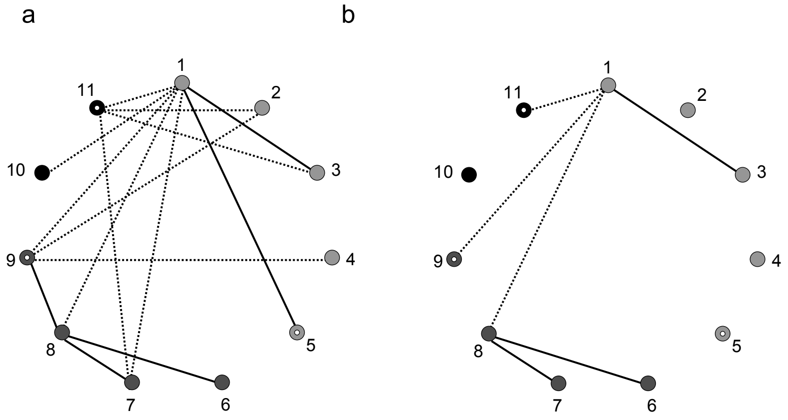


Figure 9. Differences in establishment success between life history strategies (see Fig. 5). Solid lines define significant differences at P < 0.05 between strategies from a same general cluster (as defined by the tree regression) and dashed lines differences between strategies from different clusters. In all cases, the likelihood of success is higher for the species with the lower brood value. The three strategies with the lowest brood values are identified with a white dot. The significance has been estimated with a binomial GLMM with the life history strategy (from S1 to S11) as fixed effect and species and country of introduction as random factors (a). The significance has also been assessed when including propagule size, habitat generalism and relative brain size in the model (b). The fact that some significant paths turn out non-significant in the second model primarily reflects reductions in sample size.



Appendix B

Chapter 3. Biotic resistance, niche opportunities and the invasion of natural habitats

Table 1. List of the 81 bird species censed in the Collserola Park in the period 1987-2010. English and latin names from Clements et al. (2011).

Latin name	English name	Abbreviation
Anas platyrhynchos L.	Mallard	MAL
Circus aeruginosus L.	Marsh Harrier	MHR
Accipiter nisus L.	Eurasian Sparrowhawk	SPA
Accipiter gentilis L.	Northern Goshawk	GSH
Buteo buteo L.	Common Buzzard	BUZ
Falco tinnunculus L.	Common Kestrel	KES
Falco peregrinus Tunstall	Peregrine Falcon	PER
Alectoris rufa L.	Red-legged Partridge	RLP
Phasianus colchicus L.	Common Pheasant	PHE
Larus michahellis Naumann	Yellow-legged Gull	YLG
Columba palumbus L.	Common Wood Pigeon	WPG
Columba livia Gmelin	Rock Pigeon	RPG
Streptopelia turtur L.	European Turtle Dove	TTD
Streptopelia decaocto Frivaldszky	Eurasian Collared Dove	COD
Psittacula krameri Scopoli	Rose-ringed Parakeet	RRP
Myiopsitta monachus Boddaert	Monk Parakeet	MPK
Cuculus canorus L.	Common Cuckoo	CUC
Clamator glandarius L.	Great Spotted Cuckoo	GSC
Athene noctua Scopoli	Little Owl	LOW
Caprimulgus ruficollis Temminck	Red-necked Nightjar	RNN
Merops apiaster L.	European Bee-eater	BEE
Coracias garrulus L.	European Roller	ROL
Upupa epops L.	Eurasian Hoopoe	HOP
Jynx torquilla L.	Eurasian Wryneck	WRY
Picus viridis L.	Green Woodpecker	GWP
Dendrocopos major L.	Great Spotted Woodpecker	GSW
Lullula arborea L.	Woodlark	WOL
Anthus trivialis L.	Tree Pipit	TRP
Anthus pratensis L.	Meadow Pipit	MEP
Motacilla alba L.	White Wagtail	WWG
Motacilla cinerea Tunstall	Grey Wagtail	GWG
Troglodytes troglodytes L.	Eurasian Wren	WRE
Prunella modularis L.	Dunnock	DUN
Prunella collaris Scopoli	Alpine Accentor	AAC
Erithacus rubecula L.	European Robin	ROB

Luscinia megarhynchos Brehm	Common Nightingale	NIG
Phoenicurus phoenicurus L.	Common Redstart	CRD
Phoenicurus ochruros Gmelin	Black Redstart	BRD
Saxicola rubetra L.	Winchat	WIN
Saxicola rubicola L.	European Stonechat	STO
Oenanthe oenanthe L.	Northern Wheather	NOW
Oenanthe hispanica L.	Black-eared Wheather	BEW
Monticola saxatilis L.	Common Rock Trush	RTR
Monticola solitarius L.	Blue Rock Trush	BRT
Turdus merula L.	Common Blackbird	BLB
Turdus philomelos Brehm	Song Trush	STR
Turdus iliacus L.	Redwing	RDW
Turdus viscivorus L.	Mistle Trush	MTR
Cisticola juncidis Rafinesque	Zitting Cisticola	ZCIS
Cettia cetti Temminck	Cetti's Warbler	CET
Hippolais polyglotta Vieillot	Melodious Warbler	MWR
Sylvia undata Boddaert	Dartford Warbler	DWR
Sylvia cantillans Pallas	Subalpine Warbler	SWR
Sylvia melanocephala Gmelin	Sardinian Warbler	SAW
Sylvia borin Boddaert	Garden Warbler	GWR
Sylvia atricapilla L.	Eurasian Blackcap	BLK
Sylvia hortensis Gmelin	Western Orphean Warbler	OWR
Phylloscopus bonelli Vieillot	Western Bonelli’s Warbler	BWR
Phylloscopus trochilus L.	Willow Warbler	WWR
Phylloscopus collybita Vieillot	Common Chiffchaff	CHI
Regulus regulus L.	Goldcrest	GOL
Regulus ignicapilla Temminck	Common Firecrest	FIR
Ficedula hypoleuca Pallas	Pied Flycatcher	PFL
Muscicapa striata Pallas	Spotted Flycatcher	SFL
Leiothrix lutea Scopoli	Red-billed Leiothrix	RBL
Aegithalos caudatus L.	Long-tailed Tit	LTT
Lophophanes cristatus L.	Crested Tit	CRT
Periparus ater L.	Coal Tit	COT
Cyanistes caeruleus L.	Blue Tit	BLT
Parus major L.	Great Tit	GRT
Certhia brachydactyla Brehm	Short-toed Treecreeper	TRE
Lanius meridionalis Temminck	Southern Grey Shrike	SGS
Lanius senator L.	Woodchat Shrike	WSH
Sturnus unicolor Temminck	Spottless Starling	SST
Sturnus vulgaris L.	European Starling	EST
Oriolus oriolus L.	Eurasian Golden Oriole	ORI
Garrulus glandarius L.	Eurasian Jay	JAY
Pica pica L.	Eurasian Magpie	MAG
Corvus corax L.	Northern Raven	RAV
Passer montanus L.	Eurasian Tree Sparrow	TRS
Passer domesticus L.	House Sparrow	HSP

Fringilla coelebs L.	Common Chaffinch	CHA
Coccothraustes coccothraustes L.	Hawfinch	HAW
Serinus serinus L.	European Serin	SER
Carduelis spinus L.	Eurasian Siskin	SIS
Carduelis chloris L.	European Greenfinch	GRE
Carduelis carduelis L.	European Goldfinch	GLD
Pyrrhula pyrrhula L.	Eurasian Bullfinch	BUL
Carduelis cannabina L.	Common Linnet	LIN
Loxia curvirostra L.	Red Crossbill	CRO
Emberiza cirlus L.	Cirl Bunting	CBU
Emberiza citrinella L.	Yellowhammer	YLH

Table 2. Body condition measures for the species in Collserola Park in winter and spring *.

Winter

Fat

Variables		Estimate	MCMCmean	HPD95lower	HPD95upper	pMCMC	n
Species	Long-tailed Tit	0.168	0.180	-1.690	2.001	0.842	6
	Short-toed Treecreeper	-1.861	-1.849	-3.612	-0.155	0.043	12
	Cettia's Warbler	-0.097	-0.091	-1.491	1.393	0.911	8
	European Robin	0.035	0.055	-1.723	1.627	0.946	175
	Common Chaffinch	-0.751	-0.717	-2.715	1.264	0.457	10
	Eurasian Jay	-3.373	-3.335	-6.947	0.174	0.067	5
	Blue Tit	-0.279	-0.263	-1.905	1.404	0.728	45
	Crested Tit	-0.681	-0.664	-2.367	1.143	0.416	11
	Great Tit	-1.404	-1.387	-3.127	0.329	0.105	34
	Common Chiffchaff	0.132	0.148	-1.162	1.537	0.834	11
	Dunnock	0.214	0.220	-1.622	1.926	0.785	14
	Common Firecrest	-0.611	-0.602	-2.353	1.122	0.465	26
	Sardinian Warbler	0.253	0.267	-1.016	1.618	0.680	15
	Eurasian Blackcap	-0.612	-0.595	-1.839	0.656	0.349	60
	Eurasian Wren	0.325	0.338	-1.748	2.346	0.737	6
	Common Blackbird	-2.260	-2.228	-4.797	0.382	0.096	56
	Song Trush	-0.848	-0.827	-3.251	1.782	0.521	10
Third primary feather		1.697	1.675	-1.210	4.810	0.277	
Age		0.049	0.049	-0.114	0.211	0.558	

Random effects		Std. Dev.	MCMCmedian	MCMCmean	HPD95lower	HPD95upper
Family		0.264	0.255	0.303	0.000	0.788
Season		0.000	0.028	0.053	0.000	0.189

Muscle

Variables		Estimate	MCMCmean	HPD95lower	HPD95upper	pMCMC	n
Species	Long-tailed Tit	-0.180	-0.182	-0.621	0.295	0.412	6
	Short-toed Treecreeper	0.015	0.012	-0.413	0.451	0.945	12
	Cettia's Warbler	-0.215	-0.214	-0.562	0.158	0.241	8
	European Robin	-0.377	-0.379	-0.809	0.028	0.065	175
	Common Chaffinch	-0.636	-0.636	-1.124	-0.118	0.018	10
	Eurasian Jay	-0.431	-0.434	-1.319	0.430	0.329	5
	Blue Tit	-0.205	-0.207	-0.637	0.208	0.289	45
	Crested Tit	-0.222	-0.223	-0.660	0.220	0.281	11
	Great Tit	-0.250	-0.252	-0.678	0.196	0.219	34
	Common Chiffchaff	-0.305	-0.307	-0.636	0.040	0.078	11
	Dunnock	-0.126	-0.127	-0.560	0.320	0.535	14
	Common Firecrest	-0.277	-0.280	-0.719	0.164	0.190	26
	Sardinian Warbler	-0.248	-0.250	-0.583	0.071	0.129	15
	Eurasian Blackcap	-0.478	-0.479	-0.791	-0.170	0.002	60
	Eurasian Wren	0.122	0.119	-0.381	0.634	0.641	6
	Common Blackbird	-0.776	-0.778	-1.418	-0.105	0.022	56
	Song Trush	-0.733	-0.735	-1.394	-0.129	0.026	10
Third primary		0.407	0.407	-0.378	1.119	0.289	

feather						
Age	-0.003	-0.003	-0.044	0.040	0.891	

Random effects	Std. Dev.	MCMCmedian	MCMCmean	HPD95lower	HPD95upper
Family	0.065	0.062	0.076	0.000	0.203
Season	0.107	0.110	0.121	0.049	0.218

Spring

Fat

Variables		Estimate	MCMCmean	HPD95lower	HPD95upper	pMCMC	n
Species	Long-tailed Tit	0.072	0.076	-0.935	1.201	0.861	7
	Short-toed Treecreeper	-0.747	-0.741	-1.715	0.239	0.105	13
	Cettia's Warbler	-0.128	-0.131	-0.883	0.555	0.716	7
	European Robin	0.172	0.170	-0.857	1.128	0.590	64
	Common Chaffinch	-0.097	-0.100	-1.417	1.189	0.876	6
	Eurasian Jay	1.722	1.709	-0.747	4.145	0.171	7
	Melodious Warbler	0.027	0.030	-0.416	0.475	0.899	16
	Common Nightingale	0.194	0.187	-1.055	1.255	0.702	11
	Blue Tit	-0.164	-0.171	-1.139	0.840	0.618	22
	Crested Tit	-1.062	-1.067	-2.147	0.067	0.061	4
	Great Tit	0.176	0.171	-0.831	1.220	0.657	18
	Common Firecrest	-1.005	-1.001	-2.164	0.089	0.072	11
	European Serin	0.148	0.150	-0.910	1.175	0.709	12
	Sardinian Warbler	-0.348	-0.354	-1.272	0.515	0.447	4
	Eurasian Blackcap	0.054	0.053	-0.373	0.465	0.789	41
	Eurasian Wren	-0.848	-0.843	-2.319	0.568	0.231	4
	Common Blackbird	1.029	1.021	-0.772	2.723	0.247	60
	Song Trush	1.305	1.304	-0.577	3.041	0.148	4
Third primary feather		-2.434	-2.426	-4.641	0.107	0.048	
Age		0.030	0.030	-0.141	0.203	0.728	

Random effects	Std. Dev.	MCMCmedian	MCMCmean	HPD95lower	HPD95upper
Family	0.197	0.173	0.217	0.000	0.596
Season	0.185	0.212	0.241	0.056	0.505

Muscle

Variables		Estimate	MCMCmean	HPD95lower	HPD95upper	pMCMC	n
Species	Long-tailed Tit	-0.097	-0.098	-0.389	0.196	0.433	7
	Short-toed Treecreeper	-0.005	-0.006	-0.274	0.269	0.953	13
	Cettia's Warbler	-0.016	-0.015	-0.227	0.173	0.877	7
	European Robin	-0.213	-0.214	-0.476	0.062	0.089	64
	Common Chaffinch	-0.146	-0.147	-0.498	0.215	0.389	6
	Eurasian Jay	0.427	0.422	-0.232	1.124	0.219	7
	Melodious Warbler	-0.232	-0.232	-0.356	-0.111	0.000	16
	Common Nightingale	-0.181	-0.182	-0.518	0.123	0.214	11
	Blue Tit	-0.276	-0.276	-0.556	-0.006	0.052	22
	Crested Tit	-0.420	-0.424	-0.738	-0.091	0.018	4
	Great Tit	-0.131	-0.131	-0.402	0.162	0.250	18

Common Firecrest	-0.275	-0.272	-0.569	0.033	0.070	11
European Serin	-0.267	-0.268	-0.550	0.026	0.063	12
Sardinian Warbler	-0.288	-0.288	-0.527	-0.024	0.025	4
Eurasian Blackcap	-0.344	-0.344	-0.460	-0.225	0.000	41
Eurasian Wren	-0.194	-0.192	-0.598	0.197	0.323	4
Common Blackbird	-0.105	-0.108	-0.576	0.380	0.657	60
Song Trush	-0.003	-0.005	-0.511	0.483	0.991	4
Third primary feather	-0.649	-0.644	-1.305	0.020	0.058	
Age	0.002	0.002	-0.049	0.050	0.948	

Random effects	Std. Dev.	MCMCmedian	MCMCmean	HPD95lower	HPD95upper
Family	0.055	0.049	0.061	0.000	0.165
Season	0.066	0.072	0.080	0.024	0.156

*Fat and muscle index of Leiothrix relative to resident native species, taking into the account age and body size. Taxonomic family and banding season are included in the model as random factors. Body size (third primary feather length, in mm.) is log-transformed. Only adults are used in the analyses. All species are included for comparison purposes. The estimate for Leiothrix has been set to zero, and all the other species are compared to it (Leiothrix winter n=4, spring n=81).

Table 3. Phylogenetic mean pairwise distance among Collserola habitats*.

Spring

Habitat	nº of taxa	observed MPD	random MPD	SD	rank	SES	quantile	runs
Dry grasslands	32	13.679	10.237	1.119	1001	3.076	1.000	1000
Orchards	34	11.770	10.943	0.855	837	0.967	0.836	1000
Abandoned arable land	28	12.753	10.962	0.872	982	2.053	0.981	1000
Maquis shrubland	27	11.564	11.004	0.843	741	0.665	0.740	1000
Conifer woodland	24	9.731	11.018	0.847	69	-1.520	0.069	1000
Holm oak forest	23	9.089	10.747	0.995	48	-1.666	0.048	1000
Riparian forest	29	9.876	10.920	0.897	122	-1.164	0.122	1000

Winter

Habitat	nº of taxa	observed MPD	random MPD	SD	rank	SES	quantile	runs
Dry grasslands	28	12.698	10.114	1.012	999	2.553	0.998	1000
Orchards	35	9.568	9.334	1.234	605	0.189	0.604	1000
Abandoned arable land	31	10.834	9.910	1.079	803	0.857	0.802	1000
Maquis shrubland	25	11.796	10.195	0.999	947	1.603	0.946	1000
Conifer woodland	20	9.274	10.245	1.013	176	-0.959	0.176	1000
Holm oak forest	22	9.246	10.157	1.066	216	-0.855	0.216	1000
Riparian forest	27	8.932	10.373	0.938	59	-1.537	0.059	1000

*Abbreviations are: MPD, mean pairwise distance; observed MPD, observed MPD in each habitat; random MPD, mean MPD in null habitats; SD, standard deviation of MPD in null habitats; rank, rank of observed MPD vs. null habitats; SES, standardized effect size of MPD vs. null habitats; quantile, p-value of observed MPD vs. null habitats. Positive SES values (> 0) and high quantiles (> 0.95) indicate phylogenetic evenness, while negative SES values and low quantiles (< 0.05) indicate phylogenetic clustering.

Table 4. Comparison of specialization index between Leiothrix and native forest species of similar size*.

Variables		Estimate	MCMCmean	HPD95lower	HPD95upper	pMCMC
Species	Long-tailed Tit	-0,551	-0,550	-0,941	-0,151	0,014
	European Robin	-0,297	-0,296	-0,681	0,104	0,112
	Blue Tit	-0,557	-0,557	-0,943	-0,166	0,012
	Crested Tit	-0,374	-0,373	-0,750	0,033	0,058
	Great Tit	-0,696	-0,697	-1,077	-0,298	0,004
	Common Firecrest	-0,607	-0,606	-1,010	-0,209	0,011
	Eurasian Blackcap	-0,572	-0,571	-0,865	-0,275	0,001
	Common Blackbird	-0,905	-0,905	-1,289	-0,518	0,001

Random effects	Std.Dev.	MCMCmedian	MCMCmean	HPD95lower	HPD95upper
Family	0,120	0,045	0,063	0,000	0,196

*The estimate for Leiothrix has been set to zero, and all the other species are compared to it. All models taxonomic family as random factor.

Table 5. Differences in the foraging niche components of Leiothrix respect to that of native species*.

Breeding season

Foraging height

		Estimate	MCMCmean	HPD95lower	HPD95upper	pMCMC	n
Species	Long-tailed Tit	0.638	0.636	-0.814	2.031	0.216	26
	European Robin	-1.828	-1.838	-3.155	-0.380	0.025	24
	Blue Tit	0.683	0.682	-0.663	2.020	0.181	93
	Crested Tit	0.925	0.913	-0.469	2.279	0.119	20
	Great Tit	-0.282	-0.288	-1.721	1.003	0.463	29
	Common Firecrest	0.697	0.702	-0.713	2.016	0.178	35
	Eurasian Blackcap	0.373	0.385	0.055	0.707	0.021	37
	Common Blackbird	-1.559	-1.563	-2.935	-0.171	0.037	19

Tree height

		Estimate	MCMCmean	HPD95lower	HPD95upper	pMCMC	n
Species	Long-tailed Tit	0.732	0.726	-0.819	2.193	0.183	26
	European Robin	-2.314	-2.337	-3.879	-0.913	0.013	24
	Blue Tit	0.594	0.585	-0.885	2.069	0.248	93
	Crested Tit	0.786	0.769	-0.724	2.259	0.184	20
	Great Tit	-0.247	-0.261	-1.682	1.277	0.529	29
	Common Firecrest	0.702	0.699	-0.839	2.132	0.208	35
	Eurasian Blackcap	0.392	0.400	0.066	0.744	0.020	37
	Common Blackbird	-1.944	-1.960	-3.430	-0.495	0.023	19

Group size

		Estimate	MCMCmean	HPD95lower	HPD95upper	pMCMC	n
Species	Long-tailed Tit	0.464	0.465	-0.216	1.188	0.130	16
	European Robin	-0.371	-0.371	-1.055	0.359	0.178	21
	Blue Tit	-0.097	-0.102	-0.767	0.600	0.563	73
	Crested Tit	-0.132	-0.141	-0.805	0.591	0.527	13
	Great Tit	-0.230	-0.232	-0.949	0.443	0.311	24
	Common Firecrest	-0.398	-0.393	-1.078	0.311	0.159	28
	Eurasian Blackcap	-0.258	-0.253	-0.419	-0.091	0.002	35
	Common Blackbird	-0.275	-0.280	-0.963	0.444	0.260	18

Foraging location

		Estimate	Std.Error	z value	Pr(>|z|)	n
Species	Long-tailed Tit	-0.916	0.232	-3.949	0.000	26
	European Robin	-0.996	0.239	-4.171	0.000	24
	Blue Tit	0.358	0.162	2.216	0.027	93
	Crested Tit	-1.179	0.256	-4.609	0.000	20
	Great Tit	-0.807	0.223	-3.614	0.000	29
	Common Firecrest	-0.619	0.210	-2.953	0.003	35
	Eurasian Blackcap	-0.564	0.206	-2.736	0.006	37
	Common Blackbird	-1.230	0.261	-4.716	0.000	19

Foraging substrate

		Estimate	Std.Error	z value	Pr(>|z|)	n
Species	Long-tailed Tit	-0.916	0.232	-3.949	0.000	26
	European Robin	-0.996	0.239	-4.171	0.000	24
	Blue Tit	0.358	0.162	2.216	0.027	93
	Crested Tit	-1.179	0.256	-4.609	0.000	20
	Great Tit	-0.807	0.223	-3.614	0.000	29
	Common Firecrest	-0.619	0.210	-2.953	0.003	35
	Eurasian Blackcap	-0.564	0.206	-2.736	0.006	37
	Common Blackbird	-1.230	0.261	-4.716	0.000	19

Foraging technnique

		Estimate	Std.Error	z value	Pr(>|z|)	n
Species	Long-tailed Tit	-0.634	0.243	-2.612	0.009	26
	European Robin	-0.714	0.249	-2.865	0.004	24
	Blue Tit	0.630	0.177	3.562	0.000	92
	Crested Tit	-1.059	0.282	-3.761	0.000	17
	Great Tit	-0.560	0.237	-2.362	0.018	28
	Common Firecrest	-0.491	0.232	-2.116	0.034	30
	Eurasian Blackcap	-0.308	0.220	-1.404	0.160	36
	Common Blackbird	-0.947	0.270	-3.505	0.000	19

Non-breeding season

Foraging height

		Estimate	MCMCmean	HPD95lower	HPD95upper	pMCMC	n
Species	Long-tailed Tit	0.382	0.392	-0.679	1.568	0.317	17
	European Robin	-1.745	-1.738	-2.814	-0.609	0.012	23
	Blue Tit	0.888	0.892	-0.188	1.968	0.082	97
	Crested Tit	0.643	0.655	-0.445	1.815	0.165	16
	Great Tit	-0.825	-0.818	-1.881	0.278	0.098	21
	Common Firecrest	0.527	0.522	-0.669	1.534	0.210	30
	Eurasian Blackcap	0.327	0.334	-0.042	0.690	0.075	23
	Common Blackbird	-0.510	-0.510	-1.604	0.601	0.219	24

Tree height

		Estimate	MCMCmean	HPD95lower	HPD95upper	pMCMC	n
Species	Long-tailed Tit	0.549	0.553	-0.810	1.820	0.249	17
	European Robin	-2.200	-2.201	-3.492	-0.884	0.009	23
	Blue Tit	0.745	0.738	-0.502	2.057	0.148	97
	Crested Tit	0.678	0.680	-0.619	2.043	0.187	16
	Great Tit	-0.926	-0.927	-2.309	0.281	0.104	21
	Common Firecrest	0.613	0.615	-0.757	1.834	0.209	30
	Eurasian Blackcap	0.364	0.368	-0.028	0.764	0.069	23
	Common Blackbird	-0.730	-0.735	-2.009	0.604	0.166	24

Group size

		Estimate	MCMCmean	HPD95lower	HPD95upper	pMCMC	n
Species	Long-tailed Tit	-0.561	-0.561	-1.217	0.048	0.062	12
	European Robin	-1.238	-1.237	-1.856	-0.629	0.004	22
	Blue Tit	-1.059	-1.068	-1.653	-0.423	0.007	87
	Crested Tit	-0.997	-1.006	-1.623	-0.365	0.011	12
	Great Tit	-1.126	-1.135	-1.754	-0.506	0.005	19
	Common Firecrest	-1.124	-1.127	-1.758	-0.515	0.005	26
	Eurasian Blackcap	-1.139	-1.143	-1.345	-0.943	0.000	22
	Common Blackbird	-1.162	-1.161	-1.812	-0.591	0.005	23

Foraging location

		Estimate	Std.Error	z value	Pr(>|z|)	n
Species	Long-tailed Tit	-1.294	0.274	-4.726	0.000	17
	European Robin	-0.992	0.244	-4.062	0.000	23
	Blue Tit	0.448	0.163	2.753	0.006	97
	Crested Tit	-1.355	0.280	-4.831	0.000	16
	Great Tit	-1.083	0.253	-4.288	0.000	21
	Common Firecrest	-0.726	0.222	-3.264	0.001	30
	Eurasian Blackcap	-0.992	0.244	-4.062	0.000	23
	Common Blackbird	-0.949	0.240	-3.948	0.000	24

Foraging substrate

		Estimate	Std.Error	z value	Pr(>|z|)	n
Species	Long-tailed Tit	-1.294	0.274	-4.726	0.000	17
	European Robin	-0.992	0.244	-4.062	0.000	23
	Blue Tit	0.427	0.163	2.614	0.009	95
	Crested Tit	-1.355	0.280	-4.831	0.000	16
	Great Tit	-1.083	0.253	-4.288	0.000	21
	Common Firecrest	-0.726	0.222	-3.264	0.001	30
	Eurasian Blackcap	-0.992	0.244	-4.062	0.000	23
	Common Blackbird	-0.949	0.240	-3.948	0.000	24

Foraging technnique

		Estimate	Std.Error	z value	Pr(>|z|)	n
Species	Long-tailed Tit	-1.056	0.290	-3.639	0.000	16
	European Robin	-0.738	0.259	-2.845	0.004	22
	Blue Tit	0.715	0.180	3.972	0.000	94
	Crested Tit	-1.344	0.324	-4.145	0.000	12
	Great Tit	-0.884	0.273	-3.242	0.001	19
	Common Firecrest	-0.427	0.235	-1.821	0.069	30
	Eurasian Blackcap	-0.833	0.268	-3.110	0.002	20
	Common Blackbird	-0.693	0.255	-2.714	0.007	23

* The estimate for Leiothrix has been set to zero, and all the other species are compared to it (Leiothrix breeding season n=65, non-breeding season n=62). All models include species and hour as fixed factors and taxonomic family plus transect as random factors.

Table 6. Differences in the foraging niche components of Leiothrix and native species between breeding respect to non-breeding season*.

Species	Variable	Estimate	MCMC mean	HPD95 lower	HPD95 upper	pMCMC	n	Variable	Estimate	Std. Error	z value	Pr(>|z|)	n
Red-billed Leiothrix	Foraging height	-0.055	-0.049	-0.362	0.281	0.761	127	Location	-0.047	0.178	-0.266	0.790	127
	Tree height	0.026	0.040	-0.299	0.389	0.814	127	Substrate	-0.047	0.178	-0.266	0.790	127
	Group size	0.830	0.825	0.583	1.073	0.000	88	Technique	-0.063	0.205	-0.308	0.758	95
Long-tailed Tit	Foraging height	-0.201	-0.207	-0.628	0.203	0.322	43	Location	-0.425	0.312	-1.362	0.173	43
	Tree height	-0.086	-0.078	-0.390	0.218	0.610	43	Substrate	-0.425	0.312	-1.362	0.173	43
	Group size	-0.229	-0.252	-0.745	0.231	0.304	28	Technique	-0.486	0.318	-1.528	0.127	42
European Robin	Foraging height	0.336	0.268	-0.027	0.575	0.079	47	Location	-0.043	0.292	-0.146	0.884	47
	Tree height	0.442	0.320	-0.050	0.691	0.091	47	Substrate	-0.043	0.292	-0.146	0.884	47
	Group size	-0.050	-0.048	-0.120	0.019	0.170	43	Technique	-0.087	0.295	-0.295	0.768	46
Blue Tit	Foraging height	0.209	0.207	-0.062	0.468	0.126	190	Location	0.042	0.145	0.290	0.772	190
	Tree height	0.247	0.247	0.008	0.483	0.044	190	Substrate	0.021	0.146	0.146	0.884	188
	Group size	-0.147	-0.142	-0.271	-0.005	0.037	160	Technique	0.022	0.147	0.147	0.883	186
Crested Tit	Foraging height	-0.113	-0.027	-0.760	0.697	0.944	36	Location	-0.323	0.287	-1.126	0.260	36
	Tree height	0.135	0.154	-0.471	0.764	0.618	36	Substrate	-0.323	0.287	-1.126	0.260	36
	Group size	-0.045	-0.038	-0.350	0.278	0.801	25	Technique	-0.388	0.297	-1.305	0.192	29
Great Tit	Foraging height	-0.670	-0.667	-1.427	0.021	0.069	50	Location	-0.154	0.249	-0.620	0.536	50
	Tree height	-0.685	-0.688	-1.533	0.200	0.117	50	Substrate	-0.154	0.249	-0.620	0.536	50
	Group size	-0.031	-0.042	-0.242	0.141	0.652	43	Technique	0.000	0.258	0.000	1.000	47
Common Firecrest	Foraging height	-0.127	-0.165	-0.493	0.160	0.310	65	Location	-0.154	0.249	-0.620	0.536	65
	Tree height	0.046	0.038	-0.202	0.281	0.766	65	Substrate	-0.154	0.249	-0.620	0.536	65
	Group size	0.101	0.102	-0.002	0.202	0.053	54	Technique	0.000	0.258	0.000	1.000	60
Eurasian Blackcap	Foraging height	-0.127	-0.165	-0.493	0.160	0.310	60	Location	-0.475	0.266	-1.790	0.073	60
	Tree height	0.046	0.038	-0.202	0.281	0.766	60	Substrate	-0.475	0.266	-1.790	0.073	60
	Group size	0.101	0.102	-0.002	0.202	0.053	57	Technique	-0.588	0.279	-2.108	0.035	56
Common Blackbird	Foraging height	1.131	1.134	0.391	1.919	0.004	43	Location	0.234	0.307	0.761	0.447	43
	Tree height	1.400	1.393	0.426	2.329	0.007	43	Substrate	0.234	0.307	0.761	0.447	43
	Group size	-0.065	-0.062	-0.201	0.081	0.395	41	Technique	0.191	0.310	0.616	0.538	42

*All models include species and hour as fixed factors and taxonomic family plus transect as random factors.

Table 7. Comparison of residual brain size between Leiothrix and native forest species of similar size*.

Variables		Estimate	MCMCmean	HPD95lower	HPD95upper	pMCMC
Species	European Robin	-0.375	-0.376	-0.519	-0.232	0.001
	Coal Tit	-0.399	-0.400	-0.668	-0.155	0.003
	Blue Tit	-0.285	-0.286	-0.485	-0.077	0.007
	Great Tit	-0.122	-0.122	-0.290	0.046	0.140
	Common Chiffchaff	-1.000	-1.001	-1.262	-0.747	0.000
	Dunnock	-0.207	-0.206	-0.345	-0.073	0.013
	Eurasian Blackcap	-0.368	-0.369	-0.467	-0.273	0.000
	Garden Warbler	-0.432	-0.431	-0.576	-0.290	0.000
	Eurasian Wren	-0.471	-0.473	-0.719	-0.214	0.001
	Common Blackbird	0.545	0.548	0.196	0.930	0.006
	Song Trush	0.369	0.371	0.075	0.663	0.017
Body mass (log-transformed)		0.095	0.093	-0.122	0.309	0.395

Random effects	Std. Dev	MCMCmean	HPD95lower	HPD95upper	pMCMC
Family	0.171	0.173	0.178	0.123	0.244

*The estimate for Leiothrix has been set to zero, and all the other species are compared to it. All models include species as fixed factor and taxonomic family as random factor.

Table 8. Comparison of body mass between Leiothrix and native forest species with which the invader coexist either in spring or in winter*.

Fixed effects Species	Estimate	MCMCmean	HPD95lower	HPD95upper	pMCMC
Eurasian Sparrowhawk	1.927	1.929	1.754	2.087	0.000
Long-tailed Tit	-1.181	-1.180	-1.259	-1.106	0.000
European Goldfinch	-0.416	-0.416	-0.519	-0.314	0.000
European Greenfinch	0.073	0.074	-0.012	0.170	0.097
Short-toed Treecreeper	-1.017	-1.016	-1.090	-0.942	0.000
Cetti's Warbler	-0.600	-0.599	-0.643	-0.555	0.000
Hawfinch	0.841	0.842	0.712	0.965	0.000
European Robin	-0.288	-0.287	-0.358	-0.220	0.000
Common Chaffinch	-0.070	-0.069	-0.142	0.009	0.068
Eurasian Jay	1.946	1.946	1.867	2.020	0.000
Melodious Warbler	-0.730	-0.730	-0.772	-0.689	0.000
Eurasian Wryneck	0.410	0.409	0.250	0.581	0.000
Common Nightingale	-0.063	-0.063	-0.143	0.015	0.097
European Golden Oriole	1.094	1.094	0.929	1.264	0.000
Coal Tit	-0.995	-0.996	-1.166	-0.827	0.000
Blue Tit	-0.793	-0.793	-0.859	-0.717	0.000
Crested Tit	-0.746	-0.746	-0.824	-0.673	0.000
Great Tit	-0.277	-0.277	-0.350	-0.206	0.000
House Sparrow	0.113	0.113	0.023	0.204	0.021
Eurasian Tree Sparrow	-0.327	-0.329	-0.501	-0.165	0.000
Red Blackstart	-0.463	-0.462	-0.630	-0.295	0.000
Common Chiffchaff	-1.244	-1.244	-1.294	-1.196	0.000
Green Woodpecker	2.089	2.088	1.922	2.247	0.000
Dunnock	-0.144	-0.144	-0.227	-0.067	0.006
Common Firecrest	-1.523	-1.523	-1.595	-1.449	0.000
Eurasian Serin	-0.703	-0.703	-0.780	-0.621	0.000
Sardinian Warbler	-0.631	-0.631	-0.670	-0.588	0.000
Eurasian Blackcap	-0.252	-0.252	-0.274	-0.228	0.000
Eurasian Wren	-0.934	-0.933	-1.014	-0.852	0.000
Common Blackbird	1.341	1.341	1.270	1.410	0.000
Song Trush	1.127	1.127	1.050	1.203	0.000

Random effects	Std.Dev.	MCMCmedian	MCMCmean	HPD95lower	HPD95upper
Season	0.015	0.014	0.017	0.000	0.045
Year	0.029	0.028	0.029	0.016	0.042

*Body mass in grams. Ringing season and taxonomic family are included in the model as random factors. Only adults are used in the analyses.

Table 9. Population trends of native resident species for the riparian forest before (1987-1997) and after (1998-2010) the arrival of Leiothrix, as well as for the Holm oak and conifer forests (period 1998-2010)*.

Species	Habitat (Period)	ARMA	DF	Slope	Std. Error	DF	t-value	p-value
Red-billed Leiothrix	Riparian (87-97)	-	-	-	-	-	-	-
	Riparian (98-10)	0,2	2	8.471	1.932	11	4.382	0.011
	Holm oak (98-10)	-	-	-	-	-	-	-
	Conifer (98-10)	-	-	-	-	-	-	-
Great Tit	Riparian (87-97)	0,2	2	-0.190	0.183	7	-1.037	0.334
	Riparian (98-10)	0,1	2.943	1.004	1.478	11	0.679	0.511
	Holm oak (98-10)	0,1	2	2.744	2.062	10	1.331	0.213
	Conifer (98-10)	0,1	2	-1.161	0.537	11	-2.164	0.053
Crested Tit	Riparian (87-97)	2,0	2	1.081	0.138	7	7.844	0.000
	Riparian (98-10)	0,1	2.793	0.820	0.523	11	1.566	0.146
	Holm oak (98-10)	0,0	2	-0.985	0.920	10	-1.070	0.310
	Conifer (98-10)	2,1	2	-0.095	0.499	11	-0.191	0.852
Blue Tit	Riparian (87-97)	2,0	4.492	0.571	0.251	7	2.273	0.057
	Riparian (98-10)	0,0	4.421	-6.572	5.710	11	-1.151	0.274
	Holm oak (98-10)	2,0	2	0.963	0.826	10	1.166	0.271
	Conifer (98-10)	2,0	4.621	-6.110	4.684	11	-1.304	0.219
Coal Tit	Riparian (87-97)	0,0	2	1.437	1.588	7	0.905	0.396
	Riparian (98-10)	0,2	2	0.129	0.128	11	1.007	0.336
	Holm oak (98-10)	2,2	2	0.664	0.073	10	9.097	0.000
	Conifer (98-10)	2,2	2	0.214	0.135	11	1.591	0.140
Long-tailed Tit	Riparian (87-97)	0	2	-0.133	0.787	7	-0.170	0.870
	Riparian (98-10)	2,2	2	0.589	0.761	11	0.773	0.456
	Holm oak (98-10)	2,2	2	2.047	0.140	10	14.590	0.000
	Conifer (98-10)	0,2	2	3.037	0.430	11	7.064	0.000
Common Firecrest	Riparian (87-97)	0,0	2.000	0.361	0.715	7	0.505	0.629
	Riparian (98-10)	2,2	2	2.303	0.348	11	6.623	0.000
	Holm oak (98-10)	0,1	2	2.757	0.810	10	3.405	0.007
	Conifer (98-10)	2,0	7.679	-3.265	6.087	11	-0.536	0.602
Eurasian Blackcap	Riparian (87-97)	0,0	3.000	1.660	1.382	7	1.201	0.269
	Riparian (98-10)	0,1	2	-1.711	0.371	11	-4.614	0.001
	Holm oak (98-10)	0,2	2	1.536	0.550	10	2.795	0.019
	Conifer (98-10)	0,1	2	0.985	0.375	11	2.626	0.024
Common Blackbird	Riparian (87-97)	0,0	2	1.112	0.375	7	2.966	0.021
	Riparian (98-10)	0,1	2	0.344	0.301	11	1.143	0.277
	Holm oak (98-10)	0,2	4.133	-2.732	1.836	10	-1.488	0.168
	Conifer (98-10)	2,0	6.675	-1.773	2.111	11	-0.840	0.419
Cettis' Warbler	Riparian (87-97)	0,0	2	-0.265	0.180	7	-1.467	0.186
	Riparian (98-10)	0,0	2	-0.041	0.263	11	-0.157	0.878
	Holm oak (98-10)	-	-	-	-	-	-	-
	Conifer (98-10)	-	-	-	-	-	-	-
EurasianWren	Riparian (87-97)	0,0	4.788	12.728	6.875	7	1.851	0.107
	Riparian (98-10)	0,0	2	1.796	1.682	11	1.068	0.309
	Holm oak (98-10)	0,0	2	1.418	2.405	10	0.590	0.568
	Conifer (98-10)	0,1	2	2.109	0.300	11	7.033	0.000
European Robin	Riparian (87-97)	0,0	9	18.936	0.002	7	11817.030	0.000
	Riparian (98-10)	0,1	2	3.091	1.159	11	2.667	0.022

	Holm oak (98-10)	0,0	2	0.824	1.671	10	0.493	0.633
	Conifer (98-10)	2,2	2	4.300	0.117	11	36.757	0.000

*We present the auto-regressive moving average (ARMA) serial correlation structure and the amount of smoothing (degrees of freedom) for each model (Zuur et al. 2009b). The population trend is specified by the slope parameter. A significantly positive slope indicates a population increase whereas a negative slope indicates a population decline.

Figure 1. Kilometric abundance index (KAI, median and percentiles) of Leiothrix for the period 2005-2010, compared to the abudance of native species. Leiothrix position is marked with an arrow. For species names abbreviations see Appendix B: Table 1.

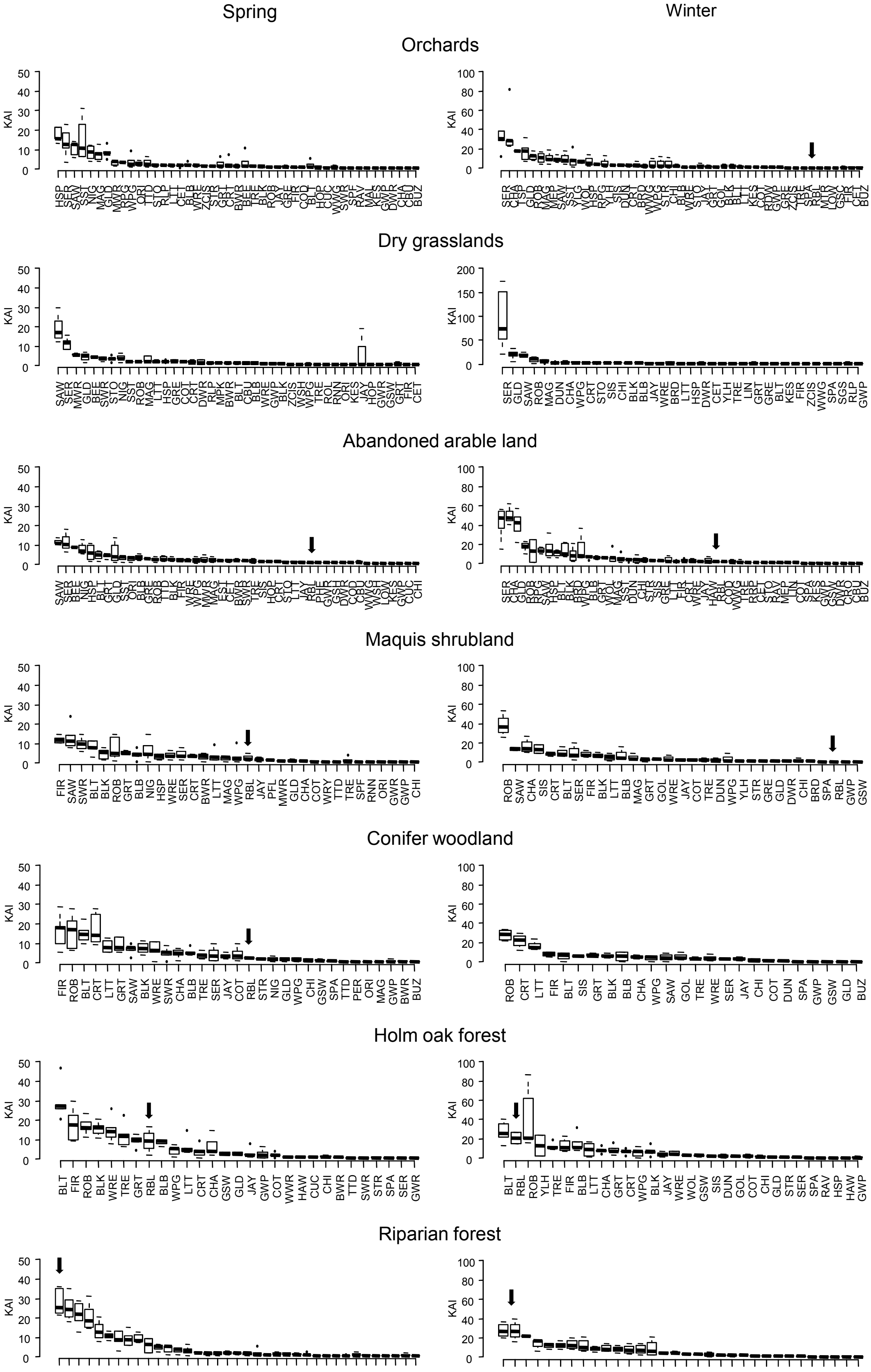


Figure 2. Frequency of captures and recaptures of leiothrixs compared to native species for the period 2003-2009. Abbreviations are: C, captures; RC, recaptures. For recaptures, Age refers to the age of the bird when it was captured for the first time. Leiothrix position is marked with an arrow. We used only captures carried out during spring. Only species with 15 captures or more have been included. Asterisks denote the species that have recapture rates larger than Leiothrix, according to a chi-square test with 1 degree of freedom. See Appendix B: Table 1 for full species names.

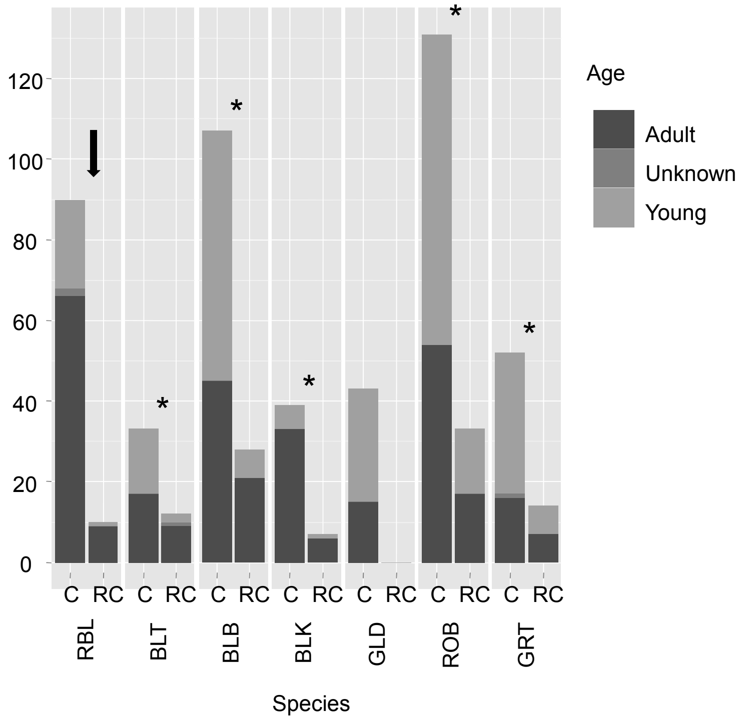


Figure 3. Comparison of the captures of leiothrixs in spring and winter for the period 2003-2009.

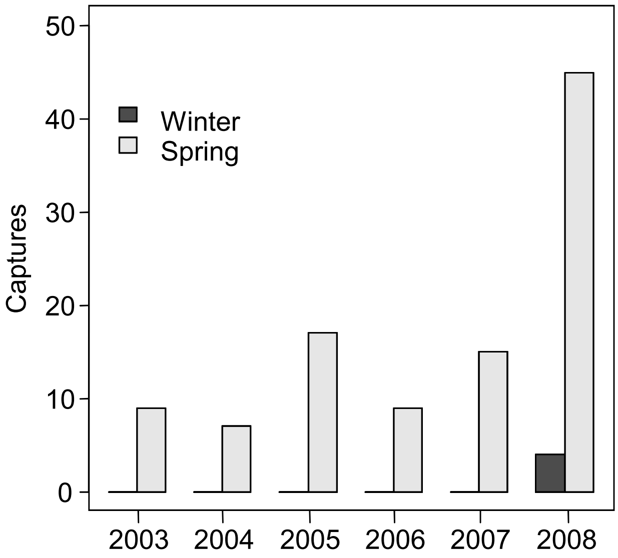


Figure 4. Phylogenetic relationships among the 53 bird species present in Collserola censuses during the period 1995-2001.

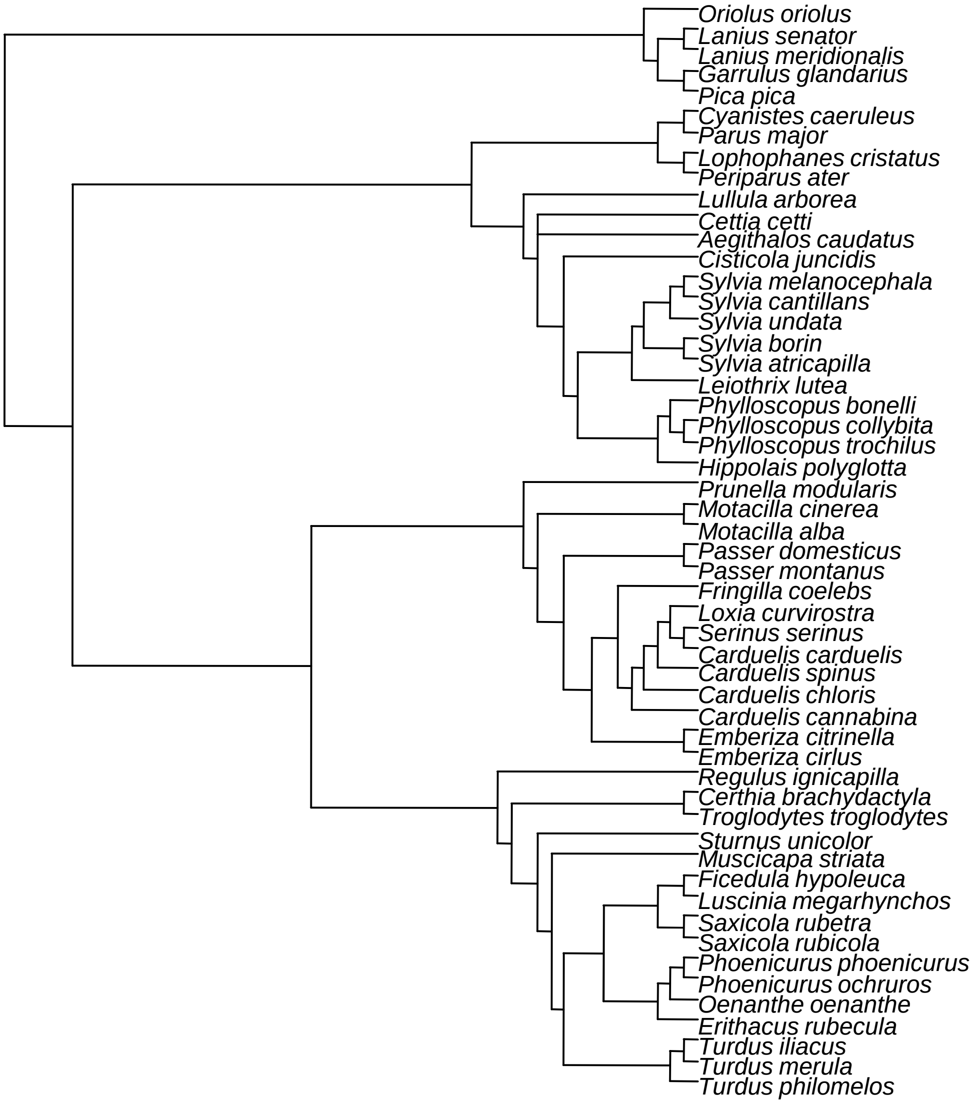


Figure 5. Phylogenetic relationships among bird species present in Collserola censuses during the period 1995-2001 in each habitat in spring (51) and winter (37).

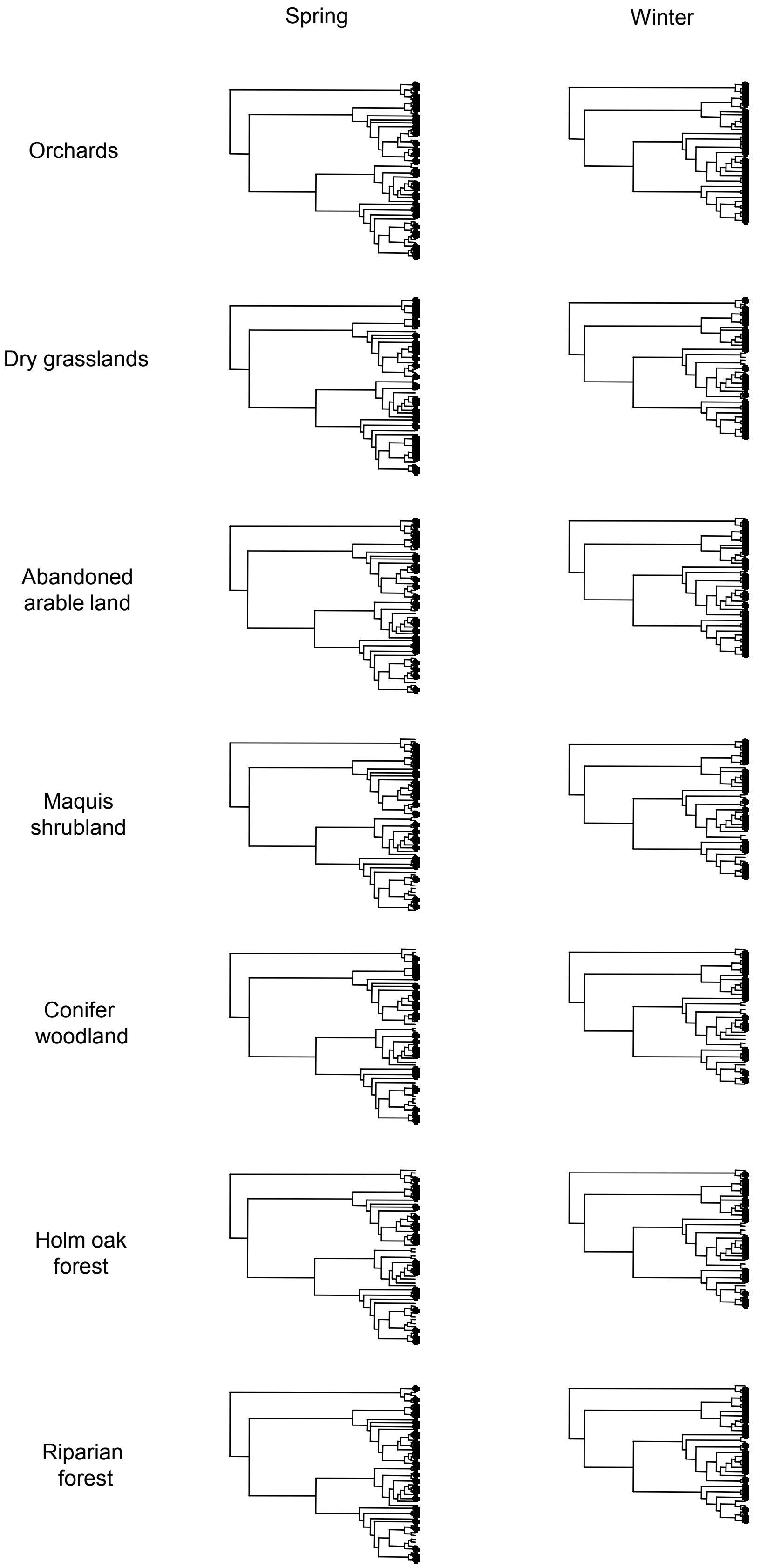


Figure 6. Foraging niche components of Leiothrix and native species. Asterisks indicate a significant difference respect to Leiothrix. See Appendix B: Table 5 for significance tests. See Appendix B: Table 1 for full species names.

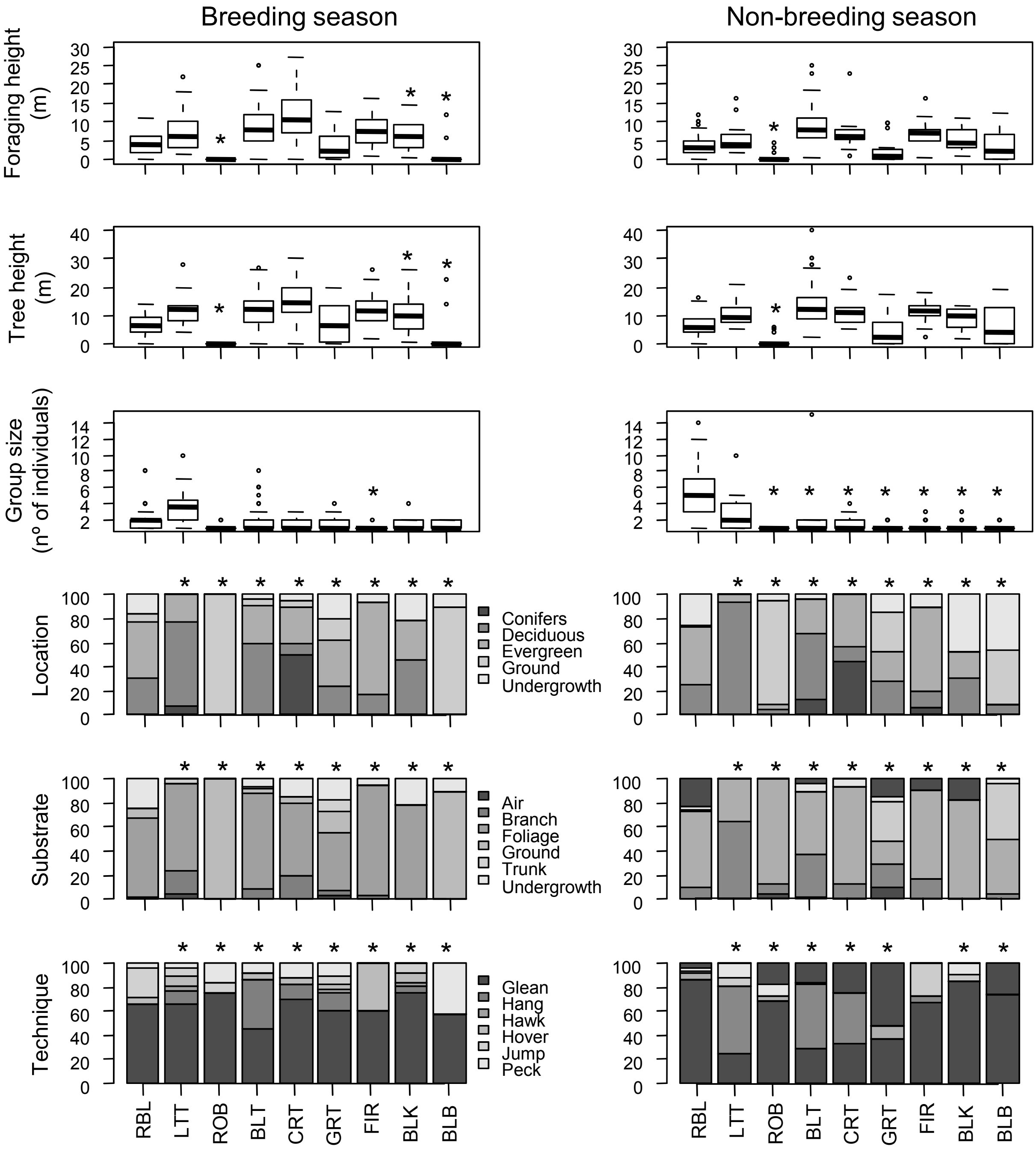


Figure 7. Comparison of relative brain size between Leiothrix and native forest species. Relative brain size comes from a global life history traits database with a single mean value for each species. Leiothrix position is marked with an arrow. See Appendix B: Table 1 for full species names.

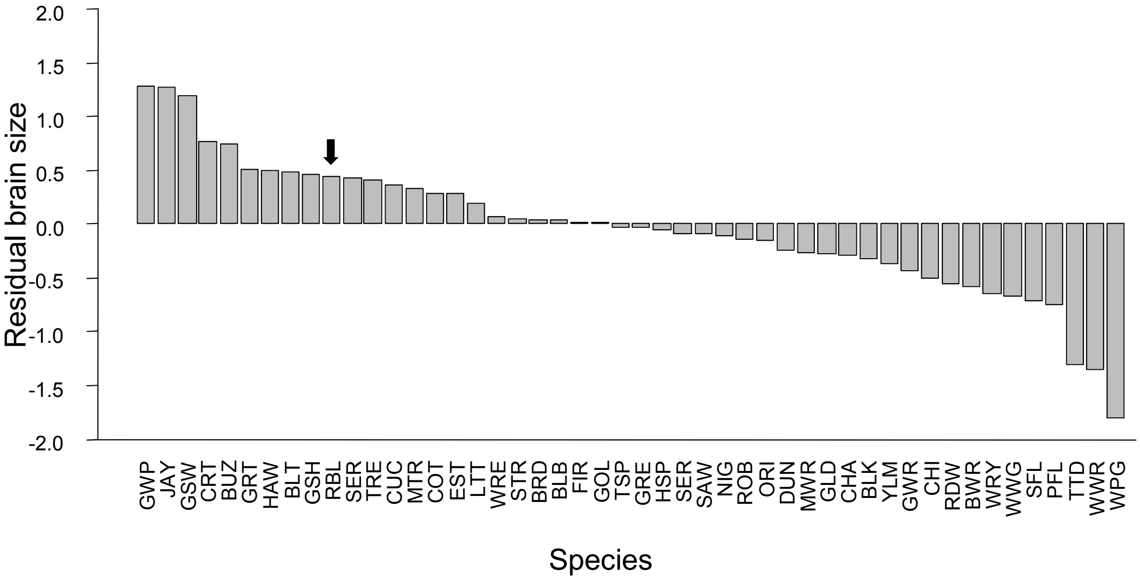


Figure 8. Frequency of observed vs. expected visits to the experimental feeders of leiothrixs and native species. Expected visits have been estimated based on the average abundance of each species in the surroundings of the experimental sites. Positive signs denote species with a visit rate significantly larger and minus signs species with a visit rate significantly lesser than Leiothrix, according to a chi-square test with 1 degree of freedom. Leiothrix position is marked with an arrow. See Appendix B: Table 1 for full species names.

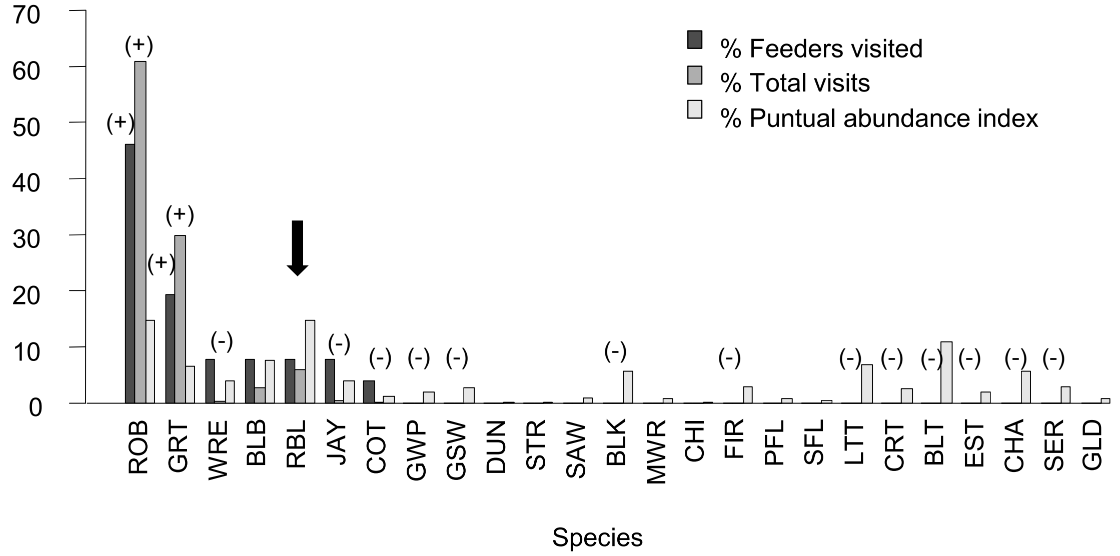
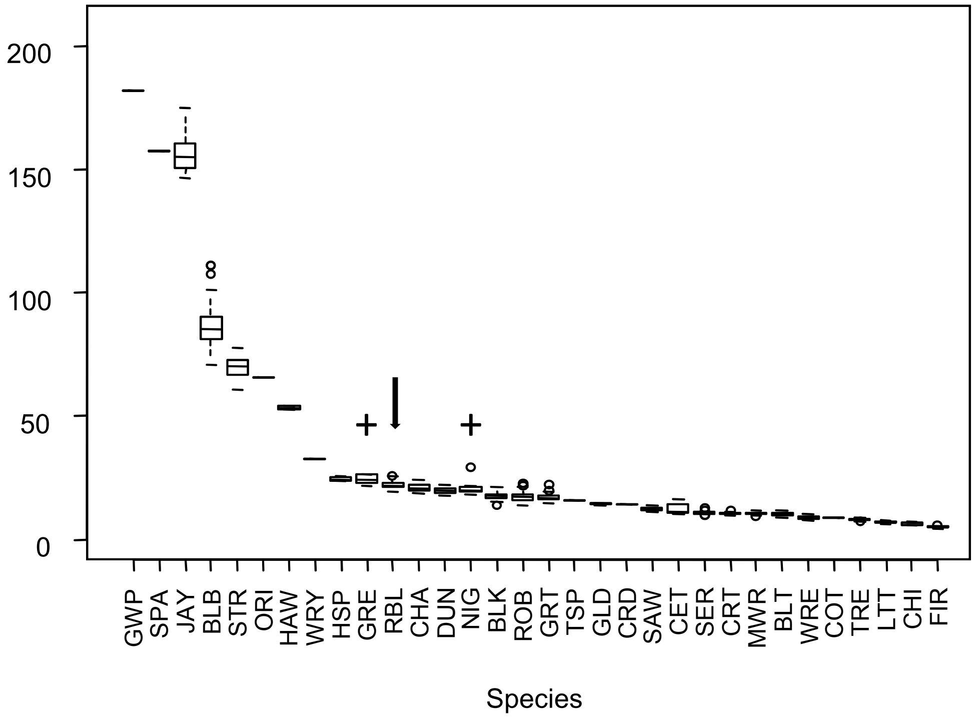


Figure 9. Comparison of body mass between Leiothrix and native forest species with which the invader coexist either in spring or in winter. Only adults are used in the analyses. Leiothrix position is marked with an arrow andcrosses indicate a non-significant difference respect to Leiothrix (see Appendix B: Table 8 for statistics). See Appendix B: Table 1 for full species names.



Appendix C

Chapter 4. A global risk assessment for the success of bird introductions

Table 1. Abbreviated data set of the introduction events compiled in the database. Information of the taxonomic position of the species (Sibley and Monroe Jr 1993), time and country of introduction, and the final outcome is provided. When more than one introduction event coincides for a country and year, more details on the place of introduction are given between parentheses ().

Order	Family	Scientific name	Time of introduction	Country of introduction	Outcome
Anseriformes	Anatidae	Aix galericulata	1861	Australia	Extinct
Anseriformes	Anatidae	Aix galericulata	1928	British Isles	Established
Anseriformes	Anatidae	Aix galericulata	1983	South Africa	Extinct
Anseriformes	Anatidae	Aix sponsa	1899	New Zealand	Extinct
Anseriformes	Anatidae	Alopochen aegyptiacus	1901	British Isles	Extinct
Anseriformes	Anatidae	Alopochen aegyptiacus	1967	The Netherlands	Established
Anseriformes	Anatidae	Anas acuta	1897	New Zealand	Extinct
Anseriformes	Anatidae	Anas platyrhynchos	1866	Australia	Extinct
Anseriformes	Anatidae	Anas platyrhynchos	1867	New Zealand	Extinct
Anseriformes	Anatidae	Anas platyrhynchos	1870	New Zealand	Established
Anseriformes	Anatidae	Anas platyrhynchos	1871	Australia	Extinct
Anseriformes	Anatidae	Anas platyrhynchos	1873	New Zealand	Established
Anseriformes	Anatidae	Anas platyrhynchos	1893	New Zealand	Extinct
Anseriformes	Anatidae	Anas platyrhynchos	1896	New Zealand	Established
Anseriformes	Anatidae	Anas platyrhynchos	1907	New Zealand	Established
Anseriformes	Anatidae	Anas platyrhynchos	1910	New Zealand	Established
Anseriformes	Anatidae	Anas platyrhynchos	1939	New Zealand	Established
Anseriformes	Anatidae	Anas platyrhynchos	1959	French Southern and Antarctic Lands Territory	Extinct
Anseriformes	Anatidae	Anser anser	1769	New Zealand	Extinct
Anseriformes	Anatidae	Anser anser	1867	New Zealand	Extinct
Anseriformes	Anatidae	Anser caerulescens	1877	New Zealand	Extinct
Anseriformes	Anatidae	Anser indicus	1972	The Netherlands	Established
Anseriformes	Anatidae	Anser indicus	1981	Finland	Established
Anseriformes	Anatidae	Aythya ferina	1894	New Zealand	Extinct
Anseriformes	Anatidae	Aythya fuligula	1870	New Zealand	Extinct
Anseriformes	Anatidae	Branta canadensis	1876	New Zealand	Extinct
Anseriformes	Anatidae	Branta canadensis	1905	New Zealand	Extinct
Anseriformes	Anatidae	Branta canadensis	1906	New Zealand	Established
Anseriformes	Anatidae	Branta canadensis	1912	New Zealand	Established
Anseriformes	Anatidae	Branta canadensis	1920	New Zealand	Established
Anseriformes	Anatidae	Branta canadensis	1936	Norway	Extinct
Anseriformes	Anatidae	Branta canadensis	1958	Norway	Extinct
Anseriformes	Anatidae	Branta canadensis	1960	Finland	Established
Anseriformes	Anatidae	Branta canadensis	1963	Norway	Extinct
Anseriformes	Anatidae	Branta canadensis	1965	Norway (Trondheimsfjord)	Established
Anseriformes	Anatidae	Branta canadensis	1965	Norway (Oslo)	Established
Anseriformes	Anatidae	Branta canadensis	1970	Norway	Extinct
Anseriformes	Anatidae	Branta canadensis	1972	Norway (Bomlo)	Extinct
Anseriformes	Anatidae	Branta canadensis	1972	Norway (Oslo)	Extinct
Anseriformes	Anatidae	Branta canadensis	1972	Norway (Storeval)	Extinct
Anseriformes	Anatidae	Branta canadensis	1981	Russia	Established

Anseriformes	Anatidae	Branta sandvicensis	?	New Zealand	Extinct
Anseriformes	Anatidae	Cairina moschata	1885	New Zealand	Extinct
Anseriformes	Anatidae	Cairina moschata	?	USA	Extinct
Anseriformes	Anatidae	Cereopsis novaehollandiae	1868	New Zealand	Extinct
Anseriformes	Anatidae	Cereopsis novaehollandiae	1871	New Zealand	Extinct
Anseriformes	Anatidae	Cereopsis novaehollandiae	1914	New Zealand	Extinct
Anseriformes	Anatidae	Cereopsis novaehollandiae	1917	New Zealand	Extinct
Anseriformes	Anatidae	Cereopsis novaehollandiae	1972	Australia	Established
Anseriformes	Anatidae	Cygnus atratus	1864	New Zealand (Auckland)	Established
Anseriformes	Anatidae	Cygnus atratus	1864	New Zealand (Canterbury)	Established
Anseriformes	Anatidae	Cygnus atratus	1864	New Zealand (Nelson)	Established
Anseriformes	Anatidae	Cygnus atratus	1866	New Zealand	Established
Anseriformes	Anatidae	Cygnus atratus	1869	New Zealand	Established
Anseriformes	Anatidae	Cygnus olor	1853	Australia	Extinct
Anseriformes	Anatidae	Cygnus olor	1866	Australia	Extinct
Anseriformes	Anatidae	Cygnus olor	1866	New Zealand (Canterbury)	Established
Anseriformes	Anatidae	Cygnus olor	1866	New Zealand (Christchurch, Canterbury)	Extinct
Anseriformes	Anatidae	Cygnus olor	1867	New Zealand	Extinct
Anseriformes	Anatidae	Cygnus olor	1868	New Zealand	Extinct
Anseriformes	Anatidae	Cygnus olor	1886	Australia	Extinct
Anseriformes	Anatidae	Cygnus olor	1897	Australia	Established
Anseriformes	Anatidae	Cygnus olor	1910	USA	Established
Anseriformes	Anatidae	Cygnus olor	1920	Australia	Extinct
Anseriformes	Anatidae	Cygnus olor	1948	USA	Established
Anseriformes	Anatidae	Cygnus olor	1962	USA	Established
Anseriformes	Anatidae	Cygnus olor	1977	Japan	Established
Anseriformes	Anatidae	Oxyura jamaicensis	1952	British Isles	Established
Anseriformes	Anatidae	Plectropterus gambensis	1929	Australia	Extinct
Anseriformes	Dendrocygnidae	Dendrocygna autumnalis	1967	Trinidad and Tobago (Tobago)	Extinct
Anseriformes	Dendrocygnidae	Dendrocygna autumnalis	1967	Trinidad and Tobago (Trinidad)	Extinct
Apodiformes	Apodidae	Collocalia vanikorensis	1962	Hawaiian Islands	Established
Ciconiiformes	Ardeidae	Bubulcus ibis	1933	Australia	Extinct
Ciconiiformes	Ardeidae	Bubulcus ibis	1955	British Indian Ocean Territory	Established
Ciconiiformes	Ardeidae	Bubulcus ibis	1959	Hawaiian Islands (Hawaii)	Established
Ciconiiformes	Ardeidae	Bubulcus ibis	1959	Hawaiian Islands (Oahu)	Established
Ciconiiformes	Ardeidae	Nycticorax nycticorax	1887	British Isles	Extinct
Ciconiiformes	Ardeidae	Nycticorax nycticorax	1950	British Isles	Established
Ciconiiformes	Charadriidae	Pluvialis apricaria	1877	New Zealand	Extinct
Ciconiiformes	Charadriidae	Pluvialis apricaria	1897	New Zealand	Extinct
Ciconiiformes	Charadriidae	Pluvialis squatarola	1867	New Zealand	Extinct
Ciconiiformes	Charadriidae	Pluvialis squatarola	1881	New Zealand	Extinct
Ciconiiformes	Charadriidae	Vanellus vanellus	1872	New Zealand	Extinct
Ciconiiformes	Charadriidae	Vanellus vanellus	1873	New Zealand	Extinct
Ciconiiformes	Charadriidae	Vanellus vanellus	1897	New Zealand	Extinct
Ciconiiformes	Charadriidae	Vanellus vanellus	1904	New Zealand (Westland)	Extinct
Ciconiiformes	Charadriidae	Vanellus vanellus	1904	New Zealand (Wellington)	Extinct
Ciconiiformes	Phalacrocoracidae	Phalacrocorax carbo	1890	Hawaiian Islands	Extinct
Ciconiiformes	Phoenicopteridae	Phoenicopterus ruber	?	Hawaiian Islands	Extinct
Ciconiiformes	Pteroclidae	Pterocles exustus	1863	Australia	Extinct
Ciconiiformes	Pteroclidae	Pterocles exustus	1864	Australia	Extinct
Ciconiiformes	Pteroclidae	Pterocles exustus	1959	USA	Extinct
Ciconiiformes	Pteroclidae	Pterocles exustus	1961	Hawaiian Islands (Hawaii)	Established
Ciconiiformes	Pteroclidae	Pterocles exustus	1961	Hawaiian Islands (Kauai)	Extinct
Ciconiiformes	Pteroclidae	Pterocles exustus	1961	Hawaiian Islands (Molokai)	Extinct
Ciconiiformes	Spheniscidae	Aptenodytes patagonicus	1936	Norway	Extinct

Columbiformes	Columbidae	Columba palumbus	1910	USA	Extinct
Columbiformes	Columbidae	Columba picturata	1652	Saint Helena	Extinct
Columbiformes	Columbidae	Geopelia cuneata	1937	Australia	Extinct
Columbiformes	Columbidae	Geopelia striata	1937	Australia	Extinct
Columbiformes	Columbidae	Geopelia striata	1950	French Polynesia	Established
Columbiformes	Columbidae	Geopelia striata	1960	British Indian Ocean Territory	Established
Columbiformes	Columbidae	Geopelia striata	1961	Hawaiian Islands	Established
Columbiformes	Columbidae	Geopelia striata	1965	Malaysia	Established
Columbiformes	Columbidae	Geopelia striata	1969	Glorioso Islands	Established
Columbiformes	Columbidae	Geophaps lophotes	1876	New Zealand	Extinct
Columbiformes	Columbidae	Geophaps lophotes	1883	New Zealand	Extinct
Columbiformes	Columbidae	Geophaps lophotes	1887	New Zealand	Extinct
Columbiformes	Columbidae	Geophaps lophotes	1937	Australia	Extinct
Columbiformes	Columbidae	Geophaps lophotes	1964	Hawaiian Islands	Extinct
Columbiformes	Columbidae	Geophaps plumifera	1940	Australia	Extinct
Columbiformes	Columbidae	Leucosarcia melanoleuca	1864	New Zealand (Otago)	Extinct
Columbiformes	Columbidae	Leucosarcia melanoleuca	1864	New Zealand (Wellington)	Extinct
Columbiformes	Columbidae	Leucosarcia melanoleuca	1868	New Zealand	Extinct
Columbiformes	Columbidae	Leucosarcia melanoleuca	1946	Australia	Extinct
Columbiformes	Columbidae	Phaps chalcoptera	1864	New Zealand	Extinct
Columbiformes	Columbidae	Phaps chalcoptera	1867	New Zealand	Extinct
Columbiformes	Columbidae	Phaps chalcoptera	1884	New Zealand	Extinct
Columbiformes	Columbidae	Streptopelia bitorquata	1867	New Zealand	Extinct
Columbiformes	Columbidae	Streptopelia chinensis	1861	Australia	Established
Columbiformes	Columbidae	Streptopelia chinensis	1881	Australia	Established
Columbiformes	Columbidae	Streptopelia decaocto	1971	New Zealand	Established
Columbiformes	Columbidae	Streptopelia senegalensis	1989	Mascarenes	Established
Columbiformes	Columbidae	Streptopelia turtur	1872	Australia	Extinct
Columbiformes	Columbidae	Zenaida asiatica	1959	USA	Established
Columbiformes	Columbidae	Zenaida asiatica	1961	Hawaiian Islands	Extinct
Columbiformes	Columbidae	Zenaida macroura	1962	Hawaiian Islands	Established
Coraciformes	Dacelonidae	Dacelo novaeguineae	1866	New Zealand	Extinct
Coraciformes	Dacelonidae	Dacelo novaeguineae	1876	New Zealand	Extinct
Coraciformes	Dacelonidae	Dacelo novaeguineae	1926	Australia	Established
Craciformes	Cracidae	Crax rubra	1923	USA	Extinct
Craciformes	Cracidae	Ortalis vetula	1923	USA	Established
Craciformes	Megapodiidae	Leipoa ocellata	1911	Australia	Extinct
Galliformes	Numididae	Numida meleagris	1700	Trinidad and Tobago	Extinct
Galliformes	Numididae	Numida meleagris	1870	Australia	Extinct
Galliformes	Numididae	Numida meleagris	1890	USA	Extinct
Galliformes	Numididae	Numida meleagris	1929	USA	Extinct
Galliformes	Odontophoridae	Callipepla californica	1851	British Isles	Extinct
Galliformes	Odontophoridae	Callipepla californica	1852	USA	Extinct
Galliformes	Odontophoridae	Callipepla californica	1857	USA (Texas)	Extinct
Galliformes	Odontophoridae	Callipepla californica	1857	USA (Washington)	Extinct
Galliformes	Odontophoridae	Callipepla californica	1862	New Zealand	Established
Galliformes	Odontophoridae	Callipepla californica	1864	Australia	Established
Galliformes	Odontophoridae	Callipepla californica	1865	New Zealand	Established
Galliformes	Odontophoridae	Callipepla californica	1867	New Zealand	Established
Galliformes	Odontophoridae	Callipepla californica	1868	New Zealand	Extinct
Galliformes	Odontophoridae	Callipepla californica	1870	British Isles	Extinct
Galliformes	Odontophoridae	Callipepla californica	1873	New Zealand	Extinct
Galliformes	Odontophoridae	Callipepla californica	1874	New Zealand	Established
Galliformes	Odontophoridae	Callipepla californica	1874	USA	Established

Galliformes	Odontophoridae	Callipepla californica	1879	Australia	Extinct
Galliformes	Odontophoridae	Callipepla californica	1907	Canada	Extinct
Galliformes	Odontophoridae	Callipepla californica	1914	USA (Oregon)	Established
Galliformes	Odontophoridae	Callipepla californica	1914	USA (Portland, Oregon)	Extinct
Galliformes	Odontophoridae	Callipepla californica	1920	Argentina	Established
Galliformes	Odontophoridae	Callipepla californica	1936	Hawaiian Islands	Established
Galliformes	Odontophoridae	Callipepla californica	1943	Argentina	Established
Galliformes	Odontophoridae	Callipepla californica	1946	USA	Extinct
Galliformes	Odontophoridae	Callipepla californica	1959	Hawaiian Islands	Established
Galliformes	Odontophoridae	Callipepla californica	1960	France	Established
Galliformes	Odontophoridae	Callipepla californica	?	USA	Established
Galliformes	Odontophoridae	Callipepla douglasii	1959	Hawaiian Islands	Extinct
Galliformes	Odontophoridae	Callipepla gambelii	1885	USA	Established
Galliformes	Odontophoridae	Callipepla gambelii	1890	USA	Extinct
Galliformes	Odontophoridae	Callipepla gambelii	1912	USA (California)	Extinct
Galliformes	Odontophoridae	Callipepla gambelii	1912	USA (San Clemente Island, California)	Extinct
Galliformes	Odontophoridae	Callipepla gambelii	1919	USA	Extinct
Galliformes	Odontophoridae	Callipepla gambelii	1960	Hawaiian Islands	Established
Galliformes	Odontophoridae	Callipepla squamata	1913	USA	Extinct
Galliformes	Odontophoridae	Callipepla squamata	1915	USA	Established
Galliformes	Odontophoridae	Callipepla squamata	1961	Hawaiian Islands	Extinct
Galliformes	Odontophoridae	Colinus virginianus	1860	British Isles	Extinct
Galliformes	Odontophoridae	Colinus virginianus	1872	Germany	Extinct
Galliformes	Odontophoridae	Colinus virginianus	1887	Sweden	Extinct
Galliformes	Odontophoridae	Colinus virginianus	1898	New Zealand (Canterbury)	Extinct
Galliformes	Odontophoridae	Colinus virginianus	1898	New Zealand (New Plymouth, Taranaki)	Extinct
Galliformes	Odontophoridae	Colinus virginianus	1898	New Zealand (Otago)	Extinct
Galliformes	Odontophoridae	Colinus virginianus	1898	New Zealand (Stratford, Taranaki)	Extinct
Galliformes	Odontophoridae	Colinus virginianus	1898	New Zealand (Wellington)	Extinct
Galliformes	Odontophoridae	Colinus virginianus	1899	Canada	Extinct
Galliformes	Odontophoridae	Colinus virginianus	1899	New Zealand (Auckland)	Extinct
Galliformes	Odontophoridae	Colinus virginianus	1899	New Zealand (Marlborough)	Extinct
Galliformes	Odontophoridae	Colinus virginianus	1899	New Zealand (Gisborne)	Extinct
Galliformes	Odontophoridae	Colinus virginianus	1899	New Zealand (Lake Waikaremoana, Hawke's Bay)	Established
Galliformes	Odontophoridae	Colinus virginianus	1899	New Zealand (Napier, Hawke's Bay)	Extinct
Galliformes	Odontophoridae	Colinus virginianus	1899	New Zealand (South Island)	Extinct
Galliformes	Odontophoridae	Colinus virginianus	1899	New Zealand (Manawatu-Wanganui)	Extinct
Galliformes	Odontophoridae	Colinus virginianus	1900	Canada	Extinct
Galliformes	Odontophoridae	Colinus virginianus	1905	Canada (Vernon, British Columbia)	Extinct
Galliformes	Odontophoridae	Colinus virginianus	1905	Canada (Shuswap, British Columbia)	Extinct
Galliformes	Odontophoridae	Colinus virginianus	1956	British Isles	Extinct
Galliformes	Odontophoridae	Colinus virginianus	1957	British Isles	Extinct
Galliformes	Odontophoridae	Colinus virginianus	1965	British Isles	Extinct
Galliformes	Odontophoridae	Colinus virginianus	1971	Canada	Extinct
Galliformes	Odontophoridae	Colinus virginianus	1983	British Isles	Extinct
Galliformes	Odontophoridae	Cyrtonyx montezumae	1961	Hawaiian Islands	Extinct
Galliformes	Odontophoridae	Oreortyx pictus	1876	New Zealand	Extinct
Galliformes	Odontophoridae	Oreortyx pictus	1881	New Zealand	Extinct
Galliformes	Odontophoridae	Oreortyx pictus	1960	Hawaiian Islands	Extinct
Galliformes	Phasianidae	Alectoris barbara	1892	New Zealand	Extinct
Galliformes	Phasianidae	Alectoris barbara	1900	Madeira	Extinct
Galliformes	Phasianidae	Alectoris barbara	1959	Hawaiian Islands	Extinct
Galliformes	Phasianidae	Alectoris barbara	1960	USA (California)	Extinct
Galliformes	Phasianidae	Alectoris barbara	1960	USA (Fresno County, California)	Extinct

Galliformes	Phasianidae	Alectoris barbara	1960	USA (Nevada)	Extinct
Galliformes	Phasianidae	Alectoris barbara	1960	USA (Tulare County, California)	Extinct
Galliformes	Phasianidae	Alectoris barbara	1961	Hawaiian Islands (Lanai)	Extinct
Galliformes	Phasianidae	Alectoris barbara	1961	Hawaiian Islands (Maui)	Extinct
Galliformes	Phasianidae	Alectoris barbara	1961	Hawaiian Islands (Molokai)	Extinct
Galliformes	Phasianidae	Alectoris chukar	1864	Australia	Extinct
Galliformes	Phasianidae	Alectoris chukar	1900	South Africa	Extinct
Galliformes	Phasianidae	Alectoris chukar	1920	New Zealand	Extinct
Galliformes	Phasianidae	Alectoris chukar	1926	New Zealand (Canterbury)	Established
Galliformes	Phasianidae	Alectoris chukar	1926	New Zealand (Otago)	Established
Galliformes	Phasianidae	Alectoris chukar	1928	New Zealand	Established
Galliformes	Phasianidae	Alectoris chukar	1929	New Zealand	Extinct
Galliformes	Phasianidae	Alectoris chukar	1932	New Zealand	Established
Galliformes	Phasianidae	Alectoris chukar	1932	USA	Established
Galliformes	Phasianidae	Alectoris chukar	1933	USA	Established
Galliformes	Phasianidae	Alectoris chukar	1934	USA (Missouri)	Extinct
Galliformes	Phasianidae	Alectoris chukar	1934	USA (Nevada)	Established
Galliformes	Phasianidae	Alectoris chukar	1934	USA (Wyoming)	Established
Galliformes	Phasianidae	Alectoris chukar	1935	USA (Box Elder County, Utah)	Extinct
Galliformes	Phasianidae	Alectoris chukar	1935	USA (Connor Spring, Box Elder County, Utah)	Extinct
Galliformes	Phasianidae	Alectoris chukar	1936	USA (Delaware County, New York)	Extinct
Galliformes	Phasianidae	Alectoris chukar	1936	USA (Pennsylvania)	Extinct
Galliformes	Phasianidae	Alectoris chukar	1937	USA	Extinct
Galliformes	Phasianidae	Alectoris chukar	1938	USA (Brigham City, Box Elder County, Utah)	Extinct
Galliformes	Phasianidae	Alectoris chukar	1938	USA (Cedar Breaks, Iron County, Utah)	Extinct
Galliformes	Phasianidae	Alectoris chukar	1938	USA (Idaho)	Established
Galliformes	Phasianidae	Alectoris chukar	1938	USA (Matanuska Valley, Alaska)	Extinct
Galliformes	Phasianidae	Alectoris chukar	1938	USA (Matanuska Valley, Alaska)	Extinct
Galliformes	Phasianidae	Alectoris chukar	1938	USA (Washington)	Established
Galliformes	Phasianidae	Alectoris chukar	1940	Canada	Established
Galliformes	Phasianidae	Alectoris chukar	1940	USA (Arsenal Springs, Davis County, Utah)	Extinct
Galliformes	Phasianidae	Alectoris chukar	1940	USA (Berry Springs, Washington County, Utah)	Extinct
Galliformes	Phasianidae	Alectoris chukar	1940	USA (Gunlock State Park, Washington County, Utah)	Extinct
Galliformes	Phasianidae	Alectoris chukar	1940	USA (Saint George, Washington County, Utah)	Extinct
Galliformes	Phasianidae	Alectoris chukar	1940	USA (Santa Clara, Washington County, Utah)	Extinct
Galliformes	Phasianidae	Alectoris chukar	1941	USA	Extinct
Galliformes	Phasianidae	Alectoris chukar	1946	USA	Extinct
Galliformes	Phasianidae	Alectoris chukar	1947	USA	Established
Galliformes	Phasianidae	Alectoris chukar	1948	USA (Deweyville, Box Elder County, Utah)	Extinct
Galliformes	Phasianidae	Alectoris chukar	1948	USA (Salt Lake County, Utah)	Extinct
Galliformes	Phasianidae	Alectoris chukar	1949	Hawaiian Islands	Established
Galliformes	Phasianidae	Alectoris chukar	1949	New Zealand	Extinct
Galliformes	Phasianidae	Alectoris chukar	1949	USA	Extinct
Galliformes	Phasianidae	Alectoris chukar	1950	France (Boches-du-Rhone and Hérault)	Extinct
Galliformes	Phasianidae	Alectoris chukar	1950	France (Lot)	Extinct
Galliformes	Phasianidae	Alectoris chukar	1950	France (lower Pyrenees)	Extinct
Galliformes	Phasianidae	Alectoris chukar	1950	France (Upper Garonne)	Extinct
Galliformes	Phasianidae	Alectoris chukar	1951	USA	Established
Galliformes	Phasianidae	Alectoris chukar	1952	USA	Extinct
Galliformes	Phasianidae	Alectoris chukar	1957	USA (Jerome, Yavapai County, Arizona)	Established
Galliformes	Phasianidae	Alectoris chukar	1957	USA (Snake Gulch, Coconino County, Arizona)	Established
Galliformes	Phasianidae	Alectoris chukar	1960	USA (San Diego, California)	Established
Galliformes	Phasianidae	Alectoris chukar	1960	USA (Colorado)	Established
Galliformes	Phasianidae	Alectoris chukar	1960	USA (Kennedy Tables, Tulare County, California)	Established

Galliformes	Phasianidae	Alectoris chukar	1960	USA (Little Rock Canyon, Kern County, California)	Established
Galliformes	Phasianidae	Alectoris chukar	1960	USA (San Ardo, Monterey County, California)	Established
Galliformes	Phasianidae	Alectoris chukar	1960	USA (Shasta Valley, Shasta County, California)	Established
Galliformes	Phasianidae	Alectoris chukar	1961	Hawaiian Islands	Extinct
Galliformes	Phasianidae	Alectoris chukar	1961	USA	Established
Galliformes	Phasianidae	Alectoris chukar	1964	South Africa	Established
Galliformes	Phasianidae	Alectoris chukar	1964	USA	Extinct
Galliformes	Phasianidae	Alectoris chukar	?	USA	Established
Galliformes	Phasianidae	Alectoris graeca	1897	New Zealand	Extinct
Galliformes	Phasianidae	Alectoris graeca	1912	New Zealand (Northland)	Extinct
Galliformes	Phasianidae	Alectoris graeca	1912	New Zealand (Waikato)	Extinct
Galliformes	Phasianidae	Alectoris graeca	1953	Ukraine	Established
Galliformes	Phasianidae	Alectoris graeca	1960	Ukraine	Extinct
Galliformes	Phasianidae	Alectoris rufa	1867	New Zealand	Extinct
Galliformes	Phasianidae	Alectoris rufa	1873	Australia	Extinct
Galliformes	Phasianidae	Alectoris rufa	1899	New Zealand	Extinct
Galliformes	Phasianidae	Alectoris rufa	1925	Madeira	Established
Galliformes	Phasianidae	Alectoris rufa	1952	USA	Extinct
Galliformes	Phasianidae	Alectoris rufa	1955	USA (Cottle County, Texas)	Extinct
Galliformes	Phasianidae	Alectoris rufa	1955	USA (Lipscomb County, Texas)	Extinct
Galliformes	Phasianidae	Alectoris rufa	1961	USA (California)	Extinct
Galliformes	Phasianidae	Alectoris rufa	1961	USA (Oklahoma)	Extinct
Galliformes	Phasianidae	Alectoris rufa	1961	USA (Texas)	Extinct
Galliformes	Phasianidae	Alectoris rufa	1961	USA (Washington)	Extinct
Galliformes	Phasianidae	Alectoris rufa	1963	USA	Extinct
Galliformes	Phasianidae	Alectoris rufa	1968	USA	Extinct
Galliformes	Phasianidae	Alectoris rufa	1972	USA	Extinct
Galliformes	Phasianidae	Ammoperdix griseogularis	1959	Hawaiian Islands	Extinct
Galliformes	Phasianidae	Ammoperdix heyi	1937	Cyprus	Extinct
Galliformes	Phasianidae	Bambusicola thoracica	1961	Hawaiian Islands	Extinct
Galliformes	Phasianidae	Bonasa bonasia	1905	USA	Extinct
Galliformes	Phasianidae	Bonasa umbellus	1884	USA	Extinct
Galliformes	Phasianidae	Bonasa umbellus	1900	USA (Green Bay, Washington Island, Wisconsin)	Extinct
Galliformes	Phasianidae	Bonasa umbellus	1900	USA (Detroit Harbour, Washington Island, Wisconsin	Extinct
Galliformes	Phasianidae	Bonasa umbellus	1911	USA	Extinct
Galliformes	Phasianidae	Bonasa umbellus	1923	USA	Extinct
Galliformes	Phasianidae	Bonasa umbellus	1931	USA	Extinct
Galliformes	Phasianidae	Bonasa umbellus	1940	USA	Extinct
Galliformes	Phasianidae	Bonasa umbellus	1948	USA (Beaver Island, Michigan)	Established
Galliformes	Phasianidae	Bonasa umbellus	1948	USA (Bois Blanc Island, Michigan)	Established
Galliformes	Phasianidae	Bonasa umbellus	1948	USA (Drummond Island, Michigan)	Established
Galliformes	Phasianidae	Bonasa umbellus	1956	Canada	Established
Galliformes	Phasianidae	Chrysolophus pictus	1883	USA	Extinct
Galliformes	Phasianidae	Chrysolophus pictus	1885	USA	Extinct
Galliformes	Phasianidae	Chrysolophus pictus	1900	USA	Extinct
Galliformes	Phasianidae	Chrysolophus pictus	1930	USA	Extinct
Galliformes	Phasianidae	Chrysolophus pictus	1975	British Isles	Established
Galliformes	Phasianidae	Coturnix chinensis	1862	Australia	Established
Galliformes	Phasianidae	Coturnix chinensis	1864	Australia	Extinct
Galliformes	Phasianidae	Coturnix chinensis	1971	Australia	Extinct
Galliformes	Phasianidae	Coturnix chinensis	1976	Australia	Extinct
Galliformes	Phasianidae	Coturnix coturnix	1862	Australia	Extinct
Galliformes	Phasianidae	Coturnix coturnix	1876	USA	Extinct
Galliformes	Phasianidae	Coturnix coturnix	1877	USA	Extinct

Galliformes	Phasianidae	Coturnix coturnix	1881	USA	Extinct
Galliformes	Phasianidae	Coturnix japonica	1904	USA	Extinct
Galliformes	Phasianidae	Coturnix japonica	1923	USA	Extinct
Galliformes	Phasianidae	Coturnix japonica	1955	USA	Extinct
Galliformes	Phasianidae	Coturnix japonica	1957	USA (Kentucky)	Extinct
Galliformes	Phasianidae	Coturnix japonica	1957	USA (Illinois)	Extinct
Galliformes	Phasianidae	Coturnix ypsilophora	1864	New Zealand	Established
Galliformes	Phasianidae	Coturnix ypsilophora	1866	New Zealand	Extinct
Galliformes	Phasianidae	Coturnix ypsilophora	1868	New Zealand	Extinct
Galliformes	Phasianidae	Coturnix ypsilophora	1872	New Zealand	Extinct
Galliformes	Phasianidae	Coturnix ypsilophora	1875	New Zealand	Established
Galliformes	Phasianidae	Francolinus adspersus	1963	Hawaiian Islands	Extinct
Galliformes	Phasianidae	Francolinus capensis	1865	Saint Helena	Extinct
Galliformes	Phasianidae	Francolinus clappertoni	1958	Hawaiian Islands	Extinct
Galliformes	Phasianidae	Francolinus erckelii	1957	Hawaiian Islands (Hawaii)	Established
Galliformes	Phasianidae	Francolinus erckelii	1957	Hawaiian Islands (Kauai)	Established
Galliformes	Phasianidae	Francolinus erckelii	1957	Hawaiian Islands (Lanai)	Established
Galliformes	Phasianidae	Francolinus erckelii	1959	USA	Extinct
Galliformes	Phasianidae	Francolinus erckelii	1960	Hawaiian Islands (Molokai)	Established
Galliformes	Phasianidae	Francolinus erckelii	1960	Hawaiian Islands (Oahu)	Established
Galliformes	Phasianidae	Francolinus erckelii	1969	USA	Extinct
Galliformes	Phasianidae	Francolinus francolinus	1894	British Isles	Extinct
Galliformes	Phasianidae	Francolinus francolinus	1932	British Isles	Established
Galliformes	Phasianidae	Francolinus francolinus	1957	USA (South Carolina)	Extinct
Galliformes	Phasianidae	Francolinus francolinus	1957	USA (Virginia)	Extinct
Galliformes	Phasianidae	Francolinus francolinus	1959	Hawaiian Islands	Established
Galliformes	Phasianidae	Francolinus francolinus	1959	USA	Extinct
Galliformes	Phasianidae	Francolinus francolinus	1960	USA (Alabama)	Extinct
Galliformes	Phasianidae	Francolinus francolinus	1960	USA (Arkansas)	Extinct
Galliformes	Phasianidae	Francolinus francolinus	1960	USA (Florida)	Established
Galliformes	Phasianidae	Francolinus francolinus	1960	USA (Kentucky)	Extinct
Galliformes	Phasianidae	Francolinus francolinus	1960	USA (New Mexico)	Extinct
Galliformes	Phasianidae	Francolinus francolinus	1960	USA (Oklahoma)	Extinct
Galliformes	Phasianidae	Francolinus francolinus	1961	Mariana Islands	Established
Galliformes	Phasianidae	Francolinus francolinus	1961	USA	Established
Galliformes	Phasianidae	Francolinus francolinus	1963	USA	Extinct
Galliformes	Phasianidae	Francolinus francolinus	1970	USA	Extinct
Galliformes	Phasianidae	Francolinus icterorhynchus	1961	Hawaiian Islands	Extinct
Galliformes	Phasianidae	Francolinus leucoscepus	1959	Hawaiian Islands	Extinct
Galliformes	Phasianidae	Francolinus pintadeanus	1962	Hawaiian Islands	Extinct
Galliformes	Phasianidae	Francolinus pondicerianus	1862	Mascarenes	Established
Galliformes	Phasianidae	Francolinus pondicerianus	1954	USA	Extinct
Galliformes	Phasianidae	Francolinus pondicerianus	1959	Hawaiian Islands	Established
Galliformes	Phasianidae	Francolinus pondicerianus	1959	USA (Nevada)	Extinct
Galliformes	Phasianidae	Francolinus pondicerianus	1959	USA (Texas)	Extinct
Galliformes	Phasianidae	Francolinus pondicerianus	1960	USA (New Mexico)	Extinct
Galliformes	Phasianidae	Francolinus pondicerianus	1960	USA (Oklahoma)	Extinct
Galliformes	Phasianidae	Francolinus pondicerianus	1961	Hawaiian Islands (Lanai)	Established
Galliformes	Phasianidae	Francolinus pondicerianus	1961	Hawaiian Islands (Maui)	Established
Galliformes	Phasianidae	Francolinus pondicerianus	1961	Hawaiian Islands (Molokai)	Established
Galliformes	Phasianidae	Francolinus pondicerianus	1961	Mariana Islands	Established
Galliformes	Phasianidae	Francolinus pondicerianus	1967	USA	Extinct
Galliformes	Phasianidae	Gallus gallus	1839	Trinidad and Tobago	Extinct
Galliformes	Phasianidae	Gallus gallus	1961	USA (Alabama)	Extinct
Galliformes	Phasianidae	Gallus gallus	1961	USA (Oklahoma)	Extinct

Galliformes	Phasianidae	Gallus gallus	1962	USA	Extinct
Galliformes	Phasianidae	Gallus gallus	1963	USA (Florida)	Extinct
Galliformes	Phasianidae	Gallus gallus	1963	USA (Georgia)	Extinct
Galliformes	Phasianidae	Gallus gallus	1963	USA (Louisiana)	Extinct
Galliformes	Phasianidae	Gallus gallus	1964	USA	Extinct
Galliformes	Phasianidae	Gallus gallus	1966	Australia	Extinct
Galliformes	Phasianidae	Gallus gallus	1966	USA	Extinct
Galliformes	Phasianidae	Gallus sonneratii	1962	Hawaiian Islands	Extinct
Galliformes	Phasianidae	Lagopus lagopus	1873	New Zealand	Extinct
Galliformes	Phasianidae	Lagopus lagopus	1905	USA	Extinct
Galliformes	Phasianidae	Lagopus lagopus	1939	Germany	Extinct
Galliformes	Phasianidae	Lagopus lagopus	1948	USA	Extinct
Galliformes	Phasianidae	Lophophorus impejanus	1871	Australia (Gembrook Reserve, Victoria)	Extinct
Galliformes	Phasianidae	Lophophorus impejanus	1871	Australia (Phillip Island, Victoria)	Extinct
Galliformes	Phasianidae	Lophura ignita	1871	Australia	Extinct
Galliformes	Phasianidae	Lophura leucomelanos	1926	USA	Extinct
Galliformes	Phasianidae	Lophura leucomelanos	1941	USA	Extinct
Galliformes	Phasianidae	Lophura leucomelanos	1958	USA	Extinct
Galliformes	Phasianidae	Lophura leucomelanos	1962	Hawaiian Islands	Established
Galliformes	Phasianidae	Lophura leucomelanos	1964	USA	Extinct
Galliformes	Phasianidae	Lophura leucomelanos	1966	USA	Extinct
Galliformes	Phasianidae	Lophura leucomelanos	1969	USA	Extinct
Galliformes	Phasianidae	Meleagris gallopavo	1910	Canada	Extinct
Galliformes	Phasianidae	Meleagris gallopavo	1958	Hawaiian Islands	Established
Galliformes	Phasianidae	Meleagris gallopavo	1959	Germany	Extinct
Galliformes	Phasianidae	Meleagris gallopavo	1961	Canada	Established
Galliformes	Phasianidae	Pavo cristatus	1867	New Zealand	Extinct
Galliformes	Phasianidae	Pavo cristatus	1870	Australia (Victoria)	Extinct
Galliformes	Phasianidae	Pavo cristatus	1870	Australia (Melbourne, Victoria)	Extinct
Galliformes	Phasianidae	Perdicula argoondah	1915	Mascarenes	Extinct
Galliformes	Phasianidae	Perdix dauurica	1956	Russia	Extinct
Galliformes	Phasianidae	Perdix perdix	1867	New Zealand (Auckland)	Extinct
Galliformes	Phasianidae	Perdix perdix	1867	New Zealand (Canterbury)	Extinct
Galliformes	Phasianidae	Perdix perdix	1869	New Zealand (Otago)	Extinct
Galliformes	Phasianidae	Perdix perdix	1869	New Zealand (Wellington)	Extinct
Galliformes	Phasianidae	Perdix perdix	1894	New Zealand	Extinct
Galliformes	Phasianidae	Perdix perdix	1899	New Zealand	Extinct
Galliformes	Phasianidae	Perdix perdix	1899	USA (Illinois)	Extinct
Galliformes	Phasianidae	Perdix perdix	1899	USA (Indiana)	Extinct
Galliformes	Phasianidae	Perdix perdix	1900	USA	Established
Galliformes	Phasianidae	Perdix perdix	1901	USA	Established
Galliformes	Phasianidae	Perdix perdix	1904	Canada	Established
Galliformes	Phasianidae	Perdix perdix	1906	USA	Established
Galliformes	Phasianidae	Perdix perdix	1908	Canada (Alberta)	Established
Galliformes	Phasianidae	Perdix perdix	1908	Canada (British Columbia)	Extinct
Galliformes	Phasianidae	Perdix perdix	1908	USA (California)	Extinct
Galliformes	Phasianidae	Perdix perdix	1908	USA (Washington)	Established
Galliformes	Phasianidae	Perdix perdix	1909	Canada (Alberta)	Established
Galliformes	Phasianidae	Perdix perdix	1909	Canada (James Island, British Columbia)	Extinct
Galliformes	Phasianidae	Perdix perdix	1909	Canada (South Pender Island, British Columbia)	Extinct
Galliformes	Phasianidae	Perdix perdix	1909	Canada (Sydney Island, British Columbia)	Extinct
Galliformes	Phasianidae	Perdix perdix	1909	USA	Established
Galliformes	Phasianidae	Perdix perdix	1910	USA	Established
Galliformes	Phasianidae	Perdix perdix	1911	USA	Extinct
Galliformes	Phasianidae	Perdix perdix	1913	USA	Established

Galliformes	Phasianidae	Perdix perdix	1914	USA	Established
Galliformes	Phasianidae	Perdix perdix	1915	USA	Established
Galliformes	Phasianidae	Perdix perdix	1921	USA	Established
Galliformes	Phasianidae	Perdix perdix	1923	USA	Extinct
Galliformes	Phasianidae	Perdix perdix	1924	Canada	Established
Galliformes	Phasianidae	Perdix perdix	1924	USA	Established
Galliformes	Phasianidae	Perdix perdix	1925	USA (Idaho)	Established
Galliformes	Phasianidae	Perdix perdix	1925	USA (Utah)	Extinct
Galliformes	Phasianidae	Perdix perdix	1926	USA	Established
Galliformes	Phasianidae	Perdix perdix	1936	Australia	Extinct
Galliformes	Phasianidae	Perdix perdix	1959	New Zealand (Canterbury)	Established
Galliformes	Phasianidae	Perdix perdix	1959	New Zealand (North Island)	Extinct
Galliformes	Phasianidae	Perdix perdix	1969	USA	Extinct
Galliformes	Phasianidae	Perdix perdix	1970	USA (Colorado)	Extinct
Galliformes	Phasianidae	Perdix perdix	1970	USA (Pennsylvania)	Extinct
Galliformes	Phasianidae	Phasianus colchicus	-325	Mariana Islands	Established
Galliformes	Phasianidae	Phasianus colchicus	1730	USA	Extinct
Galliformes	Phasianidae	Phasianus colchicus	1842	New Zealand	Extinct
Galliformes	Phasianidae	Phasianus colchicus	1851	New Zealand (Auckland)	Established
Galliformes	Phasianidae	Phasianus colchicus	1851	New Zealand (Otago)	Established
Galliformes	Phasianidae	Phasianus colchicus	1855	Australia (Churchill Island, Victoria)	Extinct
Galliformes	Phasianidae	Phasianus colchicus	1855	Australia (Phillip Island, Victoria)	Extinct
Galliformes	Phasianidae	Phasianus colchicus	1855	Australia (Western Australia)	Extinct
Galliformes	Phasianidae	Phasianus colchicus	1858	Australia	Extinct
Galliformes	Phasianidae	Phasianus colchicus	1864	Australia (Phillip Island, Victoria)	Extinct
Galliformes	Phasianidae	Phasianus colchicus	1864	Australia (Victoria)	Extinct
Galliformes	Phasianidae	Phasianus colchicus	1865	Hawaiian Islands	Established
Galliformes	Phasianidae	Phasianus colchicus	1865	New Zealand	Established
Galliformes	Phasianidae	Phasianus colchicus	1867	New Zealand (Canterbury)	Established
Galliformes	Phasianidae	Phasianus colchicus	1867	New Zealand (Canterbury)	Established
Galliformes	Phasianidae	Phasianus colchicus	1869	New Zealand	Extinct
Galliformes	Phasianidae	Phasianus colchicus	1874	New Zealand	Established
Galliformes	Phasianidae	Phasianus colchicus	1877	USA	Established
Galliformes	Phasianidae	Phasianus colchicus	1879	New Zealand	Established
Galliformes	Phasianidae	Phasianus colchicus	1881	USA	Extinct
Galliformes	Phasianidae	Phasianus colchicus	1883	Canada	Established
Galliformes	Phasianidae	Phasianus colchicus	1886	Canada	Extinct
Galliformes	Phasianidae	Phasianus colchicus	1886	Chile	Extinct
Galliformes	Phasianidae	Phasianus colchicus	1889	USA	Extinct
Galliformes	Phasianidae	Phasianus colchicus	1890	Canada (Pender Island, British Columbia)	Established
Galliformes	Phasianidae	Phasianus colchicus	1890	Canada (Prevost Island, British Columbia)	Extinct
Galliformes	Phasianidae	Phasianus colchicus	1895	New Zealand	Extinct
Galliformes	Phasianidae	Phasianus colchicus	1897	USA	Established
Galliformes	Phasianidae	Phasianus colchicus	1912	USA	Established
Galliformes	Phasianidae	Phasianus colchicus	1917	USA	Established
Galliformes	Phasianidae	Phasianus colchicus	1926	USA	Established
Galliformes	Phasianidae	Phasianus colchicus	1927	Canada	Established
Galliformes	Phasianidae	Phasianus colchicus	1928	Australia	Established
Galliformes	Phasianidae	Phasianus colchicus	1928	USA	Established
Galliformes	Phasianidae	Phasianus colchicus	1931	USA	Established
Galliformes	Phasianidae	Phasianus colchicus	1933	USA	Established
Galliformes	Phasianidae	Phasianus colchicus	1937	USA	Established
Galliformes	Phasianidae	Phasianus colchicus	1949	USA	Extinct
Galliformes	Phasianidae	Phasianus colchicus	1958	Russia	Extinct
Galliformes	Phasianidae	Phasianus colchicus	1958	Ukraine	Extinct

Galliformes	Phasianidae	Phasianus colchicus	1959	Hawaiian Islands	Established
Galliformes	Phasianidae	Phasianus colchicus	1960	USA	Established
Galliformes	Phasianidae	Phasianus colchicus	1961	Australia	Established
Galliformes	Phasianidae	Phasianus colchicus	1963	USA	Extinct
Galliformes	Phasianidae	Phasianus colchicus	1963	USA	Established
Galliformes	Phasianidae	Phasianus colchicus	1964	USA	Established
Galliformes	Phasianidae	Phasianus colchicus	1965	USA	Established
Galliformes	Phasianidae	Phasianus colchicus	1967	USA	Established
Galliformes	Phasianidae	Phasianus colchicus	?	Russia	Extinct
Galliformes	Phasianidae	Phasianus colchicus	?	USA	Established
Galliformes	Phasianidae	Syrmaticus reevesii	1870	British Isles	Extinct
Galliformes	Phasianidae	Syrmaticus reevesii	1889	USA	Extinct
Galliformes	Phasianidae	Syrmaticus reevesii	1897	New Zealand	Extinct
Galliformes	Phasianidae	Syrmaticus reevesii	1914	USA	Extinct
Galliformes	Phasianidae	Syrmaticus reevesii	1931	USA	Extinct
Galliformes	Phasianidae	Syrmaticus reevesii	1940	USA	Extinct
Galliformes	Phasianidae	Syrmaticus reevesii	1947	USA	Extinct
Galliformes	Phasianidae	Syrmaticus reevesii	1954	USA	Extinct
Galliformes	Phasianidae	Syrmaticus reevesii	1957	Hawaiian Islands	Extinct
Galliformes	Phasianidae	Syrmaticus reevesii	1959	USA (Arkansas)	Extinct
Galliformes	Phasianidae	Syrmaticus reevesii	1959	USA (Kentucky)	Extinct
Galliformes	Phasianidae	Syrmaticus reevesii	1960	Hawaiian Islands	Extinct
Galliformes	Phasianidae	Syrmaticus reevesii	1960	USA	Extinct
Galliformes	Phasianidae	Syrmaticus reevesii	1963	USA	Extinct
Galliformes	Phasianidae	Syrmaticus reevesii	1964	USA (Missouri)	Extinct
Galliformes	Phasianidae	Syrmaticus reevesii	1964	USA (Tennessee)	Extinct
Galliformes	Phasianidae	Syrmaticus reevesii	1969	USA	Extinct
Galliformes	Phasianidae	Syrmaticus reevesii	1970	British Isles	Extinct
Galliformes	Phasianidae	Syrmaticus soemmerringii	1885	USA	Extinct
Galliformes	Phasianidae	Tetrao tetrix	1879	New Zealand	Extinct
Galliformes	Phasianidae	Tetrao tetrix	1886	Canada (Nicomen Lake, British Columbia)	Extinct
Galliformes	Phasianidae	Tetrao tetrix	1886	Canada (Vancouver Island, British Columbia)	Extinct
Galliformes	Phasianidae	Tetrao tetrix	1900	New Zealand	Extinct
Galliformes	Phasianidae	Tetrao tetrix	1900	USA	Extinct
Galliformes	Phasianidae	Tetrao tetrix	1904	USA	Extinct
Galliformes	Phasianidae	Tetrao tetrix	1906	Canada	Extinct
Galliformes	Phasianidae	Tetrao tetrix	1906	USA	Extinct
Galliformes	Phasianidae	Tetrao urogallus	1893	USA	Extinct
Galliformes	Phasianidae	Tetrao urogallus	1895	USA	Extinct
Galliformes	Phasianidae	Tetrao urogallus	1903	Canada	Extinct
Galliformes	Phasianidae	Tetrao urogallus	1904	USA	Extinct
Galliformes	Phasianidae	Tetrao urogallus	1906	Canada (Lake Bunsen, British Columbia)	Extinct
Galliformes	Phasianidae	Tetrao urogallus	1906	Canada (Vancouver Island, British Columbia)	Extinct
Galliformes	Phasianidae	Tetrao urogallus	1906	USA (Bay Pond Reserve, New York)	Extinct
Galliformes	Phasianidae	Tetrao urogallus	1906	USA (Adirondacks, New York)	Extinct
Galliformes	Phasianidae	Tetrao urogallus	1907	Canada	Extinct
Galliformes	Phasianidae	Tetrao urogallus	1950	USA	Extinct
Galliformes	Phasianidae	Tetraogallus himalayensis	1960	USA	Extinct
Galliformes	Phasianidae	Tetraogallus himalayensis	1963	USA	Established
Galliformes	Phasianidae	Tympanuchus cupido	1861	Germany	Extinct
Galliformes	Phasianidae	Tympanuchus cupido	1874	British Isles	Extinct
Galliformes	Phasianidae	Tympanuchus cupido	1895	Hawaiian Islands (Niihau)	Extinct
Galliformes	Phasianidae	Tympanuchus cupido	1895	Hawaiian Islands (Kauai)	Extinct
Galliformes	Phasianidae	Tympanuchus cupido	1895	Hawaiian Islands (Oahu)	Extinct
Galliformes	Phasianidae	Tympanuchus phasianellus	1876	New Zealand	Extinct

Galliformes	Phasianidae	Tympanuchus phasianellus	1889	USA	Extinct
Galliformes	Phasianidae	Tympanuchus phasianellus	1904	USA	Extinct
Galliformes	Phasianidae	Tympanuchus phasianellus	1932	Hawaiian Islands	Extinct
Galliformes	Phasianidae	Tympanuchus phasianellus	1938	USA	Extinct
Galliformes	Phasianidae	Tympanuchus phasianellus	1939	USA	Extinct
Gruiformes	Rallidae	Gallirallus australis	1962	New Zealand	Established
Passeriformes	Alaudidae	Alauda arvensis	1850	Australia	Extinct
Passeriformes	Alaudidae	Alauda arvensis	1852	USA	Extinct
Passeriformes	Alaudidae	Alauda arvensis	1855	Australia	Established
Passeriformes	Alaudidae	Alauda arvensis	1856	Australia	Established
Passeriformes	Alaudidae	Alauda arvensis	1862	Australia (Adelaide)	Established
Passeriformes	Alaudidae	Alauda arvensis	1862	Australia (Tasmania)	Established
Passeriformes	Alaudidae	Alauda arvensis	1864	New Zealand	Established
Passeriformes	Alaudidae	Alauda arvensis	1867	New Zealand (Auckland)	Established
Passeriformes	Alaudidae	Alauda arvensis	1867	New Zealand (Otago)	Established
Passeriformes	Alaudidae	Alauda arvensis	1867	New Zealand (Canterbury)	Established
Passeriformes	Alaudidae	Alauda arvensis	1871	USA	Extinct
Passeriformes	Alaudidae	Alauda arvensis	1874	New Zealand	Established
Passeriformes	Alaudidae	Alauda arvensis	1879	New Zealand	Established
Passeriformes	Alaudidae	Alauda arvensis	1889	USA	Extinct
Passeriformes	Alaudidae	Alauda arvensis	1896	USA	Extinct
Passeriformes	Alaudidae	Alauda arvensis	1902	Canada	Established
Passeriformes	Alaudidae	Alauda arvensis	1908	USA	Extinct
Passeriformes	Alaudidae	Lullula arborea	1852	USA	Extinct
Passeriformes	Alaudidae	Lullula arborea	1872	New Zealand	Extinct
Passeriformes	Alaudidae	Lullula arborea	1889	USA	Extinct
Passeriformes	Corvidae	Corvus brachyrhynchos	1876	Caribbean British Islands	Established
Passeriformes	Corvidae	Corvus frugilegus	1862	New Zealand (Canterbury)	Established
Passeriformes	Corvidae	Corvus frugilegus	1862	New Zealand (Nelson)	Extinct
Passeriformes	Corvidae	Corvus frugilegus	1869	New Zealand (Auckland)	Extinct
Passeriformes	Corvidae	Corvus frugilegus	1869	New Zealand (Hawke's Bay)	Established
Passeriformes	Corvidae	Corvus frugilegus	1890	South Africa	Extinct
Passeriformes	Corvidae	Corvus monedula	1868	New Zealand	Extinct
Passeriformes	Corvidae	Corvus splendens	1898	Malaysia	Established
Passeriformes	Corvidae	Corvus splendens	1994	The Netherlands	Established
Passeriformes	Corvidae	Cyanopica cyana	1974	China	Extinct
Passeriformes	Corvidae	Gymnorhina tibicen	1864	New Zealand	Established
Passeriformes	Corvidae	Gymnorhina tibicen	1865	New Zealand	Established
Passeriformes	Corvidae	Gymnorhina tibicen	1867	New Zealand	Established
Passeriformes	Corvidae	Gymnorhina tibicen	1874	New Zealand	Established
Passeriformes	Corvidae	Paradisaea apoda	1912	British Virgin Islands	Extinct
Passeriformes	Fringillidae	Agelaius phoeniceus	1869	New Zealand	Extinct
Passeriformes	Fringillidae	Cardinalis cardinalis	1880	USA	Extinct
Passeriformes	Fringillidae	Carduelis cannabina	1865	Australia	Extinct
Passeriformes	Fringillidae	Carduelis cannabina	1865	New Zealand	Extinct
Passeriformes	Fringillidae	Carduelis cannabina	1867	New Zealand (Canterbury)	Extinct
Passeriformes	Fringillidae	Carduelis cannabina	1867	New Zealand (Otago)	Extinct
Passeriformes	Fringillidae	Carduelis cannabina	1881	New Zealand	Extinct
Passeriformes	Fringillidae	Carduelis cannabina	1889	USA (Oregon)	Extinct
Passeriformes	Fringillidae	Carduelis cannabina	1889	USA (Portland, Oregon)	Extinct
Passeriformes	Fringillidae	Carduelis carduelis	1852	USA	Extinct
Passeriformes	Fringillidae	Carduelis carduelis	1856	Australia	Established
Passeriformes	Fringillidae	Carduelis carduelis	1856	Australia	Established
Passeriformes	Fringillidae	Carduelis carduelis	1862	New Zealand	Established
Passeriformes	Fringillidae	Carduelis carduelis	1867	New Zealand (Auckland)	Established

Passeriformes	Fringillidae	Carduelis carduelis	1867	New Zealand (Otago)	Established
Passeriformes	Fringillidae	Carduelis carduelis	1871	New Zealand	Established
Passeriformes	Fringillidae	Carduelis carduelis	1877	New Zealand	Established
Passeriformes	Fringillidae	Carduelis carduelis	1879	Australia	Established
Passeriformes	Fringillidae	Carduelis carduelis	1889	USA	Extinct
Passeriformes	Fringillidae	Carduelis chloris	1862	New Zealand	Extinct
Passeriformes	Fringillidae	Carduelis chloris	1863	Australia (Victoria)	Established
Passeriformes	Fringillidae	Carduelis chloris	1863	Australia (South Australia)	Established
Passeriformes	Fringillidae	Carduelis chloris	1863	New Zealand	Established
Passeriformes	Fringillidae	Carduelis chloris	1865	New Zealand	Established
Passeriformes	Fringillidae	Carduelis chloris	1868	New Zealand	Established
Passeriformes	Fringillidae	Carduelis chloris	1869	Saint Helena	Extinct
Passeriformes	Fringillidae	Carduelis chloris	1879	Australia	Established
Passeriformes	Fringillidae	Carduelis chloris	1889	USA	Extinct
Passeriformes	Fringillidae	Carduelis flammea	1868	New Zealand (Canterbury)	Established
Passeriformes	Fringillidae	Carduelis flammea	1868	New Zealand (Otago)	Established
Passeriformes	Fringillidae	Carduelis flammea	1871	New Zealand	Established
Passeriformes	Fringillidae	Carduelis flammea	1875	New Zealand	Established
Passeriformes	Fringillidae	Carduelis flavirostris	1871	New Zealand	Extinct
Passeriformes	Fringillidae	Carduelis flavirostris	1880	New Zealand	Extinct
Passeriformes	Fringillidae	Carduelis spinus	1864	Australia	Extinct
Passeriformes	Fringillidae	Carduelis spinus	1866	Australia	Extinct
Passeriformes	Fringillidae	Carduelis spinus	1879	New Zealand (Canterbury)	Extinct
Passeriformes	Fringillidae	Carduelis spinus	1879	New Zealand (Wellington)	Extinct
Passeriformes	Fringillidae	Carduelis spinus	1889	USA	Extinct
Passeriformes	Fringillidae	Drepanidini cantans	1967	Midway Islands (Eastern Island)	Extinct
Passeriformes	Fringillidae	Drepanidini cantans	1967	Midway Islands (Pearl and Hermes Atoll)	Established
Passeriformes	Fringillidae	Drepanidini cantans	1967	Midway Islands (Tern Island)	Extinct
Passeriformes	Fringillidae	Emberiza cirlus	1871	New Zealand	Established
Passeriformes	Fringillidae	Emberiza cirlus	1879	New Zealand	Extinct
Passeriformes	Fringillidae	Emberiza cirlus	1880	New Zealand	Established
Passeriformes	Fringillidae	Emberiza citrinella	1862	New Zealand	Established
Passeriformes	Fringillidae	Emberiza citrinella	1862	New Zealand	Extinct
Passeriformes	Fringillidae	Emberiza citrinella	1863	Australia	Extinct
Passeriformes	Fringillidae	Emberiza citrinella	1865	New Zealand	Established
Passeriformes	Fringillidae	Emberiza citrinella	1868	New Zealand	Established
Passeriformes	Fringillidae	Emberiza citrinella	1879	New Zealand	Extinct
Passeriformes	Fringillidae	Emberiza hortulana	1863	Australia	Extinct
Passeriformes	Fringillidae	Emberiza hortulana	1885	New Zealand	Extinct
Passeriformes	Fringillidae	Emberiza schoeniclus	1871	New Zealand	Extinct
Passeriformes	Fringillidae	Emberiza schoeniclus	1873	New Zealand	Extinct
Passeriformes	Fringillidae	Fringilla coelebs	1802	New Zealand	Extinct
Passeriformes	Fringillidae	Fringilla coelebs	1863	Australia	Extinct
Passeriformes	Fringillidae	Fringilla coelebs	1864	New Zealand	Established
Passeriformes	Fringillidae	Fringilla coelebs	1867	New Zealand	Established
Passeriformes	Fringillidae	Fringilla coelebs	1868	New Zealand	Established
Passeriformes	Fringillidae	Fringilla coelebs	1874	New Zealand	Established
Passeriformes	Fringillidae	Fringilla coelebs	1879	New Zealand	Extinct
Passeriformes	Fringillidae	Fringilla coelebs	1889	USA	Extinct
Passeriformes	Fringillidae	Fringilla coelebs	1892	USA	Extinct
Passeriformes	Fringillidae	Fringilla coelebs	1898	South Africa	Established
Passeriformes	Fringillidae	Fringilla montifringilla	1868	New Zealand	Extinct
Passeriformes	Fringillidae	Fringilla montifringilla	1874	New Zealand	Extinct
Passeriformes	Fringillidae	Fringilla montifringilla	1879	Australia	Extinct
Passeriformes	Fringillidae	Paroaria coronata	1977	South Africa	Extinct

Passeriformes	Fringillidae	Paroaria coronata	1977	South Africa	Extinct
Passeriformes	Fringillidae	Piranga rubra	1868	New Zealand	Extinct
Passeriformes	Fringillidae	Pyrrhula pyrrhula	1875	New Zealand	Extinct
Passeriformes	Fringillidae	Pyrrhula pyrrhula	1879	Australia	Extinct
Passeriformes	Fringillidae	Pyrrhula pyrrhula	1889	USA	Extinct
Passeriformes	Fringillidae	Serinus canaria	1859	Australia	Extinct
Passeriformes	Fringillidae	Serinus canaria	1910	Midway Islands (Sand Island)	Established
Passeriformes	Fringillidae	Serinus canaria	1910	Midway Islands (Sand Island)	Established
Passeriformes	Fringillidae	Serinus canaria	1939	British Isles	Extinct
Passeriformes	Fringillidae	Serinus mozambicus	1977	Seychelles Islands	Established
Passeriformes	Fringillidae	Sicalis flaveola	1951	Panama	Established
Passeriformes	Fringillidae	Sturnella neglecta	1869	New Zealand	Extinct
Passeriformes	Fringillidae	Tiaris canora	1963	The Bahamas	Established
Passeriformes	Maluridae	Malurus cyaneus	1923	New Zealand	Extinct
Passeriformes	Meliphagidae	Manorina melanocephala	1874	New Zealand	Extinct
Passeriformes	Meliphagidae	Manorina melanocephala	1879	New Zealand	Extinct
Passeriformes	Meliphagidae	Manorina melanocephala	1880	New Zealand	Extinct
Passeriformes	Meliphagidae	Manorina melanophrys	1874	New Zealand	Extinct
Passeriformes	Menuridae	Menura novaehollandiae	1934	Australia	Established
Passeriformes	Menuridae	Menura novaehollandiae	1945	Australia	Established
Passeriformes	Muscicapidae	Copsychus saularis	1922	Hawaiian Islands	Established
Passeriformes	Muscicapidae	Erithacus rubecula	1852	USA	Extinct
Passeriformes	Muscicapidae	Erithacus rubecula	1857	Australia	Extinct
Passeriformes	Muscicapidae	Erithacus rubecula	1868	New Zealand	Extinct
Passeriformes	Muscicapidae	Erithacus rubecula	1883	New Zealand	Extinct
Passeriformes	Muscicapidae	Erithacus rubecula	1885	New Zealand	Extinct
Passeriformes	Muscicapidae	Erithacus rubecula	1889	USA	Extinct
Passeriformes	Muscicapidae	Luscinia megarhynchos	1857	Australia	Extinct
Passeriformes	Muscicapidae	Luscinia megarhynchos	1891	USA	Extinct
Passeriformes	Muscicapidae	Luscinia megarhynchos	1897	USA	Extinct
Passeriformes	Muscicapidae	Luscinia megarhynchos	1901	USA	Extinct
Passeriformes	Muscicapidae	Turdus merula	1852	Saint Helena	Extinct
Passeriformes	Muscicapidae	Turdus merula	1852	USA	Extinct
Passeriformes	Muscicapidae	Turdus merula	1862	Australia	Established
Passeriformes	Muscicapidae	Turdus merula	1862	New Zealand	Established
Passeriformes	Muscicapidae	Turdus merula	1863	Australia	Established
Passeriformes	Muscicapidae	Turdus merula	1865	New Zealand (Auckland)	Established
Passeriformes	Muscicapidae	Turdus merula	1865	New Zealand (Canterbury)	Established
Passeriformes	Muscicapidae	Turdus merula	1865	New Zealand (Otago)	Established
Passeriformes	Muscicapidae	Turdus merula	1889	USA	Extinct
Passeriformes	Muscicapidae	Turdus philomelos	1852	USA	Extinct
Passeriformes	Muscicapidae	Turdus philomelos	1859	Australia	Established
Passeriformes	Muscicapidae	Turdus philomelos	1862	New Zealand	Extinct
Passeriformes	Muscicapidae	Turdus philomelos	1863	New Zealand	Established
Passeriformes	Muscicapidae	Turdus philomelos	1864	Australia	Extinct
Passeriformes	Muscicapidae	Turdus philomelos	1865	New Zealand	Established
Passeriformes	Muscicapidae	Turdus philomelos	1867	New Zealand	Established
Passeriformes	Muscicapidae	Turdus philomelos	1878	New Zealand	Established
Passeriformes	Muscicapidae	Turdus philomelos	1889	USA	Extinct
Passeriformes	Muscicapidae	Turdus philomelos	1900	Saint Helena	Extinct
Passeriformes	Passeridae	Amandava amandava	1858	India	Extinct
Passeriformes	Passeridae	Estrilda astrild	1964	Hawaiian Islands	Established
Passeriformes	Passeridae	Estrilda melpoda	1965	Hawaiian Islands	Established
Passeriformes	Passeridae	Estrilda melpoda	1965	USA	Established
Passeriformes	Passeridae	Euplectes albonotatus	1931	Australia	Extinct

Passeriformes	Passeridae	Euplectes franciscanus	1971	Puerto Rico	Established
Passeriformes	Passeridae	Euplectes orix	1926	Australia	Extinct
Passeriformes	Passeridae	Euplectes orix	1982	Puerto Rico	Extinct
Passeriformes	Passeridae	Foudia madagascariensis	1977	Seychelles Islands	Established
Passeriformes	Passeridae	Foudia sechellarum	1965	Seychelles Islands	Extinct
Passeriformes	Passeridae	Lonchura castaneothorax	1861	New Zealand	Extinct
Passeriformes	Passeridae	Lonchura castaneothorax	1864	New Zealand	Extinct
Passeriformes	Passeridae	Lonchura castaneothorax	1867	New Zealand	Extinct
Passeriformes	Passeridae	Lonchura malabarica	1972	Hawaiian Islands	Established
Passeriformes	Passeridae	Lonchura malacca	1929	Australia	Extinct
Passeriformes	Passeridae	Lonchura malacca	1938	China	Extinct
Passeriformes	Passeridae	Lonchura malacca	1965	USA	Extinct
Passeriformes	Passeridae	Lonchura punctulata	1868	New Zealand	Extinct
Passeriformes	Passeridae	Lonchura punctulata	1947	Australia	Established
Passeriformes	Passeridae	Neochmia temporalis	1867	New Zealand	Extinct
Passeriformes	Passeridae	Neochmia temporalis	1868	New Zealand	Extinct
Passeriformes	Passeridae	Padda oryzivora	1856	Australia	Extinct
Passeriformes	Passeridae	Padda oryzivora	1867	New Zealand	Extinct
Passeriformes	Passeridae	Passer domesticus	1845	Mascarenes	Established
Passeriformes	Passeridae	Passer domesticus	1850	Australia	Established
Passeriformes	Passeridae	Passer domesticus	1851	USA	Extinct
Passeriformes	Passeridae	Passer domesticus	1852	USA	Established
Passeriformes	Passeridae	Passer domesticus	1855	New Zealand	Established
Passeriformes	Passeridae	Passer domesticus	1859	New Zealand	Established
Passeriformes	Passeridae	Passer domesticus	1863	Australia	Established
Passeriformes	Passeridae	Passer domesticus	1866	New Zealand	Established
Passeriformes	Passeridae	Passer domesticus	1868	New Zealand	Established
Passeriformes	Passeridae	Passer domesticus	1868	USA	Established
Passeriformes	Passeridae	Passer domesticus	1870	Caribbean British Islands	Established
Passeriformes	Passeridae	Passer domesticus	1871	Hawaiian Islands	Established
Passeriformes	Passeridae	Passer domesticus	1871	New Zealand	Established
Passeriformes	Passeridae	Passer domesticus	1873	Argentina	Established
Passeriformes	Passeridae	Passer domesticus	1882	India	Established
Passeriformes	Passeridae	Passer domesticus	1922	Cape Verde Islands	Established
Passeriformes	Passeridae	Passer domesticus	1958	Argentina	Extinct
Passeriformes	Passeridae	Passer domesticus	1968	New Zealand	Established
Passeriformes	Passeridae	Passer domesticus	1976	Papua-New Guinea	Extinct
Passeriformes	Passeridae	Passer montanus	1863	Australia	Established
Passeriformes	Passeridae	Passer montanus	1868	New Zealand (Auckland)	Extinct
Passeriformes	Passeridae	Passer montanus	1868	New Zealand (Otago)	Extinct
Passeriformes	Passeridae	Passer montanus	1870	USA	Established
Passeriformes	Passeridae	Passer montanus	1964	Malaysia	Established
Passeriformes	Passeridae	Ploceus cucullatus	1993	Cape Verde Islands	Extinct
Passeriformes	Passeridae	Ploceus philippinus	1970	China	Established
Passeriformes	Passeridae	Prunella modularis	1867	New Zealand (Auckland)	Established
Passeriformes	Passeridae	Prunella modularis	1867	New Zealand (Canterbury)	Established
Passeriformes	Passeridae	Prunella modularis	1868	New Zealand	Established
Passeriformes	Passeridae	Prunella modularis	1880	New Zealand	Established
Passeriformes	Passeridae	Stagonopleura bella	1870	New Zealand	Extinct
Passeriformes	Passeridae	Stagonopleura bella	1884	New Zealand	Extinct
Passeriformes	Passeridae	Stagonopleura guttata	1874	New Zealand	Extinct
Passeriformes	Passeridae	Stagonopleura guttata	?	Hawaiian Islands	Extinct
Passeriformes	Passeridae	Taeniopygia guttata	1884	New Zealand	Extinct
Passeriformes	Passeridae	Taeniopygia guttata	1937	Australia	Extinct
Passeriformes	Passeridae	Taeniopygia guttata	1961	Nauru	Extinct

Passeriformes	Pycnonotidae	Pycnonotus cafer	1917	Australia	Extinct
Passeriformes	Pycnonotidae	Pycnonotus cafer	1928	Tonga	Established
Passeriformes	Pycnonotidae	Pycnonotus jocosus	1891	Mascarenes	Established
Passeriformes	Pycnonotidae	Pycnonotus jocosus	1960	USA	Established
Passeriformes	Pycnonotidae	Pycnonotus jocosus	1965	Hawaiian Islands	Established
Passeriformes	Sturnidae	Acridotheres tristis	1862	Australia	Established
Passeriformes	Sturnidae	Acridotheres tristis	1871	New Zealand	Extinct
Passeriformes	Sturnidae	Acridotheres tristis	1875	New Zealand	Established
Passeriformes	Sturnidae	Acridotheres tristis	1885	Saint Helena	Established
Passeriformes	Sturnidae	Acridotheres tristis	1888	South Africa	Established
Passeriformes	Sturnidae	Acridotheres tristis	1918	Australia	Established
Passeriformes	Sturnidae	Acridotheres tristis	1918	French Polynesia	Established
Passeriformes	Sturnidae	Acridotheres tristis	1941	Mariana Islands	Extinct
Passeriformes	Sturnidae	Acridotheres tristis	1954	British Indian Ocean Territory	Established
Passeriformes	Sturnidae	Acridotheres tristis	1968	Australia	Established
Passeriformes	Sturnidae	Gracula religiosa	1960	Hawaiian Islands	Established
Passeriformes	Sturnidae	Mimus polyglottos	1892	USA	Established
Passeriformes	Sturnidae	Sturnus vulgaris	1852	Saint Helena	Extinct
Passeriformes	Sturnidae	Sturnus vulgaris	1860	Australia	Established
Passeriformes	Sturnidae	Sturnus vulgaris	1863	Australia	Established
Passeriformes	Sturnidae	Sturnus vulgaris	1865	New Zealand	Established
Passeriformes	Sturnidae	Sturnus vulgaris	1867	New Zealand (Canterbury)	Established
Passeriformes	Sturnidae	Sturnus vulgaris	1867	New Zealand (Otago)	Established
Passeriformes	Sturnidae	Sturnus vulgaris	1877	New Zealand	Established
Passeriformes	Sturnidae	Sturnus vulgaris	1881	Australia	Established
Passeriformes	Sturnidae	Sturnus vulgaris	1889	USA	Extinct
Passeriformes	Sturnidae	Sturnus vulgaris	1890	USA	Established
Passeriformes	Sturnidae	Sturnus vulgaris	1897	South Africa	Established
Passeriformes	Sturnidae	Sturnus vulgaris	1949	Venezuela	Extinct
Passeriformes	Sturnidae	Sturnus vulgaris	1954	Russia	Extinct
Passeriformes	Sylviidae	Cettia diphone	1930	Hawaiian Islands	Established
Passeriformes	Sylviidae	Garrulax caerulatus	1928	Hawaiian Islands	Established
Passeriformes	Sylviidae	Garrulax leucolophus	1969	Hawaiian Islands	Extinct
Passeriformes	Sylviidae	Leiothrix lutea	1898	France	Extinct
Passeriformes	Sylviidae	Leiothrix lutea	1905	British Isles	Extinct
Passeriformes	Sylviidae	Sylvia atricapilla	1872	New Zealand	Extinct
Passeriformes	Sylviidae	Sylvia atricapilla	1900	USA	Extinct
Passeriformes	Sylviidae	Sylvia communis	?	New Zealand	Extinct
Passeriformes	Zosteropidae	Zosterops japonicus	1928	Hawaiian Islands	Established
Psittaciformes	Psittacidae	Agapornis fischeri	1928	Tanzania	Established
Psittaciformes	Psittacidae	Agapornis personatus	1928	Tanzania	Established
Psittaciformes	Psittacidae	Agapornis roseicollis	1965	Australia	Extinct
Psittaciformes	Psittacidae	Amazona autumnalis	1968	USA	Established
Psittaciformes	Psittacidae	Amazona finschi	1976	USA	Established
Psittaciformes	Psittacidae	Brotogeris jugularis	1970	USA	Extinct
Psittaciformes	Psittacidae	Eolophus roseicapillus	1886	Saint Helena	Extinct
Psittaciformes	Psittacidae	Melopsittacus undulatus	1871	New Zealand	Extinct
Psittaciformes	Psittacidae	Melopsittacus undulatus	1961	USA	Established
Psittaciformes	Psittacidae	Myiopsitta monachus	1968	USA	Extinct
Psittaciformes	Psittacidae	Myiopsitta monachus	1985	Czech Republic	Established
Psittaciformes	Psittacidae	Nandayus nenday	1968	USA	Established
Psittaciformes	Psittacidae	Nandayus nenday	1975	USA	Established
Psittaciformes	Psittacidae	Platycercus elegans	1961	Australia	Extinct
Psittaciformes	Psittacidae	Psittacula cyanocephala	1979	South Africa	Extinct
Psittaciformes	Psittacidae	Psittacula krameri	1967	Germany	Established

Psittaciformes	Psittacidae	Pyrrhura leucotis	1971	Brazil	Extinct
Strigiformes	Strigidae	Athene noctua	1842	British Isles	Extinct
Strigiformes	Strigidae	Athene noctua	1874	British Isles	Established
Strigiformes	Strigidae	Athene noctua	1906	New Zealand	Established
Strigiformes	Strigidae	Bubo virginianus	1927	French Polynesia	Established
Strigiformes	Tytonidae	Tyto alba	1899	New Zealand	Extinct
Strigiformes	Tytonidae	Tyto alba	1922	Australia	Extinct
Strigiformes	Tytonidae	Tyto alba	1951	Seychelles Islands	Established
Strigiformes	Tytonidae	Tyto alba	1958	Hawaiian Islands	Established
Strigiformes	Tytonidae	Tyto alba	1959	Hawaiian Islands	Established
Struthioniformes	Casuaridae	Dromaius novaehollandiae	1926	Australia	Extinct
Struthioniformes	Rheidae	Rhea americana	1899	France	Extinct
Struthioniformes	Rheidae	Rhea americana	1941	Ukraine	Extinct
Struthioniformes	Struthionidae	Struthio camelus	1879	Saint Helena	Extinct
Struthioniformes	Struthionidae	Struthio camelus	1919	Australia	Established
Tinamiformes	Tinamidae	Eudromia elegans	1970	USA	Extinct
Tinamiformes	Tinamidae	Eudromia elegans	1971	USA	Extinct
Tinamiformes	Tinamidae	Nothoprocta ornata	1969	USA	Extinct
Tinamiformes	Tinamidae	Nothoprocta perdicaria	1966	Hawaiian Islands	Extinct
Tinamiformes	Tinamidae	Nothoprocta perdicaria	1977	USA	Extinct
Tinamiformes	Tinamidae	Nothura darwinii	1970	USA	Extinct
Tinamiformes	Tinamidae	Nothura maculosa	1966	USA	Extinct
Tinamiformes	Tinamidae	Nothura maculosa	1968	USA	Extinct
Tinamiformes	Tinamidae	Rhynchotus rufescens	1970	USA	Extinct
Tinamiformes	Tinamidae	Tinamus major	1923	USA	Extinct

Table 2. Complete set list of solutions for random effects. Random effects are: taxonomic hierarchy (orders, families within orders, genus within families and species within genus) and biome of introduction (Australasian, Ethiopian, Nearctic, Neotropical, Oriental and Palaearctic). Asterisk (*) marks $P<0.05$.

Effect	order	family	genus	species	biomeintro	Estimate	Pred	DF	t Value	Pr>|t|
order	Apodifor					0.05506	0.4094	616	0.13	0.8930
order	Ciconiif					-0.1000	0.3641	616	-0.27	0.7836
order	Columbif					0.1766	0.3523	616	0.50	0.6163
order	Coracifo					-0.03583	0.4034	616	-0.09	0.9293
order	Cracifor					0.08160	0.4055	616	0.20	0.8406
order	Gallifor					-0.3285	0.3132	616	-1.05	0.2946
order	Gruiform					0.03981	0.4103	616	0.10	0.9227
order	Passerif					-0.2098	0.2841	616	-0.74	0.4606
order	Psittaci					0.09989	0.3708	616	0.27	0.7877
order	Strigifo					-0.08537	0.3912	616	-0.22	0.8273
order	Struthio					0.006853	0.4008	616	0.02	0.9864
order	Tinamifo					-0.1331	0.3982	616	-0.33	0.7382
family(order)	Anserifo	Anatidae				0	.	.	.	.
family(order)	Anserifo	Dendrocy				0	.	.	.	.
family(order)	Apodifor	Apodidae				0	.	.	.	.
family(order)	Ciconiif	Ardeidae				0	.	.	.	.
family(order)	Ciconiif	Charadri				0	.	.	.	.
family(order)	Ciconiif	Phalacro				0	.	.	.	.
family(order)	Ciconiif	Phoenico				0	.	.	.	.
family(order)	Ciconiif	Pterocli				0	.	.	.	.
family(order)	Ciconiif	Sphenisc				0	.	.	.	.
family(order)	Columbif	Columbid				0	.	.	.	.
family(order)	Coracifo	Daceloni				0	.	.	.	.
family(order)	Cracifor	Cracidae				0	.	.	.	.
family(order)	Cracifor	Megapodi				0	.	.	.	.
family(order)	Gallifor	Numidida				0	.	.	.	.
family(order)	Gallifor	Odontoph				0	.	.	.	.
family(order)	Gallifor	Phasiani				0	.	.	.	.
family(order)	Gruiform	Rallidae				0	.	.	.	.

family(order)	Passerif	Alaudida		0	.	.	.	.
family(order)	Passerif	Corvidae		0	.	.	.	.
family(order)	Passerif	Fringill		0	.	.	.	.
family(order)	Passerif	Malurida		0	.	.	.	.
family(order)	Passerif	Meliphag		0	.	.	.	.
family(order)	Passerif	Menurida		0	.	.	.	.
family(order)	Passerif	Muscicap		0	.	.	.	.
family(order)	Passerif	Passerid		0	.	.	.	.
family(order)	Passerif	Pycnonot		0	.	.	.	.
family(order)	Passerif	Sturnida		0	.	.	.	.
family(order)	Passerif	Sylviida		0	.	.	.	.
family(order)	Passerif	Zosterop		0	.	.	.	.
family(order)	Psittaci	Psittaci		0	.	.	.	.
family(order)	Strigifo	Strigida		0	.	.	.	.
family(order)	Strigifo	Tytonida		0	.	.	.	.
family(order)	Struthio	Casuarid		0	.	.	.	.
family(order)	Struthio	Rheidae		0	.	.	.	.
family(order)	Struthio	Struthio		0	.	.	.	.
family(order)	Tinamifo	Tinamida		0	.	.	.	.
genus(family)		Alaudida	Alauda	0	.	.	.	.
genus(family)		Anatidae	Aix	0	.	.	.	.
genus(family)		Anatidae	Alopoche	0	.	.	.	.
genus(family)		Anatidae	Anas	0	.	.	.	.
genus(family)		Anatidae	Anser	0	.	.	.	.
genus(family)		Anatidae	Aythya	0	.	.	.	.
genus(family)		Anatidae	Branta	0	.	.	.	.
genus(family)		Anatidae	Cairina	0	.	.	.	.
genus(family)		Anatidae	Cereopsi	0	.	.	.	.
genus(family)		Anatidae	Cygnus	0	.	.	.	.
genus(family)		Anatidae	Oxyura	0	.	.	.	.
genus(family)		Anatidae	Plectrop	0	.	.	.	.
genus(family)		Apodidae	Collocal	0	.	.	.	.
genus(family)		Ardeidae	Bubulcus	0	.	.	.	.
genus(family)		Ardeidae	Nycticor	0	.	.	.	.

genus(family)	Casuarid	Dromaius	0	.	.	.	.
genus(family)	Charadri	Pluviali	0	.	.	.	.
genus(family)	Charadri	Vanellus	0	.	.	.	.
genus(family)	Columbid	Columba	0	.	.	.	.
genus(family)	Columbid	Geopelia	0	.	.	.	.
genus(family)	Columbid	Geophaps	0	.	.	.	.
genus(family)	Columbid	Leucosar	0	.	.	.	.
genus(family)	Columbid	Phaps	0	.	.	.	.
genus(family)	Columbid	Streptop	0	.	.	.	.
genus(family)	Columbid	Zenaida	0	.	.	.	.
genus(family)	Corvidae	Corvus	0	.	.	.	.
genus(family)	Corvidae	Cyanopic	0	.	.	.	.
genus(family)	Corvidae	Gymnorhi	0	.	.	.	.
genus(family)	Corvidae	Paradise	0	.	.	.	.
genus(family)	Cracidae	Crax	0	.	.	.	.
genus(family)	Cracidae	Ortalis	0	.	.	.	.
genus(family)	Daceloni	Dacelo	0	.	.	.	.
genus(family)	Dendrocy	Dendrocy	0	.	.	.	.
genus(family)	Fringill	Agelaius	0	.	.	.	.
genus(family)	Fringill	Cardinal	0	.	.	.	.
genus(family)	Fringill	Cardueli	0	.	.	.	.
genus(family)	Fringill	Emberiza	0	.	.	.	.
genus(family)	Fringill	Fringill	0	.	.	.	.
genus(family)	Fringill	Paroaria	0	.	.	.	.
genus(family)	Fringill	Piranga	0	.	.	.	.
genus(family)	Fringill	Pyrrhula	0	.	.	.	.
genus(family)	Fringill	Serinus	0	.	.	.	.
genus(family)	Fringill	Sicalis	0	.	.	.	.
genus(family)	Fringill	Sturnell	0	.	.	.	.
genus(family)	Fringill	Tiaris	0	.	.	.	.
genus(family)	Malurida	Malurus	0	.	.	.	.
genus(family)	Megapodi	Leipoa	0	.	.	.	.
genus(family)	Meliphag	Manorina	0	.	.	.	.
genus(family)	Menurida	Menura	0	.	.	.	.

genus(family)	Muscicap	Copsychu	0	.	.	.	.
genus(family)	Muscicap	Erithacu	0	.	.	.	.
genus(family)	Muscicap	Luscinia	0	.	.	.	.
genus(family)	Muscicap	Turdus	0	.	.	.	.
genus(family)	Numidida	Numida	0	.	.	.	.
genus(family)	Odontoph	Callipep	0	.	.	.	.
genus(family)	Odontoph	Colinus	0	.	.	.	.
genus(family)	Odontoph	Cyrtonyx	0	.	.	.	.
genus(family)	Odontoph	Oreortyx	0	.	.	.	.
genus(family)	Passerid	Amandava	0	.	.	.	.
genus(family)	Passerid	Estrilda	0	.	.	.	.
genus(family)	Passerid	Euplecte	0	.	.	.	.
genus(family)	Passerid	Foudia	0	.	.	.	.
genus(family)	Passerid	Lonchura	0	.	.	.	.
genus(family)	Passerid	Neochmia	0	.	.	.	.
genus(family)	Passerid	Padda	0	.	.	.	.
genus(family)	Passerid	Passer	0	.	.	.	.
genus(family)	Passerid	Ploceus	0	.	.	.	.
genus(family)	Passerid	Prunella	0	.	.	.	.
genus(family)	Passerid	Stagonop	0	.	.	.	.
genus(family)	Passerid	Taeniopy	0	.	.	.	.
genus(family)	Phalacro	Phalacro	0	.	.	.	.
genus(family)	Phasiani	Alectori	0	.	.	.	.
genus(family)	Phasiani	Ammoperd	0	.	.	.	.
genus(family)	Phasiani	Bambusic	0	.	.	.	.
genus(family)	Phasiani	Bonasa	0	.	.	.	.
genus(family)	Phasiani	Chrysolo	0	.	.	.	.
genus(family)	Phasiani	Coturnix	0	.	.	.	.
genus(family)	Phasiani	Francoli	0	.	.	.	.
genus(family)	Phasiani	Gallus	0	.	.	.	.
genus(family)	Phasiani	Lagopus	0	.	.	.	.
genus(family)	Phasiani	Lophopho	0	.	.	.	.
genus(family)	Phasiani	Lophura	0	.	.	.	.
genus(family)	Phasiani	Meleagri	0	.	.	.	.

genus(family)	Phasiani	Pavo	0	.	.	.	.
genus(family)	Phasiani	Perdix	0	.	.	.	.
genus(family)	Phasiani	Phasianu	0	.	.	.	.
genus(family)	Phasiani	Syrmatic	0	.	.	.	.
genus(family)	Phasiani	Tetrao	0	.	.	.	.
genus(family)	Phasiani	Tetraoga	0	.	.	.	.
genus(family)	Phasiani	Tympanuc	0	.	.	.	.
genus(family)	Phoenico	Phoenico	0	.	.	.	.
genus(family)	Psittaci	Agaporni	0	.	.	.	.
genus(family)	Psittaci	Amazona	0	.	.	.	.
genus(family)	Psittaci	Brotoger	0	.	.	.	.
genus(family)	Psittaci	Eolophus	0	.	.	.	.
genus(family)	Psittaci	Melopsit	0	.	.	.	.
genus(family)	Psittaci	Myiopsit	0	.	.	.	.
genus(family)	Psittaci	Nandayus	0	.	.	.	.
genus(family)	Psittaci	Platycer	0	.	.	.	.
genus(family)	Psittaci	Psittacu	0	.	.	.	.
genus(family)	Psittaci	Pyrrhura	0	.	.	.	.
genus(family)	Pterocli	Pterocle	0	.	.	.	.
genus(family)	Pycnonot	Pycnonot	0	.	.	.	.
genus(family)	Rallidae	Galliral	0	.	.	.	.
genus(family)	Rheidae	Rhea	0	.	.	.	.
genus(family)	Sphenisc	Aptenody	0	.	.	.	.
genus(family)	Strigida	Athene	0	.	.	.	.
genus(family)	Strigida	Bubo	0	.	.	.	.
genus(family)	Struthio	Struthio	0	.	.	.	.
genus(family)	Sturnida	Acridoth	0	.	.	.	.
genus(family)	Sturnida	Gracula	0	.	.	.	.
genus(family)	Sturnida	Mimus	0	.	.	.	.
genus(family)	Sturnida	Sturnus	0	.	.	.	.
genus(family)	Sylviida	Garrulax	0	.	.	.	.
genus(family)	Sylviida	Leiothri	0	.	.	.	.
genus(family)	Sylviida	Sylvia	0	.	.	.	.
genus(family)	Tinamida	Eudromia	0	.	.	.	.

genus(family)	Tinamida	Nothopro		0	.	.	.	.	
genus(family)	Tinamida	Nothura		0	.	.	.	.	
genus(family)	Tinamida	Rhynchot		0	.	.	.	.	
genus(family)	Tinamida	Tinamus		0	.	.	.	.	
genus(family)	Tytonida	Tyto		0	.	.	.	.	
genus(family)	Zosterop	Zosterop		0	.	.	.	.	
species(genus)		Acridoth	ACRTRI	0.2927	0.6957	616	0.42	0.6741	
species(genus)		Agaporni	AGAFIS	0.3943	10.225	616	0.39	0.6999	
species(genus)		Agaporni	AGAPER	0.5510	10.074	616	0.55	0.5846	
species(genus)		Agaporni	AGAROS	-0.3815	10.241	616	-0.37	0.7096	
species(genus)		Agelaius	AGEPHO	-0.2848	10.408	616	-0.27	0.7844	
species(genus)		Aix	AIXGAL	0.1360	0.8720	616	0.16	0.8761	
species(genus)		Aix	AIXSPO	-0.3159	10.346	616	-0.31	0.7602	
species(genus)		Alauda	ALAARV	0.7213	0.5090	616	1.42	0.1570	
species(genus)		Alectori	ALEBAR	-11.949	0.8102	616	-1.47	0.1408	
species(genus)		Alectori	ALECHU	0.9533	0.3720	616	2.56	0.0106	*
species(genus)		Alectori	ALEGRA	0.3400	0.8618	616	0.39	0.6934	
species(genus)		Alectori	ALERUF	-0.3909	0.7519	616	-0.52	0.6034	
species(genus)		Alopoche	ALOAEG	0.8592	0.9847	616	0.87	0.3833	
species(genus)		Amandava	AMAAMA	-0.3819	10.228	616	-0.37	0.7090	
species(genus)		Amazona	AMAAUT	0.5503	10.078	616	0.55	0.5852	
species(genus)		Amazona	AMAFIN	0.5510	10.100	616	0.55	0.5856	
species(genus)		Ammoperd	AMMGRI	-0.1829	10.694	616	-0.17	0.8642	
species(genus)		Ammoperd	AMMHEY	-0.06784	11.148	616	-0.06	0.9515	
species(genus)		Anas	ANAACU	-0.4370	10.155	616	-0.43	0.6671	
species(genus)		Anas	ANAPLA	0.4236	0.6132	616	0.69	0.4899	
species(genus)		Anser	ANSANS	-0.5994	0.9567	616	-0.63	0.5312	
species(genus)		Anser	ANSCAE	-0.4735	10.104	616	-0.47	0.6395	
species(genus)		Anser	ANSIND	17.582	0.9260	616	1.90	0.0581	
species(genus)		Aptenody	APTPAT	-0.1460	10.834	616	-0.13	0.8929	
species(genus)		Athene	ATHNOC	-0.1952	0.9093	616	-0.21	0.8301	
species(genus)		Aythya	AYTFER	-0.2965	10.393	616	-0.29	0.7755	
species(genus)		Aythya	AYTFUL	-0.2666	10.464	616	-0.25	0.7990	
species(genus)		Bambusic	BAMTHO	-0.1554	10.789	616	-0.14	0.8855	

species(genus)	Bonasa	BONBON	-0.08854	11.055	616	-0.08	0.9362
species(genus)	Bonasa	BONUMB	12.185	0.6180	616	1.97	0.0491 *
species(genus)	Branta	BRACAN	0.6535	0.5540	616	1.18	0.2387
species(genus)	Branta	BRASAN	-0.1861	10.690	616	-0.17	0.8618
species(genus)	Brotoger	BROJUG	-0.3174	10.355	616	-0.31	0.7593
species(genus)	Bubo	BUBVIR	0.3076	10.396	616	0.30	0.7674
species(genus)	Bubulcus	BUBIB	0.8544	0.8125	616	1.05	0.2934
species(genus)	Cairina	CAIMOS	-0.6059	0.9559	616	-0.63	0.5264
species(genus)	Callipep	CALCAL	12.593	0.4629	616	2.72	0.0067 *
species(genus)	Callipep	CALDOU	-0.1804	10.706	616	-0.17	0.8663
species(genus)	Callipep	CALGAM	0.8102	0.7688	616	1.05	0.2924
species(genus)	Callipep	CALSQU	0.6814	0.9352	616	0.73	0.4665
species(genus)	Cardinal	CARCAR	-0.3019	10.370	616	-0.29	0.7710
species(genus)	Cardueli	CARCAN	-14.474	0.7873	616	-1.84	0.0665
species(genus)	Cardueli	CARCHL	0.4972	0.6301	616	0.79	0.4304
species(genus)	Cardueli	CARCRD	11.107	0.6338	616	1.75	0.0802
species(genus)	Cardueli	CARFLA	10.832	0.8652	616	1.25	0.2111
species(genus)	Cardueli	CARFLV	-0.8438	0.9203	616	-0.92	0.3595
species(genus)	Cardueli	CARSPI	-0.9035	0.8743	616	-1.03	0.3018
species(genus)	Cereopsi	CERNOV	0.09879	0.8353	616	0.12	0.9059
species(genus)	Chrysolo	CHRPIC	0.6104	0.9108	616	0.67	0.5030
species(genus)	Colinus	COLVIR	-13.033	0.6535	616	-1.99	0.0465 *
species(genus)	Collocal	COLVAN	0.4223	10.200	616	0.41	0.6790
species(genus)	Columba	COLPAL	-0.1779	10.720	616	-0.17	0.8683
species(genus)	Copsychu	COPSAU	0.6395	0.9988	616	0.64	0.5222
species(genus)	Corvus	CORBRA	0.4584	10.116	616	0.45	0.6506
species(genus)	Corvus	CORFRU	-0.9336	0.7484	616	-1.25	0.2127
species(genus)	Corvus	CORMON	-0.5991	10.009	616	-0.60	0.5497
species(genus)	Corvus	CORSPL	0.8803	0.9343	616	0.94	0.3464
species(genus)	Coturnix	COTCHI	0.7018	0.9369	616	0.75	0.4542
species(genus)	Coturnix	COTCOT	-0.3773	0.9930	616	-0.38	0.7041
species(genus)	Coturnix	COTJAP	-0.7647	0.9037	616	-0.85	0.3977
species(genus)	Coturnix	COTYPS	0.7055	0.7767	616	0.91	0.3641
species(genus)	Crax	CRARUB	-0.06848	11.148	616	-0.06	0.9510

species(genus)	Cyanopic	CYACYN	-0.3700	10.264	616	-0.36	0.7186
species(genus)	Cygnus	CYGATR	20.874	0.7783	616	2.68	0.0075 *
species(genus)	Cygnus	CYGOLO	0.6494	0.6280	616	1.03	0.3015
species(genus)	Cyrtonyx	CYRMON	-0.1419	10.838	616	-0.13	0.8959
species(genus)	Dacelo	DACNOV	-0.2748	0.8689	616	-0.32	0.7519
species(genus)	Dendrocy	DENAUT	-0.8161	0.9371	616	-0.87	0.3842
species(genus)	Dromaius	DRONOV	-0.1207	10.929	616	-0.11	0.9121
species(genus)	Emberiza	EMBCIR	0.5241	0.8254	616	0.63	0.5257
species(genus)	Emberiza	EMBCIT	0.05682	0.7055	616	0.08	0.9358
species(genus)	Emberiza	EMBHOR	-0.3618	10.072	616	-0.36	0.7196
species(genus)	Emberiza	EMBSCH	-0.3109	10.217	616	-0.30	0.7610
species(genus)	Eolophus	EOLROS	-0.4997	10.104	616	-0.49	0.6211
species(genus)	Erithacu	ERIRUB	-10.147	0.8519	616	-1.19	0.2341
species(genus)	Estrilda	ESTAST	0.3628	10.262	616	0.35	0.7238
species(genus)	Estrilda	ESTMLP	11.602	0.9058	616	1.28	0.2007
species(genus)	Eudromia	EUDELE	-0.4052	10.007	616	-0.40	0.6857
species(genus)	Euplecte	EUPALB	-0.1339	10.869	616	-0.12	0.9020
species(genus)	Euplecte	EUPFRA	0.7840	10.050	616	0.78	0.4356
species(genus)	Euplecte	EUPORI	-0.6108	0.9710	616	-0.63	0.5296
species(genus)	Foudia	FOUMAD	0.3243	10.321	616	0.31	0.7534
species(genus)	Foudia	FOUSEC	-0.4529	10.108	616	-0.45	0.6543
species(genus)	Francoli	FRAADS	-0.1715	10.732	616	-0.16	0.8731
species(genus)	Francoli	FRACAP	-0.08230	11.082	616	-0.07	0.9408
species(genus)	Francoli	FRACLA	-0.1175	10.934	616	-0.11	0.9144
species(genus)	Francoli	FRAERC	13.934	0.6728	616	2.07	0.0388 *
species(genus)	Francoli	FRAFRA	0.3071	0.5468	616	0.56	0.5746
species(genus)	Francoli	FRAICT	-0.1715	10.732	616	-0.16	0.8731
species(genus)	Francoli	FRALEU	-0.4046	10.194	616	-0.40	0.6916
species(genus)	Francoli	FRAPIN	-0.2544	10.484	616	-0.24	0.8084
species(genus)	Francoli	FRAPON	0.02955	0.5829	616	0.05	0.9596
species(genus)	Fringill	FRICOE	0.3804	0.5941	616	0.64	0.5222
species(genus)	Fringill	FRIMON	-0.9216	0.8962	616	-1.03	0.3042
species(genus)	Galliral	GALAUS	0.3053	10.406	616	0.29	0.7693
species(genus)	Gallus	GALGAL	-16.142	0.7665	616	-2.11	0.0356 *

species(genus)	Gallus	GALSON	-0.3425	10.292	616	-0.33	0.7394
species(genus)	Garrulax	GARCAE	0.4138	10.165	616	0.41	0.6841
species(genus)	Garrulax	GARLEU	-0.3941	10.191	616	-0.39	0.6991
species(genus)	Geopelia	GEOCUN	-0.1855	10.697	616	-0.17	0.8624
species(genus)	Geopelia	GEOSTR	11.635	0.7555	616	1.54	0.1241
species(genus)	Geophaps	GEOLOP	-0.7115	0.9135	616	-0.78	0.4363
species(genus)	Geophaps	GEOPLU	-0.06350	11.170	616	-0.06	0.9547
species(genus)	Gracula	GRAREL	0.4305	10.141	616	0.42	0.6714
species(genus)	Gymnorhi	GYMTIB	0.7728	0.9044	616	0.85	0.3931
species(genus)	Lagopus	LAGLAG	-0.4738	0.9645	616	-0.49	0.6234
species(genus)	Leiothri	LEILUT	-0.6689	0.9472	616	-0.71	0.4803
species(genus)	Leipoa	LEIOCE	-0.08970	11.057	616	-0.08	0.9354
species(genus)	Leucosar	LEUMEL	-0.4512	0.9786	616	-0.46	0.6449
species(genus)	Lonchura	LONCAS	-0.6914	0.9234	616	-0.75	0.4543
species(genus)	Lonchura	LONMAL	0.3067	10.359	616	0.30	0.7673
species(genus)	Lonchura	LONMLA	-0.5503	0.9536	616	-0.58	0.5641
species(genus)	Lonchura	LONPUN	0.1962	0.9127	616	0.21	0.8298
species(genus)	Lophopho	LOPIMP	-0.1010	10.983	616	-0.09	0.9268
species(genus)	Lophura	LOPIGN	-0.02166	11.379	616	-0.02	0.9848
species(genus)	Lophura	LOPLEU	-0.1388	0.7911	616	-0.18	0.8608
species(genus)	Luscinia	LUSMEG	-0.7413	0.9165	616	-0.81	0.4189
species(genus)	Malurus	MALCYA	-0.4836	10.072	616	-0.48	0.6313
species(genus)	Manorina	MANMEL	-16.312	0.8351	616	-1.95	0.0512
species(genus)	Manorina	MANMLA	-0.3335	10.305	616	-0.32	0.7463
species(genus)	Meleagri	MELGAL	12.923	0.8457	616	1.53	0.1270
species(genus)	Melopsit	MELUND	0.1503	0.9101	616	0.17	0.8689
species(genus)	Menura	MENNOV	0.6280	0.9608	616	0.65	0.5136
species(genus)	Mimus	MIMPOL	0.4237	10.154	616	0.42	0.6766
species(genus)	Myiopsit	MYIMON	-0.2649	0.9223	616	-0.29	0.7741
species(genus)	Nandayus	NANNEN	10.145	0.9244	616	1.10	0.2729
species(genus)	Neochmia	NEOTEM	-0.5284	0.9678	616	-0.55	0.5853
species(genus)	Nothopro	NOTORN	-0.1478	10.830	616	-0.14	0.8915
species(genus)	Nothura	NOTMAC	-0.3312	10.191	616	-0.32	0.7453
species(genus)	Numida	NUMMEL	-0.5102	0.9561	616	-0.53	0.5938

species(genus)	Nycticor	NYCNYC	0.6923	0.9636	616	0.72	0.4728
species(genus)	Oreortyx	OREPIC	-0.6663	0.9281	616	-0.72	0.4731
species(genus)	Ortalis	ORTVET	0.7840	10.080	616	0.78	0.4370
species(genus)	Oxyura	OXYJAM	0.7787	10.070	616	0.77	0.4396
species(genus)	Padda	PADORY	-0.7429	0.9319	616	-0.80	0.4256
species(genus)	Paradise	PARAPO	-0.6296	0.9988	616	-0.63	0.5287
species(genus)	Paroaria	PARCOR	-0.4131	0.9926	616	-0.42	0.6775
species(genus)	Passer	PASDOM	0.8128	0.6041	616	1.35	0.1790
species(genus)	Passer	PASMON	0.3775	0.7350	616	0.51	0.6077
species(genus)	Pavo	PAVCRI	-0.1369	10.816	616	-0.13	0.8993
species(genus)	Perdix	PERDAU	-0.2180	10.595	616	-0.21	0.8371
species(genus)	Perdix	PERPER	0.8174	0.4180	616	1.96	0.0509
species(genus)	Phalacro	PHACAR	-0.1911	10.682	616	-0.18	0.8581
species(genus)	Phaps	PHACHA	-0.6048	0.9467	616	-0.64	0.5231
species(genus)	Phasianu	PHACOL	11.134	0.4342	616	2.56	0.0106 *
species(genus)	Phoenico	PHORUB	-0.1572	10.791	616	-0.15	0.8842
species(genus)	Piranga	PIRRUB	-0.1866	10.687	616	-0.17	0.8614
species(genus)	Platycer	PLATELE	-0.5767	10.064	616	-0.57	0.5668
species(genus)	Plectrop	PLEGAM	-0.1286	10.891	616	-0.12	0.9060
species(genus)	Ploceus	PLOCUC	-0.5405	10.027	616	-0.54	0.5900
species(genus)	Ploceus	PLOPHI	0.6578	10.011	616	0.66	0.5113
species(genus)	Pluviali	PLUAPR	-0.3426	10.140	616	-0.34	0.7356
species(genus)	Pluviali	PLUSQU	-0.3887	10.026	616	-0.39	0.6984
species(genus)	Prunella	PRUMOD	10.749	0.8511	616	1.26	0.2071
species(genus)	Psittacu	PSICYA	-0.4350	10.178	616	-0.43	0.6692
species(genus)	Psittacu	PSIKRA	0.3961	10.231	616	0.39	0.6988
species(genus)	Pterocle	PTEEXU	-0.1686	0.8282	616	-0.20	0.8388
species(genus)	Pycnonot	PYCCAF	0.4440	0.9263	616	0.48	0.6318
species(genus)	Pycnonot	PYCJOC	0.9592	0.8901	616	1.08	0.2816
species(genus)	Pyrrhula	PYRPYR	-0.6273	0.9356	616	-0.67	0.5028
species(genus)	Pyrrhura	PYRLEU	-0.3662	10.283	616	-0.36	0.7219
species(genus)	Rhea	RHEAME	-0.1390	10.830	616	-0.13	0.8979
species(genus)	Rhynchot	RHYRUF	-0.1041	10.994	616	-0.09	0.9246
species(genus)	Serinus	SERCAN	0.6360	0.7863	616	0.81	0.4189

species(genus)	Serinus	SERMOZ		0.4452	10.117	616	0.44	0.6601
species(genus)	Sicalis	SICFLA		10.487	10.440	616	1.00	0.3156
species(genus)	Stagonop	STABEL		-0.5605	0.9618	616	-0.58	0.5602
species(genus)	Stagonop	STAGUT		-0.6421	0.9508	616	-0.68	0.4997
species(genus)	Streptop	STRBIT		-0.2779	10.438	616	-0.27	0.7901
species(genus)	Streptop	STRCHI		12.659	0.9103	616	1.39	0.1648
species(genus)	Streptop	STRDEC		0.8159	10.084	616	0.81	0.4188
species(genus)	Streptop	STRPIC		-0.2240	10.578	616	-0.21	0.8324
species(genus)	Streptop	STRSEN		0.5739	10.035	616	0.57	0.5676
species(genus)	Streptop	STRTUR		-0.1612	10.775	616	-0.15	0.8811
species(genus)	Struthio	STRCAM		0.3122	0.9297	616	0.34	0.7371
species(genus)	Sturnell	STUNEG		-0.2464	10.505	616	-0.23	0.8146
species(genus)	Sturnus	STUVUL		0.2850	0.5846	616	0.49	0.6261
species(genus)	Sylvia	SYLATR		-0.4519	0.9832	616	-0.46	0.6460
species(genus)	Sylvia	SYLCOM		-0.2040	10.627	616	-0.19	0.8478
species(genus)	Syrmatic	SYRREE		-22.313	0.7055	616	-3.16	0.0016 *
species(genus)	Syrmatic	SYRSOE		-0.05864	11.192	616	-0.05	0.9582
species(genus)	Taeniopy	TAEGUT		-0.6797	0.9256	616	-0.73	0.4630
species(genus)	Tetrao	TETTET		-10.847	0.8487	616	-1.28	0.2017
species(genus)	Tetrao	TETURO		-0.7439	0.8980	616	-0.83	0.4078
species(genus)	Tetraoga	TETHIM		0.6300	0.9434	616	0.67	0.5045
species(genus)	Tiaris	TIACAN		0.3741	10.230	616	0.37	0.7147
species(genus)	Tinamus	TINMAJ		-0.03277	11.321	616	-0.03	0.9769
species(genus)	Turdus	TURMER		0.2079	0.6446	616	0.32	0.7472
species(genus)	Turdus	TURPHI		0.1612	0.5991	616	0.27	0.7879
species(genus)	Tympanuc	TYMCUP		-0.4386	0.9760	616	-0.45	0.6533
species(genus)	Tympanuc	TYMPHA		-0.5527	0.9406	616	-0.59	0.5570
species(genus)	Tyto	TYTALB		-0.7671	0.8209	616	-0.93	0.3504
species(genus)	Vanellus	VANVAN		-0.9199	0.8787	616	-1.05	0.2956
species(genus)	Zenaida	ZENASI		0.1351	0.9224	616	0.15	0.8836
species(genus)	Zenaida	ZENMAC		0.2581	10.501	616	0.25	0.8059
species(genus)	Zosterop	ZOSJAP		0.2797	10.419	616	0.27	0.7885
biomeintro			Australa	0	.	.	.	.
biomeintro			Ethiopia	0	.	.	.	.

biomeintro	Nearctic	0	.	.	.	.
biomeintro	Neotropi	0	.	.	.	.
biomeintro	Oriental	0	.	.	.	.
biomeintro	Palaearc	0	.	.	.	.

Supplementary references. List of data sources for the species traits.

del Hoyo, J., Elliot, A. & Sargatal, J. (2006) *Handbook of the Birds of the World*, Vol. 12. Lynx Editions, Barcelona, Spain.

Ehrlich, P.R., Dobkin, D.S., Wheye, D. & Pimm S.L. (1994) *The Birdwatchwer's Handbook. A guide to the natural history of the birds of Britain and Europe*. Oxford University Press, Oxford, UK.

Cassey, P. (2002a) Comparative analyses of establishment among introduced land bird. Ph.D. thesis, Griffin University, Queensland, Australia.

Feare, C. & Craig, A. (1998). *Starlings and Mynas*. Christopher Helm, London, UK.

Iwaniuk, A.N. (2003) The evolution of brain size and structure in birds. Ph.D thesis, Monash University, Clayton, Australia.

Juniper, T. & Parr, M. (1998) *Parrots. A Guide to the Parrots of the World*. Pica Press, London, UK.

Long, J.L. (1981) *Introduced Birds of the World*. David and Charles, London, UK.

Madge, S. & Burn, H. (1999) *Crows & Jays. A Guide to the Crows, Jays and Magpies of the World*. Christopher Helm, London, UK.

Madge, S. & McGowan, P. (2002) *Pheasants, Partidges & Grouse. Including buttonquails, sandgrouses and allies*. Christopher Helm, London, UK.

McLain, D.K., Moulton, M.P. & Sanderson, J.G. (1999) Sexual selection and extinction: The fate of plumage-dimorphic and plumage-monomorphic birds introduced onto islands. *Evolutionary Ecology Research*, **1**, 549-565.

Mlíkovský, J. (1989a) Brain size in birds: 1. Tinamiformes through Ciconiiformes. *Vést. Cs. Spolec. Zool*. **53**, 33-45.

Mlíkovský, J. (1989b) Brain size in birds: 2. Falconiformes through Gaviiformes. *Vést. Cs. Spolec. Zool*. **53**, 200-213.

Mlíkovský, J. (1989c) Brain size in birds: 3. Columbiformes through Gaviiformes. *Vést. Cs. Spolec. Zool*. **53**, 252-264.

Mlíkovský, J. (1990) Brain size in birds: 4. Passeriformes. *Acta Soc Zool. Bohemoslov*. **54**, 27-37.

Sorci, G., Moller, A.P. & Clobert, J. (1998) Plumage dichromatism of birds predict introduction success in New Zealand. *Journal of Animal Ecology*, **67**, 263-269.

Taylor, B. & van Perlo, B. (1998) *Rails. A Guide to the Rails, Crakes, Gallinules and Coots of the World*. Pica Press, London, UK.

Questionnaire. Establishment risk assessment questionnaire and scoring system. Adapted from Bomford (2003).

Probability escaped or released individuals will establish a free-living population

1. Degree of climate match between species overseas range and Australia
    - Calculate the Climate Match Index: CMI=60(number of 10% grid squares) + 6(number of 20% grid squares) + (number of 30% grid squares) + (number of 40% grid squares) + (number of 50% grid squares)
    - Convert CMI to a climate match (1) score:
        - 1 = 1 (very low) CMI <150
        - 1 = 2 (low) CMI = 150-799
        - 1 = 3 (moderate) CMI = 800-1,999
        - 1 = 4 (high) CMI = 2,000-2,599
        - 1 = 5 (very high) CMI = 2,600-4,499
        - 1 = 6 (extreme) CMI ≥ 4,600 or overseas range unknown and climate match to Europe* unknown

    Climate match score 1 = 1-6

2. Exotic population overseas
    - No exotic population ever established = 0
    - Exotic populations only established on small islands less than 50,000 square kilometers (Tasmania is 67,800 square kilometers) = 2
    - Exotic populations only established on a island larger than 50,000 square kilometers or anywhere on a continent = 4

    Exotic elsewhere score 2 = 0-4

3. Taxonomic class
    - Bird = 0
    - Mammal, reptile or amphibian = 1

    Taxonomic class score 3 = 0-1

4. Non-migratory behavior
    - Migratory in its native range = 0
    - Non-migratory in its native range or unknown = 1

    Non-migratory behavior score 4 = 0-1

5. Diet
    - Specialist with a restricted range of foods = 0
    - Generalist with a broad diet of many food types or diet unknown = 1

    Diet score 5 = 0-1

6. Lives in disturbed habitats

- Only in undisturbed (natural) habitats = 0
- Can live in human-disturbed habitats (including grazing and agricultural lands, forests that are intensively managed or planted for timber harvesting and/or urban-suburban environments) or habitat use unknown = 1

Disturbed habitat score 6 = 0-1

Decision process

Establishment risk score: 1 + 2+ 3 + 4 + 5 + 6 (1-14)

For birds and mammals:

B < 7	low establishment risk
B = 7-8	moderate establishment risk
B = 9-10	high establishment risk
B > 10	extreme establishment risk

Appendix D

Chapter 5. From journals to plans: the importance of using scientific advice in invasive species management.

Table 1. Data set of the exotic birds species present in Catalonia. Information of the taxonomic position of the species (Sibley and Monroe Jr 1993), region of origin, primary source for the introduction, classification (AERC 2001) and their evaluation according to the risk assessment is provided.

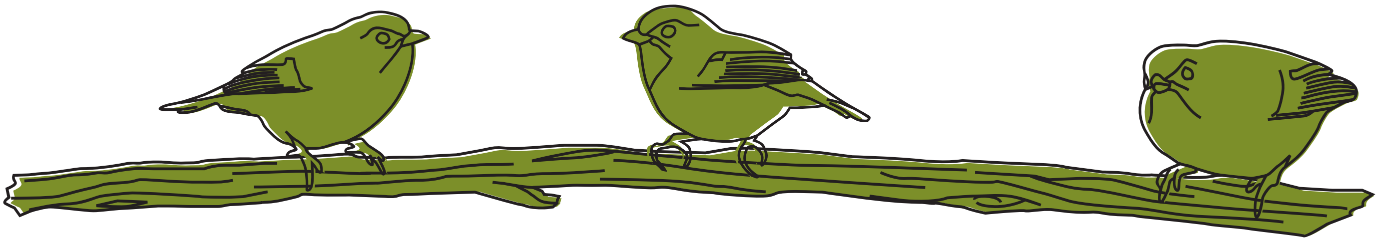
Scientific name	Taxonomical order	Region	Primary source	AERC classification	Risk assessment evaluation	Risk assessment category
Acridotheres ginginianus	Passeriformes	Asia	Pet	E3	0.24	Low risk
Acridotheres tristis	Passeriformes	Asia	Pet	E3	0.63	High risk
Agapornis canus	Psittaciformes	Africa	Pet	E3	0.63	High risk
Agapornis fischeri	Psittaciformes	Africa	Pet	E2	0.24	Low risk
Agapornis pullarius	Psittaciformes	Africa	Pet	E3	0.63	High risk
Agapornis roseicollis	Psittaciformes	Africa	Pet	E3	0.24	Low risk
Aix galericulata	Anseriformes	Asia	Ornamental	C5	0.24	Low risk
Aix sponsa	Anseriformes	North America	Ornamental	E3	0.24	Low risk
Alectoris chukar	Galliformes	Cosmopolitan	Game	E3	0.28	Low risk
Alectoris graeca	Galliformes	Cosmopolitan	Game	E3	0.28	Low risk
Alopochen aegyptiacus	Anseriformes	Africa	Ornamental	E2	0.2	Low risk
Amadina fasciata	Passeriformes	Africa	Pet	E3	0.63	High risk
Amandava amandava	Passeriformes	Asia	Pet	E1	0.28	Low risk
Amandava subflava	Passeriformes	Africa	Pet	E2	0.28	Low risk
Amazona aestiva	Psittaciformes	Central and South America	Pet	E3	0.63	High risk
Amazona amazonica	Psittaciformes	Central and South America	Pet	E3	0.63	High risk
Amazona ochrocephala	Psittaciformes	Central and South America	Pet	E3	0.63	High risk
Anas acuta	Anseriformes	Cosmopolitan	Ornamental	E3	0.24	Low risk
Anas bahamensis	Anseriformes	Central and South America	Ornamental	E3	0.24	Low risk
Anas cyanoptera	Anseriformes	Cosmopolitan	Ornamental	E3	0.24	Low risk
Anas discors	Anseriformes	North America	Ornamental	E3	0.24	Low risk
Anas falcata	Anseriformes	Asia	Ornamental	E3	0.24	Low risk
Anas formosa	Anseriformes	Asia	Ornamental	E3	0.28	Low risk
Anas penelope	Anseriformes	Cosmopolitan	Ornamental	E3	0.24	Low risk
Anas platyrhynchos	Anseriformes	Cosmopolitan	Ornamental/ Food	E3	0.24	Low risk
Anas rhynchotis	Anseriformes	Oceania	Ornamental	E3	0.24	Low risk

Anas sibilatrix	Anseriformes	Central and South America	Ornamental	E3	0.24	Low risk
Anser anser	Anseriformes	Cosmopolitan	Ornamental/ Food	E3	0.24	Low risk
Anser cygnoides	Anseriformes	Asia	Ornamental	E3	0.24	Low risk
Anser indicus	Anseriformes	Asia	Ornamental	E3	0.24	Low risk
Ara ararauna	Psittaciformes	Central and South America	Pet	E3	0.24	Low risk
Aratinga acuticaudata	Psittaciformes	Central and South America	Pet	E1	0.63	High risk
Aratinga aurea	Psittaciformes	Central and South America	Pet	E3	0.63	High risk
Aratinga erythrogenys	Psittaciformes	Central and South America	Pet	E2	0.63	High risk
Aratinga holochlora	Psittaciformes	Central and South America	Pet	E3	0.24	Low risk
Aratinga jandaya	Psittaciformes	Central and South America	Pet	E3	0.24	Low risk
Aratinga leucophthalmus	Psittaciformes	Central and South America	Pet	E3	0.63	High risk
Aratinga mitrata	Psittaciformes	Central and South America	Pet	E1	0.63	High risk
Aratinga nana	Psittaciformes	Central and South America	Pet	E3	0.24	Low risk
Barnardius zonarius	Psittaciformes	Oceania	Pet	E3	0.63	High risk
Branta canadensis	Anseriformes	North America	Ornamental	C5	0.48	Medium risk
Branta leucopsis	Anseriformes	Europe	Ornamental	E3	0.24	Low risk
Branta sandvicensis	Anseriformes	Oceania	Ornamental	E3	0.24	Low risk
Cacatua galerita	Psittaciformes	Oceania	Pet	E3	0.63	High risk
Cacatua sulphurea	Psittaciformes	Asia	Pet	E3	0.24	Low risk
Cairina moschata	Anseriformes	Central and South America	Ornamental/ Food	E2	0.24	Low risk
Callipepla californica	Galliformes	North America	Game	E3	0.2	Low risk
Callonetta leucophrys	Anseriformes	Central and South America	Ornamental	E3	0.24	Low risk
Carduelis yarrellii	Passeriformes	Central and South America	Pet	E3	0.24	Low risk
Chenonetta jubata	Anseriformes	Oceania	Ornamental	E3	0.28	Low risk
Chrysolophus amherstiae	Galliformes	Asia	Ornamental	E3	0.24	Low risk
Chrysolophus pictus	Galliformes	Asia	Ornamental	E3	0.24	Low risk
Ciconia abdimii	Ciconiiformes	Africa	Ornamental	E3	0.48	Medium risk
Ciconia ciconia	Ciconiiformes	Cosmopolitan	Fauna improvement	E3	0.24	Low risk
Colinus virginianus	Galliformes	Cosmopolitan	Game	E2	0.24	Low risk
Columba livia	Columbiformes	Cosmopolitan	Food	C2	0.48	Medium risk
Coturnix japonica	Galliformes	Asia	Game	E3	0.24	Low risk
Cyanoliseus	Psittaciformes	Central and	Pet	E2	0.24	Low risk

patagonus		South America				
Cygnus atratus	Anseriformes	Oceania	Ornamental	E3	0.24	Low risk
Cygnus olor	Anseriformes	Cosmopolitan	Ornamental	E2	0.24	Low risk
Dendrocygna autumnalis	Anseriformes	Central and South America	Ornamental	E3	0.24	Low risk
Dendrocygna bicolor	Anseriformes	Cosmopolitan	Ornamental	E3	0.24	Low risk
Dendrocygna viduata	Anseriformes	Cosmopolitan	Ornamental	E3	0.24	Low risk
Dromaius novaehollandiae	Struthioniformes	Oceania	Ornamental	E3	0.2	Low risk
Emberiza bruniceps	Passeriformes	Asia	Pet	E3	0.63	High risk
Eophona migratoria	Passeriformes	Africa	Pet	E3	0.45	Medium risk
Estrilda astrild	Passeriformes	Africa	Pet	C1	0.28	Low risk
Estrilda caerulescens	Passeriformes	Africa	Pet	E3	0.28	Low risk
Estrilda melpoda	Passeriformes	Africa	Pet	E1	0.28	Low risk
Estrilda rhodopyga	Passeriformes	Africa	Pet	E3	0.28	Low risk
Estrilda troglodytes	Passeriformes	Africa	Pet	E1	0.24	Low risk
Euplectes afer	Passeriformes	Africa	Pet	E2	0.63	High risk
Euplectes fransciscanus	Passeriformes	Africa	Pet	E3	0.24	Low risk
Euplectes hordeaceus	Passeriformes	Africa	Pet	E3	0.63	High risk
Euplectes jacksoni	Passeriformes	Africa	Pet	E3	0.24	Low risk
Euplectes macrourus	Passeriformes	Africa	Pet	E3	0.63	High risk
Euplectes nigroventris	Passeriformes	Africa	Pet	E3	0.24	Low risk
Euplectes orix	Passeriformes	Africa	Pet	E3	0.24	Low risk
Falco biarmicus	Ciconiiformes	Cosmopolitan	Falconry	E3	0.63	High risk
Falco cherrug	Ciconiiformes	Cosmopolitan	Falconry	E3	0.24	Low risk
Francolinus francolinus	Galliformes	Asia	Game	E3	0.2	Low risk
Gallus gallus	Galliformes	Asia	Ornamental/ Food	E3	0.28	Low risk
Geopelia cuneata	Columbiformes	Oceania	Ornamental	E3	0.28	Low risk
Gracula religiosa	Passeriformes	Asia	Pet	E3	0.24	Low risk
Haliaeetus leucocephalus	Ciconiiformes	North America	Falconry	E3	0.63	High risk
Lagonosticta senegala	Passeriformes	Africa	Pet	E3	0.2	Low risk
Lamprotornis chalybaeus	Passeriformes	Africa	Pet	E3	0.24	Low risk
Lamprotornis purpureus	Passeriformes	Africa	Pet	E3	0.63	High risk
Lamprotornis superbus	Passeriformes	Africa	Pet	E3	0.63	High risk
Leiothrix lutea	Passeriformes	Asia	Pet	C1	0.63	High risk
Leptoptilos crumeniferus	Ciconiiformes	Africa	Ornamental	E3	0.24	Low risk
Lonchura	Passeriformes	Africa	Pet	E3	0.28	Low risk

cucullata						
Lonchura maja	Passeriformes	Asia	Pet	E3	0.28	Low risk
Lonchura malacca	Passeriformes	Asia	Pet	E3	0.63	High risk
Lonchura nigriceps	Passeriformes	Africa	Pet	E3	0.28	Low risk
Lonchura punctulata	Passeriformes	Asia	Pet	E3	0.28	Low risk
Lonchura striata	Passeriformes	Asia	Pet	E3	0.28	Low risk
Meleagris gallopavo	Galliformes	North America	Ornamental/ Food	E3	0.2	Low risk
Melopsittacus undulatus	Psittaciformes	Oceania	Pet	E3	0.63	High risk
Mycteria ibis	Ciconiiformes	Africa	Ornamental	E3	0.24	Low risk
Myiopsitta monachus	Psittaciformes	Central and South America	Pet	C1	0.63	High risk
Nandayus nenday	Psittaciformes	Central and South America	Pet	E2	0.24	Low risk
Netta rufina	Anseriformes	Cosmopolitan	Ornamental	E3	0.24	Low risk
Numida meleagris	Galliformes	Africa	Ornamental/ Food	E3	0.28	Low risk
Bubo scandiacus	Strigiformes	Cosmopolitan	Falconry	E3	0.24	Low risk
Nymphicus hollandicus	Psittaciformes	Oceania	Pet	E3	0.63	High risk
Oena capensis	Columbiformes	Cosmopolitan	Ornamental	E3	0.28	Low risk
Oxyura jamaicensis	Anseriformes	North America	Ornamental	C5	0.24	Low risk
Padda oryzivora	Passeriformes	Asia	Pet	E3	0.63	High risk
Parabuteo unicinctus	Ciconiiformes	Central and South America	Falconry	E3	0.63	High risk
Paroaria coronata	Passeriformes	Central and South America	Pet	E2	0.24	Low risk
Passer luteus	Passeriformes	Africa	Pet	E3	0.63	High risk
Pavo cristatus	Galliformes	Asia	Ornamental	E3	0.24	Low risk
Pelecanus onocrotalus	Ciconiiformes	Cosmopolitan	Ornamental	E3	0.24	Low risk
Phasianus colchicus	Galliformes	Asia	Game	C1	0.48	Medium risk
Phoenicopterus ruber	Ciconiiformes	Central and South America	Ornamental	E3	0.24	Low risk
Platycercus elegans	Psittaciformes	Oceania	Pet	E3	0.63	High risk
Platycercus eximius	Psittaciformes	Oceania	Pet	E3	0.63	High risk
Ploceus cucullatus	Passeriformes	Africa	Pet	E2	0.63	High risk
Ploceus galbula	Passeriformes	Africa	Pet	E2	0.63	High risk
Ploceus manyar	Passeriformes	Asia	Pet	E3	0.24	Low risk
Ploceus melanocephalus	Passeriformes	Africa	Pet	E3	0.24	Low risk
Ploceus nigerrimus	Passeriformes	Africa	Pet	E3	0.63	High risk
Ploceus vitellinus	Passeriformes	Africa	Pet	E3	0.24	Low risk
Poicephalus crassus	Psittaciformes	Africa	Pet	E3	0.24	Low risk
Poicephalus senegalus	Psittaciformes	Africa	Pet	E2	0.24	Low risk

Psephotus haematonotus	Psittaciformes	Oceania	Pet	E3	0.63	High risk
Psittacula alexandri	Psittaciformes	Asia	Pet	E3	0.63	High risk
Psittacula eupatria	Psittaciformes	Asia	Pet	E3	0.63	High risk
Psittacula krameri	Psittaciformes	Cosmopolitan	Pet	C1	0.63	High risk
Psittacus erithacus	Psittaciformes	Africa	Pet	E3	0.63	High risk
Pytilia melba	Passeriformes	Asia	Pet	E3	0.63	High risk
Pycnonotus jocosus	Passeriformes	Central and South America	Pet	E3	0.63	High risk
Pyrrhura frontalis	Psittaciformes	Africa	Pet	E3	0.24	Low risk
Quelea erythrops	Passeriformes	Africa	Pet	E3	0.45	Medium risk
Quelea quelea	Passeriformes	Africa	Pet	E1	0.45	Medium risk
Rhea americana	Struthioniformes	Central and South America	Ornamental/ Food	E3	0.28	Low risk
Sarkidiornis melanotos	Anseriformes	Cosmopolitan	Ornamental	E3	0.24	Low risk
Serinus atrogularis	Passeriformes	Cosmopolitan	Pet	E3	0.63	High risk
Serinus canaria	Passeriformes	Africa	Pet	E3	0.63	High risk
Serinus dorsostriatus	Passeriformes	Africa	Pet	E3	0.24	Low risk
Serinus mozambicus	Passeriformes	Africa	Pet	E3	0.63	High risk
Sicalis flaveola	Passeriformes	Central and South America	Pet	E3	0.63	High risk
Streptopelia roseogrisea	Columbiformes	Cosmopolitan	Ornamental	E2	0.28	Low risk
Streptopelia senegalensis	Columbiformes	Cosmopolitan	Ornamental	E3	0.48	Medium risk
Struthio camelus	Struthioniformes	Africa	Ornamental	E3	0.24	Low risk
Sturnus malabaricus	Passeriformes	Asia	Pet	E3	0.63	High risk
Sturnus sinensis	Passeriformes	Asia	Pet	E3	0.63	High risk
Tadorna ferruginea	Anseriformes	Cosmopolitan	Ornamental	E2	0.24	Low risk
Tadorna radjah	Anseriformes	Oceania	Ornamental	E3	0.24	Low risk
Taeniopygia bichenovii	Passeriformes	Oceania	Pet	E3	0.28	Low risk
Taeniopygia guttata	Passeriformes	Oceania	Pet	E3	0.48	Medium risk
Threskiornis aethiopicus	Ciconiiformes	Africa	Ornamental	E2	0.63	High risk
Trichoglossus haematodus	Psittaciformes	Oceania	Pet	E3	0.24	Low risk
Uraeginthus bengalus	Passeriformes	Africa	Pet	E3	0.28	Low risk
Vidua chalybeata	Passeriformes	Africa	Pet	E3	0.28	Low risk
Vidua macroura	Passeriformes	Africa	Pet	E3	0.28	Low risk
Vidua paradisaea	Passeriformes	Africa	Pet	E3	0.28	Low risk



CREAF

UAB
Universitat Autònoma
de Barcelona