Universitat Autònoma de Barcelona

Spatio-temporal variability of bee/wasp communities and their host-parasitoid interaction networks

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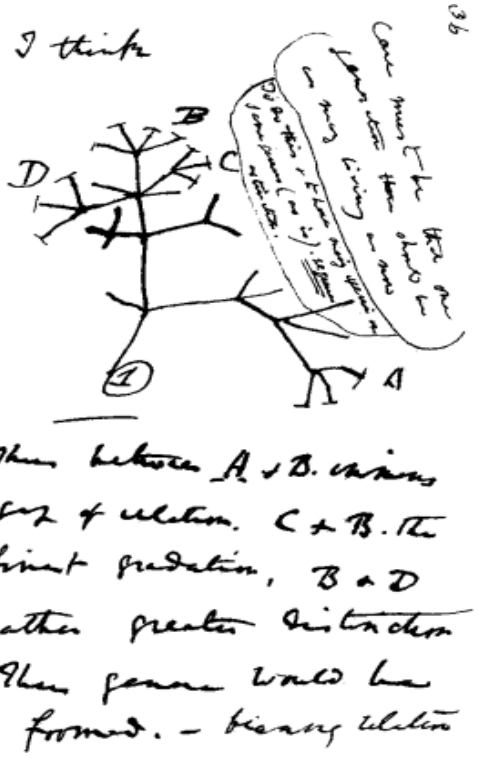
“... Yo creo que existe, y lo siento dentro de mí, un instinto de la verdad, o del conocimiento, o del descubrimiento, (...) y el hecho de que tengamos ese instinto es razón suficiente para las investigaciones científicas aunque no se deriven de ellas ningún resultado práctico”.

— Charles Darwin



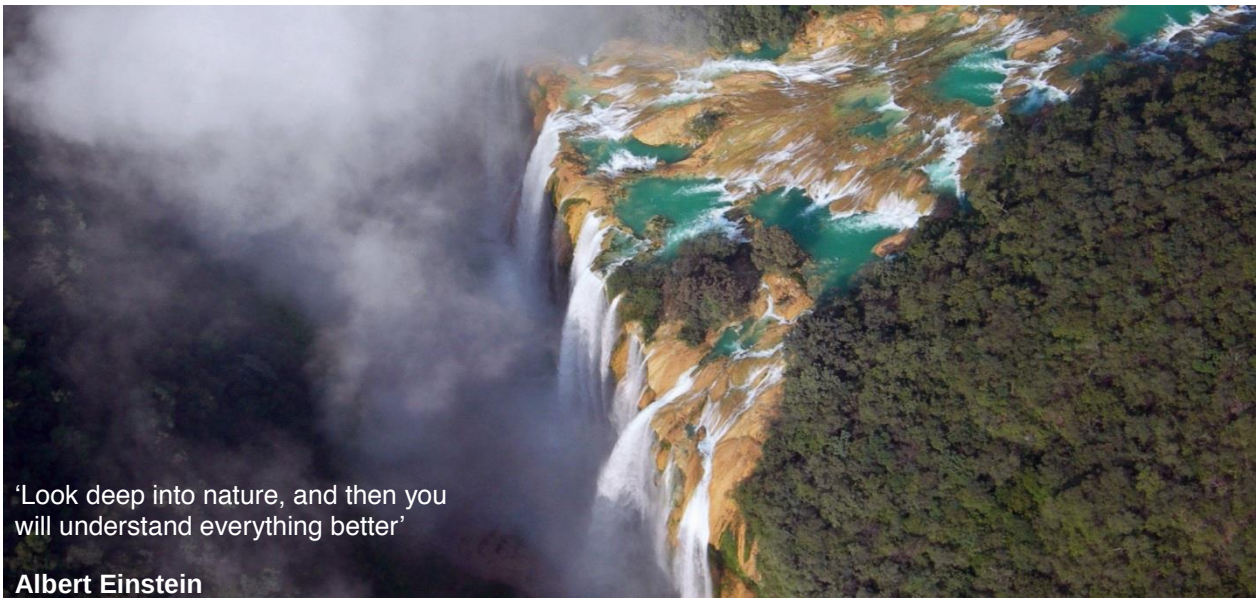
"Árbol evolutivo" bosquejado por Darwin en su primera "libreta de notas sobre la transmutación de las especies" (Notebook B, 1837), con el comentario: "I think" añadido, arriba a la izquierda. La interpretación del texto manuscrito es la siguiente:

"I think case must be that one generation should have as many living as now. To do this and to have as many species in same genus (as is) requires extinction. Thus between A+B the immense gap of relation. C+B the finest gradation, B+D rather greater distinction. Thus genera would be formed.- bearing relation"... (y sigue en la siguiente página) ..."to ancient types with several extinct forms".

— Charles Darwin

Siempre me he sentido atraído y maravillado por la Naturaleza. Si ese fue el primer instinto, el primer paso en este camino, sin duda el segundo paso fue conocer las ideas sobre la evolución biológica de Darwin y Wallace. Probablemente ninguna otra idea científica me ha marcado tanto (y lo sigue haciendo), y probablemente ninguna otra idea subyace, vertebra e impregna tanto el conocimiento y la investigación biológica actual en todos sus campos, siguiendo (como no podía ser de otra manera) su propio proceso de cambio y adaptación a los nuevos descubrimientos y paradigmas científicos.

Sirvan estas palabras como humilde homenaje a estos pensadores y a su legado (y a todos los que posteriormente lo han hecho “evolucionar”), con todo mi respeto, agradecimiento y admiración.


‘Look deep into nature, and then you
will understand everything better’
Albert Einstein

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A mis amigos y a mi Familia de ambos lados del Atlántico.

A mis padres, y muy especialmente a mi madre, responsable directa de que yo esté aquí, en todos los sentidos, guía en momentos decisivos de mi vida. Una dedicatoria especial para ti, con todo mi amor.

A Verónica, compañera de vida, gracias por tu plena compresión e implicación durante todo este proceso, gracias por tu apoyo emocional y literal, socorriendo con amor a la piltrafa humana que llegaba del campo muchos días, o viniendo conmigo a los muestreos innumerables días, atrapando ingentes cantidades de *Hylaeus*, sufriendo las inclemencias de la meteorología e incluso alguna picada de *Anthophora*! (¿A que no dolió tanto? ;)). También para ti, con todo mi amor.

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Thesis General Abstract

One of the main goals in ecology is to understand how biodiversity is spatial and temporally structured, and which are the mechanisms underlying biodiversity gradients at different spatial and temporal scales. In this thesis, I analyze spatial and temporal variability in bee/wasp (hosts) and their parasitoid communities, and in the antagonistic interaction networks between them. Bees, wasps and their parasitoids are related to key ecosystem functions (e.g., pollination or herbivore populations control). Bee and wasp species show notably seasonal differences in their phenology. Bee species also show different thermoregulatory capabilities in relation with their body size (the bigger the bee species, the more 'endothermic' the species are). So, it could be hypothesized a relationship between body size (~endothermic capabilities) and ambient temperature in the period of adult flying activity. Bee and wasp communities also have been shown to be spatially heterogeneous in response to food and nesting resources. Temporal and spatial changes in bee/wasp communities are expected to impact in their parasitoid communities, as they depend on their host communities. Moreover, if host and parasitoid community structure and composition change over space and time, their functional traits, interaction patterns, network structure and ecosystem functionality are also expected to change spatio-temporally.

In Chapter 1 we tested the body size-temperature relationship along an intra-annual, seasonal environmental temperature gradient using a Mediterranean regional bee fauna. We expected to find larger bee species (i.e. more endothermic species) in colder seasons, and progressively smaller bee species towards warmer seasons. This approaches to the Bergmann's rule along a temporal temperature gradient (instead of their classical formulation along geographical gradients). We found a different relationship between body size and ambient temperature for large ('endothermic') and small (ectothermic) bee species: species larger than 27.81 mg (dry weight) followed Bergmann's rule, whereas species below this threshold did not (no relationship at all). Our results extend Bergmann's rule to a temporal gradient and are coherent with the physiological mechanism proposed originally by Bergmann himself ("thermoregulatory hypothesis").

In order to analyze spatial and temporal variability in antagonistic interaction networks, we used cavity-nesting bees and wasp communities ('CNBW', acting as 'hosts'), and their interacting 'parasitoid' communities in a temperate zone (Chapters 2 and 3).

In Chapter 2, we studied the effects of seasonality (spring vs. summer) on taxonomic and functional structure and composition of CNBW and their parasitoid communities, and on their interaction networks. We found strong seasonal changes in taxonomic and functional structure and composition of both the CNBW host and their parasitoid communities. However, we did not find seasonal shifts in percent parasitism, and the few seasonal changes in the structure of the host-parasitoid interaction network appeared to be mostly driven by changes in network size. Our results underscore the need to consider functional traits and to incorporate a temporal component into network analysis if we are to understand the global relationship between network structure and ecosystem function.

Finally, in Chapter 3 we studied the effects of local (nesting environment: farms vs tree stands) and landscape (forest-cropland gradient) spatial factors on taxonomic structure and composition of CNBW hos and their parasitoid communities, and on their interaction networks. CNBW host community structure and composition, as well as network structure, were much more dependent on local than on landscape factors. Open habitats associated with extensively farmed exploitations favor local CNBW diversity (especially bees) and result in more complex host–parasitoid interaction networks in comparison to forested areas. This study highlights the conservation value of this kind of open habitat in view of the progressive abandonment of extensively cultivated farmland in favor of agricultural intensification and reforestation taking place in Europe.

Resumen General de la Tesis

Uno de los principales objetivos de la ecología es comprender cómo la biodiversidad está estructurada espacial y temporalmente, y cuáles son los mecanismos subyacentes a los gradientes de biodiversidad en diferentes escalas espaciales y temporales. En esta tesis, analizo la variabilidad espacio-temporal de comunidades de abejas/avispas (huéspedes) y de sus parasitoides, y de las redes de interacción huésped-parasitoide que se establecen entre ellas. Las especies de abejas y avispas muestran notables diferencias temporales en su fenología, y, por otro lado, las especies de abejas muestran diferentes capacidades termorreguladoras en relación con su tamaño corporal (cuanto más grandes es una, mayor es su capacidad termoreguladora). Por tanto, se podría hipotetizar una relación entre el tamaño corporal (~'grado de endotermia') y la temperatura ambiente durante el período de vuelo del adulto. Las comunidades de abejas y avispas también muestran una considerable heterogeneidad espacial en respuesta a sus recursos alimentarios y de nidificación. Estos cambios espacio-temporales en las comunidades de abejas/avispas podrían conllevar cambios en sus 'rasgos funcionales', y podrían tener un impacto en sus comunidades de parasitoides y, en consecuencia, esto podría reflejarse en cambios en la estructura de sus redes de interacción y en las funciones ecosistémicas asociadas.

En el capítulo 1 se analizó la relación entre el tamaño corporal y la temperatura a lo largo de un gradiente de temperatura ambiental intra-anual, utilizando una fauna regional de abejas mediterráneas. Esperábamos encontrar especies más grandes (más endotérmicas) en las estaciones más frías, y especies progresivamente más pequeñas hacia estaciones más cálidas. Esto se puede considerar un test a la 'norma de Bergmann' a lo largo de un gradiente de temperatura temporal (en lugar de su formulación clásica a lo largo de gradientes geográficos). Encontramos una relación diferente entre el tamaño corporal y la temperatura ambiente de las especies para las abejas grandes ('endotérmicas') y para las pequeñas (ectotérmicas): las especies mayores que 27,81 mg (peso seco) siguieron la norma de Bergmann, mientras que las especies por debajo de este umbral no mostraban ningún patrón. Nuestros resultados

extienden la norma de Bergmann a un gradiente temporal y son coherentes con el mecanismo fisiológico propuesto originalmente por el propio Bergmann ("hipótesis termorreguladora").

Para estudiar las redes de interacción huésped-parasitode se utilizaron comunidades de abejas y avispas nidificantes en cavidades preestablecidas (AANCP), que actúan como 'huéspedes', y sus comunidades de parasitoides, en una zona templada (Capítulos 2 y 3).

En el capítulo 2 se estudiaron los efectos de la estacionalidad (primavera vs verano) sobre la estructura y composición taxonómica y funcional de las comunidades de AANCP y de sus parasitoides, y sobre sus redes de interacción. Se encontraron notables cambios estacionales en la estructura taxonómica y funcional, y en la composición tanto de la comunidad de AANCP como de parasitoides. Sin embargo, no encontramos cambios estacionales en el porcentaje de parasitismo, y los pocos cambios estacionales en la estructura de la red de interacción parecían principalmente motivados por cambios en el tamaño de la red.

Por último, en el capítulo 3 se estudiaron los efectos de los factores espaciales locales (ambiente de nidificación: granjas vs agrupaciones de árboles) y paisajísticos (gradiente de cobertura agrícola) sobre la estructura taxonómica y la composición de las comunidades de AANCP y de sus parasitoides, y sobre sus redes de interacción. La estructura y composición de la comunidad AANCP, así como la estructura de la red, fueron mucho más dependientes de los factores locales que de los factores del paisaje. Los hábitats abiertos asociados con explotaciones extensivas favorecen la diversidad local de AANCP (especialmente abejas) lo que origina redes de interacción huésped-parasitoide más complejas en comparación con áreas boscosas.

General Introduction

General Introduction

Spatio-temporal patterns of biodiversity

One of the main goals in ecology is to understand how biodiversity is structured both spatial and temporally, and which are the mechanisms underlying biodiversity patterns at different spatial and temporal scales (Ricklefs 1987, Chesson 2000, Kneitel & Chase 2004). Biodiversity dynamics is influenced by the complex interplay of biotic (e.g. competition, facilitation, dispersal limitation) and abiotic (e.g. climate, geology) factors. Local community structure and composition result from a series of drivers operating at different spatio-temporal scales. First, evolutionary and historical factors set the regional species pool. Then, environmental filtering and dispersal barriers, set the limit on which species might potentially occur in a local community (Cornell & Harrison 2014). Finally, the realized composition of the local community depends on biotic interactions, operating at predominantly local scales (Silvertown et al. 2006). Two of the main environmental filters shaping biodiversity along spatial and temporal gradients are climate and disturbance. For instance, broad-scale spatial patterns of species richness and species interactions are often correlated with contemporary climate (e.g., Gaston 1996, Dunn et al. 2009, Dalsgaard et al. 2011, Schleuning et al. 2012). Similarly, species richness and community composition also change throughout the year in relation to climate variables (Petanidou et al. 1995, Cros et al. 1997, Bosch et al. 1997, González et al. 2003, Standfuss & Standfuss 2006, Leong et al. 2016). Meanwhile, the role of disturbance in shaping biodiversity is widely recognized (Dornelas 2010, Mouillot et al. 2013), and many different patterns of variation in community diversity across disturbance gradients have been observed in nature depending on disturbance type and regime. For example, intermediate levels of disturbance can even enhance biodiversity (Wilkinson 1999). However, it is widely accepted that land-use change is one of the main drivers of biodiversity loss (McGill 2015).

Biodiversity dimensions and ecosystem function

Ecologists have traditionally studied biodiversity patterns keeping the focus on the variation of the number and abundance of species along environmental gradients (i.e., taxonomic diversity). However, such a taxonomic approach misses relevant information about processes and functions. Thus, the study of other biodiversity components, such as the phylogenetic, functional, and interaction components of biodiversity, can better shed light on the structuring patterns of biotic communities (Pavoine & Bonsall 2011) as well as the evolutionary history of a community and their functionality (Webb et al. 2002, Petchey & Gaston 2006).

Functional diversity reflects the diversity of morphological, physiological, and phenological features measurable at an individual level in each species found in a community (Petchey & Gaston 2006, Violle et al. 2007). Any of these measurable features could be considered as 'functional traits' if they impact species fitness indirectly via its effects on growth, reproduction and survival (Violle et al. 2007). Functional traits differentiate in 'response traits' if the trait varies in response to changes in environmental conditions, and 'effect traits' if they reflect the effects of a species on environmental conditions, community or ecosystem properties (e.g., energy flow, nutrient cycling) (Violle et al. 2007). Thus, depending on which effect traits are mostly present in a community, they will determine the rate and magnitude of ecosystem processes and functions (e.g., seed dissemination, pollination, control of insect populations, parasitism) (Díaz & Cabido 2001, Lavorel & Garnier 2002). In this way, traits can be mechanistically linked to ecological patterns or processes of interest (Díaz & Cabido 2001), and inferences are generalizable to other organisms and systems that possess similar trait values. This is more informative than citing the contributions of specific species from a taxonomic diversity approach (McGill et al. 2006). Furthermore, non-overlapping trait values in a community can provide insights into niche differences among species, suggesting, for instance, that resource partitioning mechanisms are at work. These mechanisms have often been invoked to explain the positive effect of species richness on ecosystem properties such as biomass production and resource use (Loreau & Hector 2001, Cardinale et al. 2006).

Functional diversity can also give insights into potential redundancy among species in their effects on ecosystem processes, which allows estimation of how many species can be lost before there are significant ecosystem consequences (Rosenfeld 2002). Finally, the analysis of functional response traits may allow us to better understand and predict community responses to global change, by linking traits that make species more or less vulnerable to warming, overexploitation, and other anthropogenic activities (Mouillot et al. 2013).

One of the most important and studied functional trait in animals is body size. Body size provides a functional link between individual-level processes such as metabolism, physiology or behavior, and higher-level ecological processes such as the strength and outcome of trophic interactions, which regulate the flow of energy and nutrients within and across ecosystems (Peters 1983, Chown & Gaston 2010). Since the mid-19th century, a number of macroecological rules describing intra- and interspecific variation in body size have been put forth, among which Bergmann's rule (Bergmann 1847, Gaston et al. 2008) is the most well-known. This rule originally described an increase in body size along decreasing environmental temperature spatial gradients (e.g. with increasing latitude) in closely related species of warm-blooded animals. Bergmann pointed out a possible mechanism behind this pattern. Given that body volume scales with a higher exponent than body surface and that the former is related to heat production and the latter to heat loss, Bergmann proposed that larger animals are better enabled to conserve heat in colder climates (nowadays known as 'heat conservation' or 'thermoregulatory hypothesis').

Functional traits are determinant in species interactions. First, trait-mediated environmental filtering drives species distribution and abundance, and therefore affects the probability that two species may co-occur and potentially interact. Second, trait-mediated morphological and phenological matching drives interactions between potential interaction partners (Vázquez et al. 2009, Eklöf et al. 2013, Bartomeus et al. 2016). Thus, functional diversity might be in close association with interaction diversity. Interaction diversity describes the ways in which individuals can interact with their con-specifics and/or with other species in a community. Dynamic biotic

processes such as competition, predation, parasitism or mutualistic interactions play an essential role in creating and maintaining biodiversity (Stoufer & Bascompte 2010, Pfenning & Pfenning 2012, Pascual-García & Bastolla 2017). On an ecological time-scale, interspecific competition or predation can restrict the number of co-existing species but, simultaneously, lead to a diversification of species' traits. At an evolutionary time scale, interspecific interactions account for the evolutionary generation of biodiversity; in the course of the coevolution of species new biological traits continuously develop. However, the relationship between biodiversity and ecosystem functioning is still the subject of intense debates (reviewed in Loreau et al. 2001).

Methods based in 'network theory' have been recently developed to allow the quantification of ecological interactions at the community level (ecological networks analysis) (Müller et al. 1999, Bascompte 2007). This sophisticated analysis gives a more robust description of community structure, and provide insights into the dynamic processes that structure ecological communities (Morris et al. 2004). The information contained in food webs can be summarized and compared between webs through the computation of various quantitative weighted descriptors or 'metrics' describing different aspects of network structure (Bersier et al. 2002). These methods have considerable potential for quantifying the effect of human activities on networks of interacting species (Henneman & Memmott 2001). Ultimately, the study of interaction networks has contributed to better understand ecosystem functioning and community stability, since functionality is often reflected in interaction network structure (Bascompte 2010, Thompson et al. 2012, Allesina & Tang 2012, Peralta et al. 2014).

Ecosystem properties and function greatly depend on biodiversity in terms of both organism functional traits and the distribution and abundance of organisms over space and time. Species traits interact with the effects of climate, resource availability, and disturbance regimes on influencing ecosystem properties and functions (i.e. predation, pollination, pest control, parasitism) (Hooper et al. 2000).

The study system

In this thesis, I use solitary bees (although also a few social species) and wasps communities, as well as their 'natural enemies' (parasitoids, cleptoparasites and predator/scavengers) communities, as a study model to analyze spatial and temporal patterns and processes structuring biotic communities and species interaction networks. Solitary wasps and bees (Insecta: Hymenoptera) are important components of natural and agroforestry systems (Tylianakis et al. 2005, Buschini & Woiski 2008) due to their relevant functionality. Predatory solitary wasps play a key role in reducing crop pests such as Lepidoptera larvae (Tylianakis et al., 2005), aphids (O'Neill 2001) and/or Orthoptera nymphs (Soares et al. 2001), while also have some role in pollination service (O'Neill 2001). Solitary bees are the most important pollinators of native and cultivated plants, both in terms of flower visitation rates and pollination efficiency. Their decline due to human-driven disturbances (e.g. land-use changes) may have negative impacts on crop yields (Klein et al. 2003, Kremen et al. 2007, Ricketts et al. 2008, Giannini et al. 2015). Both hymenopteran groups have also been widely used as bioindicators of environmental quality, since they are sensitive to changes in microclimate conditions and food resources availability (Klein et al. 2002, Tylianakis et al. 2004, 2005, 2006, Buschini & Woiski 2008).

These solitary bees and wasps also act as 'hosts', as their nests (specifically their larvae, their food provisions, or both), are attacked by a wide range of 'natural enemies' (parasitoids, cleptoparasites and predators/scavengers; henceforth 'parasitoids'), that are also important components of natural and agroforestry systems. Parasitoids include many taxonomical groups (Hymenoptera, Diptera, Coleoptera, Lepidoptera, Acari), but parasitoid wasps are between the most specious and ubiquitous organisms (Pennacchio & Strand 2006). Host-parasitoid interactions are prevalent within natural ecosystems, and parasitoid organisms, especially parasitoid wasps, are considered to be one the most important biological control agents used in agriculture and conservation (Pennacchio & Strand 2006, Mills & Wajnberg 2008, Pennisi 2010, Henri & van Veen 2011).

Solitary bees and wasps gather a set of traits that make of them a good model of study. Both of them are highly specious (especially bees with ~20.000 species currently described worldwide, Ascher & Pickering 2016). They have short activity periods (as flying adults), which make possible a high seasonal species turnover. In addition, bee and wasp species show very contrasted functional traits, such as phenology (e.g. the time when they initiate their adult flight period and its duration) or body size. Differences in body size imply, among others, differences in energetic requirements, foraging ranges and dispersal abilities. In general, both bees and wasps are highly mobile organisms (especially bees); however, they show high spatial variability in the structure and composition of their communities at small spatial scales (Herrera 1988, Minckley et al. 1999, Janovský et al. 2013, Torné-Noguera et al. 2014).

Considering that bees and wasps have short activity periods, high species number and are active nearly all year round (at least in the case of bees), they are a good study system to analyze community seasonal changes. Moreover, bees (and some wasps) show 'endothermic capabilities', which depend on body size (with better capabilities as larger the species are; Heinrich 1974, Stone & Willmer 1989, Heinrich 1993) until a size threshold, below which species behave as ectothermic (Bishop & Armbruster 1999). Endothermic species are better capable of maintain flight activity in thermal adverse conditions (Stone & Willmer 1989, Willmer & Stone 2004). Since bee species considerable differ in phenology, a relationship between bee body size (i.e. endothermic capabilities) and phenology might be expected. Thus, it is likely to find larger species (i.e. more endothermic species) in colder seasons of the year, and progressively smaller species appear as temperature increases towards warmer seasons. This could be considered as a test for the Bergmann's rule along a temporal (seasonal) temperature gradient (instead of their classical formulation along geographical gradients).

Since structure and composition of Hymenopteran communities are known to change over space (Herrera 1988, Minckley et al. 1999, Janovský et al. 2013, Torné-Noguera et al. 2014) and time (Olesen et al. 2008, Petanidou et al. 2008), parasitoid

communities are also expected to change in parallel, as they are highly dependent on their hosts (Steffan-Dewenter 2003, Albrecht et al. 2007, Tylianakis et al. 2007, Fabian et al. 2013). Consequently, interaction patterns and the resulting host-parasitoid interaction networks structure are also expected to change at multiple spatial and temporal scales. Solitary bees and wasps also constitute a very useful study system to study spatio-temporal changes in communities' structure and composition and in their interactions. Particularly, the study of communities of cavity-nesting bees and wasps (henceforth CNBW) is very interesting. These species use naturally pre-existing cavities to construct their nests, and easily use artificial nesting structures (drilled wood blocks and/or bundles of reeds). These 'trap-nesting units' have been shown to be very useful, as allow to obtain information on community structure and composition (species richness and abundance) simultaneously in different locations, so that sampling effort can be standardized and replicated (Tschanrtke et al. 1998). These trap-nests are especially interesting to study species interactions: they allow characterizing qualitative and quantitatively the communities of parasitoids interacting with CNBW communities ('hosts').

Objectives

The general objective of this dissertation is to study spatio-temporal patterns and factors determining changes in bee and wasp (acting as 'hosts'), and in their parasitoid communities structure and composition, and in the host-parasitoid interaction networks established between them. This thesis is composed of three chapters:

In **Chapter 1**, we test the extension of Bergmann's rule to a temporal (seasonal) climatic gradient (instead of latitudinal or geographical), using a regional bee fauna (mostly solitary but some social species) from a Mediterranean area (~1600 Km^2). We used two different methodological approaches: cross-species and assemblage-based analyses. We particularly aim: (1) to establish whether the temporal distribution of body sizes in a bee fauna follows a seasonal pattern congruent with temperature; (2) to establish whether this pattern is consistent throughout the entire

range of body sizes. Given that Bergmann's pattern is consistent for endotherms but not for ectotherms, we hypothesize a negative relationship between body size and temperature for large species, but not for small ones.

In **Chapter 2**, we study the effects of seasonality (spring vs. summer) on a community of CNBW (acting as 'hosts') and their parasitoids in a temperate zone (Mediterranean climate with continental influence). We analyze seasonal changes in the taxonomic and functional structure and composition of the host-parasitoid community and in the resulting interaction network along the whole phenology of CNBW communities. We have three objectives: a) To analyze seasonal changes in species richness, abundance and composition of the host and parasitoid communities; b) To establish whether these changes result in changes in community functional structure; c) To establish whether taxonomic and functional seasonal changes result in changes in parasitism rates and network structure.

In **Chapter 3**, we investigate the effects of local and landscape factors on a community of CNBW and their parasitoids, and on the structure of their interactions along an agricultural–forest gradient (in the same temperate zone as Chapter 2). Our objectives are to understand how local (nesting environment) and regional (landscape composition) factors modify abundance, species richness, and composition of hosts and parasitoids, and consequently, how these community changes result in changes in levels of parasitism and host–parasitoid network structure.

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Chapter 1

Body size phenology in a regional bee fauna: a temporal extension of Bergmann's rule

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Abstract

Bergmann's rule originally described a positive relationship between body size and latitude in warm-blooded animals. Larger animals, with a smaller surface/volume ratio, are better enabled to conserve heat in cooler climates (thermoregulatory hypothesis). Studies on endothermic vertebrates have provided support for Bergmann's rule, whereas studies on ectotherms have yielded conflicting results. If the thermoregulatory hypothesis is correct, negative relationships between body size and temperature should occur in temporal in addition to geographical gradients. To explore this possibility, we analysed seasonal activity patterns in a bee fauna comprising 245 species. In agreement with our hypothesis of a different relationship for large (endothermic) and small (ectothermic) species, we found that species larger than 27.81 mg (dry weight) followed Bergmann's rule, whereas species below this threshold did not. Our results represent a temporal extension of Bergmann's rule and indicate that body size and thermal physiology play an important role in structuring community phenology.

Keywords: Apiformes, ectothermy, endothermy, heterothermy, seasonality, temperature, thermoregulation.

1.1. Introduction

Bergmann's relationship between body size and latitude is one of the oldest rules in biogeography and macroecology (Bergmann 1847; Gaston et al. 2008). Originally, it described a broad-scale increase in body size with increasing latitude in related species of warm-blooded animals. Given that body volume scales with a higher exponent than body surface and that the former is related to heat production and the latter to heat loss, Bergmann proposed that larger animals are better enabled to conserve heat in colder climates (heat conservation or thermoregulatory hypothesis). Since its formulation, Bergmann's rule has been extended to altitudinal and other geographical clines, and tested on ectotherms in addition to endotherms at inter and intraspecific levels (e.g. Blackburn et al. 1999; Watt et al. 2010).

Most studies on endotherms (birds and mammals) corroborate Bergmann's rule (e.g. Meiri & Dayan 2003; Clauss et al. 2013). However, beyond the consistency of the observed patterns, the validity of the physiological and evolutionary mechanisms proposed by Bergmann has been variously contested. First, other factors besides environmental temperature, such as primary productivity, predation, and competition, may also covary with latitudinal/geographical gradients, and are likely to impose selective pressure on body size (Dayan & Simberloff 1998; Watt et al. 2010). Second, the observed body-size temperature patterns could result from a plastic response to environmental conditions rather than (or in addition to) adaptation (Dayan & Simberloff 1998).

On the other hand, the search for Bergmann's patterns in ectotherms has yielded highly heterogeneous results. Some studies confirm Bergmann's rule, but others show other patterns, including positive relationships between body size and temperature ('converse Bergmann's rule') and no relationship at all (e.g. Shelomi 2012; Vinarski 2014). These heterogeneous results in ectotherms have contributed to fuel the debate over the mechanisms underlying geographical body size patterns. For example, in relation to thermoregulation, large body size could favour heat retention in ectotherms, but could also decrease their ability to warm up from external heat

sources (Stevenson 1985). For this reason, the 'heat conservation' hypothesis is often considered inadequate for ectotherms (Watt et al. 2010), although some authors argue that it may still be valid in certain groups such as lizards and frogs, which show behavioural compensatory mechanisms to gain heat faster (Cruz et al. 2005; Olalla-Tárraga & Rodrıguez 2007). As with endotherms, it has been argued that the observed patterns could result from a plastic response to ambient conditions (body size-temperature reaction norms or temperature-size rule, Atkinson 1994). Ultimately, it is likely that several correlated factors interact to determine body size–temperature relationships in ectotherms, thus resulting in the various patterns reported in the literature (Vinarski 2014). There is also disagreement on whether the original mechanism proposed by Bergmann should be considered part of the rule (Watt et al. 2010). In this sense, some authors refer to 'Bergmann's rule sensu lato' to include any clinal variation in morphometrics over geographical ranges, irrespective of the underlying mechanism (Olalla-Tárraga 2011; Shelomi 2012).

If the thermoregulatory hypothesis is correct, negative relationships between body size and temperature could occur not only across geographical but also across temporal gradients. Some studies report daily or seasonal variation in the body size of active insects at intra or interspecific levels possibly related to temperature (Shmida & Dukas 1990; Willmer & Stone 2004; Schuldiner-Harpaz & Coll 2013). However, we know of no study explicitly exploring whether Bergmann's patterns occur along temporal temperature gradients at the community or faunal level. This approach is important because such a relationship would indicate that body size, and possibly thermal physiology, play a role in structuring community phenology. This issue is particularly relevant in the current scenario of climate change and in the face of reports of recent phenological shifts in various taxonomic groups (Scaven & Rafferty 2013).

In this study, we explore the relationship between body size, flight phenology and temperature in a species-rich bee fauna (Hymenoptera: Apoidea) in a Mediterranean area. Mediterranean regions combine a long period of temperatures adequate for insect flight, with relatively large temperature differences between seasons, thus

providing a wide temporal temperature gradient. Bees are appropriate organisms to address this topic because bee communities are highly specious (may contain over 200 species) and encompass a wide range of body weights (~ 200-fold interspecific differences and relatively low intraspesific variation, see below). In addition, Mediterranean bee communities are highly seasonal, with some species becoming active as early as early winter and others as late as midsummer. Finally, several bee species have been shown to be able to regulate body temperature by physiological means, and this endogenous thermoregulatory ability is positively related to body size (Stone & Willmer 1989; Heinrich 1993; Bishop & Armbruster 1999). In a bee fauna in Alaska, Bishop & Armbruster (1999) established the body size threshold above which bees had endogenous thermoregulatory capacity at 16 mg (dry weight). Thus, a typical bee fauna might be expected to show a range of thermoregulatory capabilities from large, highly endothermic bumblebees to small, ectothermic solitary bees. This affords a rare opportunity to test Bergmann's rule on both endotherms and ectotherms within a group of phylogenetically related species.

The aim of this study is to establish whether Bergmann's rule can be extended to a temporal dimension. Our specific objectives are as follows: (1) to establish whether the temporal distribution of body sizes in a bee fauna follows a seasonal pattern congruent with temperature; (2) to establish whether this pattern is consistent throughout the entire range of body sizes. Given that Bergmann's pattern is consistent for endotherms but not for ectotherms (geographic patterns consistent with Bergmann's rule have been found in only 22% of the studies on insects at interspecific level; Shelomi 2012), we hypothesize a negative relationship between body size and temperature for large species, but not for small ones. Our results corroborate this hypothesis. We found a Bergmann's pattern only for species above a certain body size threshold, thus supporting the idea that Bergmann's thermoregulatory hypothesis can be used to explain body size distributions along temporal clines.

1.2. Material and Methods

1.2.1. Study area

We obtained bee records from various localities within an area of 1626 km² around the city of Barcelona (north-eastern Iberian Peninsula) (Fig. 1), at 0–300 m a.s.l. The climate in the region is typically Mediterranean, with mild winters and dry summers. Most precipitation takes place in spring and autumn. Weather conditions are fairly homogeneous across the study area (see below).

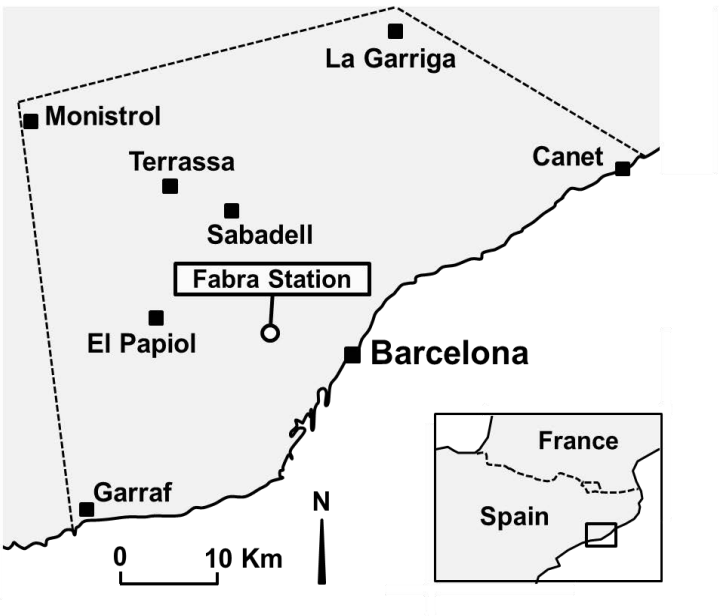

Figure 1. Map of the study area indicating the main localities sampled and the weather station from which temperature data were obtained.

1.2.2. Data collection

We obtained bee records (locality and date of collection) from three sources: (1) Our own surveys; including intensive weekly (1–2 days per week) visual surveys

conducted year-round at two localities (Papiol and Garraf) in 2010; (2) published faunistic accounts (Bofill 1905; Vergés 1964); and (3) museum collections; basically our own collection (CREAF, Bellaterra) and the collection at the Museum of Natural Sciences of Barcelona. In all, we compiled a data set comprising 8275 bee records (species/date) representing 290 species.

1.2.3. Temperature

To characterize the temperature regime of the study area, we worked with a climatic series (94 years, 1914–2007) from the Fabra Weather Station (Fig. 1). Monthly temperatures of this climatic series were highly correlated with those from the localities included in the study (for all localities, $P < 0.0001$, $r \geq 0.99$, $n = 12$ months) (http://www.es.climate-data.org data base). The year was divided into 52 weeks. Each week was characterized by a measure of maximum temperature. To obtain this measure, we first averaged the daily maximum temperatures of each week and year and then computed a weekly mean of the 94 years. We chose to work with maximum daily temperatures because, in general, bees concentrate their flight activity to the warmest part of the day, and because we were interested in establishing how early in the year each species was active (see below). We call this variable 'weekly temperature'. We define the variable 'species temperature' as the weekly temperature of the week in which a species began its flight activity (earliest annual record; henceforth variable 'species week'). It might be argued that the temperature of the coldest week in which a species is active instead of the temperature in which a species begins its activity should be used. For the majority of species (83%), which become active before the hottest week of the year (week 30, late July), the two temperatures (first week and coldest) coincide. For the remaining species (17%), which begin their activity in late summer, the coldest temperature occurs in autumn or early winter. However, these cold temperatures affect only the tail end of the activity period, when only a few, old females are still active, and their reproductive success is very low (Tepedino & Torchio 1982; Bosch & Vicens 2005, 2006). Thus, temperatures experienced at the beginning of the flying period, when females are

young and their cell provisioning rates are highest are likely to exert a much stronger selection on flying phenology. For this reason, we used the temperature of the week in which a species became active to characterize each species. We nonetheless repeated all analyses using the coldest temperature for each species (henceforth 'coldest species temperature') (see Appendix 1: Table A1.1). Weekly temperature and species temperature were log-transformed (log_{10}) in all analyses to match normality and homoscedasticity of statistical model residuals.

1.2.4. Bee phenology

For each of the 290 species, flight activity periods were established based on the weeks in which the species was first and last recorded (Appendix 1: Table A1.2). However, some species were represented by just one or a few records, and therefore their flying period could not be properly characterized (bee species in temperate zones fly for 1 month or longer; Westrich 1989). For this reason, we excluded from the analyses 44 species with artificially short (< 4 weeks) flying periods. These excluded species encompass a wide range of phenologies and body sizes (Appendix 1: Table A1.2.). The honey bee, *Apis mellifera* was also excluded from the analyses because its phenology and abundance are strongly conditioned by bee-keeping practices. Thus, all analyses were conducted on the remaining 245 species.

1.2.5. Body size

Most bees show body size sexual dimorphism, with females usually being larger than males. All our analyses are based on female body sizes. We used intertegular span (hereafter ITS) as a measure of body size. ITS is the standard measure of body size in bees (e.g. Peters et al. 2016), and it is highly related to dry body weight (R2 = 0.97; Cane 1987). The use of ITS is especially adequate in our study, as it may also reflect thermorregulatory capability, given that flight muscles, which occupy most of the thorax volume, are the main heat generators in bees (Heinrich 1993). Measurements

were done on pinned specimens using a stereomicroscope (magnification 8–35x) with a calibrated ocular micrometer (resolution = 0.029–0.133 mm). When possible, we measured ≥ 3 specimens per species (mean = 3.53, Appendix 1, Table A1.2). Small sample sizes are justified given that interspecific variability in body size is much larger (range: 0.99 to 198.9 mg; 202-fold differences) than intraspecific variability (mean ± SE of 44 species with ≥ 5 measurements: 1.62 ± 0.05-fold differences), and our hypothesis is based on interspecific differences. ITS was log-transformed (log_{10}) to match normality and homoscedasticity of statistical model residuals.

1.2.6. Statistical analysis

To test our hypothesis, we used both cross-species and assemblage-based approaches (see below). These two approaches are complementary and have been widely used in studies testing relationships between functional traits and environmental variables, including studies on Bergmann's rule (Gaston et al. 2008; Olalla-Tárraga et al. 2010). All statistical analyses were performed in R ver. 3.1.3. (R Development Core Team 2015). In all cases, residuals were checked to confirm adequacy to normality and homoscedasticity.

Cross-species approach

Using the 245 bee species as replicates, we analyzed the relationship of species body size (log_{10} ITS; dependent variable) with species week and species temperature separately (both log_{10}-transformed). These models took into account phylogenetic relatedness. We used phylogenetic generalized least squares (pGLS) models with a variance–covariance matrix of the data based on the inferred phylogenetic tree of the 245 species. The tree was constructed based on various sources of phylogenetic information available for bees, and ultrametricized with Grafen's method (Grafen 1989) (Appendix 1: Appendix A1.3, Fig. A1.3). Lambda (k), the character describing

the phylogenetic signal (Pagel 1999), was estimated by maximum likelihood (ML) in all cases. For pGLS analyses, we used the R packages 'ape' and 'caper'.

Given that we expected different relationships for large (endothermic) and small (ectothermic) species, we looked for a possible body size break-point in the body size–temperature relationship. To this effect, we conducted a piecewise linear regression analysis across the entire body size range. In this analysis, two or more functions are fitted between one or more unknown points (break-points). Piecewise linear regression is based on 'broken-stick' models, and is commonly used to identify ecological thresholds (Appendix 1: Appendix A1.4). To account for phylogenetic relatedness, we developed an R algorithm using a pGLS function in which the phylogenetic tree was adjusted to each break-point tested (Appendix1: App. A1.5).

Assemblage-based approach

For each week, we computed a mean ITS (log_{10}-transformed) considering all species flying in that week (henceforth 'weekly mean body size'). Then, we analyzed the relationship of weekly mean body size (dependent variable) with week (1–52), and with weekly temperature, separately. Given that weekly temperatures increase from January to August and decrease from August to December, for the former relationship we fitted a quadratic model (weekly mean body size ~ week + $week^2$). For the weekly mean body size-weekly temperature, we fitted a linear model. Because the species assemblages of consecutive weeks are likely to be similar, we tested model residuals for temporal autocorrelation. In both relationships (body size-week and body size-weekly temperature), we found autocorrelation effects. For this reason, we used generalized least squares (GLS) models with four different temporal covariance structures (compound symmetry structure, AR-1 correlation structure, and two different values of auto-regressive moving average; Zuur et al. 2009). Then, for each relationship, we compared these four models and the model with no covariance structure (computed with maximum likelihood methods of parameter estimation), and selected the best-fit model using second-order Akaike information criterion

(Zuur et al. 2009). Finally, to obtain unbiased parameter estimates, we recalculated the selected model with restricted maximum likelihood estimates. GLS analyses were conducted with the R package 'nlme'. Adjusted-pseudo R^2 of these GLS models were calculated based on the likelihood-ratio test performed with the 'r.squaredLR' function of R package 'MuMIn'.

1.3. Results

1.3.1. Bee community

Body sizes and flying periods of the 290 bee species recorded are shown in Appendix 1 (Table A1.2). The 245 species included in the analyses (Appendix 1: Table A1.2) were distributed in five families as follows: Megachilidae (70 species, 28.6%), Apidae (68, 27.7%), Halictidae (42, 17.1%), Andrenidae (39, 16.0%) and Colletidae (26, 10.6%). Species body size (ITS) ranged from 0.75 mm (*Ceratina parvula*) to 6.67 mm (*Xylocopa valga*). We recorded bee activity year-round (from week 1 to 52). The number of species per week followed a unimodal distribution, with a peak in spring (200 species in week 20, mid May). The earliest species appeared in week 1 and the latest in week 29 (mid July). The species temperature ranged from a minimum of 9.9 °C (week 1) to a maximum of 28.2 °C (week 30, late July).

1.3.2. Cross-species approach

Phylogenetic generalized least squares analyses yielded a significant negative linear relationship between body size (ITS $\log_{10}$-transformed) and species week, but the explanatory power was very low ($t = -2.51$, $P = 0.0128$, adjusted-$R^2 = 0.02$, $\lambda = 1$). As regards the relationship between body size and species temperature (both $\log_{10}$-transformed), pGLS analyses yielded a significant negative linear relationship, again with a very low explanatory power ($t = -2.62$, $P = 0.0092$, adjusted-$R^2 = 0.02$, $\lambda = 1$).

When we used the coldest species temperature instead of species temperature, we obtained similar results (Appendix 1,Table A1.1).

We predicted a different pattern for large and small bees. For the relationship between species temperature and ITS (both log_{10}-transformed), the phylogenetic piecewise algorithm yielded a body size break-point at ITS (log_{10}-transformed) = 0.473 (95% CI = 0.394–0.542) (which corresponds to an ITS of 2.97 mm, 95% CI: 2.48–3.49 mm; and a dry body weight of 27.81 mg, 95% CI: 17.86–41.14 mg) (Fig. 2). This break-point separates the 54 largest species from the remaining 191, indicating a different species temperature–body size relationship between the two groups. This relationship was in fact highly significant for the group of large species (pGLS model t = -4.87, P < 0.0001, adjusted-R^2 = 0.30, λ = 0.0), but not for the group of smaller species (t = -1.20, P = 0.23, adjusted-R^2 = 0.0023, λ = 0.55) (Fig. 2). The pattern found for large species could be strongly conditioned by the three largest species (see Fig. 2). We, therefore, removed these species from the analysis and the relationship remained significant (break-point = 0.476, CI = 0.40–0.54; pGLS for 'large' group: λ = 0.0, adjusted-R^2 = 0.18, t = -3.45, P = 0.0012, n = 50; pGLS for 'small' group: λ = 0.55, adjusted-R^2 = 0.002, t = -1.17, P = 0.24, n = 192).

1.3.3. Assemblage-based approach

The GLS model yielded a highly significant quadratic relationship between weekly mean body size (ITS log_{10}-transformed) and week (week: t = -8.87, P < 0.0001; $week^2$: t = 9.05, P < 0.0001; pseudo-R^2 = 0.63) (Fig. 3a). Residuals inspection revealed four outliers (weeks 1, 2, 51 and 52) that strengthened the fit. We thus re-ran the analysis without these 4 weeks and obtained similar results and greater explanatory power (week: t =-17.13, P < 0.0001; $week^2$: t = 16.03, P < 0.0001; pseudo-R^2 = 0.87) (Fig. 3a). The GLS model yielded a highly significant negative linear relationship between weekly mean body size (log_{10}-transformed) and weekly temperature (log_{10}-transformed) (t = -7.06, P < 0.0001, pseudo-R^2 = 0.50) (Fig. 3b). Residuals inspection

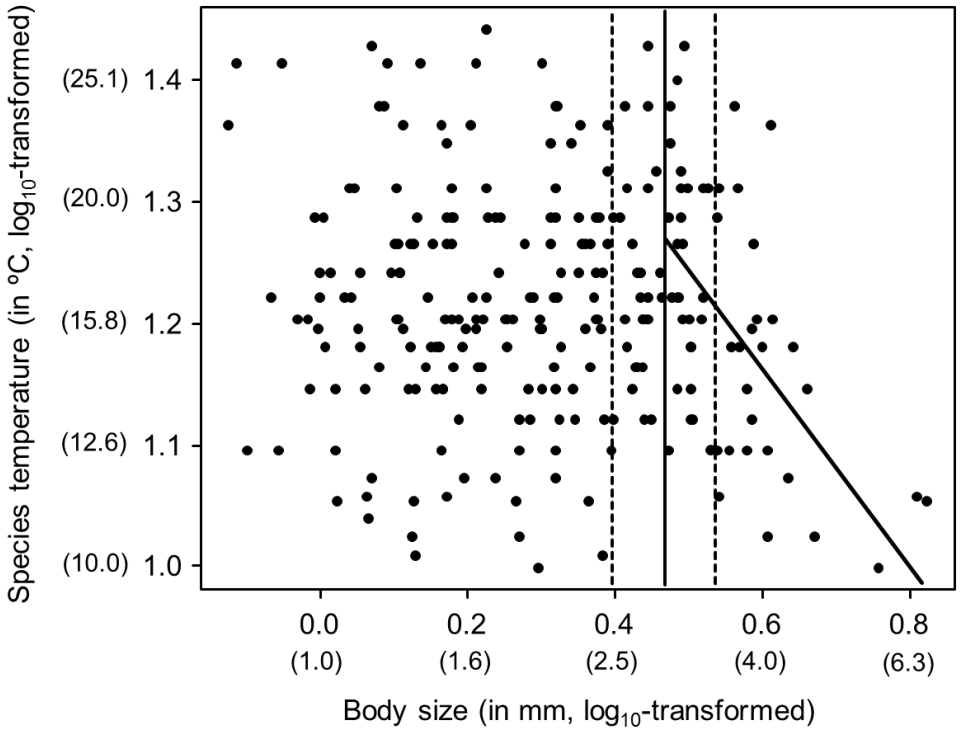

Figure 2. Relationship (phylogenetic generalized least squares model) between 'species temperature' (temperature of the first week in which a species is active) and body size (inter-tegular span in mm, log_{10}-transformed; n = 245 species). Vertical lines indicate the break-point for body size (0.47; solid line), and the 95% confidence intervals (dashed lines) obtained from phylogenetic piecewise regression analysis. The slanted line represents the model fit for the 54 species with body size above the break-point. Numbers in parentheses indicate untransformed values.

revealed the same four outlier weeks. We re-ran the analyses without these 4 weeks, and again obtained a better fit ($t = -13.36$, $P < 0.0001$, pseudo-$R^2 = 0.79$) (Fig. 3b).

1.4. Discussion

The aim of this study was to establish whether Bergmann's rule could be extended to a temporal dimension. In agreement with Bergmann's rule, the temporal distribution of body sizes in our bee community was negatively related to temperature. To our knowledge, this is the first time Bergmann's rule is used to explain the seasonal distribution of body sizes in an animal community or fauna. Our findings are consistent regardless of the methodological approach used. Importantly, in the cross-

species analysis, a Bergmann's pattern is apparent only for species above a certain size threshold (dry body weight, 27.81 mg; 95% CI: 17.86–41.14 mg). This weight is higher than the threshold found between endothermic and ectothermic species in an Alaskan bee community (Bishop & Armbruster 1999). In that community, thermoregulatory ability increased with body weight above 16 mg, and bees with body sizes below this threshold did not show endogenous thermoregulatory capability. The difference between our body weight break-point and the threshold reported by Bishop & Armbruster (1999) may be explained by the highly contrasting climatic differences between arctic Alaska and our Mediterranean study area. Endothermic capabilities should be higher in cold-adapted species, because warm-up rates are expected to have evolved to match ambient conditions (Stone & Willmer 1989). Therefore, it is plausible that endothermic capabilities are reached at lower body sizes in colder climates in which the selective pressure to forage at low temperatures should be higher. At any rate, the fact that a Bergmann's pattern was found only for large (endothermic) species is in agreement with the existing literature on geographic temperature gradients, consistently finding Bergmann's patterns in endotherms (birds and mammals) (e.g. Meiri & Dayan 2003; Clauss et al. 2013), but not in ectotherms (no pattern found in 53% of interspecific studies in insects; Shelomi 2012). Some studies on ectotherms (25% of interspecific insect studies; Shelomi 2012), have found an inverse Bergmann's pattern. Larger body sizes at lower latitudes may arise in species with the capacity to extend their feeding periods in response to long periods of temperatures adequate for growth (Mousseau & Roff 1989). However, this possibility is not available to bees for two reasons. First, larvae have no control over the amount of food consumed (which is determined by the parental generation). Second, nesting females with long nesting periods provision more cells, but do not store larger provisions (Bosch & Vicens 2006). Finally, other studies on ectotherms have found patterns congruent with Bergmann's rule (22% of interspecific insect studies; Shelomi 2012). Although large body size would hinder the ability to warm up in ectotherms, it could still favour heat retention (Stevenson 1985; Cruz et al. 2005; Olalla-Tárraga & Rodríguez 2007). As far as bees are concerned, studies analyzing the distribution of body sizes along geographic gradients have

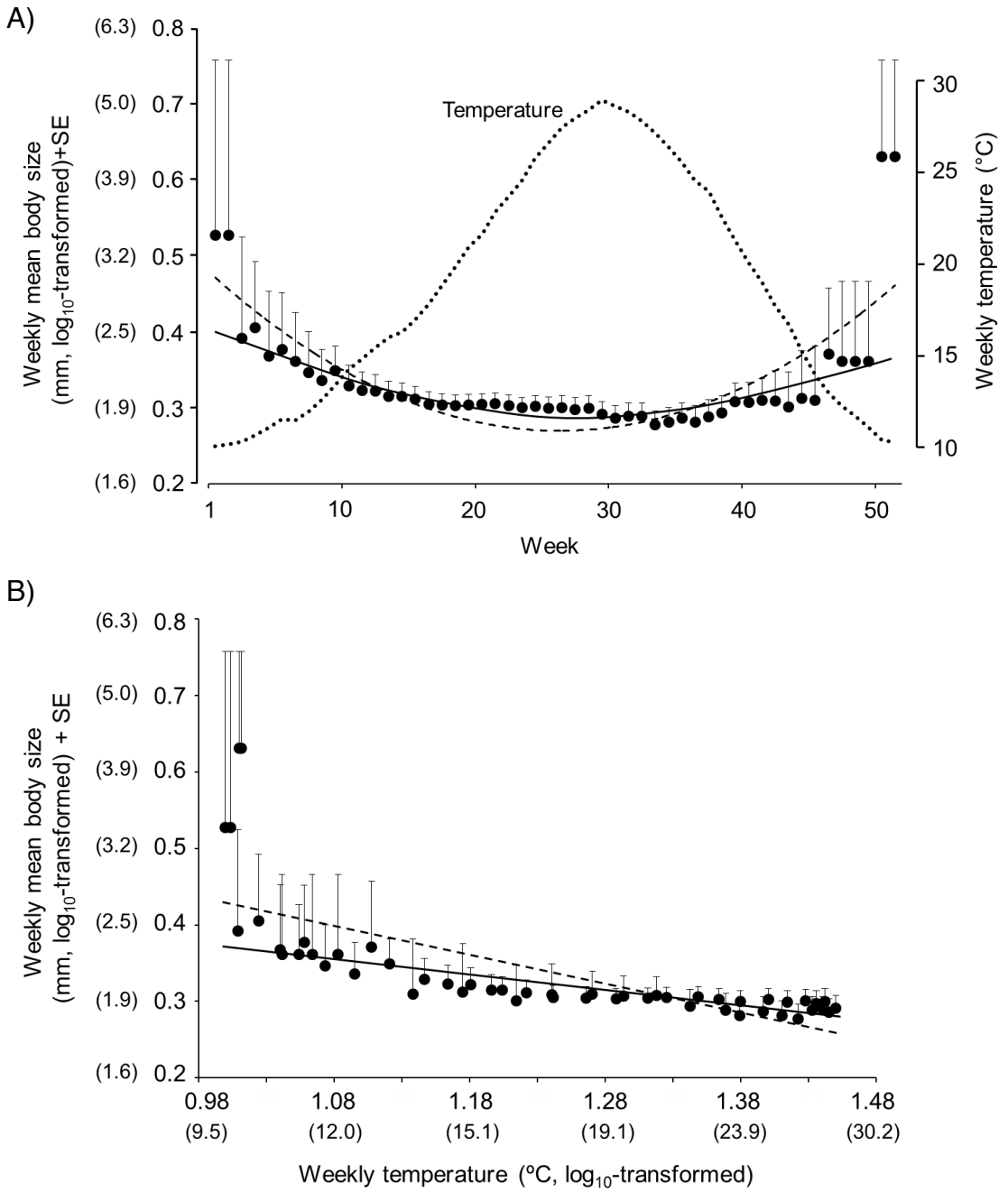

Figure 3. Results of the assemblage-based analyses. **(a)** Relationship (generalized least squares – GLS-model) between weekly mean body size (mean of inter-tegular span of species active in each week, in mm, log_{10}- transformed; dots with + SE bars) and week. The dashed line represents the fitted quadratic function. The solid line represents the same function with four outliers (first 2 and last 2 weeks) excluded. The dotted line represents weekly temperature (weekly average of maximum temperatures). **(b)** Relationship (GLS model) between weekly mean body size and weekly temperature (dots with + SE bars). The dashed line represents the fitted linear function. The solid line represents the same function with four outliers (first 2 and last 2 weeks) excluded. In both graphs, numbers in parentheses indicate untransformed values.

yielded conflicting results. Some have found patterns congruent with Bergmann's rule (Malo & Baonza 2002; Hoiss et al. 2012; Peters et al. 2016) but others have not (Hawkins 1995; Peat et al. 2005; Nagano et al. 2014).

The physiological mechanisms proposed to explain Bergmann's patterns in endothermic vertebrates ('thermoregulatory hypothesis' or 'heat conservation hypothesis'; Bergmann 1847; Blackburn et al. 1999; Watt et al. 2010) also apply to large bees. Bees generate endogenous heat by contraction of the thoracic flight muscles (Heinrich 1993). Large species, with a greater flight muscle mass and a lower surface-to-volume ratio are good endogenous thermoregulators (Heinrich 1993). Consequently, large bees are able to warm up faster and initiate flight activity at lower temperatures (earlier in the morning, on colder days, in alpine habitats) (Willmer & Stone 2004; Peters et al. 2016). Our results suggest that this thermoregulatory ability may also allow large bees to start flying early in the season. As the season progresses and environmental temperatures rise, progressively smaller species within the group of large species (and therefore with lower endogenous thermoregulatory capacity) are added to the community. In temperate latitudes, large amounts of floral resources are available in the spring (Fitter & Fitter 2002; Bosch et al. 2009; Aldridge et al. 2011; Filella et al. 2013). Therefore, the capacity to fly early in the year provides access to abundant floral resources at a time when temperatures are still suboptimal for most pollen/nectar feeding insects (Peters et al. 2016). This is particularly important for large bees, which require large pollen-nectar provisions to produce an offspring (Müller et al. 2006). In Mediterranean ecosystems, characterized by severe summer droughts during which very few plants are in bloom (Bosch et al. 2009), the imbalance between available floral resources and pollinator activity results in a strong increase in flower visitation rates (pollinator visits per flower and minute) from late-winter to summer (Bosch et al. 2009; Filella et al. 2013).

While our results provide evidence for the existence of a Bergmann's pattern in the seasonal distribution of body sizes in our regional fauna, other factors in addition to physiological thermoregulatory ability are likely to have influenced the evolution of the timing of activity periods in bees. First, in the cross-species analysis for large

species, a considerable amount of variability remains unexplained by the temperature-body size relationship (adjusted-R^2 = 0.30). Second, in the assemblage-based analyses, mean bee body size was more strongly related to week than to weekly temperature.

Deviations from an ideal body size–temperature relationship may arise because, in addition to endogenous thermoregulation, bees (both large and small) have other mechanisms to control their body temperature. Several studies show that some small bee species are able to fly at cold ambient temperatures by means of behavioural thermoregulation, including basking, foraging in favourable microclimates such as sun-exposed plants and flowers with elevated intra-floral temperature (Herrera 1995), and restricting foraging activity to the hottest parts of the day (Willmer & Stone 2004). Most small species flying in winter in our community are *Andrena* or *Lasioglossum*, two genera known to fly at lower thoracic temperatures than would be expected for their body size (Bishop & Armbruster 1999). The rest of the small species flying in winter are *Nomada* and *Sphecodes*, which are cleptoparasitic on *Andrena* and *Lasioglossum*. Possibly in relation to the fact that they do not transport pollen-nectar loads, cleptoparasitic bees are also able to fly with lower thoracic temperatures than would be expected for their size (Stone & Willmer 1989). On the other hand, large bees have developed various behavioural mechanisms to fly at hot temperatures. These include interrupting their activity during the hottest part of the day (Willmer & Stone 2004), and increasing flight speed, thus favouring heat loss by convection (Heinrich 1993). In addition, physiological regulation of heat loss has been reported in some large bees, which avoid overheating by diverting haemolymph flow from the thorax to cooler body parts, such as the abdomen and the legs (Heinrich 1993; Peat et al. 2005). Another trait potentially affecting thermoregulation is pilosity. Both length and density of thorax fur have been shown to favour heat conservation at low temperatures (Heinrich 1993; Peters et al. 2016). A recent study found that bees with greater hair length were active at lower temperatures and bee communities along an altitudinal gradient included species with increasing pilosity at increasing elevations (Peters et al. 2016). However, major differences were found between bumblebees (typical of high altitudes) and other bees. Our regional bee

fauna includes only three bumblebee species. In addition to thermoregulation in relation to foraging, pilosity in bumblebees may be related to brood incubation (Heinrich 1993).

Besides the capacity to exploit abundant floral resources available early in the year when temperatures are low, other ecological factors are likely to exert selective pressure on the timing of bee activity periods. Most bee species are polylectic (collect pollen from a variety of plants from different families), but others are oligolectic or even monolectic (collect pollen from only one plant family or genus respectively). The flying period of these species is expected to be under selective pressure to coincide with the flowering period of their main host plants (Willmer & Stone 2004). Cleptoparasitic bee species (18% in our bee fauna) lay their eggs in active nests of other bees (Stephen et al. 1969; Westrich 1989). Therefore, their activity periods are expected to trace the evolution of the activity periods of their hosts (usually a restricted number of closely related species from a given genus). However, because cleptoparasitic bees feed on the host's provisons, their body sizes are similar to those of their hosts (Stephen et al. 1969). Therefore, we do not expect cleptoparasitic species to follow a different body size–temperature pattern from that of nesting species.

Finally, flight phenology is likely to be conditioned by life cycle constraints. Most bees in temperate regions overwinter in the prepupal stage, but some overwinter as adults (Westrich 1989), a condition that allows them to become active early in the year (Bosch et al. 2001). Importantly, the wintering stage appears to be unrelated to body size, and shows a high level of variability even among congeneric species (Bosch et al. 2001). In our fauna, the subfamily Xylocopinae includes the smallest (*Ceratina parvula*) and the largest (*Xylocopa valga*) species, both of which winter as adults (Stephen et al. 1969). Unfortunately, the wintering stage for many of the species in our fauna is not known. A second life history trait that may result in deviations from an ideal body size–temperature pattern is the duration of the life cycle. Most bee species in temperate zone have short (1–2 months) activity periods (Stephen et al. 1969; Westrich 1989). However, some species (including social species such as

Bombus, some *Lasioglossum*, some *Halictus*, but also long-lived solitary species such as *Xylocopa* and some multivoltine species) may be active for most of the season (Stephen et al. 1969; Westrich 1989). At least in the assemblage-based analyses, these differences among species in duration of the activity period are likely to confound body size–temperature relationships. Importantly, however, duration of the activity period is not related to body size in our bee fauna (PGLS model: $\log_{10}$ (ITS) ~ duration of the activity period: $\lambda = 1.00$, adjusted-$R^2 = -0.00024$, $t = 0.97$, $P = 0.33$, $n = 245$).

To our knowledge, our study is the first to extend Bergmann's rule to a year-round temporal temperature cline. Notwithstanding other factors that may have influenced the evolution of activity periods in bees, we propose that species with greater thermoregulatory capacity have some selective advantage by flying early in the year, when temperatures are low. Being active during periods of marginal weather allows these species to exploit abundant flower resources at a time when few pollen-nectar feeding insects are active and flower visitation rates are low (Bosch et al. 2009; Filella et al. 2013). Our results suggest that body size and thermal physiology play a role in structuring community phenology. This is particularly relevant in the current context of global warming, with species experiencing phenological shifts (Scaven & Rafferty 2013). Global warming is expected to cause a reduction in adult body size (Scaven & Rafferty 2013) as a result of temperature size rules (Atkinson 1994). Thermoregulatory strategies could also be affected by global warming, as behavioural thermoregulation seems to be more effective than physiological thermoregulation under hot conditions (Gunderson & Stillman 2015). Finally, an extension of the period with temperatures appropriate for development may result in the addition of extra generations, as has already been reported in several insects (Robinet & Roques 2010). In consequence, climate change is expected to induce important modifications in species body size, themoregulatory strategies, and phonological traits, which may have profound effects on structural and temporal community patterns.

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Chapter 2

Seasonal dynamics in a cavity-nesting bee-wasp community: shifts in community structure, functional diversity and host-parasitoid network structure

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Abstract

Ecological communities are composed of species that interact giving rise to complex interaction networks. Although interaction networks have been usually treated as static entities, interactions show high levels of temporal variation. These variation is mainly due to temporal species turnover. Consequently, analyses based on observations aggregated over long periods are inflated with 'forbidden links', as they put together species with non-overlapping phenologies. Changes in taxonomic composition are likely to bring about in changes in functional trait composition. Because functional traits influence the likelihood that two species interact, temporal changes in functional composition and structure may ultimately affect interactin network structue. Here, we study the seasonality (spring vs. winter) of a community of cavity-nesting solitary bees and wasps ('hosts') and their nests associates ('parasitoids'). We analyze seasonal changes in taxonomic compostion and structure of the host and parasitoid communities, as well as in functional traits. We also analyze whether these seasonal changes result in changes in percent parasitism and interaction network structure. Our host and parasitoid communities are strongly seasonal. Host species richness increases from spring (almost exclusively bees) to summer (both bees and wasps). This results in important seasonal changes in functional composition of the host community. The spring community is characterized by large, univoltine, adult-wintering host species. The summer community is dominated by smaller, bivoltine, prepupa-wintering species. Host functional diversity is higher in summer than in spring. Importantly, these functional changes are not explained by the addition of wasp species in summer. Functional changes in the parasitoid community are much less pronounced, probably due to the lower parasitoid species turnover. Despite these important taxonomic and functional changes, levels of parasitism did not change with season. Two network metrics (generality and interaction evenness) increased from spring to summer. However, these canges can be explained by the seasonal increase in species richness (and therefore network size). Our study underscores the need to consider functional traits and to incorporate a temporal component into network analysis to fully understand the relationship between network structure and ecosystem function.

Key-words: body size, cleptoparasites, functional traits, host-parasite food web, parasitoids, phenology, trap-nesting, temporal variation

2.1. Introduction

Ecological communities are composed of species that interact among themselves in various ways including antagonistic and mutualistic relationships, giving rise to complex interaction networks (Woodward et al. 2005a, Bascompte & Jordano 2007, Ings et al. 2009, Montoya et al. 2006). Ultimately, the structure of these networks reflects ecosystem functioning and community stability (Bascompte 2010, Thompson et al. 2012, Peralta et al. 2014, Harvey et al. 2017, Allesina & Tang 2012). Although we often implicitly treat interaction networks as static entities ("the food web of a given locality", "the pollination network of a given habitat"), interactions show high levels of temporal variation (e.g. Olesen 2010). Abiotic conditions such as temperature and precipitation fluctuate periodically in a more or less predictably way throughout the year (seasonality), and the timing of the life cycle of organisms (phenology) has evolved in response to these changes. Especially in communities of organisms with short activity periods, seasonality results in changes in community composition. Consequently, network analyses based on observations aggregated over long periods are inflated with 'forbidden links' (Jordano et al. 2003) as they put together species with non-overlapping phenologies. This results in apparent low connectance (indicative of low cohesion) and high specialization (Petanidou et al. 2008). For this reason, interaction network studies are progressively moving from static to dynamic analyses, providing a more meaningful relationship with ecosystem function (Olesen 2010, Burkle & Alarcon 2012, Poissot et al. 2015). Several network studies split data into successive time slices, and demonstrate important differences among temporal subnetworks and between the metanetwork and the various temporal sub-networks (Schoenly & Cohen 1991, Tavares-Cromar & Williams 1996, Basilio et al. 2006, Olesen et al. 2008). These differences are mainly due to the temporal turnover of interacting species, which creates temporal assemblages with decreasing compositional similarity as assemblages are further apart in time (Basilio et al. 2006). Even though seasonality clearly affects species composition, there is no consensus about how seasonal changes in community structure and composition translate into seasonal

changes in network structure. Some works show concomitant changes in community and network structure (Laliberté & Tylianakis 2010, Gagig et al. 2012, López-Carretero et al. 2014), while others have found changes in community structure but not in network structure (Lewis et al. 2002, Kemp et al. 2017).

Temporal changes in community structure and composition are likely to lead to changes in community functional trait composition (Ramírez et al. 2015, Samnegard et al. 2015, Kendall & Ward 201). Compared to classical taxonomic-based approaches, trait-based approaches provide an improved mechanistic understanding of species–environment relationships (Keddy 1992, Townsend & Hildrew 1994). A functional approach is especially important for the study of interaction networks, because functional traits influence species interactions at two levels. First, trait-mediated environmental filtering drives species distribution and abundance, and therefore affects the probability that two species may co-occur and potentially interact. Second, trait-mediated morphological and phenological matching drives interactions between potential interaction partners (Vázquez et al. 2009, Eklöf et al. 2013, Bartomeus et al. 2016). In this regard, some studies demonstrate that particular functional traits are fundamental to understand the structure and the degree of specialization of ecological networks (Eklöf et al. 2013, Dehling et al. 2015). For instance, in plant-frugivore and plant-pollinator networks, consumer morphological specialization results in specialized functional roles (Maglianesi et al. 2014, Dehling et al. 2015, Watts et al. 2016). In aphid-parasitoid networks, certain host traits (e.g., degree of food and habitat specialization, mobility, body size, colony organization) are associated with high parasitoid specialization (Gagic et al. 2016). However, it is still unclear how changes in functional trait composition relate to variation in overall network structure.

Here, we study the seasonality of a community of cavity-nesting solitary bees and wasps (henceforth 'hosts') and their nests associates (including parasitoids, cleptoparasites and predators/scavengers; henceforth 'parasitoids') in a temperate zone. Cavity-nesting bees and wasps have been used to study host-parasite

interactions in relation to landscape factors such as habitat composition (Tylianakis et al. 2007, Albrecht et al. 2007, Laliberté & Tylianakis 2010, Osorio et al. 2015). We sampled our community periodically, which affords us with an opportunity to incorporate a temporal dimension to the study of bee-wasp communities and their interactions with parasitoids. We analyze seasonal changes in the taxonomic and functional structure and composition of the host-parasitoid community and in the resulting interaction network. We have three objectives: a) To analyze seasonal changes in species richness, abundance and composition of the host and parasitoid communities; b) To establish whether these changes result in changes in community functional structure; c) To establish whether taxonomic and functional seasonal changes result in changes in parasitism rates and network structure.

Our study area (NE Iberian Peninsula) shows a strong seasonality in climate and food resources for host species (pollen and nectar for bees, nectar and arthropod prey for wasps). Springs are cool and wet compared to summers (ICC 2008). As a consequence, floral resources are much more abundant and diverse in spring than in summer (Bosch et al. 1997, Flo et al. unpublished). Aphids, caterpillars and spiders, the main prey of cavity nesting wasps, also exhibit strong seasonal patterns typical of temperate zones (aphids: Müller et al. 1999, Jansen & Hautier 2007, Yoldas et al. 2011; caterpillars: Mooney & Linhart 2006, Burger et al. 2012, CBMS 2017; spiders: Cardoso et al. 2007, Castro Gil 2009, Barrientos et al. 2014). Therefore, and given that solitary bees and wasps usually have short activity periods (Krombein 1969, Westrich 1989), we expect a high species turnover between seasons. If so, we expect these changes in composition to lead to seasonal changes in functional traits. For example, body size in bee assemblages decreases from spring to summer as environmental temperature increases (Osorio-Canadas et al. 2016). As mentioned, it is unclear to what extent these seasonal changes in composition and functional traits may result in changes in percent parasitism and interaction network structure. In this sense, changes in parasitism rates and/or in network structure have been described in association with changes in community taxonomic structure and composition through temporal (Laliberté & Tylianakis 2010, Gagig et al. 2012, López-Carretero et

al. 2014, but see Lewis et al. 2002, Kemp et al. 2017) and spatial gradients (Maunsell et al. 2015, Morris et al. 2015, Staab et al. 2016).

2.2. Materials & Methods

2.2.1. Study area and sites

The study area covers a surface of about 100 km2 around the city of Olot (Catalonia, NE Spain, 42º11'N, 2º29'E; 443 m above sea level). The climate is Mediterranean with continental influence. Mean annual temperature and cumulative annual precipitation are 13ºC and 1000 L/m2, respectively. Climate presents a marked seasonality, especially in temperature (spring (March-June): mean temperature, 13.7ºC; cumulative precipitation, 322 L/m^2; summer (June-September): mean temperature, 20.4ºC; cumulative precipitation, 289L/m^2)). The natural vegetation is a mixed forest with Mediterranean species (Quercus ilex) alongside mid-elevation continental species (Quercus robur, Fagus sylvatica). Urban development and agricultural areas (mainly cereals) are intermixed within the forest matrix forming a complex small-scale mosaic. We selected 14 sites along a gradient of forest–cropland cover. Distance between sites ranged from 1.4 to 13 km.

2.2.2. Trap-Nesting

Cavity-nesting bees and wasps (henceforth CNBW) nest in pre-established cavities such as abandoned beetle burrows in dead trees, and their nests are attacked by a suite of natural enemies, including parasitoids, cleptoparasites and nest predators/scavengers (henceforth 'parasitoids'). At each site, we placed 'trap-nests' consisting in drilled wood blocks (10x10x16 cm) with inserted paper straws (trap-nest). Each trap-nest accommodated 25 straws of a given diameter (2, 3, 4, 5, 6, 7 or 8 mm). Paper straw length was 5 cm for the 2 and 3 mm diameters and 15 cm for the rest. We arranged these trap-nests in nesting stations. Each nesting station had 7

trap-nests, one of each diameter. Each nesting station was attached to a relatively isolated farm building in each of the 14 chosen sites, approximately at 150 cm above the ground facing SE.

To obtain data on host and parasitoid seasonality, we sampled throughout the entire bee-wasp nesting season (mid-March, to October) in 1991. During this period, we made biweekly visits to each site and replaced filled straws by empty ones to make sure there would be cavities of all diameters available at all times. Straws containing nests were taken to the laboratory and kept at 25 ºC until October, when they were transferred to an unheated storage unit (2-10 ºC) for wintering. In the following spring, straws were exposed to room temperature (22-25 ºC) to stimulate larval development. Then, nests were dissected and their contents recorded, and hosts and parasitoids were reared and identified.

We established two main nesting periods (seasons), of equal duration: spring (nests collected from early April to late June), and summer (nests collected from early July to late September). These two periods differ in climatic conditions (see above) and floral resource availability. In spring, floral resources (pollen and nectar) are abundant and diverse, including wild flowers (Brassicaceae, Prunus, Crataegus, Cistaceae, Papaver, Ranunculus, Boraginaceae) and entomophilous crops (rape, turnip). In summer, floral resources are much less abundant and diverse, including wild flowers (Reseda, Labiatae, Fabaceae, Compositae), and entomophilous crops (sunflower, alfalfa).

2.2.3. Taxonomic community structure

To describe taxonomic community structure, we computed host species richness, host abundance (number of host cells produced), parasitoid species richness and parasitoid abundance (number of parasitized cells) for each nesting station and season.

2.2.4. Functional community structure and composition

For each species of hosts and parasitoid, we compiled information on five and six functional traits, respectively. Hosts were characterized based on: 1) body size, 2) larval diet, 3) wintering stage, 4) voltinism (number of generations per year), and 5) nest-building materials. Parasitoids were characterized based on: 1) body size, 2) parasitic behavior (cleptoparasite, parasitoid or scavenger/predator), 3) wintering stage, 4) voltinism, and 5) gregariousness (solitary: one individual parasitoid develops per individual host; gregarious: several individual parasitoids developed per individual host). For a detailed definition and methodology of these traits see Appendix 2: Table A2.1. These traits are assumed to be important to general species' performance (Moretti et al. 2009, Forrest et al. 2015) and likely to affect the establishment of interactions with other species (Appendix 2: Table A2.1).

We characterized the functional composition of host and parasitoid communities at each site and season by computing two functional indices for each trait: 1) Trait average; it is indicative of the most common trait in a community. For continuous traits (body size), trait average was computed as the weighted community mean (mean of the trait values of all species composing the community weighted by their abundance). In the case of categorical traits, each level of the trait was converted into a separate variable and the proportion of individuals of each species accounting for each level was computed (Laliberté & Legendre 2010, Laliberté et al. 2014); and 2) Functional dispersion (FDis); it provides a measure of functional trait diversity and indicates the extent to which species within a community differ in their traits (Laliberté & Legendre 2010). This index quantifies the mean distance of each species from its community centroid in a multivariate space defined by all included traits. FDis is mathematically independent of species richness and was calculated as an abundance-weighted (quantitative) metric (Hinners et al. 2012, Hoiss et al. 2012). FDis was computed for each single trait and for all traits together. To calculate trait average and FDis indices, we used the function 'dbFD' in 'FD' package (Laliberté & Legendre 2010, Laliberté et al 2014) for R version 3.3.1 (R Development Core Team

2016). We used "lingoes" correction for non-Euclidean distances (Legendre & Anderson 1999, Laliberté & Legendre 2010).

2.2.5. Percentage of parasitism and host-parasitoid network structure

Parasitism was expressed as the percentage of cells that were parasitized. To describe host-parasitoid network structure, we first built two interaction host-parasitoid networks for each nesting station, one for spring and another for summer (28 networks). We then computed the following quantitative metrics related to network specialization: 1) generality (weighted average number of host species per parasitoid) (Bersier et al. 2002); 2) vulnerability (weighted average number of parasitoid species per host) (Bersier et al. 2002); 3) interaction evenness (Shannon's diversity of interactions / ln (hosts richness * parasitoid richness) (Dormann et al. 2009); and 4) the specialization index H2', a measure of the degree of complementary specialization at the network level. This metric, which accounts for the interaction frequency (number of parasitized brood cells) of each species, is not affected by network size and ranges between 0 (maximum generalization) and 1 (maximum specialization) (Blüthgen et al. 2006). Three of our 28 networks were too small to obtain a reliable computation of network metrics, so they were excluded from all network analyses. All metrics were calculated with 'bipartite' v.1.16 (Dormann et al. 2009) for R.

2.2.6. Statistical analyses

Effects of seasonality on host and parasitoid taxonomic community structure

We used general linear mixed models (GLMM) ('nlme' package for R; Pinheiro et al. 2012) to analyze the effects of season on each response variable (host abundance, host richness, parasitoid abundance, parasitoid richness). To account for repeated temporal measures (spring and summer), we included site as a random factor. Some

studies have found parasitoid richness and parasitoid abundance to be correlated to host richness and/or abundance (Steffan-Dewenter 2003, Albrecht et al. 2007, Holzschuh et al. 2009, Osorio et al. 2015). Thus, analyses of parasitoid-related variables were repeated controlling for potential host effects. Host abundance was not affected by season (see results). Therefore, we only used host richness as controlling variable. Host richness was strongly related to season (see results). Thus, it could not be included as a covariate with season in the same model. Therefore, to extract the effects of host richness on parasitoid richness and abundance we first built a GLMM with the response variable (parasitoid richness or parasitoid abundance, respectively) and only host richness as explanatory variable, and then we extracted the residuals of these models as new response variables.

Effects of seasonality on community taxonomic composition

To explore the effects of season on taxonomic community composition, we used permutational multivariate analysis of variance (PERMANOVA) ('adonis' function, Vegan Library (Oksanen et al. 2012) for R), separately for hosts and parasitoids. Abundance data for each plot in both seasons were square-root transformed, and distance matrices were calculated with the Bray-Curtis dissimilarity index. We run 9999 permutations per test. Because we used the same nesting stations along the two seasons, they were grouped by site using the function strata, which constrains the number of permutations within groups (stations) similarly to a random factor. We also run qualitative (presence/absence) versions of these PERMANOVAs to evaluate if possible seasonal community shifts are just due to changes in relative abundances, or mainly due to species turnover. To visualize differences in community composition among stations in each season (separately for hosts and parasitoids) we conducted multidimensional scaling (NMDS) based on the Bray-Curtis dissimilarity index ('metaMDS' function, 'Vegan' Library for R (Oksanen et al. 2012)). We selected the number of dimensions (k) considering ''stress'' values (a measure of goodness of fit

based on the Bray-Curtis dissimilarity index and distance in graphical representation).

Effects of seasonality on community functional composition

We used GLMMs to analyze the effects of season (spring vs summer) on each functional response variable: 1) trait average index for each trait (for categorical traits that only had two levels, analyses were conducted just for one level); and 2) FDis for each trait and for the entire pool of traits. All analyses were conducted separately for hosts and parasitoids. In each model we checked the residuals for the assumptions of normality and homoscedasticity, and transformations (log10, square, square root, arcsine) were applied in some variables to meet these assumptions.

Effects of seasonality on parasitism and network structure

We again used GLMMs to analyze the effects of season (spring vs summer) on percentage of parasitism and on the specialization network metrics (vulnerability, generality, interaction evenness and H_2'). As with taxonomic community structure variables, the percentage of parasitism and network structure metrics may be affected by certain covariates (Steffan-Dewenter 2003, Albrecht et al. 2007, Holzschuh et al. 2009). So, we repeated these analyses controlling for potential effects of these covariates. Some studies show correlations of percent parasitism with host richness and/or abundance (Steffan-Dewenter 2003, Albrecht et al. 2007, Holzschuh et al. 2009), and parasitoid richness (Veddeler et al 2010). As host abundance was not related to season in our study (see results), and parasitoid richness was related to season through the effect of host richness (see results), we used host richness as a controlling variable. Host richness was strongly related to season (see results). Thus, it could not be included as a covariate with season in the same model. Therefore, to extract the effects of host richness on percentage of parasitism, we first build a GLMM with the response variable (percentage of parasitism) and only host richness as

explanatory variable, and then we extracted the residuals of these models as new response variables in a new analysis with season as a response variable. Vulnerability, generality and interaction evenness may be affected by network size (Tylianakis et al. 2007, Dormann et al. 2009, Gagic et al. 2011). For this reason, we tried to use network size (host richness + parasitoid richness) as a controlling variable in the seasonality analyses. However, network size and season were related (mean network size ± SE: spring, 9.3 ± 1.2; summer, 15.0 ± 0.8; GLMM: $F_{1,10} = 26.8$, $P = 0.0004$), and therefore could not be used in the same analysis. As a result, we followed the same procedure as for percent parasitism: we first built a general linear mixed model of the response variable (vulnerability, generality, interaction evenness) with network size as explanatory variable, and then we extracted the residuals of these three models as new response variables in three new analyses with season as a response variable. In all GLMMs, adjusted-pseudo R2 was calculated based on Likelihood-ratio tests with the r.squaredLR function (MuMIn package, Bartoń 2015). Transformations (log_{10}, square root) were applied as needed to meet the assumptions of normality and homoscedasticity.

2.3. Results

2.3.1. General description of the community

We obtained 1491 nests amounting to 5703 cells. About half of the nests (57.9 %) corresponded to 16 bee species (13 Megachilidae, 3 Colletidae) (Appendix 2: Table A2.2). The remaining nests corresponded to 11 wasp species (6 Crabronidae, 4 Eumenidae, 1 Sphecidae). In addition, we found 19 species of parasitoids (Appendix 2: Table A2.2). We collected a similar number of nests in the two seasons (719 in spring, 772 in summer), but more cells in spring (3485) than in summer (2218).

2.3.2. Effects of seasonality on community taxonomic structure and composition

There were no differences in host abundance between spring and summer, but host richness was significantly higher in summer (mean ± SE: 8.4 ± 0.5) than in spring (3.9 ± 0.6) (Table 1, Fig. 1). Wasps were very rare in spring. Therefore, the increase in host richness in summer might be simply due to the addition of wasp species. To test this possibility, we repeated the abundance and richness analyses only with bee hosts. Bee abundance was higher in spring (mean ± SE: 242.5 ± 55.4) than in summer (41.4 ± 6.9), but there were no seasonal differences in mean bee richness (spring: 3.1 ± 0.5, summer: 3.7 ± 0.3). As for parasitoids, there were no differences in abundance between spring and summer, but richness, although not significantly, tended to be higher in summer (6.6 ± 0.5) than in spring (5.4 ± 0.7), (Table 1, Fig. 1). Once controlled for host richness, the effect of season on parasitoid richness was non-significant (Table 1).

Bee activity began in early spring and continued through the summer, showing a strong seasonality. Two bee species occurred only in spring, seven in spring and summer, and seven only in summer. On the other hand, wasp activity did not start until late spring. The wasp community also showed a strong seasonality. Five wasp species occurred in late spring and summer, and six only in summer. Consequently, there was a significant seasonal change in taxonomic host community composition (PERMANOVA for quantitative host species composition data: df=1, F=8.4; p=0.0001, pseudo-R2=0.2) (Fig. 2A). This change was not only due to changes in relative frequencies of different host species, but to species turnover, as qualitative results also showed a significant change in taxonomic host community composition (Appendix 2: Table A2.4). Since wasps were very rare in spring, we repeated these analyses only with bee host species, and again we found clear significant differences in community composition between seasons, both quantitatively (df=1, F=4.3, p=0.001, pseudo-R2=0.14) and qualitatively (Appendix 2: Table A2.4).

Table 1. Summary of linear mixed model outputs analyzing the effect of season (reference level: summer) on various community and network metrics. Six of the analyses (parasitoid abundance, parasitoid richness, percentage of parasitism, vulnerability, generality and interaction evenness) were repeated controlling for the effects of particular covariates (controlled variable).

Response variable	*t*	Pseudo-R^2	*P*	Controlled variable	*t*	Pseudo-R^2	*P*
Host abundance	-0.78	0.02	0.45	None	-	-	-
Host richness	11.4	0.50	**<0.0001**	None	-	-	-
Parasitoid abundance	-0.27	0.003	0.79	Host richness	1.20	0.05	0.25
Parasitoid richness	1.93	0.12	0.076	Host richness	1.51	0.08	0.16
Percentage of Parasitism	0.07	0.001	0.95	Host richness	0.82	0.03	0.43
Vulnerability	0.34	0.01	0.74	Network size	0.97	0.04	0.35
Generality	3.56	0.32	**0.005**	Network size	1.62	0.10	0.13
Interaction Evenness	2.27	0.18	**0.046**	Network size	1.40	0.08	0.19
H_2'	-0.65	0.07	0.53	None	-	-	-

The parasitoid community also changed significantly from spring to summer (Fig. 2B) (quantitative PERMANOVA: df=1, F=9.1; p=0.0001, pseudo-R2=0.3; see qualitative PERMANOVA in Appendix 2: Table A2.4). One parasitoid species was only found in spring, twelve in both spring and summer, and six only in summer. In spring, the parasitoid community was dominated by species exclusively attacking bees (Monodontomerus obsoletus, Cacoxenus indagator) (Fig. 1). In summer, the parasitoid community was dominated by species that showed a clear preference for wasp hosts (some exclusively attacked wasp hosts) (Pyemotes ventricosus, Sarcophagidae sp. 1, Sarcophagidae sp. 2), but also by species attacking indistinctly bees and wasp (Trichodes alvearius, Melittobia acasta) (Fig. 1).

2.3.3. Effects of seasonality on community functional structure and composition

Most host traits showed significant shifts in trait average index from spring to summer (Table 2). Overall, the spring community was characterized by large, univoltine, adult-wintering host species, with a pollinivorous diet and generalized host-parasite relationships. In contrast, the summer community was dominated by smaller, bivoltine, prepupa-wintering, mostly carnivorous species. The use of various nesting materials (mud, plant materials, secretions) on the other hand, did not vary across seasons. Since wasps were very rare in spring, we repeated these analyses only for bee host species, and we obtained similar results for all traits, except for the proportion of species using mud as nesting material, which significantly decreased from spring to summer (Table 2). In general, host trait FDis was higher in summer than in spring, and this pattern did not change when only bees were considered (Table 2). However, the traits involved were not entirely coincidental (all hosts: larval diet, wintering stage and nesting material; bees only: wintering stage and voltinism) (Table 2). Overall FDis (all traits together) was higher in summer than in spring (both for all hosts and for only bee hosts) (Table 2).

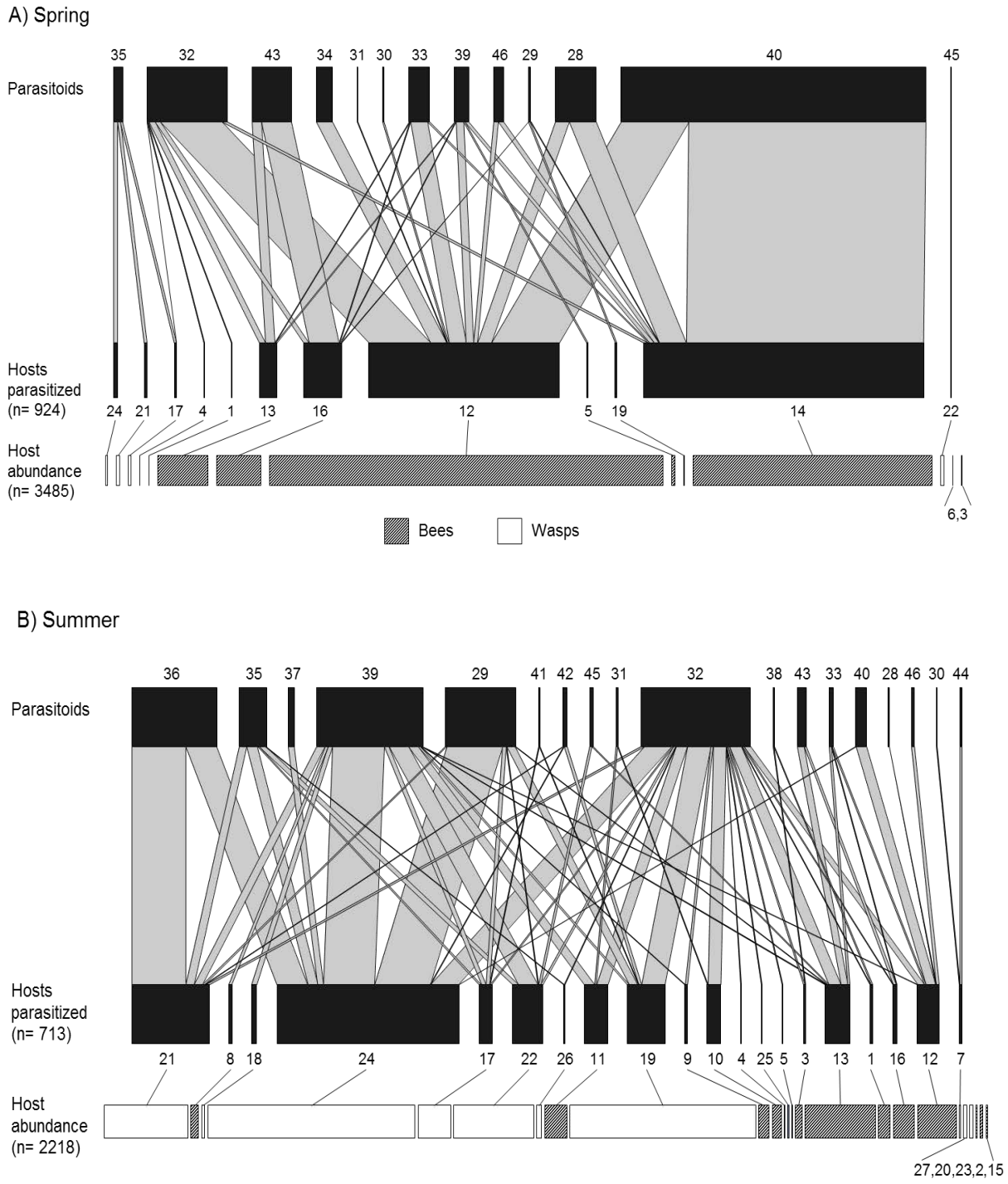

Figure 1. Spring (A) and summer (B) host-parasitoid network (data from the 14 sampled sites lumped together). Numbers correspond to species names in Appendix 2 (Tables A2.2). Width of links (grey) denotes interaction strength (number of cells parasitized). Width of red and yellow bars indicates host abundance (number of cells produced). Note different scales in spring and summer networks (n=number of cells).

Results were quite different for the parasitoid community. None of the parasitoid traits considered showed seasonal variation in trait average index (Table 2). But, in coincidence with hosts, parasitoid FDis was higher in summer than in spring for most traits (except for 'wintering stage' and 'gregariousness', which showed only marginal seasonal differences) (Table 2). Also in agreement with hosts, overall FDis (all traits together) was higher in summer than in spring (Table 2).

2.3.4. Effects of seasonality on parasitism and network structure

Despite the above-mentioned differences between seasons in taxonomic and functional community structure and composition, there were not significant differences in the percentage of parasitism between spring (mean ± SE: 22.1 % ± 4.5) and summer (32.5% ± 6.4) (Table 1). As regards network structure, generality was significantly higher in summer (1.8 ± 0.1) than in spring (1.4 ± 0.08) (Table 1, Fig. 1), but this effect disappeared after controlling by network size (Table 1). Interaction evenness showed a similar tendency, which again disappeared after controlling for network size (Table 2, Fig. 2). Vulnerability and H2' showed no differences between seasons (Table 2, Fig. 2).

2.4. Discussion

We report strong seasonal changes in taxonomic and functional structure and composition in both host and parasitoid communities. However, we found no seasonal shifts in percent parasitism, and seasonal changes in the structure of the host-parasitoid interaction network appear to be mostly driven by changes in network size.

Table 2. Summary of linear mixed model outputs analyzing the effect of season (reference level: summer) on trait average and on functional dispersion (FDis) for single traits and for all traits together in (A) host (bees + wasps), (B) (only bee hosts) and (C) parasitoid communities.

A) HOSTS

		Trait average		**FDis**	
Trait	Variable	t	p	t	p
Larval diet	% pollinivorous	-12.9	**<0.0001**	7.0	**<0.0001**
Body size	Inter-tegular span	-6.6	**<0.0001**	1.7	0.1
Wintering stage	% prepupa	20.3	**<0.0001**	3.4	**0.007**
Voltinism	% univoltine	-7.9	**<0.0001**	1.2	0.3
Nest-building material	% mud	-1.0	0.3	4.4	**0.001**
	% plant material	0.2	0.9		
	% secretions	3.5	**0.004**		
All traits	-	-	-	4.9	**0.0006**

B) ONLY BEE HOSTS

		Trait average		**FDis**	
Trait	Variable	t	p	t	p
Body size	Inter-tegular span	-4.6	**0.0005**	0.1	0.9
Wintering stage	% prepupa	5.2	**0.0002**	3.9	**0.004**
Voltinism	% univoltine	-3.0	**0.01**	2.9	**0.02**
Nest-building mat.	% mud	-3.1	**0.009**	1.5	0.2
	% plant material	1.6	0.13		
	% secretions	2.6	**0.02**		
All traits	-	-	-	3.6	**0.005**

Table 2. (continued)

C) PARASITOIDS

		Trait average		**FDis**	
Trait	variable	t	p	t	p
Parasitic behaviour	% cleptoparasite	0.3	0.8	2.0	**0.07**
	% parasitoid	-0.3	0.8		
	% scavenger	-0.02	0.9		
Body size length	Length	-1.6	0.1	4.4	**0.0009**
Wintering stage	% inmature	-0.1	0.9	1.9	0.09
Voltinism	% univoltine	-0.2	0.9	3.0	**0.006**
Gregariousness	% solitary	-1.4	0.2	2.1	**0.06**
All traits	-	-	-	3.5	**0.005**

Our bee-wasp community showed a strong seasonality. The spring community was almost exclusively composed of bees. Then, as the season progressed, wasps became increasingly specious and abundant while bees maintained their species richness but became less abundant. Other studies in Mediterranean habitats have also found greater bee abundance and/or diversity in spring and greater wasp abundance and/or diversity in summer (Petanidou et al. 1995, Bosch et al. 1997, González et al. 2003, Standfuss & Standfuss 2006, Osorio-Canadas et al. 2016, Leong et al. 2016). Importantly, the strong seasonal changes in species composition in our host community were not only due to the addition of wasps late in the season. Temporal species turnover was also important within the bee guild. Osmia spp. were the first bees to appear, followed by other Osmiini and Hylaeus, and the Megachilini occurred mostly in summer. As a result, the spring and summer host communities were drastically different.

The parasitoid community followed the dynamics of the host community. Parasitoid abundance did not change seasonally, and the close-to-significant increase in species richness from spring to summer can be explained by the increase in host species richness. This result is in agreement with other studies showing a similar relationship between host and parasitoid community structure (Steffan-Dewenter 2003, Albrecht et al. 2007, Osorio et al. 2015). Seasonal changes in parasitoid composition also parallel changes in host composition, as most parasitoid species show a certain level of specificity at the subgenus, genus or tribe level. Only 4 parasitoid species attacked both bees and wasps (10 attacked only bees and 5 only wasps).

Seasonal changes in host community structure and composition resulted in clear changes in functional composition. Most of the traits considered showed a seasonal component. Importantly, these changes were not exclusively due to the addition of wasp species in summer. Rather, the trends observed at the entire community level were maintained when only bees were considered. In addition, and in agreement with the increase in species richness late in the season, we found that functional diversity was higher in summer than in spring. Bee studies in tropical areas have found changes in trait predominance (Samnegard et al. 2015), and in functional richness (Ramírez et al. 2015) between the dry and rainy seasons. The study of Ramírez et al. (2015) did not find seasonal changes in trait means or in functional diversity. However, this study involved a taxonomically narrow group (Euglossine bees), expected to be less functionally diverse than our bee/wasp community.

We found a seasonal decrease in body size for both the overall and only bee host communities. Body size has been shown to decrease from spring to summer in a regional bee fauna close to our study area (Osorio-Canadas et al. 2016). This pattern was interpreted as a temporal extension of Bergmann's rule, whereby species with larger body sizes are better equipped to generate and conserve body heat (Stone & Willmer 1989, Heinrich 1993, Bishop & Armbruster 1999), and therefore can afford to be active in periods of cold temperatures (Osorio-Canadas et al. 2016). The decrease in host body size in our community has important consequences for the use

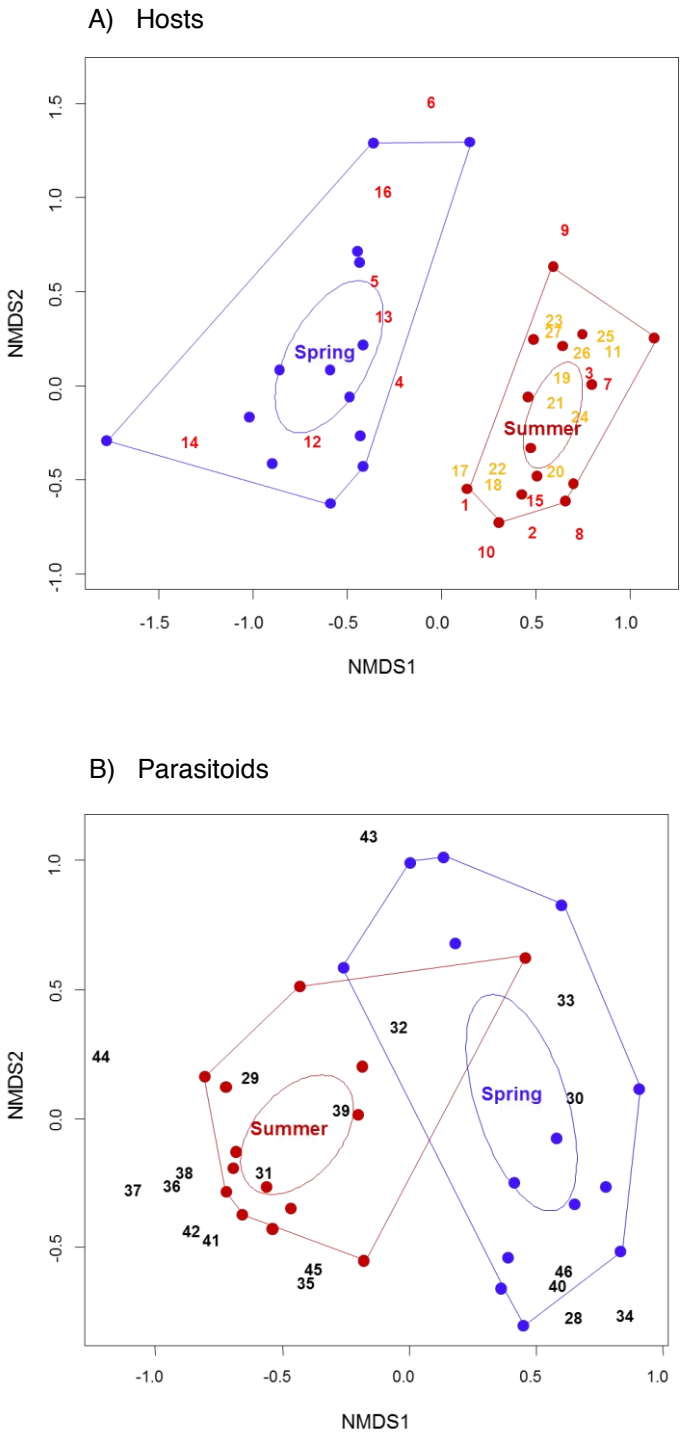

Figure 2. Nonmetric multidimensional scaling (NMDS) of (A) host and (B) parasitoid community composition in each season and sampling statition, using abundance data. Colour points represent sampling stations (Spring: blue; Summer: dark red). Colored numbers represent species codes (light red: bees; orange: wasps; black: parasitoids). For species codes, see Appendix 2 (Tables A2.2). Colored polygons encompass all sampling stations in the same season. Ellipses represent CI (0.95%) for each season. Only two of the three dimensions obtained in the analysis (k=3) are displayed.

of nesting resources. Unlike many other bee and wasp species which excavate their own nests, cavity-nesting species are totally dependent on pre-existing cavities, such as abandoned beetle burrows in dead wood, hollow stems, and abandoned bee and wasp nests (Stephen et al. 1969). Preferred cavity diameter is correlated to body size, so finding potential preexisting holes of suitable characteristics could be a limiting factor, as suggested by some studies (Holzschuh et al. 2010, Roulston & Goodell 2011). In our study, the seasonal decrease in host body size resulted in a decrease of cavity diameters occupied from spring to summer (Appendix 2: Figure A2.2).

Functional traits average indexes of our parasitoid community did not vary seasonally. This could be explained in part by longer mean activity periods of parasitoid species compared to host species (parasitoid: (mean±SE) 6.6±0.7 fortnights; bee hosts: 4.3±0.7; wasp hosts: 4.1±1.1). In fact, only 44% of the host species were found in the two seasons, compared to 63% of the parasitoid species.

Nevertheless, in agreement with the bee-wasp dominance seasonal pattern, the parasitoid community showed a higher proportion of species attacking only bees in spring (~69%), and a higher proportion of species attacking only wasps (~22%) or both guilds (~70%) in summer. Parasitoid overall functional diversity (all traits together) was higher in summer than in spring, again in agreement with taxonomically and functionally richer and more diverse summer host communities. This result contrasts with the absence of seasonal shifts in functional diversity found by other study in parasitoid communities (Kendall & Ward 2016). However, this study involved a taxonomically narrower group (Ichneumonidae and Braconidae wasp families), expected to be less functionally diverse than our parasitoid community. Factors related to host biology, such as habitat specialization, food-plant type and feeding strategy are known to be important determinants of parasitoid community structure (Hawkins 1994, Shaw 2006) and, in consequence, they probably are also important drivers of parasitoid functional diversity patterns (Santos et al. 2015). Interestingly, a study on island parasitoid assemblages along a worldwide latitudinal gradient found a positive relationship between island temperature and

functional diversity (Santos et al. 2015). The higher levels of energy available in warmer islands may increase the availability of both food and habitat resources (Wright 1983), allowing for the coexistence of a greater range of functions, and therefore higher functional diversity (Santos et al. 2015). Even though host abundance in our study did not change between the colder (spring) and the warmer (summer) periods, we found a greater functional diversity in summer, probably mediated by the greater host species availability in summer.

We found important seasonal taxonomic and functional changes in both our host and parasitoid communities. The changes in functional structure involved functional traits potentially important for the establishment of host-parasitoid interactions (Appendix 2: Table A2.1). Therefore, we expected to find changes in parasitism rates and in host-parasitoid interaction networks. However, parasitism rates in our community did not change seasonally. Some studies have found significant temporal variation in parasitism rates (Tylianakis et al. 2006, Veddeler et al. 2010, Gagic et al. 2012), but these studies use shorter temporal resolutions (monthly, weekly) and therefore do not really address seasonal changes. It is possible that these shorter time lapses reveal more subtle changes in community structure and, consequently, in parasitism rates. Our community also shows important biweekly fluctuations in percent parasitism (data not shown), but these changes show no seasonal pattern. The three above-mentioned studies find parasitism rate to be positively related to parasitoid species richness and abundance through time. Similar results have been reported in other studies along geographical gradients (Staab et al. 2016). Since we found no seasonal differences in host and parasitoid abundance, and only marginal differences in parasitoid richness, the lack of seasonal differences in parasitism rate in our community is congruent with these studies.

As opposed to parasitism rate, we found some seasonal changes in network structure (interaction evenness and generality increased from spring to summer). However, and in agreement with other studies on temporal shifts in antagonistic networks (Laliberté & Tylianakis 2010, Gagic et al. 2012, López-Carretero et al. 2014), seasonal

changes in network structure in our study are mostly explained by the seasonal increase in species richness, and therefore, network size. In this sense, some studies along geographical gradients also report changes in network structure associated to changes in taxonomic community structure and composition (Maunsell et al. 2015, Staab et al. 2016). However, another study reported changes in network structure that were independent of changes in network size (Morris et al. 2015). In mutualistic networks, seasonal changes in network structure are also related with seasonal variation in species richness (Ramos-Robles et al. 2016). Interestingly, where no temporal changes in network size have been found, very few changes in network structure have been reported (Tiedeken & Stout 2015). Irrespective of the effect of network size, it is noteworthy that vulnerability did not increase from spring to summer as generality did. This may be explained by the clear increase in host species richness in summer, while parasitoid richness keeps constant between seasons. Notwithstanding network size effects, some studies along geographical gradients suggest that temperature might have a direct effect on species interactions, as colder environments tend to hold lower parasitism rates and lower values of generality, vulnerability and interaction evenness (Hall et al. 2015, Maunsell et al. 2015).

We found important seasonal changes in taxonomic community structure and in community composition both in host and parasitoid communities. These changes result in distinct changes in functional structure (especially for hosts), which occur at two levels. First, we shift from a bee dominated community in spring to a wasp dominated community in summer. Second, even considering only bee hosts, functional trait composition and functional structure clearly changed between spring and summer communities. Functional traits considered are likely to affect host-parasitoid interactions, and therefore to have a direct effect on parasitism function (see Appendix 2: Table A2.1). Nevertheless, we found no seasonal changes in percent parasitism, and the observed changes in network structure could be explained by changes in species richness (and therefore network size). A possible explanation for the lack of relationship between changes in functional and network structure could be a compensation between traits influencing network parameters in opposite

directions. For example, considering the spring to summer decrease in host body size we would expect a decrease in vulnerability in summer (as large hosts could be attacked by parasitoids of any size, but smaller hosts would be less likely to be attacked by large parasitoids). However, the host decrease in body size from spring to summer was paralleled by a shift from mostly univoltine to mostly bivoltine hosts (with an overall longer activity period and therefore likely to be attacked by a greater number of parasitoid species, resulting in an increasing vulnerability in summer). At any rate, the consequences of the strong seasonal changes observed in our bee-wasp-parasitoid community go well beyond host-parasitoid relationships. The shift from a bee dominated community in spring to a wasp dominated community in summer implies an emphasis on pollination function in spring and an emphasis in predation function in summer, with obvious consequences on ecosystem function. In conclusion, our study underscores the need to consider functional traits and to incorporate a temporal component into network analysis if we are to understand the global relationship between network structure and ecosystem function.

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Chapter 3

Local and landscape effects in a host–parasitoid interaction network along a forest–cropland gradient

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Abstract

Land-use driven habitat modification is a major driver of biodiversity loss and impoverishment of interaction diversity. This may affect ecosystem services such as pollination and biological control. Our objective is to analyze the effects of local (nesting environment: farms vs. tree stands) and landscape (forest–cropland gradient) factors on the structure and composition of a cavity-nesting bee–wasp (CNBW) community, their nests associates (henceforth parasitoids), and their interactions. We set up 24 nest-trapping stations in a fragmented, extensively farmed area of ~100 km^2. We obtained 2035 nests containing 7572 brood cells representing 17 bee and 18 wasp species, attacked by 20 parasitoid species. Community structure and composition, as well as network structure, were much more dependent on local than on landscape factors. Host abundance and richness were higher in farms. In addition, host abundance was positively correlated to cropland cover. We also found highly significant differences between nesting environments in host community composition. Structure and composition of the parasitoid community were conditioned by the structure and composition of the host community. Network structure was affected by nesting environment but not by landscape factors. Interactions tended to be more diverse in farms. This result was mostly explained by differences in network size (greater in farms). However, generality was significantly higher in farms even after controlling for network size, indicating that differences in species' interaction patterns associated to differences in community composition between the two nesting environments are also affecting network structure. In conclusion, open habitats associated with extensively farmed exploitations favor local CNBW diversity (especially bees) and result in more complex host–parasitoid interaction networks in comparison to forested areas. The conservation value of this kind of open habitat is important in view of the progressive abandonment of extensively cultivated farmland taking place in Europe at the expense of agricultural intensification and reforestation.

Key words: crop–forest gradient; ecosystems services; extensive agriculture; extensive farming; host–parasitoid food web; pollinators; trap-nesting bees and wasps.

3.1. Introduction

Discerning the factors that generate and maintain biodiversity and their implications for the structure of relationships among species is fundamental to understand ecosystem function. In the last decades, agricultural activity has been one of the main drivers of habitat transformation, with strong consequences on community structure and biodiversity loss (Robinson and Sutherland 2002, Foley et al. 2005). Two of the main consequences of farming are the alteration and the fragmentation of natural habitats, which, depending on the degree of agricultural intensification, generate more or less complex mosaic landscapes (Bennett et al. 2006). In such fragmented environments, both local and landscape factors may have a strong effect on resident communities (Clough et al. 2007, Williams and Kremen 2007, Kennedy et al. 2013, Schüepp et al. 2014). At the local scale, most studies focus on habitat type (seminatural vs. agricultural [Berg 2002]), and habitat elements typical of agricultural landscapes (crops vs. fallows, forest edges, hedgerows, grass strips [Kruess 2003, Holzschuh et al. 2009]), as well as farm management (agricultural intensity, conventional vs. organic [Clough et al. 2007, Williams and Kremen 2007, Holzschuh et al. 2010, Kennedy et al. 2013]). At the landscape level, several studies have shown that landscape composition and spatial configuration, as well as habitat diversity, may affect community composition and structure, and that these landscape effects may be scale dependent (Tews et al. 2004, Winfree et al. 2011, Tscharntke et al. 2012, Kennedy et al. 2013). To assess the effects of habitat transformation on communities it is therefore important to simultaneously analyze local and landscape factors at different spatial scales.

Changes in community structure and composition caused by human intervention may in turn affect the identity and strength of interactions between species, potentially resulting in changes in interaction network structure (Tscharntke et al. 2005, Tylianakis et al. 2008). Ultimately, these changes may pose a threat to ecosystem services associated with certain interactions such as pollination and biological control (Costanza et al. 1997, Kremen and Ostfeld 2005). Therefore, to make agricultural

management compatible with the preservation of natural communities and ecosystem function, we need to understand the extent to which changes in community structure and composition affect interaction identity and interaction network structure.

There are several ways in which changes in community structure and composition may result in changes in network structure. First, community species richness determines network size, which is well known to influence many network metrics such as connectance, linkage density, vulnerability, and generality (Blüthgen et al. 2006, Tylianakis et al. 2007). Second, abundance may affect network structure if abundant species are more likely to interact with a high number of species simply due to their abundance (neutrality [Vázquez et al. 2009]). Abundance may also indirectly affect network size. For example, host abundance may favor parasitoid species richness (Kruess 2003, Albrecht et al. 2007). Third, species composition may affect network properties, simply because different species are likely to have different interaction patterns, such as the number of species with which they interact or their interaction diversity. Finally, interaction patterns may be context dependent, so that the same species may behave differently in different environments (Brose et al. 2005, Tylianakis et al. 2007).

A number of studies addressing the effects of habitat alteration on interaction networks have worked with cavity-nesting bees and wasps (henceforth CNBW). Using trap-nesting units, information on species richness, abundance, and interactions with nest associates (parasitoids, cleptoparasites, and nest scavengers) can be obtained simultaneously in different locations, and sampling effort can be standardized and replicated. Several studies have found that richness and abundance of CNBW depends on various local and landscape factors, such as the proportion of seminatural habitat, edge density of surrounding landscape, vegetation structure, and microclimate (Steffan-Dewenter 2002, Holzschuh et al. 2010, Batista Matos et al. 2013). The few studies that have specifically addressed community composition in CNBW (species identity and relative abundance) have found that community composition may

change depending on the degree of agricultural intensity (Tylianakis et al. 2007) and, more specifically, on the extent of habitat deforestation associated with farming (Laliberté and Tylianakis 2010). Finally, some studies have found changes in community structure and host–parasitoid network structure in relation to habitat management and agricultural intensity (Albrecht et al. 2007, Tylianakis et al. 2007).

In this study we investigate the effects of local and landscape factors on a community of CNBW and their nests associates (henceforth parasitoids), and on the structure of their interactions along an agricultural–forest gradient. At the local level we consider the two potential habitats used by CNBW as nesting environments in the study area: tree stands and farming complexes. At the landscape level we consider the proportion of the two main habitats potentially used by CNBW as foraging areas (agricultural fields and forests). Our objectives are to understand how nesting environment and landscape composition modify abundance, species richness, and composition of hosts and parasitoids, and to establish whether the observed changes result in changes in level of parasitism and host–parasitoid network structure.

3.2. Material and Methods

3.2.1. Study area and sites

The study area covers a surface of ~100 km^2 around the city of Olot (Catalonia, northeast Spain, 42º 11' N, 2º 29' E; 443 m above sea level). The climate is Mediterranean, with a mean annual temperature of 13º C and a mean rainfall of 1000 L/m^2. The natural vegetation is a mixed forest with Mediterranean species (*Quercus ilex*) alongside mid-elevation continental species (*Quercus robur*, *Fagus sylvatica*). Forests are relatively young (30–40 years), with a regular structure due to past lumber and reforestation activities. Tree density is high, with scarce understory and low volume of dead wood. Urban development and agricultural areas are intermixed within the forest matrix forming a complex small-scale mosaic (sensu Tscharntke et

al. 2005) (Fig. 1A, see Plate 1). Fields are small (1.74 ± 0.20 ha [mean ± SE], *n* = 50 randomly chosen fields), and unmanaged field margins, pine and oak coppices, and fallow fields are important elements of the agricultural landscape. Agricultural management is extensive (low input of pesticides and inorganic fertilizers). The main crops are cereals (mostly corn, ~85% cropland cover). The main entomophilous crop is alfalfa (*Medicago sativa*; 13%), but it is grown for hay, and therefore usually cut before bloom. Other minor entomophilous crops are buckwheat (*Fagopyrum esculentum*), rape (*Brassica* spp.), and sunflower (*Helianthus annuus*). Most of the study area is located within the Natural Park of Zona Volcànica de la Garrotxa. We selected 14 sites (Fig. 1A) along a gradient of forest–cropland cover. Distance between sites ranged from 1.4 to 13 km.

3.2.2. Trap-nesting

To obtain bee/wasp nests, we used drilled wood blocks (10 x 10 x 16 cm) with inserted paper straws. Each wood block accommodated 25 straws of a given diameter (2, 3, 4, 5, 6, 7, or 8 mm). Paper straw length was 5 cm for the 2- and 3-mm diameters and 15 cm for the rest. Each nesting station had seven trap-nests, one of each diameter. Nesting stations were attached to trees or to farm buildings (see next section 1.2.3. Local and landscape factors) at ~150 cm above the ground, facing southeast. We sampled throughout the entire bee–wasp nesting season (March–October) in 1991. During this period, we made visits every two weeks to each site and replaced filled straws by empty ones to make sure there would be cavities of all diameters available. Straws containing nests were taken to the laboratory and kept at 25o C until October, when they were transferred to an unheated storage unit (2o–10o C) for wintering. In the following spring, nests were dissected and their contents recorded, and hosts and parasitoids were reared and identified.

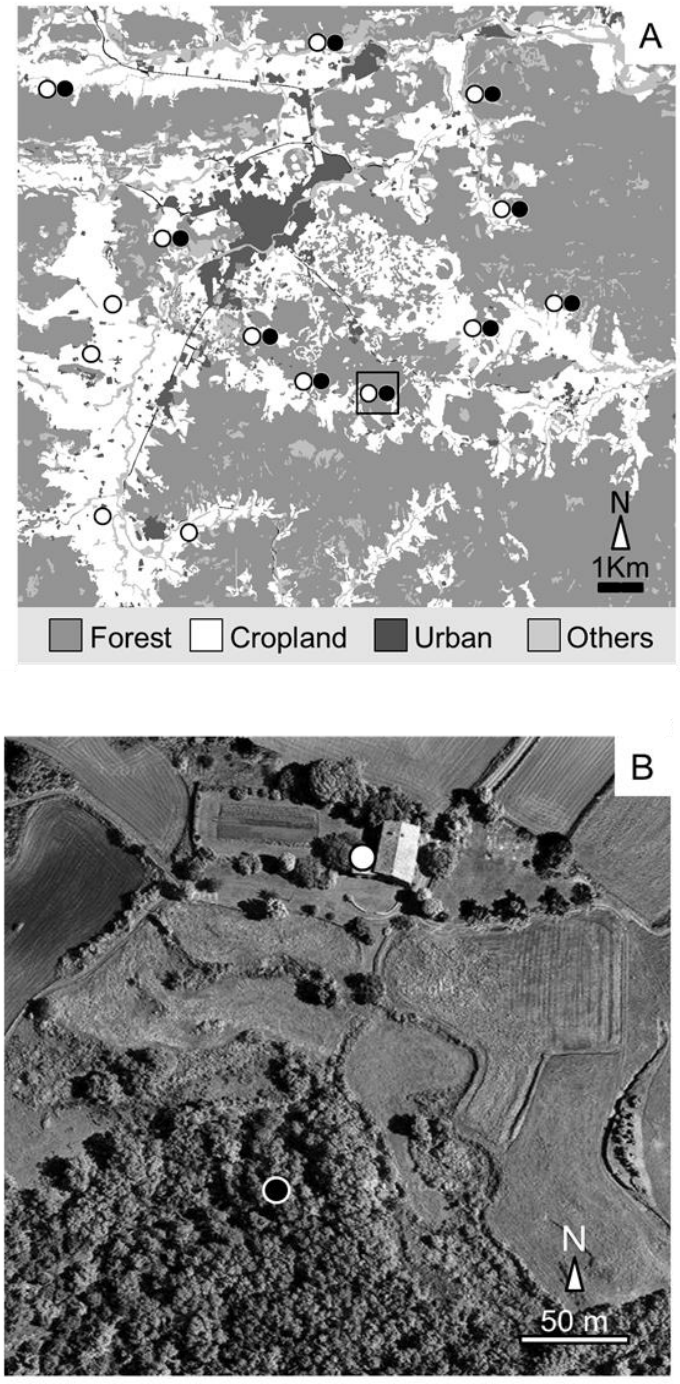

Figure. 1. (A) Land cover map of the study area with location of the 14 study sites. White circles denote nesting stations in farms and black circles denote stations in tree stands. **(B)** An orthophoto corresponding to an enlargement of the black square in Fig. 1A, showing the location of nesting stations of a paired plot.

3.2.3. Local and landscape factors

At the local level, we considered the two types of environments in which CNBW may nest in the study area (henceforth nesting environment): farm complexes (henceforth farms) and forested areas (henceforth tree stands). In 10 of the 14 sites, we set up two nesting stations, one in a farm environment and one in an adjacent tree stand (Fig. 1B). The remaining four sites were located in the middle of areas with high cropland cover. These sites were chosen to increase the cropland gradient, but because they had no adjacent forested areas, they contained only one nesting station (in the farm environment). Thus, we had a total of 24 nesting stations. The distance between paired farm and tree stand stations was ≤100 m at all sites except two, in which distance was 170 and 250 m, respectively (117 ± 18.35 m [mean ± SE]).

To describe landscape composition, we used a land cover map (DMAH 1993) on which we quantified the percentage of surface covered by different land cover types (12 categories) around each nesting station. This was done at three different spatial scales (250, 500, and 750 m radius buffers). However, differences in landscape composition across the three buffers were very small. We thus decided to work only with the 500m-buffer because several studies indicate that foraging ranges of many CNBW fall within this distance (Gathmann and Tscharntke 2002, Guédot et al. 2009, Zurbuchen et al. 2010). Two land cover categories, forest and cropland, accounted for ≥90% of the cover in most stations, and were negatively correlated ($r \geq |0.70|$ for all three buffers). For these reasons, we decided to use percentage of cropland cover to describe landscape composition. Our gradient of cropland cover (which includes not only agricultural fields per se but also associated habitats such as unpaved roads, field margins, etc.) ranged between 8% and 89%.

To describe landscape structure, we quantified the perimeter of all habitat fragments and calculated habitat diversity using Shannon's *H* (including the 12 categories in the land cover map). However, as found in other studies (Thies and Tscharntke 1999, Steffan-Dewenter et al. 2002, Schmidt et al. 2004), both total perimeter and habitat

diversity were strongly related to cropland cover. Therefore, we decided to keep cropland cover as the only landscape descriptor.

3.2.4. Community structure and host–parasitoid network structure

To describe community structure at each nesting station, we used host species richness, host abundance (number of host cells produced), parasitoid species richness, and parasitoid abundance (number of parasitized cells). In addition, we defined community composition (of hosts and parasitoids separately) as the relative abundance of each of the species in the community.

Levels of parasitism are expressed as the percentage of cells that were parasitized. In addition, we built an interaction host–parasitoid network for each nesting station (24 networks). To describe their structure, we used the quantitative metrics generality (weighted average number of host species per parasitoid), and vulnerability (weighted average number of parasitoid species per host) (Bersier et al. 2002). We also used interaction evenness (Shannon's diversity of interactions divided by ln(hosts richness x parasitoid richness) (Dormann et al. 2009). Finally, we used H_2' as a measure of the degree of specialization at the network level. This metric, which accounts for the interaction frequency (number of parasitized brood cells) of each species and is not affected by network size, ranges between 0 (maximum generalization) to 1 (maximum specialization) (Blüthgen et al. 2006). Of our 24 networks, 22 had at least 3 host and 3 parasitoid species and three species-to-species interactions. The two remaining networks (all from tree stands) were smaller and were excluded from all network analyses. All metrics were calculated with Bipartite v.1.16 (Dormann et al. 2009) for R (R Development Core Team 2012).

3.2.5. Statistical analysis

Spatial autocorrelation

We explored the spatial structure of species composition with the Mantel test. We used a matrix of geographic distances between nesting stations and a matrix of Bray-Curtis quantitative dissimilarity index of species composition (hosts + parasitoids). This was done separately for farms and tree stands to account for potential effects of nesting environment on species composition. We found no spatial autocorrelation (farms, r = 0.14, P = 0.15; tree stands, r = - 0.094, P = 0.68), and therefore we did not include spatial coordinates in our analyses.

Effect of nesting environment and cropland cover on community abundance, richness, and composition

We used general linear mixed models (*lme* function, nlme package [Pinheiro et al. 2012] for R) to analyze the effects of nesting environment (farms vs. tree stands) and cropland cover on each response variable (host abundance, host richness, parasitoid abundance, parasitoid richness). Host abundance was square-root transformed. Because nesting stations were grouped by site, we included site as a random factor. We ran four models for each response variable: one complete model (with nesting environment and cropland cover as fixed factors), two models with only one fixed factor (nesting environment or cropland cover), and a null model with no fixed factors. We then selected the best-fit model with the second-order Akaike Information Criterion, adequate for small samples (AIC_c [Burnham and Anderson 2002]). We used an estimate of maximum likelihood (ML) to compare all models, and once the model with the lowest AIC_c was identified, we used a restricted maximum likelihood estimate (REML) to obtain unbiased parameter estimates. In each case we checked that the best model complied with the assumptions of normality and homoscedasticity.

To explore the effects of nesting environment and cropland cover on community composition, we used permutational multivariate analysis of variance (PERMANOVA), separately for hosts and parasitoids (*adonis* function, Vegan Library [Oksanen et al. 2012]) for R). Abundance data were square-root transformed, and

distance matrices were calculated with the Bray-Curtis dissimilarity index. We run 9999 permutations per test. Because nesting stations were grouped by site, we used the function *strata*, which constrains the number of permutations within groups (stations) similarly to a random factor. We also calculated the determination coefficient (R^2) attributable to each source (partial R^2 based on the 9999 permutations, Vegan Library for R). To visualize differences in community composition among stations (separately for hosts and parasitoids) we conducted a multidimensional scaling (NMDS) based on the Bray-Curtis dissimilarity index (*metaMDS* function, Vegan Library for R [Oksanen et al. 2012]).

Effect of nesting environment and cropland cover on parasitism and network structure

We used general linear mixed models as described above, to analyze the effects of nesting environment (farm vs. tree stand) and cropland cover on percentage of parasitism, and the network metrics vulnerability, generality, interaction evenness, and H_2'. Some studies have found parasitoid richness, parasitoid abundance, and percentage of parasitism to be correlated to host richness and/or abundance (Steffan-Dewenter 2003, Albrecht et al. 2007, Holzschuh et al. 2009). Therefore, the analyses of parasitoid variables were repeated controlling for potential host effects. Because host richness and abundance are strongly correlated in our study (Pearson $r = 0.72$, $P = 0.0001$), only the variables explaining the highest amount of parasitoid variability (based on the AIC_c : host richness for parasitoid richness, and host abundance for parasitoid abundance) were used. However, host abundance was related to cropland cover and to nesting environment (see Results), and host richness was related to nesting environment (see Results). Thus, to extract the effect of the covariate (host richness or host abundance) we first built general linear mixed models of the response variable (parasitoid richness or parasitoid abundance) with only host richness or host abundance, and then used the residuals of these models to repeat the analyses of parasitoid variables with the explanatory variables nesting environment and cropland cover.

Generality, vulnerability, and interaction evenness may also be affected by network size (Tylianakis et al. 2007, Dormann et al. 2009, Gagic et al. 2011). For this reason, we included the variable network size (host richness + parasitoid richness) as a covariate in the analyses of generality, vulnerability and interaction evenness. However, network size and nesting environment were related (network size, farms, 20.6 ± 1.1 [mean ± SE]; tree stands, 12.8 ± 1.5; general linear mixed model, $F_{1,7} = 18.2$, $P = 0.004$). Thus, we first ran a general linear mixed model of each variable (generality, vulnerability, and interaction evenness) with network size as the only fixed factor and site as a random factor. Then, we used the residuals of each of these three models as response variables in three new models with the explanatory variables nesting environment and cropland cover.

As explained, these analyses were conducted including the four sites that had no tree environment. Because these four plots had high values of cropland cover, this might have conditioned our results. For this reason, we repeated the above analyses excluding these four plots for all the community structure and network structure metrics. We obtained similar results as when all sites were included (data not shown).

3.3. Results

3.3.1 General description of the community

We obtained 2035 nests amounting to 7572 cells. About half of the nests (57.3%) corresponded to 17 bee species (14 Megachilidae, 3 Colletidae). The remaining nests corresponded to 18 wasp species (10 Crabronidae, 6 Eumenidae, 1 Sphecidae, 1 Pompilidae) (see Plate 1 and Appendix 3: Table A3.1.1). In addition, we found 20 species of parasitoids (Appendix 3: Table A3.1.2). We collected almost four times more nests in farms (1590 nests in 14 stations) than in tree stands (445 nests in 10 stations).

3.3.2. Effects of nesting environment and cropland cover on community abundance, richness and composition

Both host and parasitoid abundance were higher in farms than in tree stands (Table 1, Fig. 2) and increased with increasing cropland cover (Table 1). Farms also favored host and parasitoid richness (Table 1, Fig. 2). However, once controlled for host abundance and richness, respectively, the effects of nesting environment and cropland cover on parasitoid abundance and richness became nonsignificant, and in both cases the best model included no explanatory variables (Table 1). Host composition differed dramatically between nesting environments (Table 2, Fig. 3A). In addition, there was a significant interaction between nesting environment and cropland cover because cropland cover affected community composition only in stations located in farms. Considering all stations (14 farms, 10 tree stands), farms hosted more bees (17 species, 68% abundance) than wasps (10 species, 32% abundance). On the other hand, tree stands hosted similar bee and wasp richness (12 species of each), but a greater relative abundance of wasps (84%) than bees (16%). Thus, the higher host species richness in farms was mostly due to an increase of bee species in this environment. Two bee species (*Osmia bicornis*, *O. cornuta*) and one wasp species (*Euodynerus posticus*) were characteristic of farm environments (had much higher relative abundance in farms than in tree stands). On the other hand, two wasp species (*Trypoxylon figulus*, *Psenulus fuscipennis*) were characteristic of tree stands. In addition, 10 host species with lower abundance were only found in farms and three were only found in tree stands (Fig. 2). The effect of cropland cover on community composition in farm environments was mostly mediated by two bee species (*O. bicornis* and *O. cornuta*) and two wasps (*Passaloecus* spp. and *Trypoxylon* spp.) that were very abundant in sites with high cropland cover and scarce in sites with low cropland cover. Parasitoid composition was also strongly dependent on nesting environment, but in this case there was no interaction with cropland cover (Table 2, Fig. 3B). Two species (*Monodontomerus obsoletus*, *Trichodes alvearius*) were characteristic of farm environments whereas three species (Sarcophagidae sp.1,

Table 1. Summary of best-fit general linear mixed models for the various response variables in relation to the two explanatory variables (Expl. var.) used: landscape composition (cropland cover: % cropland cover in a 500 m radius) and local nesting environment (farms versus tree stands; reference level: farms). Five of the analyses (parasitoid abundance, parasitoid richness, vulnerability, generality and interaction evenness) were repeated controlling for the effects of certain covariables (controlled variable).

Response variable	Expl. var. entering the best model	*t*	*P*	Controlled variable	Expl. var. entering the best model	*t*	*P*
Host abundance	Cropland cover	3.08	0.003	None	-	-	-
	Nesting environment	2.72	0.03				
Host richness	Nesting environment	4.20	0.002	None	-	-	-
Parasitoid abundance	Cropland cover	3.15	0.003	Host abundance	None	-	-
	Nesting environment	2.52	0.04				
Parasitoid richness	Nesting environment	4.6	0.001	Host richness	None	-	-
% Parasitism	None	-	-	None	-	-	-
Vulnerability	Nesting environment	1.9	0.09	Network size	None	-	-
Generality	Nesting environment	4.9	0.002	Network size	Nesting environment	3.01	0.02
Interaction Evenness	None	-	-	Network size	None	-	-
H_2'	Nesting environment	-1.9	0.09	None	-	-	-

Sarcophagidae sp. 2, and *Melittobia acasta*) were characteristic of tree stands. In addition, eight species with lower abundance were singular to farms, but there were no parasitoid species singular to tree stands (Fig. 2).

3.3.3. Effects of nesting environment and cropland cover on parasitism and network structure

The best model of percentage of parasitism included no explanatory variables (Table 1). Despite the previously mentioned differences between nesting environments in community structure and composition, percentage of parasitism per station was similar in farms (30.2% ± 2.5% [mean ± SE]) and tree stands (25.8% ± 4.9%; general linear mixed model with nesting environment as fixed factor and site as random factor, $F_{1,9} = 0.84$; $P = 0.4$). Generality was higher in farms (Table 1, Fig. 2) but was not affected by cropland cover. (The best model for generality included only nesting environment; Table 1). Importantly, the effect of nesting environment on generality persisted after controlling for network size (Table 1). Vulnerability showed a similar tendency, but the model narrowly failed significance, and the best model did not include any explanatory variable once we controlled for network size (Table 1, Fig. 2). H_2' was again marginally affected by nesting environment (with H_2' tending to be lower in farms) (Table 1, Fig. 2). The best models of interaction evenness included no explanatory variables irrespective of whether we controlled for network size or not (Table 1).

3.4. Discussion

Our study shows that nesting environment influences the structure and composition of CNBW communities and that these effects ultimately result in changes in host–parasitoid network structure. By comparison, the effects of landscape composition are much smaller and do not result in significant changes in network structure.

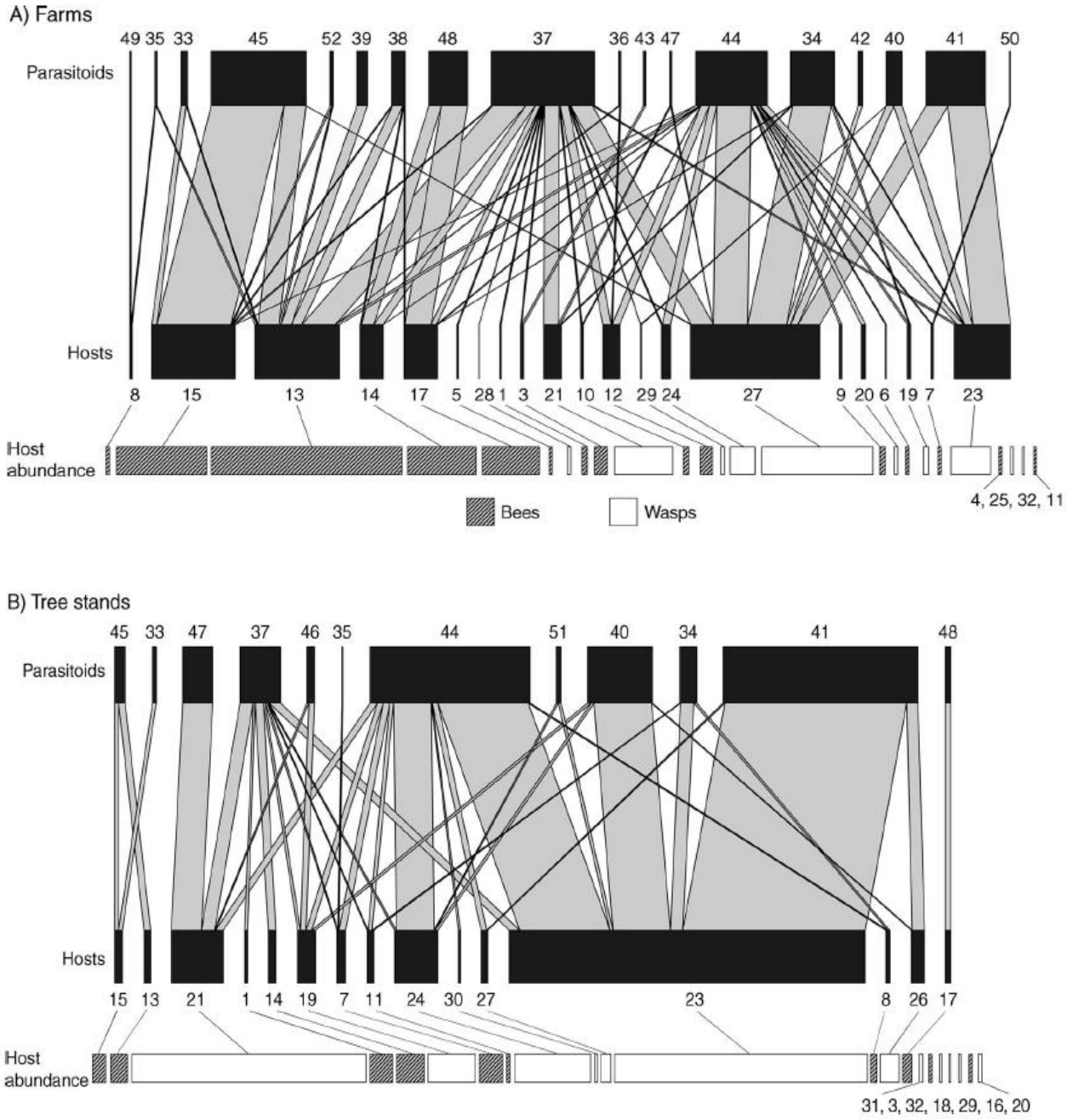

Figure. 2. Host–parasitoid networks from **(A)** farms and **(B)** tree stands built with data from the 10 sites in which both farms and tree stands were sampled. Numbers correspond to species names in Appendix 3: Table A3.1. Width of links (gray) denotes interaction strength (cells parasitized). Hatched and white bars at the bottom indicate abundance (number of cells produced) of host species (including non-parasitized species). Hosts (parasitized) and host abundance (including non-parasitized hosts) are not at the same scale.

Nesting environment had a profound effect on abundance, richness, and composition of hosts and parasitoids. Basically, the two nesting environments had similar wasp communities, but farms hosted richer, more abundant bee communities. This outcome is remarkable because differences were clear even between farm and tree stations separated by as few as 100 m. Two factors may contribute to explain these results. First, farm complexes in the area of study offer a wealth of nesting cavities. In addition to beetle burrows in wooden structures (also found in tree stands), farm buildings offer holes in bricks, thatched roofs, and cracks between rocks, as well as abandoned bee/wasp nests in mortar and adobe structures. Finding appropriate nesting resources may be more difficult for cavity-nesting than for ground-nesting bees and wasps (Gathmann et al. 1994, Tscharntke et al. 1998, Steffan-Dewenter 2003, Holzschuh et al. 2010). Farm buildings could represent an enriched source of nesting cavities compared to tree stands, as described for certain urban environments (Saure 1996, Cane and Tepedino 2001, Everaars et al. 2011). This is especially important given the young age of the forest matrix in the study area and its associated scarcity of dead wood. Second, farming environments provide good conditions for the proliferation of weedy plants, many of which produce large amounts of pollen and nectar (Westrich 1989, Klein et al. 2006). The most abundant species in our study was *O. bicornis*. In an urban environment, Everaars et al. (2011) also found this species associated to buildings and sunlit areas as opposed to trees. Other studies have also found that bees prefer open habitats over forested areas and have attributed this preference to exposure to sunlight and the associated proliferation of ruderal plants (Osborne et al. 1991, Potts and Willmer 1997, Tscharntke and Brandl 2004, Winfree et al. 2007).

Compared to nesting environment, landscape composition had a much smaller effect on host communities. Host abundance increased with cropland cover, which can be explained by the non-intensive agricultural management prevalent in the area. Fields are small, surrounded by mostly unmanaged margins and dirt roads, which, together with fallow fields provide a diversity of habitats favorable to flowering plants and insects. In addition, these structures may act as corridors between agricultural fields

Table 2. Results of multivariate permutational analysis (PERMANOVA) based on Bray-Curtis dissimilarity of host and parasitoid community composition as a function of the two explanatory variables used: Cropland cover (% cropland cover in a 500 m radius) and Nesting Environment (farms versus tree stands).

	HOSTS					**PARASITOIDS**				
Explanatory variables	R^2	df	MS	*F*	*P*	R^2	df	MS	*F*	*P*
Nesting Environment	0.20	1	0.98	6.19	0.001	0.17	1	0.86	4.88	0.0009
Cropland cover	0.09	1	0.46	2.88	0.2	0.06	1	0.30	1.70	0.8
Nesting Environment x Cropland cover	0.08	1	0.42	2.63	0.01	0.06	1	0.31	1.75	0.1
Residual		20	0.16	0.63			20	0.18	0.71	
Total		23					23			

and semi-natural habitats. These conditions have been shown to favor bee abundance (Steffan-Dewenter 2003) and wasp richness (Steffan-Dewenter 2002, Holzschuh et al. 2010). A cursory qualitative analysis of nest provisions provided additional information on the relationship between cropland cover and host abundance. Although some of the crops in the area are entomophilous, identification of pollen samples from bee nests revealed that most of the pollen utilized by bees came from ruderal plants (*Papaver*, *Echium*, *Reseda*, *Ranunculus*, *Campanula*, and several Asteraceae, Fabaceae, and Lamiaceae), forest trees (*Quercus*), and sporadic fruit trees growing in the vicinity of farms but not commercially cultivated (*Prunus*, *Malus*). As for wasp nests, of the various aphid, caterpillar, heteropteran, spider and orthopteran prey encountered, only one aphid species was associated with one of the main crops (alfalfa) in the study area. The remaining species were associated with wild plants such as herbaceous ruderal species, various shrubs, pines, oaks and fruit trees. Thus

the increase in host abundance with cropland cover seems to be related not to the crops per se, but to resources present in habitat elements typical of extensively managed farming areas. Studies comparing organic vs. conventional farms have found abundance and richness of CNBW to be related to wildflower availability (Holzschuh et al. 2007). We also found an effect of cropland cover on host composition, but only in farm stations. This effect was mediated by two bee (*O. bicornis* and *O. cornuta*) and two wasp species (*Passaloecus* spp. and *Trypoxylon* spp.) whose abundance was positively correlated to cropland cover. *O. cornuta*, *O. bicornis*, and *Trypoxylon figulus* have been associated with open agricultural habitats in other studies (Westrich 1989, Holzschuh et al. 2010, Gruber et al. 2011, Coudrain et al. 2013).

Parasitoid abundance was positively associated with farms and cropland cover, while parasitoid richness was positively associated with cropland cover. However, these relationships were not maintained when host abundance and richness were controlled for. Thus, the relationship of parasitoid richness and abundance with local and landscape factors seems to be mostly mediated by the relationship between parasitoids and their hosts. Conversely, Klein et al. (2006) found parasitoid richness and abundance, and parasitism rate, to be negatively related to isolation from forested areas and not to host community structure in a CNBW community. Importantly, and as opposed to our study, the agricultural system in which Klein and collaborators worked was intensively farmed and relatively isolated from natural habitats. In conclusion, and in agreement with other studies (Steffan-Dewenter 2003, Albrecht et al. 2007, Holzschuh et al. 2009, 2010), parasitoid community structure in our study can be mostly explained by host community structure. This is further supported by the parallel differences in host species composition and parasitoid species composition between farms and tree stands. Of the 20 parasitoid species found, 10 were unique to bees, and 6 were unique to wasps. The remaining four species parasitized both groups, but most of them showed strong preferences for one of them.

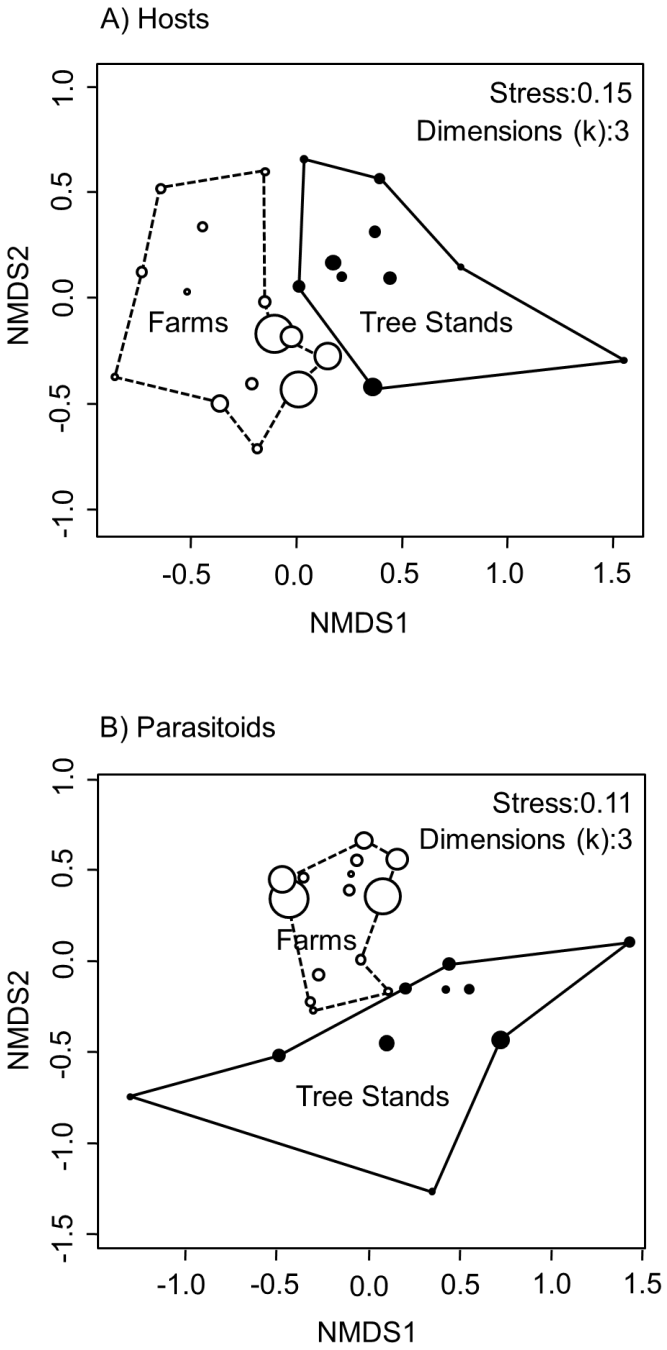

Figure. 3. NMDS (nonmetric multidimensional scaling) of **(A)** host and **(B)** parasitoid community composition. Only two of the three dimensions obtained in the analysis are displayed. Each circle represents a sampling station in a farm (white) or a tree stand (black). Circle size is proportional to the percentage of cropland cover in a radius of 500 m. "Stress" is a measure of goodness of fit based on the Bray-Curtis dissimilarity index and distance in graphical representation. The lower the stress the better the fit. "Dimensions" (k) represents the number of axes defining the solution providing the best fit.

Network structure was only influenced by nesting environment. Of the four network metrics considered, three (generality, vulnerability, and H_2') showed a tendency towards greater generalization in farms (although vulnerability and H_2' models narrowly failed significance). This result is partly explained by the higher species richness (leading to increased network size) encountered in farms. However, other factors besides species richness must be contributing to the observed differences in network structure, since generality remained higher in farms after controlling for network size. Differences between the two nesting environments in community composition imply differences in specific interaction patterns, ultimately affecting network structure. However, due to the strong relationship between nesting environment, network size, and species composition, it is difficult to disentangle the relative importance of these factors on the observed differences in network structure. Other studies have also found confounding effects of community richness and composition on network structure (Gagic et al. 2012). As opposed to nesting environment, we found no effects of cropland cover on network structure. Two factors may explain this lack of relationship. First, percentage of cropland cover did not affect host and parasitoid richness and therefore network size. Second, differences in community composition across the cropland gradient were much smaller than differences between nesting environments. A study on gall insects in oak forests (Kaartinen and Roslin 2011) also found no effect of landscape factors on host–parasitoid interaction networks. In the same study, changes in species richness and composition associated with habitat fragmentation and isolation resulted in almost no changes in network structure. Conversely, studies in agricultural habitats show changes in network structure associated to landscape factors and/or habitat management mediated by differences in community composition, with little variation in species richness (Tylianakis et al. 2007, Gagic et al. 2011). A key difference between these studies and ours is that the level of agricultural intensification was much lower in our study, suggesting that the effects of community composition on network structure are influenced by the level of disturbance.

In sum, a proposed pathway through which nesting environment could affect network structure in our community can be described as follows. Farms create an environment which, by providing additional nesting cavities, floral resources, and sun exposure, modifies the CNBW composition typical of forested areas. These changes in composition are basically mediated by an addition of bees, both in terms of abundance and richness. Wasps, on the other hand, are much less affected. The increase in host availability in farms entails an increase in parasitoid richness and abundance. Increased species richness entails a larger network size, which, together with changes in community composition, results in a more generalized network structure. Our results have important consequences for the conservation of bee and wasp diversity, and the maintenance of interaction networks and ecosystem services provided by bees and wasps. Farm environments in our study area host a qualitatively different CNBW community from the surrounding forest matrix. More specifically, farms represent a local refuge for bee species that are otherwise rare, especially in the more densely forested areas (Westrich 1996, Holzschuh et al. 2010). On the other hand, the low bee richness found in tree stands could be compensated by the much greater surface occupied by trees compared to farms and, perhaps, by a greater beta diversity as suggested by our NMDS analyses, which, especially for parasitoids, indicate a greater species turnover in tree stands than in farms (Fig. 3). Other studies have shown that moderate land modification leading to a heterogeneous extensively managed landscape, such as in our study area, enhance bee and wasp biodiversity (Tscharntke et al. 2005, Winfree et al. 2007, Schüepp et al. 2012). The last decades have seen a progressive abandonment of extensively cultivated farmland in favor of agricultural intensification and reforestation in Europe in general, and in the Mediterranean in particular (Gerard et al. 2010, Basnou et al. 2013). Under such a scenario, the conservation value of mosaic landscapes associated to extensive farming is important, not only for bees and wasps, but also for other organisms associated to open areas.

3.5. ACKNOWLEDGMENTS

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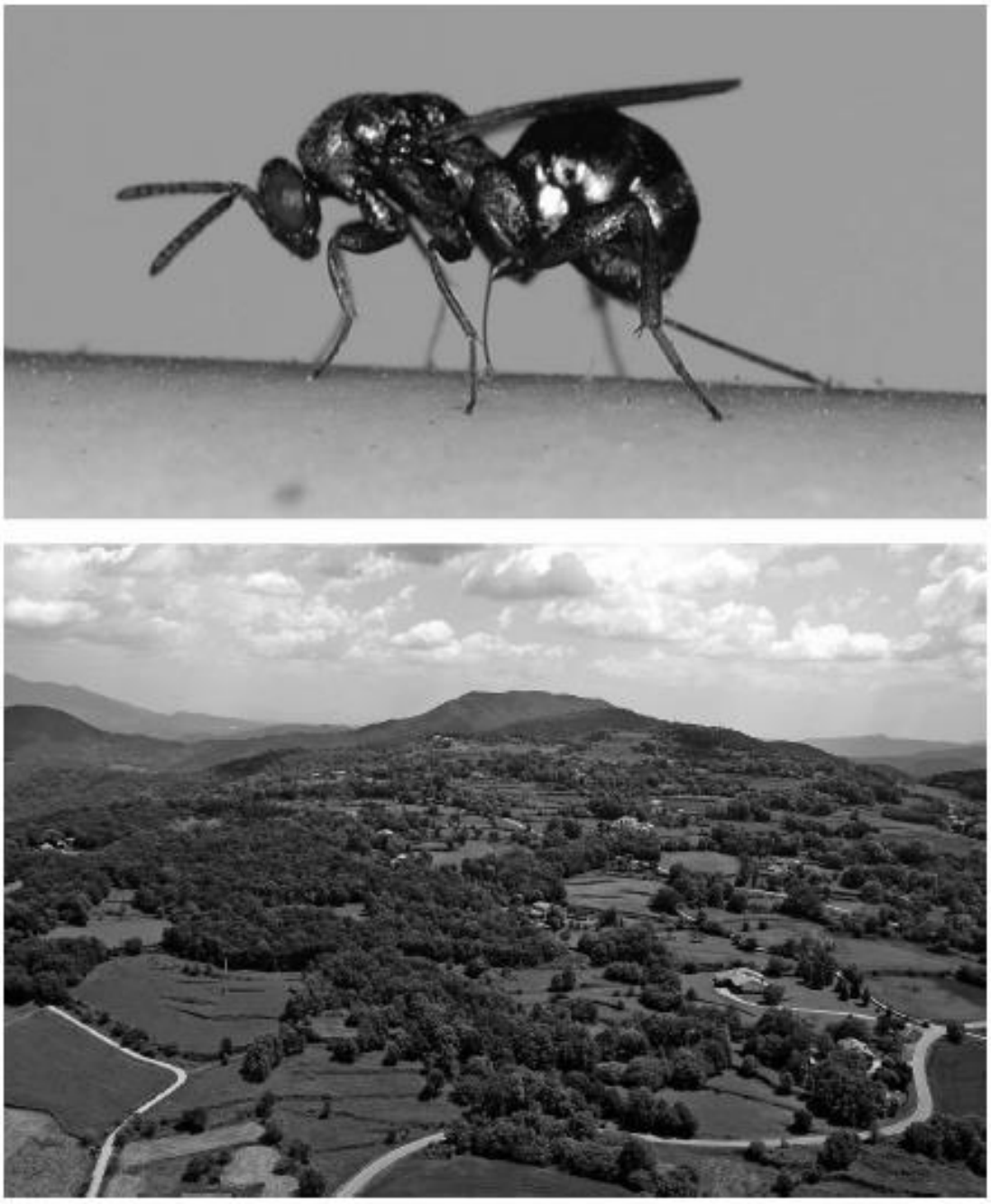

PLATE 1. (Top) Female *Monodontomerus* sp., a parasitoid of *Osmia* spp. (Bottom) Study area landscape (close to the city of Olot, Catalonia, Spain). Photo credits: top, Javier Losarcos; bottom, Pep Sau (deposited at La Garrotxa Volcanic Zone Natural Park Documentation Centre (Catalonia, Spain) #CDPNZVG).

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General Conclusions

General Conclusions

Chapter 1

- We demonstrated that Bergmann's rule can be extended to a temporal gradient using two different methodological approaches (cross-species and assemblage-based analyses).

- Using the cross-species approach we found a different body size-ambient temperature relationship for large ('endothermic') and small (ectothermic) bee species: species larger than 27.81 mg (dry weight) followed Bergmann's rule, whereas species below this threshold did not (no relationship at all).

- Using the assemblage-based approach we found a highly significant quadratic relationship between weekly mean body size and time (weeks), as well as a highly significant negative linear relationship between weekly mean body size and mean weekly temperature. Both relationships are coherent with a Bergmann's pattern.

- Our results not only confirm the pattern but are coherent with the physiological mechanism originally proposed by Bergmann himself, i.e. the"thermoregulatory hypothesis".

- We also found deviations from an ideal body size–temperature relationship, which may arise because, in addition to endogenous thermoregulation, bees (both large and small) have other mechanisms to control their body temperature ('behavioural thermoregulation', pilosity, and/or physiological adaptations).

- Notwithstanding the Bergmann's pattern found, other factors in addition to physiological thermoregulatory ability are likely to have influenced the evolution of the timing of activity periods in bees, such as the temporal distribution of floral resources (especially if bee species are highly pollen-specialized), life cycle constrains (as hibernation stage) or voltinism.

- We propose that species with greater thermoregulatory capacity have some selective advantage by flying early in the year, when temperatures are low, because during these periods of marginal weather these species can exploit abundant flower resources at a time when few pollen-nectar feeding insects are active and flower visitation rates are low.

- Our results suggest that body size and thermal physiology play a role in structuring community phenology. This is particularly relevant in the current context of global warming, with species experiencing phenological shifts.

Chapter 2

- We found important seasonal changes in taxonomic community structure and composition of both cavity-nesting bees and wasps (CNBW) host and their parasitoid communities.

- Taxonomic seasonal changes result in changes in community functional structure (especially for hosts), which occur at two levels. First, there is a shift from a bee dominated community in spring to a wasp dominated community in summer. Second, even considering only bee hosts, functional trait composition and functional structure clearly changed between spring and summer.

- As for host communities, most of the traits considered showed a seasonal component, and overall functional diversity was higher in summer than in spring. Contrarily, for parasitoid communities, no functional traits average indices did vary seasonally, which could be explained in part by longer mean activity periods of parasitoid species, that encompassed the two seasons studied. Parasitoid overall functional diversity was higher in summer than in spring, in agreement with taxonomically and functionally richer and more diverse summer host communities.

- In spite of the strong seasonal changes in taxonomic and functional structure and composition in both the CNBW host and their parasitoid communities, we found no seasonal shifts in percent parasitism, and seasonal changes in the structure of the host-parasitoid interaction network appear to be mostly driven by changes in network size.

- A possible explanation for the lack of incidence of seasonal changes in functional structure on network structure could be a compensation between traits influencing network parameters in opposite directions in each season.

- Consequences of the strong seasonal changes observed in our bee/wasp-parasitoid community go beyond host-parasitoid relationships. The shift from a bee dominated community in spring to a wasp dominated community in summer, implies an emphasis on pollination function in spring to an emphasis in predation function in summer, with obvious consequences on ecosystem function.

- Our study underscores the need to consider functional traits and to incorporate a temporal component into network analysis if we are to understand the global relationship between network structure and ecosystem function.

Chapter 3

- CNBW host community structure and composition, as well as network structure, are much more dependent on local (nesting environment, farms vs tree stands) than on landscape factors (% crop cover).

- Host abundance and richness were higher in farms than in tree stands, and we found highly significant differences between nesting environments in host community composition. In addition, host abundance was positively correlated to cropland cover. Structure and composition of the parasitoid community were conditioned by that of their hosts.

- Network structure was affected by nesting environment but not by landscape factors. Interactions tended to be more diverse in farms. This result was mostly explained by differences in network size (greater in farms). However, generality was significantly higher in farms even after controlling for network size, suggesting that other factors are also affecting network structure, as differences in community composition found between the two nesting environments.

- Open habitats associated with extensively farmed exploitations favor local cavity-nesting bee/wasp diversity (especially bees) and result in more complex host–parasitoid interaction networks in comparison to forested areas. Thus, the conservation value of this kind of open habitat is important in view of the progressive abandonment of extensively cultivated farmland taking place in Europe at the expense of agricultural intensification and reforestation.

Appendix 1

Table A1.1. Results from the additional cross-species piecewise analyses. Abbreviations: ITS, body size.

				PGLS "large"					PGLS "small"					
Model	**breakpoint**	CI		lambda	R2	t	p	n	lambda	R2	t	p	n	n total
log_{10}(Species temperature) ~ log_{10}(ITS)	0.4729905	0.3938594	0.5429498	0.00	0.30	-4.87	<0.0001	54	0.547	0.0023	-1.20	0.23	191	245
log_{10}(Coldest species temperature) ~ log_{10}(ITS)	0.4740279	0.3909748	0.5058507	0.040	0.26	-4.35	<0.0001	53	0.617	0.0019	-1.17	0.24	192	245

Table A1.2. List of the 290 bee species in our regional bee fauna indicating the first and last weeks in which they were recorded, the maximum temperature of the week in which they became active, the temperature of the coldest week in which they were recorded, and their body size (intertegular span in mm). Species without acronym (45) were not included in the analyses because their activity periods could not be properly characterized.

Acronym	Genus	Species	First week	last week	First week temperature (Species temperature) (ºC)	Coldest week temperature (ºC)	ITS (mm)	ITS SD	n
XAL	*Xylocopa*	*valga*	7	29	11,32	11,32	6,68	0,45	5
XVI	*Xylocopa*	*violacea*	6	50	11,42	11,00	6,46	0,54	9
BTE	*Bombus*	*terrestris*	1	52	9,99	9,99	5,72	0,53	4
BPA	*Bombus*	*pascuorum*	4	50	10,57	10,57	4,69	0,07	4
BPRA	*Bombus*	*pratorum*	11	25	14,01	14,01	4,60		1
ANBI	*Anthophora*	*biciliata*	13	24	15,16	15,16	4,39		1
ANFU	*Anthophora*	*fulvitarsis*	8	38	11,84	11,84	4,32		1

AFE	*Anthophora*	*femorata*	15	33	16,00	16,00	4,12	0,19	2
MLA	*Megachile*	*lagopoda*	23	40	23,12	20,79	4,09	0,05	2
OCO	*Osmia*	*cornuta*	9	20	12,45	12,45	4,06	0,43	10
ADI	*Anthophora*	*dispar*	4	23	10,57	10,57	4,06	0,18	3
ARE	*Anthophora*	*retusa*	13	24	15,16	15,16	3,99		1
AMU	*Anthophora*	*mucida*	15	22	16,00	16,00	3,92	0,09	2
ABA	*Anthophora*	*balneorum*	18	27	18,44	18,44	3,89	0,20	4
MPY	*Megachile*	*pyrenaica*	10	28	13,21	13,21	3,86	0,47	8
XIR	*Xylocopa*	*iris*	14	44	15,70	15,70	3,86	0,09	2
AAC	*Anthophora*	*acervorum*	9	40	12,45	12,45	3,79	0,07	3
ONAS	*Osmia*	*nasoproducta*	11	23	14,01	14,01	3,79	0,09	2
MCI	*Megachile*	*circumcincta*	13	23	15,16	15,16	3,72		1
TIN	*Trachusa*	*interrupta*	20	33	20,48	20,48	3,69	0,05	2
AGA	*Amegilla*	*garrula*	24	44	23,96	16,38	3,66	0,07	3

EAL	*Eucera*	*alternans*	13	21	15,16	15,16	3,62	0,24	2
EBA	*Eucera*	*barbiventris*	9	18	12,45	12,45	3,59		1
ENIG	*Eucera*	*nigrilabris*	6	21	11,42	11,42	3,49	0,05	2
AFL	*Anthidium*	*florentinum*	20	41	20,48	19,65	3,48	0,17	3
MALB	*Melecta*	*albifrons*	9	21	12,45	12,45	3,46	0,44	4
AAL	*Amegilla*	*albigena*	19	41	19,41	19,41	3,46	0,00	2
AQU	*Amegilla*	*quadrifasciata*	20	43	20,48	17,40	3,37	0,08	3
RST	*Rhodanthidium*	*sticticum*	9	26	12,45	12,45	3,35	0,30	3
LCH	*Lithurgus*	*chrysurus*	20	38	20,48	20,48	3,33	0,57	4
MALBO	*Megachile*	*albonotata*	16	37	16,66	16,66	3,33		1
ACI	*Anthidium*	*cingulatum*	15	43	16,00	16,00	3,30	0,27	3
OTR	*Osmia*	*tricornis*	10	19	13,21	13,21	3,21	0,20	4
ACR	*Anthophora*	*crassipes*	13	52	15,16	10,24	3,19	0,00	3
ALE	*Anthophora*	*leucophaea*	11	21	14,01	14,01	3,19		1

ASAL	*Anthophora*	*salviae*	10	19	13,21	13,21	3,19		1
ENI	*Eucera*	*nigrescens*	13	23	15,16	15,16	3,19	0,13	3
	Melecta	*italica*	-	-	-	-	3,19		1
AMA	*Anthidium*	*manicatum*	15	45	16,00	14,96	3,17	0,14	3
MPI	*Megachile*	*pilicrus*	20	39	20,48	20,48	3,16	0,09	4
MAL	*Megachile*	*albisecta*	27	39	26,79	22,01	3,13	0,20	3
RSE	*Rhodanthidium*	*septendentatum*	15	29	16,00	16,00	3,10	0,20	3
MME	*Megachile*	*melanopyga*	18	42	18,44	18,44	3,10	0,14	5
ETA	*Eucera*	*taurica*	20	30	20,48	20,48	3,09	0,20	6
MER	*Megachile*	*ericetorum*	19	33	19,41	19,41	3,09	0,14	2
THI	*Thyreus*	*hirtus*	21	29	21,15	21,15	3,09	0,12	4
EHI	*Eucera*	*hispaliensis*	16	30	16,66	16,66	3,08	0,06	4
ALIM	*Andrena*	*limbata*	16	24	16,66	16,66	3,06		1
AHIS	*Andrena*	*hispania*	18	22	18,44	18,44	3,06	0,19	2

ALO	*Anthidium*	*loti*	25	34	25,14	25,14	3,06	0,13	3
OLAT	*Osmia*	*latreillei*	11	23	14,01	14,01	3,06	0,24	6
CAL	*Colletes*	*albomaculatus*	16	26	16,66	16,66	3,02	0,08	3
CSU	*Colletes*	*succintus*	24	43	23,96	17,40	2,99		1
ODI	*Osmia*	*dimidiata*	22	29	22,32	22,32	2,99	0,24	3
HTRI	*Hoplitis*	*tridentata*	19	36	19,41	19,41	2,97	0,18	4
MLU	*Melecta*	*luctuosa*	9	20	12,45	12,45	2,97	0,08	3
ALAB	*Andrena*	*cf. labialis*	16	27	16,66	16,66	2,91	0,12	2
TST	*Tetraloniella*	*strigata*	17	30	17,44	17,44	2,89	0,05	2
TOR	*Thyreus*	*orbatus*	21	50	21,15	11,00	2,86		1
ECO	*Eucera*	*collaris*	10	27	13,21	13,21	2,82	0,04	3
ASA	*Amegilla*	*savignyi*	27	33	26,79	26,79	2,79		1
CAR	*Coelioxys*	*argentea*	24	42	23,96	18,64	2,79	0,07	3
HQU	*Halictus*	*quadricinctus*	16	36	16,66	16,66	2,79	0,12	3

OLAB	*Osmia*	*labialis*	15	25	16,00	16,00	2,79	0,19	2
	Apis	*mellifera*	-	-	-	-	2,79		1
HBI	*Hoplitis*	*bisulca*	20	37	20,48	20,48	2,79		1
CAB	*Colletes*	*abeillei*	15	47	16,00	12,81	2,78	0,10	3
ORUF	*Osmia*	*rufa*	10	32	13,21	13,21	2,76	0,07	4
ACA	*Andrena*	*carbonaria*	12	33	14,58	14,58	2,75	0,21	3
OAU	*Osmia*	*aurulenta*	15	29	16,00	16,00	2,75	0,21	3
OLE	*Osmia*	*leaiana*	15	24	16,00	16,00	2,75	0,04	3
AAG	*Andrena*	*agilissima*	16	25	16,66	16,66	2,73		1
CCO	*Colletes*	*collaris*	17	44	17,44	16,38	2,72	0,04	5
AFA	*Amegilla*	*fasciata*	17	42	17,44	17,44	2,70	0,08	3
APUB	*Anthophora*	*pubescens*	12	40	14,58	14,58	2,69	0,07	4
MVE	*Megachile*	*versicolor*	12	45	14,58	14,58	2,68	0,19	4
ABIM	*Andrena*	*bimaculata*	11	15	14,01	14,01	2,66		1

ANPU	*Anthidium*	*punctatum*	18	33	18,44	18,44	2,66		1
HSC	*Halictus*	*scabiosae*	13	33	15,16	15,16	2,62	0,25	3
MPIL	*Megachile*	*pilidens*	20	42	20,48	18,64	2,62	0,08	3
HOCR	*Hoplitis*	*cristata*	24	27	23,96	23,96	2,59	0,09	2
MGI	*Megachile*	*giraudi*	15	24	16,00	16,00	2,59	0,12	3
AOB	*Anthidium*	*oblongatum*	19	36	19,41	19,41	2,56		1
ALIMA	*Andrena*	*limata*	10	33	13,21	13,21	2,51	0,10	3
HANT	*Hoplitis*	*antigae*	19	25	19,41	19,41	2,50		1
ATR	*Andrena*	*trimmerana*	9	36	12,45	12,45	2,49	0,05	2
ABI	*Anthophora*	*bimaculata*	18	47	18,44	12,81	2,46	0,07	3
MFL	*Megachile*	*flabellipes*	23	30	23,12	23,12	2,46	0,07	3
TFU	*Tetraloniella*	*fulvescens*	21	24	21,15	21,15	2,46		1
EEL	*Eucera*	*elongatula*	10	27	13,21	13,21	2,44	0,10	3
ANI	*Andrena*	*nigroaenea*	3	25	10,21	10,21	2,42	0,25	17

ONI	*Osmia*	*niveata*	17	25	17,44	17,44	2,42	0,15	3
LAL	*Lasioglossum*	*albocinctum*	14	50	15,70	11,00	2,40	0,12	4
CSI	*Colletes*	*similis*	19	43	19,41	17,40	2,40	0,15	5
	Andrena	*sp.1*	-	-	-	-	2,39		1
OBR	*Osmia*	*brevicornis*	15	26	16,00	16,00	2,38	0,11	4
CCH	*Ceratina*	*chalcites*	17	36	17,44	17,44	2,37	0,10	3
MAP	*Megachile*	*apicalis*	19	37	19,41	19,41	2,37	0,08	3
HOANT	*Hoplitis*	*anthocopoides*	15	24	16,00	16,00	2,36	0,01	2
OME	*Osmia*	*melanogaster*	16	26	16,66	16,66	2,36	0,05	2
	Panurgus	*arctos*	-	-	-	-	2,36		1
AFU	*Andrena*	*fulva*	12	15	14,58	14,58	2,33		1
HBE	*Hoplitis*	*benoisti*	18	33	18,44	18,44	2,33		1
NMU	*Nomada*	*mutabilis*	7	16	11,32	11,32	2,32		1
CNI	*Colletes*	*nigricans*	18	42	18,44	18,44	2,30	0,13	18

OCAE	*Osmia*	*caerulescens*	14	33	15,70	15,70	2,29	0,36	8
CFO	*Colletes*	*foveolaris*	18	23	18,44	18,44	2,27	0,09	6
COB	*Coelioxys*	*obtusa*	23	36	23,12	23,12	2,26		1
	Andrena	*sp.2*	-	-	-	-	2,26		1
OLIG	*Osmia*	*ligurica*	17	28	17,44	17,44	2,25	0,16	6
AST	*Anthidiellum*	*strigatum*	19	41	19,41	19,41	2,24	0,04	3
	Andrena	*sp.3*	-	-	-	-	2,23	0,24	2
ARH	*Andrena*	*rhenana*	10	24	13,21	13,21	2,23	0,10	2
ANIG	*Andrena*	*nigrolivacea*	11	44	14,01	14,01	2,21	0,06	4
	Andrena	*sp.4*	-	-	-	-	2.21		1
	Andrena	*sp.5*	-	-	-	-	2,19		1
	Anthidiellum	*breviusculum*	-	-	-	-	2,19	0,09	2
LDI	*Lasioglossum*	*discum*	22	42	22,32	18,64	2,19	0,07	6
HFU	*Halictus*	*fulvipes*	13	46	15,16	13,74	2,13	0,16	5

ALI	*Pseudoanthidium*	*lituratum*	17	42	17,44	17,44	2,13	0,13	3
	Andrena	*sp.6*	-	-	-	-	2,13		1
AOV	*Andrena*	*ovatula*	10	30	13,21	13,21	2,11	0,16	6
EJU	*Epeolus*	*julliani*	24	39	23,96	22,01	2,10		1
LNI	*Lasioglossum*	*nigripes*	16	44	16,66	16,38	2,10		1
AHU	*Andrena*	*humilis*	9	33	12,45	12,45	2,10	0,05	2
ASI	*Andrena*	*similis*	11	20	14,01	14,01	2,10		1
CAF	*Coelioxys*	*afra*	19	42	19,41	18,64	2,10	0,05	2
CEC	*Coelioxys*	*echinata*	24	41	23,96	19,65	2,10	0,14	2
NSE	*Nomada*	*sexfasciata*	8	23	11,84	11,84	2,10		1
OAN	*Osmia*	*anceyi*	20	29	20,48	20,48	2,10	0,05	2
ASE	*Andrena*	*senecionis*	12	41	14,58	14,58	2,08	0,10	3
HAC	*Hoplitis*	*acuticornis*	16	28	16,66	16,66	2,08	0,14	3
EFA	*Epeolus*	*cf. fallax*	19	41	19,41	19,41	2,06		1

HPE	*Hoplitis*	*perezi*	18	24	18,44	18,44	2,06	0,07	3
	Epeolus	*sp. 1*	-	-	-	-	2,06	0,00	3
PBI	*Nomiapis*	*bispinosa*	22	35	22,32	22,32	2,06	0,12	3
	Nomada	*goodeniana*	-	-	-	-	2,05		1
	Epeolus	*sp.2*	-	-	-	-	2,04		1
ALA	*Andrena*	*lagopus*	11	24	14,01	14,01	2,01		1
DTR	*Dioxys*	*tridentata*	26	33	25,96	25,96	2,01		1
HCREN	*Halictus*	*crenicornis*	14	38	15,70	15,70	2,01	0,11	5
HAD	*Hoplitis*	*adunca*	14	31	15,70	15,70	2,00	0,18	3
	Andrena	*decipiens*	-	-	-	-	2,00	0,19	2
	Andrena	*sp.7*	-	-	-	-	2,00		1
AMUC	*Andrena*	*mucida*	15	28	16,00	16,00	1,99	0,10	2
AAN	*Andrena*	*angustior*	1	21	9,99	9,99	1,98	0,07	6
	Andrena	*sp.8*	-	-	-	-	1.98		1

	Epeolus	*sp.3*	-	-	-	-	1,98		1
ALEP	*Andrena*	*lepida*	16	21	16,66	16,66	1,95		1
AFLA	*Andrena*	*flavipes*	10	20	13,21	13,21	1,93	0,20	3
	Andrena	*sp. 9*	-	-	-	-	1.93		1
AHE	*Andrena*	*hesperia*	16	21	16,66	16,66	1,93		1
LLE	*Lasioglossum*	*leucozonium*	11	36	14,01	14,01	1,92	0,08	2
	Andrena	*sp.10*	-	-	-	-	1,91	0,01	3
NBA	*Nomada*	*basalis*	18	26	18,44	18,44	1,90	0,05	2
	Nomada	*emarginata*	-	-	-	-	1,89		1
NMA	*Nomada*	*marshamella*	10	25	13,21	13,21	1,87	0,28	8
NSU	*Nomada*	*succinta*	4	24	10,57	10,57	1,87	0,19	7
OSU	*Osmia*	*submicans*	9	26	12,45	12,45	1,86	0,12	3
APR	*Andrena*	*propinqua*	7	26	11,32	11,32	1,85	0,12	12
AGR	*Andrena*	*granulosa*	15	20	16,00	16,00	1,83	0,05	3

	Nomada	*ferruginata*	-	-	-	-	1,82	0,07	6
	Andrena	*fertoni*	-	-	-	-	1,81	0,08	4
	Epeolus	*sp.4*	-	-	-	-	1,80		1
OAND	*Osmia*	*andrenoides*	15	36	16,00	16,00	1,80	0,09	2
ORU	*Osmia*	*rufohirta*	13	26	15,16	15,16	1,80	0,24	3
PCA	*Panurgus*	*calcaratus*	15	42	16,00	16,00	1,79	0,06	2
PDI	*Nomiapis*	*diversipes*	19	42	19,41	18,64	1,76	0,19	3
HCRE	*Hoplitis*	*crenulata*	17	29	17,44	17,44	1,75	0,14	6
SRU	*Sphecodes*	*ruficrus*	8	42	11,84	11,84	1,73	0,18	10
SSI	*Stelis*	*signata*	19	38	19,41	19,41	1,73	0,07	3
	Andrena	*sp.11*	-	-	-	-	1,73		1
	Ceratina	*mocsaryi*	-	-	-	-	1,73		1
ECR	*Epeolus*	*cruciger*	19	41	19,41	19,41	1,70	0,14	2
HPO	*Halictus*	*pollinosus*	29	42	27,68	18,64	1,69	0,00	2

APU	*Ammobates*	*punctatus*	20	40	20,48	20,48	1,69	0,04	3
DCI	*Dioxys*	*cincta*	16	27	16,66	16,66	1,68	0,07	3
PCAP	*Protosmia*	*capitata*	15	21	16,00	16,00	1,66	0,28	2
HSI	*Hylaeus*	*signatus*	12	33	14,58	14,58	1,66		1
LBI	*Lasioglossum*	*bimaculatum*	11	42	14,01	14,01	1,65	0,07	5
OGA	*Osmia*	*gallarum*	12	27	14,58	14,58	1,64	0,10	3
HTR	*Heriades*	*truncorum*	26	33	25,96	25,96	1,63	0,15	7
HSU	*Halictus*	*subauratus*	15	39	16,00	16,00	1,63	0,03	3
NPU	*Nomada*	*pusilla*	14	28	15,70	15,70	1,63		1
	Osmia	*cephalotes*	-	-	-	-	1,63	0,07	4
NIN	*Nomada*	*integra*	16	21	16,66	16,66	1,62	0,02	2
	Andrena	*sp.12*	-	-	-	-	1.61		1
NSA	*Nomada*	*laevilabris*	23	26	23,12	23,12	1,60		1
	Andrena	*sp.13*	-	-	-	-	1,60		1

	Nomada	*bifasciata*	-	-	-	-	1,60		1
NMAC	*Nomada*	*maculicornis*	14	21	15,70	15,70	1,58		1
LSU	*Lasioglossum*	*subhirtum*	8	35	11,84	11,84	1,57	0,08	3
AVU	*Andrena*	*vulpecula*	13	21	15,16	15,16	1,56	0,04	3
	Andrena	*sp.14*	-	-	-	-	1.56		1
HGI	*Hylaeus*	*gibbus*	15	18	16,00	16,00	1,55	0,06	4
NZO	*Nomada*	*zonata*	10	24	13,21	13,21	1,54	0,16	5
PMA	*Pasites*	*maculatus*	19	42	19,41	18,64	1,52	0,08	3
NCA	*Nomada*	*carnifex*	12	18	14,58	14,58	1,52	0,20	2
HVE	*Halictus*	*vestitus*	19	36	19,41	19,41	1,51		1
HPI	*Hylaeus*	*pictus*	20	39	20,48	20,48	1,51		1
HVA	*Hylaeus*	*variegatus*	18	32	18,44	18,44	1,51	0,12	2
CEM	*Chelostoma*	*emarginatum*	15	26	16,00	16,00	1,51	0,04	3
SAL	*Sphecodes*	*alternatus*	19	37	19,41	19,41	1,49	0,12	7

HCR	*Heriades*	*crenulatus*	22	42	22,32	18,64	1,49	0,10	3
LME	*Lasioglossum*	*mediterraneum*	6	36	11,42	11,42	1,48	0,21	3
PDE	*Panurgus*	*dentipes*	18	43	18,44	17,40	1,48	0,10	4
HPIL	*Hylaeus*	*pilosulus*	15	24	16,00	16,00	1,48		1
ANA	*Andrena*	*nana*	11	26	14,01	14,01	1,47		1
ANIV	*Andrena*	*niveata lecana*	11	23	14,01	14,01	1,47		1
CCU	*Ceratina*	*cucurbitina*	9	44	12,45	12,45	1,46	0,07	3
	Hylaeus	*convergens*	-	-	-	-	1,46		1
NHI	*Nomada*	*hispanica*	9	18	12,45	12,45	1,46	0,12	4
HLE	*Hoplitis*	*leucomelana*	23	41	23,12	19,65	1,46		1
AALF	*Andrena*	*alfkenella*	13	21	15,16	15,16	1,46		1
HMA	*Halictus*	*maculatus*	13	39	15,16	15,16	1,45	0,14	7
CED	*Chelostoma*	*edentulum*	13	22	15,16	15,16	1,44	0,10	3
LPAL	*Lasioglossum*	*pallens*	11	15	14,01	14,01	1,44		1

HPR	*Hylaeus*	*praenotatus*	18	40	18,44	18,44	1,43	0,07	10
CCY	*Ceratina*	*cyanea*	13	44	15,16	15,16	1,42	0,04	3
	Nomada	*beaumonti*	-	-	-	-	1,40		1
ASIM	*Andrena*	*simontornyella*	16	24	16,66	16,66	1,40		1
LIN	*Lasioglossum*	*interruptum*	12	39	14,58	14,58	1,39	0,03	6
SBR	*Stelis*	*breviuscula*	26	38	25,96	23,39	1,37	0,04	3
HRU	*Heriades*	*rubicola*	19	39	19,41	19,41	1,36	0,03	3
LVI	*Lasioglossum*	*villosulum*	11	44	14,01	14,01	1,35		1
AMI	*Andrena*	*minutula*	3	25	10,21	10,21	1,35	0,07	11
	Andrena	*cf. saxonica*	-	-	-	-	1,34		1
HSP	*Hylaeus*	*spilotus*	18	40	18,44	18,44	1,34	0,09	3
LMA	*Lasioglossum*	*malachurum*	7	46	11,32	11,32	1,34	0,09	6
	Hoplitis	*annulata*	-	-	-	-	1,34		1
ATE	*Andrena*	*tenuistriata*	4	21	10,57	10,57	1,34	0,08	8

HDI	*Hylaeus*	*difformis*	18	34	18,44	18,44	1,33	0,00	2
ASEM	*Andrena*	*semilaevis*	13	24	15,16	15,16	1,32	0,06	2
HHY	*Hylaeus*	*hyalinatus*	11	41	14,01	14,01	1,32	0,08	14
HCOR	*Hylaeus*	*cornutus*	23	37	23,12	23,12	1,30		1
PEX	*Protosmia*	*exenterata*	14	27	15,70	15,70	1,30	0,06	2
SMO	*Sphecodes*	*monilicornis*	17	38	17,44	17,44	1,29	0,10	9
ASPR	*Andrena*	*spreta*	17	21	17,44	17,44	1,28	0,13	4
HBRA	*Hylaeus*	*brachycephalus*	15	26	16,00	16,00	1,28		1
ONA	*Osmia*	*nasuta*	18	22	18,44	18,44	1,28	0,12	2
	Protosmia	*glutinosa*	-	-	-	-	1,28		1
HPU	*Hylaeus*	*punctatus*	20	44	20,48	16,38	1,27	0,04	19
ADJ	*Andrena*	*djelfensis*	15	20	16,00	16,00	1,27	0,04	6
HCO	*Hylaeus*	*communis*	18	33	18,44	18,44	1,27	0,06	2
	Heriades	*sp.1*	-	-	-	-	1,27		1

	Protosmia	*asensioi*	-	-	-	-	1,25	0,38	3
SRUF	*Sphecodes*	*rufiventris*	17	31	17,44	17,44	1,25	0,18	3
HYSU	*Hylaeus*	*sulphuripes*	26	33	25,96	25,96	1,24	0,02	2
HAN	*Hylaeus*	*angustatus*	24	37	23,96	23,95	1,22		1
AVE	*Andrena*	*verticalis*	12	25	14,58	14,58	1,20	0,04	3
LCAP	*Lasioglossum*	*capitale*	24	28	23,96	23,96	1,20		1
	Osmia	*scutellaris*	-	-	-	-	1,20		1
NDI	*Nomada*	*discrepans*	8	37	11,84	11,84	1,18	0,14	2
CDA	*Ceratina*	*dallatorreana*	27	34	26,79	26,45	1,18	0,10	3
	Hylaeus	*gredleri*	-	-	-	-	1,16		1
LTR	*Lasioglossum*	*transitorium*	5	50	10,97	10,97	1,16	0,09	3
HGE	*Halictus*	*gemmeus*	6	46	11,42	11,42	1,16	0,11	16
SPU	*Sphecodes*	*puncticeps*	11	41	14,01	14,01	1,15	0,06	5
LMO	*Lasioglossum*	*morio*	13	35	15,16	15,16	1,14		1

CDE	*Ceratina*	*dentiventris*	17	40	17,44	17,44	1,13	0,07	3
SMIN	*Sphecodes*	*aff.miniatus*	14	31	15,70	15,70	1,13		1
HSM	*Halictus*	*smaragdulus*	20	45	20,48	14,96	1,12	0,21	15
NPA	*Nomada*	*panurgina*	16	33	16,66	16,66	1,11		1
LPAU	*Lasioglossum*	*pauxillum*	20	25	20,48	20,48	1,10		1
	Sphecodes	*cf. combai*	-	-	-	-	1.10		1
	Sphecodes	*hirtellus*	-	-	-	-	1.10		1
LPA	*Lasioglossum*	*pauperatum*	16	35	16,66	16,66	1,08		1
	Hylaeus	*rubicola*	-	-	-	-	1,08		1
NFL	*Nomada*	*flavoguttata*	7	24	11,32	11,32	1,06	0,05	4
NDIS	*Nomada*	*distinguenda*	9	39	12,45	12,45	1,05		1
SDU	*Sphecodes*	*dusmeti*	11	25	14,01	14,01	1,05		1
PAL	*Panurginus*	*albopilosus*	17	24	17,44	17,44	1,03	0,06	2
	Chelostoma	*foveolatum*	-	-	-	-	1,03		1

SPS	*Sphecodes*	*pseudofasciatus*	13	43	15,16	15,16	1,02	0,05	3
AmspA	*Andrena*	*sp.15*	19	25	19,41	19,41	1,01	0,02	3
	Andrena	*sp.16*	-	-	-	-	1,01		1
HCL	*Hylaeus*	*clypearis*	17	50	17,44	11,00	1,00	0,07	4
HTA	*Hylaeus*	*taeniolatus*	16	50	16,66	11,00	1,00	0,06	25
LATR	*Lasioglossum*	*atrovirens*	14	34	15,70	15,70	0,99	0,04	3
HIM	*Hylaeus*	*imparilis*	19	44	19,41	16,38	0,99	0,07	18
HBR	*Hylaeus*	*brevicornis*	11	46	14,01	13,74	0,97	0,05	13
NCO	*Nomada*	*coronata*	15	24	16,00	16,00	0,96	0,04	4
LGR	*Lasioglossum*	*griseolum*	15	50	16,00	11,00	0,93	0,03	3
LGL	*Lasioglossum*	*glabriusculum*	26	39	25,96	22,01	0,89		1
NSH	*Nomada*	*sheppardana*	9	23	12,45	12,45	0,88	0,08	6
LPO	*Lasioglossum*	*politum*	16	38	16,66	16,66	0,86	0,03	2
LMIN	*Lasioglossum*	*minutissimum*	9	28	12,45	12,45	0,80	0,00	2

	Lasioglossum	*pseudoplanulum*	-	-	-	-	0,80		1
NMI	*Nomioides*	*minutissimus*	26	38	25,96	23,39	0,77	0,03	4
CPA	*Ceratina*	*parvula*	23	37	23,12	23,12	0,75	0,02	3

Appendix A1.3. Phylogenetic relationships supplementary information

Based on different sources of phylogenetic information (morphological and molecular phylogenetic trees, taxonomical classifications; see in this Appendix 1: Table A1.3 and References of Appendix A1.3) we built a phylogenetic tree of the 245 bee species (see Appendix 1: Figure) included in the analyses (MESQUITE v.3.02; Maddison & Maddison 2015). Because this tree had no branch lengths, we applied Grafen's ultrametricizing method (Grafen 1989) using "compute.brlen" function from package "ape" for R (Paradis *et al*. 2014). With this method, each node is given a 'height', corresponding to the number of leaves of the subtree minus one (leaf height = 0). Each height is scaled to a root height = 1, and then raised to power 'rho' (> 0). Branch lengths are then computed as the difference between the height of the lower node and the height of the upper node. We tested different rho values (1, 0.5 and 0.1), and choose to work with rho = 0.5 because it yielded branch length ratios (basal family branches vs terminal species branches) (Appendix 1: Figure A1.3) similar to those in recently published molecular trees of bee families and genera (Danforth *et al.* 2006a; Cardinal & Danforth 2013). Polytomies were resolved using the "multi2d function" (package "ape" for R; Paradis *et al*. 2004).

Table A1.3. Bibliographical sources used in tree topology reconstruction

Reference	Taxa	Topology	source of data (molecular/morphology/taxonomy)	Observations
Hedtke et al 2013	SuperFam Apoidea: topology of Families inside	(AP+MEGA)+ ((COLL+HALIC)+ANDREN)	molecular	(Review)
Danforth et al 2013		(AP+MEGA)+ ((COLL+HALIC)+ANDREN)	molecular	
Cardinal & Danforth 2013		(AP+MEGA)+ ((COLL+HALIC)+ANDREN)	molecular + fossil data	
Danforth et al 2006a		(AP+MEGA)+ ((COLL+HALIC)+ANDREN)	molecular	
Danforth et al 2006b		(AP+MEGA)+ ((COLL+HALIC)+ANDREN)	molecular + morphology	
Fam. Apidae				
Payne 2014	Tribes/SubFam inside Fam. Apidae	(Anthophorini+Nomadinae) + (Apini+(Xylocopini+Eucerini))	molecular+morphological+behavioural	
Cardinal et al 2010		(Anthophorini+Nomadinae) + (Apini+(Xylocopini+Eucerini))	molecular	
Danforth et al 2013		(Anthophorini+Nomadinae) + (Apini+(Xylocopini+Eucerini))	molecular (Review)	
Cardinal & Danforth 2013		(Anthophorini+Nomadinae) + (Apini+(Xylocopini+Eucerini))	molecular + fossil data	
Litman et al 2013		Anthophorini + (Nomadinae + ((Apini+Xylocopini)+Eucerini))	molecular (5925 base pairs from four nuclear protein-coding genes and one nuclear ribosomal gene:	not used because discrepancies with the rest , but (Apini-Xylocopini-Eucerini) line supported
Brooks 1988	Subgenera topology inside Tribe Anthophorini (10sp)	(((Anthophora+Lophanthop.)+Petalosternon) + (Heliophila+Paramegilla)) + (Zebramegilla+Amegilla)	morphology	considered but not used because they do not include all subgenera present in our community
Dubitzky et al 2007		(((Petalosternon+Lophanthop.)+Anthophora) + Heliophila) falta subgen. Paramegilla + (Zebramegilla) falta subgen. Amegilla	morphology	
Michez et al 2008		(Heliophila + Anthophora) faltan el resto + (Zebramegilla+Amegilla)	morphology (based in part in Dubitzky et al 2007)	
Rehan and Schwarz 2014	SubGenera and species inside Genus Ceratina	(((Euceratina chalybea+Euceratina cyanea)+Euc. Chalcites)+Euc. Dallatorreana) + (Ceratina cucurbitina + Dalyatina parvula)	molecular	all spp present in our community included except C. dentiventris
Alexander 1994	Groups inside Genus Nomada	(Furva group+Ruficornis group)+Basalis group	morphology	not containing most of species of our community, and no others works on internal phylogeny of groups found
Ortiz-Sánchez 2011	Subgenera inside Genera Eucera		taxonomy	no work on internal phylogeny of Genus Eucera found
Fam. Megachilidae				
Litman et al 2011	Tribes inside Fam. Megachilidae	(((Osmiini+Megachilini)+Anthidiini)+Dioxyni)+Lithurgini	molecular	
González et al 2012		(((Osmiini+(Megachilini+Dioxyni))+Anthidiini)+Lithurgini	morphology (200 characters)	considered but position of Dioxyni in Litman et al molecular study is preferred
González (TESIS) 2008	Genera and Subgenera inside genus Megachile	(((((Macromegachile+Xanthosarus)+Eutricharea+Neoeutricharea)+Creightonella)+Chalicodoma))+ Genus Coelioxys	morphology (225 characters)	
Praz et al 2008	Genera inside Osmini Tribe	(((Hoplitis+Osmia sensu lato)+ Haethosmia) + (Protosmia+Heriades) +Chelostoma)	molecular	
Rightmayer et al 2013	Subgenera and species inside Osmia genus	(((Helicosmia caerulescens+Helic.niveata)+Helic. Aurulenta) + ((Pyrosmia gallarum+Pyrosmia ferruginea)+(Metalinella brevicornis+Osmia cornuta)) + (Erythrosmia andrenoides))) + Allosmia rufohirta	molecular	
Haider et al 2014		(Osmia cornuta + Metalinella brevicornis) + (Helicosmia aurulenta+Pyrosmia ferruginea)	morphology + molecular	considered but not used because they do not include all subgenera present in our community
González et al 2012	Subgenera inside Tribe Anthidiini	(((((Anthidium s.s.+Pseudoanthidium) + Anthidiellum) + Rhodanthidium) + Trachusa) + Stelis	morphology (200 characters)	
Müller 1996	Species inside Anthidium Subgenera	(((((Anthidium florentinum+ A.septemspinosum) + A.manicatum) +A. loti + A.cingulatum) +A.oblongatum)	morphology (115 characters)	
Fam. Halictidae				
Danforth et al 2008	Genera and Subgenera inside Halictidae Family	((Halictini+Sphecodini) + Nomioidinae) + Nomiinae Halictini=Lasioglosum + Halictus (L.(Evylaeus)+L.(Dialictus))+L.(Lasioglossum) (H.(Seladonia)+H.(Vestitohalictus)) + H.(Halictus)	molecular	
Danforth et al 2003	Species inside Subgenus Evylaeus	(L(Evy) mediterraneum + L(Evy) malachurum) + L(Evy) interruptum) + L(Evy) politum	molecular (ML method) (based on three protein coding genes:	also considered Danforth et al 1999, but contained less species than Danforth et al
Danforth et al 1999	Subgenera and species inside Genus Halictus	Vestitohalictus pollinosus+Vestito. Vestitus) + Seladonia gemmeus + Seladonia smaragdulus) + Seladonia subauratus) + (((((H.(Halictus) fulvipes+H(Hal.) scabiosae) + H(Hal) crenicornis) + H(Hal) maculatus) + H(Hal) quadricinctus)	molecular (ML method)	containing all 10 species present in Papiol
Habermannovà et al 2013	Species inside Genus Sphecodes	(ruficrus+pseudofasciatus) + puncticeps) +(rufiventris+monolicornis)	molecular (character state reconstruction of ancestral hosts)	including all 5 species in Papiol
Fam. Colletidae				
Kuhlmann et al 2009	Species inside Genus Colletes	(foveolaris + nigricans) + similis	molecular	
Ortiz-Sánchez 2011	Species inside Genus Colletes	C. abeillei inside "fodiens" group together with C. similis	taxonomy	
Kayaalp et al 2013	SubGenera inside Hylaeus Genera	((Prosopis + Spatulariella) + Paraprosopis) + Hylaeus	molecular (one mitochondrial and two nuclear genes)	SubGen Dentigera not included in this phylogeny, but no studies including it were found
Fam. Andrenidae				
Dubitzki et al 2005 (TESIS) and Dubitzki et al 2010	Sugenera and species inside Genera Andrena	(((Euandrena+Ptilandrena) + ((Biareolina + Agendrena)+Plastandrena))+ ((Zonandrena+Melandrena)+Simandrena)) + +Micrandrena + (Fumandrena + Chlorandrena) + (Graecandrena + Micrandrena) + (Ptilandrena+Hoplandrena)	morphology (single cladogram after succesive character reweightning a posteriori)	containing all subgenera in which are included all species in our site
Dubitzki et al 2005 (TESIS)		((Micrandrena + Chlorandrena) + (Zonandrena + Melandrena) + Simandrena) + Euandrena	molecular (mitochondrial COI)	considered but not used because they do not include all subgenera present in our community
Larkin et al 2006		(Melandrena + Plastandrena)+ (Simandrena+Micrandrena) + Melandrena + (Euandrena+Ptilandrena)	molecular	
Larkin et al 2008		((Euandrena + Ptilandrena) + (Micrandrena + Simandrena) + Melandrena)) + Plastandrena	molecular	
Shimizu et al 2014		(Euandrena+ Ptilandrena) + ((Simandrena+Chlorandrena)+ Hoplandrena) + Micrandrena)) + Melandrena) + Plastandrena	molecular	

Figure A1.3. Phylogentic tree of the 245 species included in the analyses inferred from different sources (Table S1a) and ultrametricized with Graffen's method (*rho*=0.5). See Table S1b for species names.

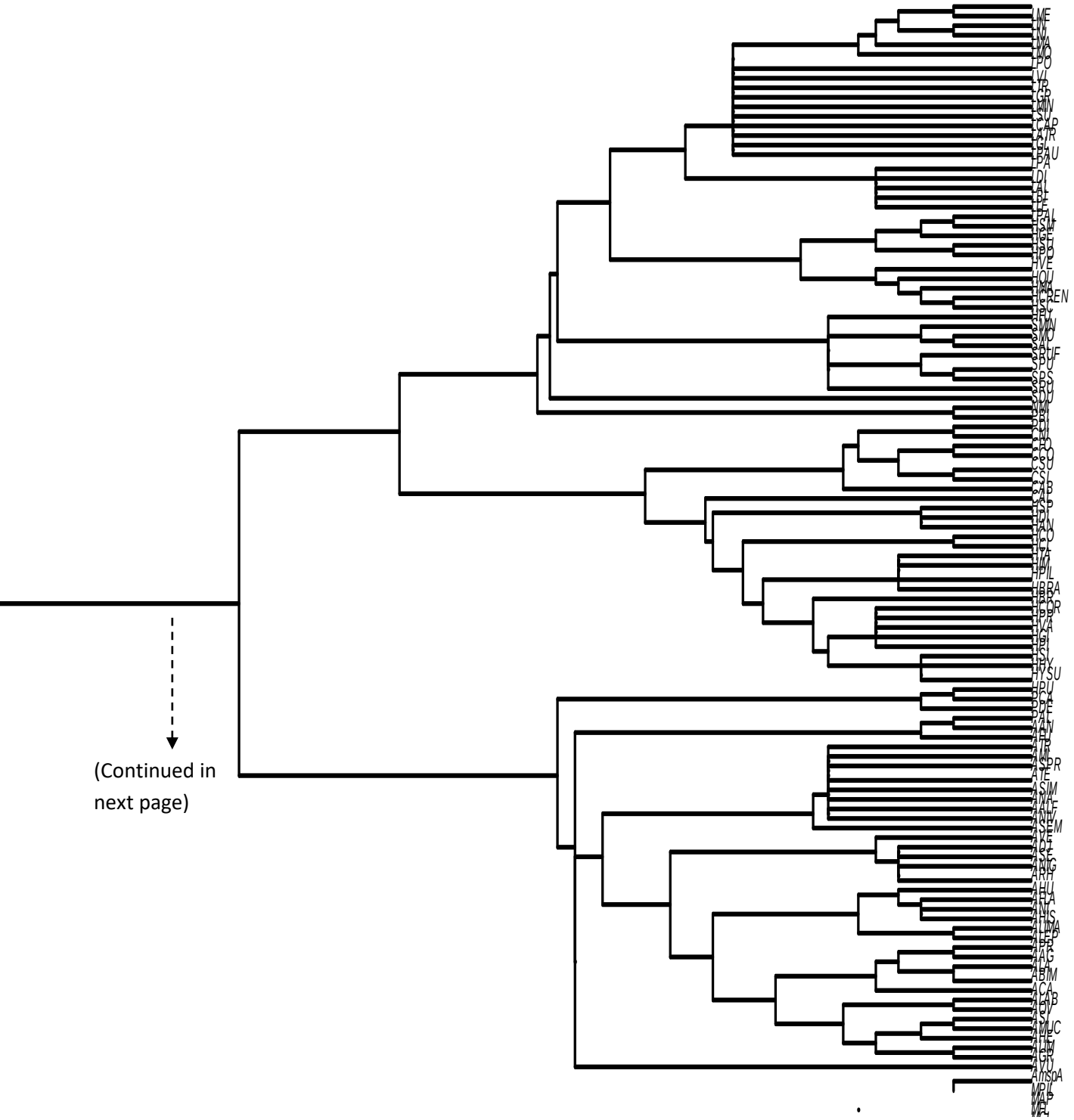
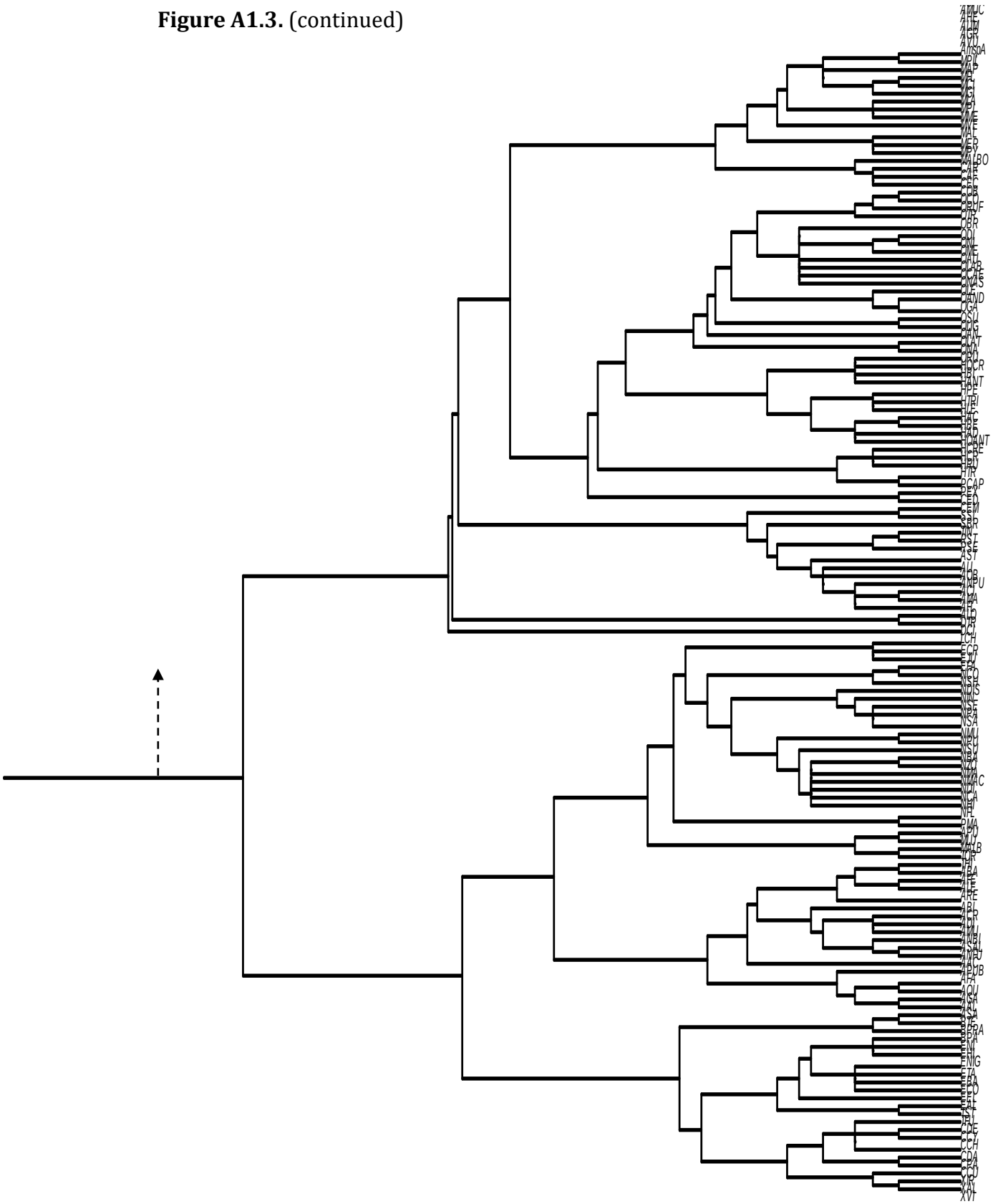


Figure A1.3. (continued)



References Appendix A1.3. and Table A1.3.

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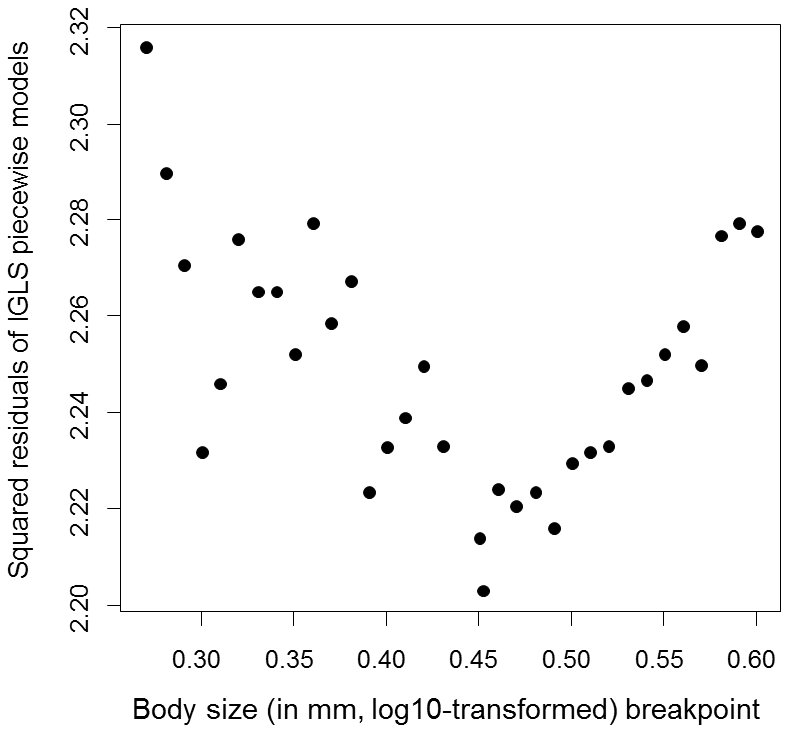
Appendix A1.4. Phylogenetic piecewise regression

Because thermoregulatory ability is dependent on body size (Bishop & Ambruster 1999; Willmer & Stone 2004), we expected a different body size – species temperature relationship for large (endothermic) and small (ectothermic) bees. The statistical significance of this transition (or "difference-in-slope" parameter) can be tested using a piecewise regression (Muggeo 2003; Toms & Lesperence 2003). Piecewise-regression models are ''broken-stick'' models, where two or more fitted functions are separated at unknown point(s), called "break-point(s)" (Toms & Lesperance 2003). Some packages in R apply this procedure to lineal models (e.g. "segmented", Muggeo 2008), but do not account for phylogenetic relatedness. For this reason, we developed an R algorithm incorporating phylogenetic information. This algorithm allowed us to use a pGLS function (instead of the lm function) and to modify the phylogenetic tree for each possible break-point tested. We use the pGLS ($\log_{10}$(species temperature) ~ $\log_{10}$(ITS)) model as a base for our phylogenetic piecewise analysis. The script for this algorithm is provided in Appendix S5.

Piecewise regressions require a sensible initial estimate of the break-point. Otherwise, if the initial estimate of the break-point is very distant from the true break-point, the algorithm may converge to a local solution rather than a global solution (Muggeo 2003; Toms & Lesperence 2003). Thus, we first inspected the scatterplot of squared residuals obtained from the pGLS function for the entire body size range in our community (calculating squared residuals for the piecewise algorithm at 0.01 intervals). We obtained an absolute minimum value of squared residuals of fitted regression lines at $\log_{10}$ body size ~ 0.45 (Figure S4). Consequently, we run our phylogenetic piecewise algorithm in the 0.40 – 0.55 interval with an intensive searching function (*optim*) to obtain a more accurate calculation of the breakpoint value. Confidence intervals (95%) for the break-point were obtained with

a percentile methodology, using a bootstrapping procedure with 1000 iterations (Efron & Tibshirani 1986) (script in Appendix S5).

Figure A1.4. Relationship between phylogenetic piecewise squared residuals (log_{10}Species temperature- log_{10} ITS model), and body size break-point calculated from phylogenetic piecewise regression model at 0.01 intervals of possible body size break-points.



References Appendix A1.4

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Appendix A1.5. Phylogenetic piecewise regression script.

```
rm(list=ls(all=TRUE))

assign("last.warning", NULL, envir = baseenv())


library(xlsx)

library(ape)

library(caper)


#Tree and species data-245sp(con DTR)(ult 9-6-16)

Tree245sp <- # phylogenetic tree


# Species data

setwd("data route")

NB245 <- read.csv2("data name",sep=";",dec=".",row.names=NULL,header=T)


# Trims the phylogenetic tree according to the input data.

prepare.cdat <- function(phy.tree,spec.data,spec.to.trim) {

 new.tree <- drop.tip(phy=phy.tree,tip=as.vector(spec.to.trim[,1])) # Trims
phylogenetic tree.

 new.tree <- compute.brlen(new.tree, method="Grafen", power=0.5)
```

```
  new.tree <- multi2di(new.tree)

  cdat <- comparative.data(data=spec.data,
phy=new.tree,names.col="acronimo",vcv=T)

  return(cdat)

}


# Splits the data into two halves and computes the residuals.

res.pgls <- function(a) {

  x <- try(pgls(logTa1a~log.AT.,a,lambda="ML"),TRUE)

  if (!inherits(x,"try-error")) {

    return(residuals(x))

  } else return(x)

}


fu <- function(bp) {

  a <- species.data[species.data$log.AT.<=bp,]

  b <- species.data[species.data$log.AT.>bp,]

  cdat.small <- prepare.cdat(tree139sp,a,b)

  cdat.large <- prepare.cdat(tree139sp,b,a)

  return(sum(res.pgls(cdat.small)^2)+sum(res.pgls(cdat.large)^2))

}
```

```
# Searches for the break point by minimizing the residuals.

species.data <- NB245

#visualization of all possibles breakpoints vs residuals

#x<- seq(0.27, 0.60,.01)

#y <- sapply(x,fu)

#plot(y~x)

#browser()


lower.bp <- .40

upper.bp <- .55

break.point <- optim(0.45,fu,method="Brent",lower=lower.bp,upper=upper.bp)$par


# Bootstraps the data to estimate confidence intervals for the break point.

bp <- break.point

nboot <- 1000

break.point.boot <- NULL

min.boot <- NULL


t <- NB245$log.AT.[NB139$log.AT.>=lower.bp & NB139$log.AT.<=upper.bp]
```

```
a <- NB139[NB139$log.AT.<=bp,]

b <- NB139[NB139$log.AT.>bp,]

cdat.small <- prepare.cdat(tree139sp,a,b)

cdat.large <- prepare.cdat(tree139sp,b,a)

fit.small <- pgls(logTa1a~log.AT.,cdat.small,lambda="ML")

fit.large <- pgls(logTa1a~log.AT.,cdat.large,lambda="ML")

pred.small <- predict(fit.small)

pred.large <- predict(fit.large)

rs <- residuals(fit.small)

rl <- residuals(fit.large)

for (i in 1:nboot) {

 cat(paste("Loop num. ",i," of ",nboot,"...\n",sep=""))

 y1 <- pred.small + sample(rs,replace=T)

 y2 <- pred.large + sample(rl,replace=T)

 species.boot <- NB139

 species.boot$logTa1a <- c(y1,y2)

 fu.boot <- function(q) {

  a <- species.boot[species.boot$log.AT.<=q,]

  b <- species.boot[species.boot$log.AT.>q,]

  res.small <- res.pgls(prepare.cdat(tree139sp,a,b))

  res.large <- res.pgls(prepare.cdat(tree139sp,b,a))
```

```
  if (!inherits(res.small,"try-error") & !inherits(res.large,"try-error")) {
    return(sum(res.small^2)+sum(res.large^2))
  } else return(NA)
 }
 z <- sapply(t,fu.boot)
 z <- z[!is.na(z)]
 break.point.boot <- c(break.point.boot,t[which.min(z)])
 min.boot <- c(min.boot, min(z))
}

# Calculates confidence intervals.
aver.boot <- mean(break.point.boot)
bias.boot <- (aver.boot-break.point)
var.boot <- sum((break.point.boot-aver.boot)^2)/nboot
se.boot<-sqrt(var.boot)/sqrt(nboot)
conf.boot <- quantile(break.point.boot,c(.025,.975))

save(break.point,break.point.boot,min.boot,aver.boot,bias.boot,var.boot,conf.boot,
   file="NB- piecewise con estimación de lambda -  codigo R Roberto (corrRob)-para
251-17sp(corrSOC-24-5-16) V4")
```

```
############################################################

#Compute pGLS for “large” and “small” groups using breakpoint obtained

bp<-break.point

a <- NB139[NB139$log.AT.<=bp,]

b <- NB139[NB139$log.AT.>bp,]

cdat.small <- prepare.cdat(tree139sp,a,b)

cdat.large <- prepare.cdat(tree139sp,b,a)

fit.small <- pgls(logTa1a~log.AT.,cdat.small,lambda="ML")

fit.large <- pgls(logTa1a~log.AT.,cdat.large,lambda="ML")

summary(fit.small)

summary(fit.large)
```

Appendix 2

Table A2.1. Functional trait description for host and parasitoids, with an explanation of potential importance of each trait for interaction with their parasitoids or host respectively.

HOSTS				
Trait	**Description**	**Type of variable**	**Potential importance for interactions with parasitoids**	**Source ***
Body size	Intertegular span (ITS), in mm. Highly correlated to body weight in bees (Cane 1987, Peters et al. 2016). It has also been used for other insects (Chifflet et al. 2011)	Continuous	Host body size may constrain parasitoid size.	Own measures
Larval diet	Pollinivorous (bees) or carnivorous (wasps)	Categorical with two levels	Parasitoid species (especially cleptoparasites) may specialize or display preferences for certain types of host provisions	Literature and own observations
Wintering stage	Adult or prepupa	Categorical with two levels	Species overwintering as adults are active earlier in the year than species wintering as prepupae (Bosch et al. 2001), thus conditioning the temporal overlap with parasite species.	Literature and own observations
Voltinism	Number of generations per year (univoltine or multivoltine)	Categorical with two levels	Multivoltine species usually have longer activity periods and therefore may be exposed to a greater range of parasitoids	Literature and own observations
Nest-building materials	Type of materials used by females use to build cell partitions and nest caps (mud, plant material, glandular secretions).	Categorical with three levels	Certain nesting materials (e.g., mud) may offer greater protection against parasitoids than others (e.g., leaves).	Literature and own observations

Table A2.1. (continued)

PARASITOIDS				
Trait	**Description**	**Type of variable**	**Potential importance for interactions with parasitoids**	**Source***
Body size	Measured as body length, in mm	Continuous	Parasitoid size may constrain suitable host size.	Literature and own measures
Parasitic behavior	parasitoids, cleptoparasites, and scavenger/predators	Categorical variable with three levels	Cleptoparasites are expected to have a narrower diet breadth than parasitoids and, especially, scavengers	Literature
Wintering stage	Adult or immature	Categorical with two levels	Species overwintering as adults tend to be active earlier in the year than species wintering immatures, thus conditioning the temporal overlap with host species.	Literature
Voltinism	Number of generations per year (univoltine or multivoltine)	Categorical with two levels	Multivoltine species usually have longer activity periods and therefore may have access to a greater variety of hosts	Literature
Gregarism	Solitary (only one parasitoid individual develops per host individual) or gregarious (several parasitoids develop)	Categorical with two levels	In multivoltine species, the capacity to increase percent parasitism is likely to be greater in gregarious species	Literature and own observations

Table A2.2.. Host and parasitoids species and their code numbers in Figure 1 in main text in Chapter 2.

Table A2.2.1. Host species and their code numbers.

Code	Family /Subfamily	*Species*
	'BEES'	
1	COLLETIDAE	*Hylaeus communis*
2	COLLETIDAE	*Hylaeus signatus*
3	COLLETIDAE	*Hylaeus taeniolatus*
4	MEGACHILIDAE	*Chelostoma campanularum*
5	MEGACHILIDAE	*Chelostoma emarginata*
6	MEGACHILIDAE	*Chelostoma florisomne*
7	MEGACHILIDAE	*Heriades truncorum*
8	MEGACHILIDAE	*Hoplitis adunca*
9	MEGACHILIDAE	*Megachile apicalis*
10	MEGACHILIDAE	*Megachile centuncularis*
11	MEGACHILIDAE	*Megachile rotundata*
12	MEGACHILIDAE	*Osmia bicornis*
13	MEGACHILIDAE	*Osmia caerulescens*
14	MEGACHILIDAE	*Osmia cornuta*
15	MEGACHILIDAE	*Osmia fulviventris*
16	MEGACHILIDAE	*Osmia submicans*
	'WASPS'	
17	CRABRONIDAE	*Passaloecus spp.*[1]
18	CRABRONIDAE	*Pison atrum*
19	CRABRONIDAE	*Psenulus fuscipennis*
20	CRABRONIDAE	*Solierella compedita*
21	CRABRONIDAE	*Trypoxylon figulus*

22	CRABRONIDAE	*Trypoxylon spp.*[2]
23	EUMENINAE	*Alastor atropos*
24	EUMENINAE	*Euodynerus posticus*
25	EUMENINAE	*Microdynerus nugdunensis*
26	EUMENINAE	*Microdynerus timidus*
27	SPHECIDAE	*Isodontia mexicana*

[1] Mostly *Passaloecus corniger* along with some *P. eremita* and *P. gracilis*.

[2] Mostly *Trypoxylon clavicerum* along with some *T. minus*

Table A2.2.2. Parasitoid species and their code numbers.

Code	Order/Infraclass	*Species*
28	ACARI	*Chaetodactylus osmiae*
29	ACARI	*Pyemotes ventricosus*
30	COLEOPTERA	*Ptinus pyrenaeus*
31	COLEOPTERA	*Ptinus sexpunctatus*
32	COLEOPTERA	*Trichodes alvearius*
33	DIPTERA	*Anthrax anthrax*
34	DIPTERA	*Cacoxenus indagator*
35	DIPTERA	*Sarcophagidae sp.1*
36	DIPTERA	*Sarcophagidae sp.2*
37	HYMENOPTERA	*Chrysis ignita*
38	HYMENOPTERA	*Gasteruption sp.*
39	HYMENOPTERA	*Melittobia acasta*
40	HYMENOPTERA	*Monodontomerus obsoletus*
41	HYMENOPTERA	*Omalus auratus*
42	HYMENOPTERA	*Perithous (=Hybomischos) septemcinctorius*
43	HYMENOPTERA	*Sapyga quinquepunctata*
44	HYMENOPTERA	*Stelis breviuscula*
45	HYMENOPTERA	*Trichrysis cyanea*
46	LEPIDOPTERA	*Plodia interpunctella*

Table A2.3. Results of GLMM analyses of season effects on hosts separating bees and wasps) richness and abundance.

Table A2.3.1. Results of GLMM models.

Host Richness (Response variable) model:

Exp.Var.	numDF	denDF	F-value	p-value
(Intercept)	1	39	152.23588	<.0001
group	1	39	6.42953	0.0153
season	1	39	54.25009	<.0001
group X season	1	39	29.52336	<.0001

Exp.Var.	Value	Std.Error	DF	t-value
(Intercept)	3.142857	0.3561800	39	8.823788
group[WASP]	-2.357143	0.4182987	39	-5.635070
season[summer]	0.571429	0.4182987	39	1.366078
group[WASP] X season[summer]	3.214286	0.5915638	39	5.433541

Inside [ ]: level of reference; Exp.Var.: Explanatory variables

Host abundance (Response variable) model:

Exp.Var.	numDF	denDF	F-value	p-value
(Intercept)	1	39	40.23699	<.0001
group	1	39	7.74219	0.0083
season	1	39	2.46595	0.1244
group X season	1	39	29.26845	<.0001

Exp.Var.	Value	Std.Error	DF	t-value
(Intercept)	242.5000	29.67329	39	8.172332
group[WASP]	-236.0714	40.75129	39	-5.792980
season[summer]	-201.1429	40.75129	39	-4.935865
group[WASP] X season[summer]	311.7857	57.63103	39	5.410032

(inside [ ]: level of reference); Exp.Var.: Explanatory variables

Table A2.3.2. Tukey Post hoc comparisons from crossed effects of GLMM model.

Host Richness (Response variable) model:

contrast	estimate	SE	df	*t* ratio	p
spring,BEE - summer,BEE	-0.5714286	0.4182987	39	-1.366	0.5277
spring,BEE - spring,WASP	2.3571429	0.4182987	39	5.635	<.0001
spring,BEE - summer,WASP	-1.4285714	0.4182987	39	-3.415	0.0079
summer,BEE - spring,WASP	2.9285714	0.4182987	39	7.001	<.0001
summer,BEE - summer,WASP	-0.8571429	0.4182987	39	-2.049	0.1880
spring,WASP - summer,WASP	-3.7857143	0.4182987	39	-9.050	<.0001

Host Abundance (Response variable) model:

contrast	estimate	SE	df	*t* ratio	p
spring,BEE - summer,BEE	0.51819298	0.1532976	39	3.380	0.0086
spring,BEE - srping,WASP	1.51310774	0.1532976	39	9.870	<.0001
spring,BEE - summer,WASP	0.08151066	0.1532976	39	0.532	0.9508
summer,BEE - spring,WASP	0.99491476	0.1532976	39	6.490	<.0001
summer,BEE - summer,WASP	-0.43668232	0.1532976	39	-2.849	0.0338
spring,WASP - summer,WASP	-1.43159708	0.1532976	39	-9.339	<.0001

Table A2.4. Results summary for PERMANOVA analyses of community composition with qualitative data.

Table A2.4.1. Quantitative data

Resp.var	Exp.var	df	sums of sqs	meansqs	F	pse-R^2	p (>F)
HOSTS	season	1	2.38	2.38	8.44	0.24	0.0001
HOST BEES	season	1	1.43	1.43	4.28	0.14	0.0013
PARASIT.	season	1	1.98	1.98	9.05	0.26	0.0001

Resp.var: response variable; Exp.var: explanatory variable; sums of sqs: sums of squares; pse-R^2: pseudo-R^2, PARASIT.: parasitoids

Table A2.4.2. Qualitative (presence/absence) data

Resp.var	Exp.var	df	sumsofsqs	meansqs	F	pse-R^2	p (>F)
HOSTS	season	1	1.72	1.72	10.39	0.29	0.0002
HOST BEES	season	1	0.87	0.87	4.40	0.14	0.0003
PARASIT.	season	1	1.11	1.11	8.49	0.24	0.0003

Resp.var: response variable; Exp.var: explanatory variable; sums of sqs: sums of squares; pse-R2: pseudo-R^2, PARASIT.: parasitoids

Figure A2. 1. Effect of season (spring/summer) and group (bee/wasp) on hosts.

Figure A2.1.1. Effect of season and group on mean host abundance.

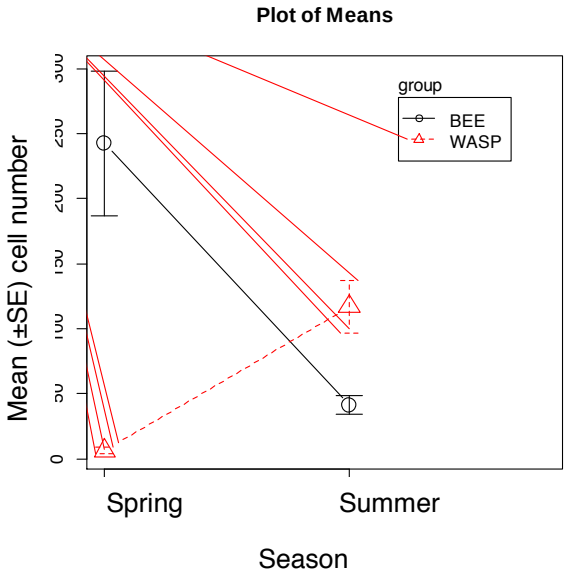


Figure A2.1.2. Effect of season and group on mean host richness.

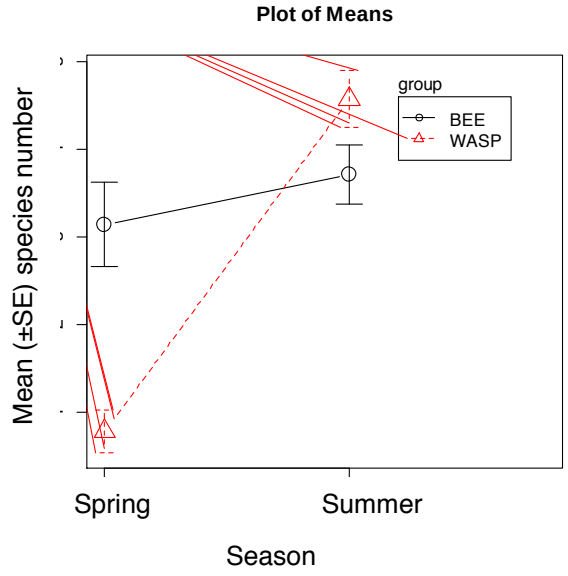
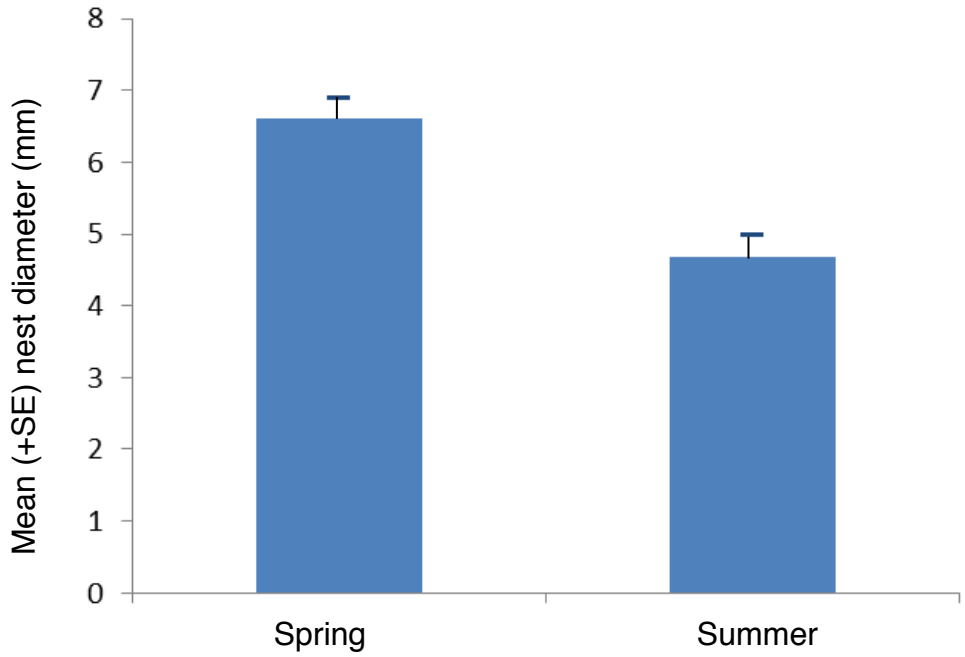


Figure A2.2.(Appendix E). Mean (+ standard error (SE)) nest diameter used by host species seasonally.



Appendix 3

TABLE A3.1. Host and parasitoids species and their code numbers in Fig. 2 in the main text of Chapter 3.

TABLE A3.1.1. Host species and their code numbers.

Code	Family /Subfamily	*Species*
	"BEES"	
1	COLLETIDAE	*Hylaeus communis*
2	COLLETIDAE	*Hylaeus signatus*
3	COLLETIDAE	*Hylaeus taeniolatus*
4	MEGACHILIDAE	*Anthidium florentinum*
5	MEGACHILIDAE	*Chelostoma campanularum*
6	MEGACHILIDAE	*Chelostoma emarginata*
7	MEGACHILIDAE	*Chelostoma florisomne*
8	MEGACHILIDAE	*Heriades truncorum*
9	MEGACHILIDAE	*Hoplitis adunca*
10	MEGACHILIDAE	*Megachile apicalis*
11	MEGACHILIDAE	*Megachile centuncularis*
12	MEGACHILIDAE	*Megachile rotundata*
13	MEGACHILIDAE	*Osmia bicornis*
14	MEGACHILIDAE	*Osmia caerulescens*
15	MEGACHILIDAE	*Osmia cornuta*
16	MEGACHILIDAE	*Osmia fulviventris*
17	MEGACHILIDAE	*Osmia submicans*
	"WASPS"	
18	CRABRONIDAE	*Lestica clypeata*

19	CRABRONIDAE	*Passaloecus spp.*[1]
20	CRABRONIDAE	*Pison atrum*
21	CRABRONIDAE	*Psenulus fuscipennis*
22	CRABRONIDAE	*Solierella compedita*
23	CRABRONIDAE	*Trypoxylon figulus*
24	CRABRONIDAE	*Trypoxylon spp.*[2]
25	EUMENINAE	*Alastor atropos*
26	EUMENINAE	*Discoelius zonalis*
27	EUMENINAE	*Euodynerus posticus*
28	EUMENINAE	*Microdynerus nugdunensis*
29	EUMENINAE	*Microdynerus timidus*
30	EUMENINAE	*Symmorphus crassicornis*
31	POMPILIDAE	*Dipogon sp*
32	SPHECIDAE	*Isodontia mexicana*

[1] Mostly *Passaloecus corniger* along with some *P. eremita* and *P. gracilis*.

[2] Mostly *Trypoxylon clavicerum* along with some *T. minus*.

TABLE A3.1.2. Parasitoids species and their code numbers.

Code	Order/Infraclass	*Species*
33	ACARI	*Chaetodactylus osmiae*
34	ACARI	*Pyemotes ventricosus*
35	COLEOPTERA	*Ptinus pyrenaeus*
36	COLEOPTERA	*Ptinus sexpunctatus*
37	COLEOPTERA	*Trichodes alvearius*
38	DIPTERA	*Anthrax anthrax*
39	DIPTERA	*Cacoxenus indagator*
40	DIPTERA	*Sarcophagidae sp.1*
41	DIPTERA	*Sarcophagidae sp.2*
42	HYMENOPTERA	*Chrysis ignita*
43	HYMENOPTERA	*Gasteruption sp.*
44	HYMENOPTERA	*Melittobia acasta*
45	HYMENOPTERA	*Monodontomerus obsoletus*
46	HYMENOPTERA	*Omalus auratus*
47	HYMENOPTERA	*Perithous septemcinctorius*
48	HYMENOPTERA	*Sapyga quinquepunctata*
49	HYMENOPTERA	*Stelis breviuscula*
50	HYMENOPTERA	*Stelis minuta*
51	HYMENOPTERA	*Trichrysis cyanea*
52	LEPIDOPTERA	*Plodia interpunctella*