Ecology and biogeography of island parasitoid faunas

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Abstract

Islands constitute natural laboratories for the study of evolutionary and ecological processes due to their discrete and isolated nature. Island biotas tend to be species–poor and disharmonic compared to the mainland; typically, interspecific competition is low, and entire groups of predators, parasitoids or pathogens are absent from their biotas, so the ecological space is often not fully saturated. Consequently, species from island assemblages often use a wider range of resources than their counterparts from the source mainland. Here, I investigate whether island parasitoid communities have proportionally more generalist species than their source mainland, and which factors determine island community structure. These questions were approached using data on the distribution of Ichneumonoidea (Hymenoptera) species worldwide and with data from a survey conducted in the Macaronesian region. Prior to the global analyses, I assessed whether islands and archipelagos follow the same species–area relationship, and identified which islands have comparable inventories. Globally, islands have proportionally more idiobionts (i.e. generalists) than continental areas. However, there is a latitudinal gradient in the level of generalism of island parasitoid faunas that correlates with some environmental factors and island characteristics; the species pool is the most important determinant of island community structure, together with temperature (for braconids) or biogeographical region (for ichneumonids). Host and parasitoid larvae collected in different islands of the Macaronesian region and adjacent mainland were assigned to Molecular Operational Taxonomic Units using a protocol based on host dissection and DNA barcoding. At this scale, mainland faunas have proportionally more koinobiont species and island communities have a greater proportion of idiobionts. Although overall parasitism rates were similar between islands and mainland, islands had higher idiobiont parasitism rates than expected by chance. In summary, results from this thesis indicate that indeed island parasitoid faunas are biased towards generalist species.

Declaration

The work presented in this thesis is entirely my own and it has not been submitted for any other academic qualification.

Co-authors on published and submitted chapters are listed as footnotes at the start of each chapter. People who provided less formal help and advice are listed in the acknowledgements.

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Chapter 1: General Introduction

1.1. Parasitoids

A parasitoid is ‘an organism which develops on or in another single ("host") organism, extracts nourishment from it, and kills it as a direct or indirect result of that development' (Eggleton & Gaston, 1990, following Kuris, 1974). This broad definition includes not only insects, but also other groups like entomophagous nematodes, some protists, entomophagous fungi, and a few crustaceans. Since most biologists use the term *parasitoid* to mention only insect taxa, in this thesis this term will also refer only to insects that exhibit the parasitic way of life.

Insect parasitoids are usually defined as insects whose larvae develop by feeding in or on the body of an arthropod host. The outcome of their development is, by definition, the death of their individual host (Eggleton & Belshaw, 1992; Godfray, 1994; Quicke, 1997). The parasitoid life style is one of the most abundant in the animal kingdom, probably comprising 10% or more of all metazoan animals (Hassell & Godfray, 1992). Although a number of insect groups have parasitoid members, the greatest number is found in the order Hymenoptera, which accounts for nearly 75% of the estimated number of parasitoid species (Feener & Brown, 1997; Belshaw *et al.*, 2003). Other orders such as Diptera, Coleoptera, Lepidoptera, Trichoptera and Neuroptera also include parasitoid species (Godfray, 1994). Most parasitoids attack other insects, including other parasitoids (i.e., hyperparasitoids); at least 19 insect orders and a few non-insect groups are utilised as hosts (Quicke, 1997), and all life stages of the host are attacked by at least some parasitoids.

1.1.1. Biology

Adult parasitoids are usually free living and highly mobile, being proficient at searching for and detecting both exposed hosts and those that are hidden in a relatively static way. Hosts are usually located by the adult female who lays her eggs either directly on or in the host or in its immediate vicinity. Hymenopteran parasitoids nearly always have well-developed ovipositors that they use to locate the host (even those protected by plant tissue or wood),

manipulate the eggs and inject various secretions into the hosts that may cause temporary or permanent paralysis, or modify the host's immune system and the metabolic functions (Godfray, 1994; Quicke, 1997). Most parasitoids attack their hosts at their juvenile stages, so they can be classified according to the stage they attack and emerge from. Thus, a host may be attacked by egg, larval, pupal, or adult parasitoids, that attack and develop in the respective stage of the host. Alternatively, there are parasitoids that lay eggs in one stage but complete development in the next stage, for example, egg-larval parasitoids, or larval-pupal parasitoids.

Depending on the feeding behaviour of their larvae, parasitoids can either be endoparasitoids, if the larvae feed inside the host's body, or ectoparasitoids, that live externally, normally with their mouthparts buried in their host's body. Solitary parasitoids usually lay one egg in a host which produces one larva (in contrast to some polyembryonic parasitoids in which multiple larvae hatch from a single egg; Strand, 1989), while gregarious parasitoids lay multiple eggs that can develop into many individuals per host. If further eggs are deposited on the host by another individual of the same parasitoid species, superparasitism is said to occur; however, if a parasitoid develops on another parasitoid it is called hyperparasitoid. A true hyperparasitoid attacks the primary parasitoid when it is still developing in or on its host (the secondary host for the hyperparasitoid), whereas pseudohyperparasitoids attack parasitoid larvae, pupae or adults when they have already left the host.

1.1.2. Idiobionts versus *koinobionts*

Parasitoids can also be divided into two different groups, depending on the host growth: koinobionts, which usually allow the host to continue its development after oviposition, and idiobionts, that do not (Askew & Shaw, 1986). In fact, idiobionts inject venom into their host during oviposition, either causing permanent paralysis or arrested development (Gauld & Bolton, 1988). This way, the developing parasitoid is never in danger of being dislodged, injured or killed by their host's movement (see examples in Gross, 1993), and the location used by the host for its own protection also serves to protect the parasitoid. Most koinobionts, on the other hand, do not paralyse the host, or do it just temporarily, and the host can continue to grow while the parasitoid larvae feed on its hemolymph or non vital organs

(Shaw, 1997). Several studies show that this dichotomy correlates with numerous other life history traits of the parasitoids (Sheehan & Hawkins, 1991; Belshaw, 1994; Quicke, 1997; Mayhew & Blackburn, 1999). Normally, koinobiont species attack young hosts, whereas idiobionts attack more mature ones (Godfray, 1994; Quicke, 1997). Many idiobionts are ectoparasitoids, feeding mostly on concealed hosts. In contrast, koinobionts are mainly endoparasitoids, attacking mobile or fairly free-ranging hosts (Askew & Shaw, 1986; Hawkins, 1994; Quicke, 1997; Mayhew & Blackburn, 1999). Idiobionts tend to have rapid larval development, long adult life span, are synovigenic (i.e. can produce eggs in their ovaries during their life; Jervis *et al.*, 2001) and attack hosts that are larger than them, whereas koinobionts have a slow or delayed larval development, short adult life spans, are pro-ovigenic (i.e. have all the eggs already mature and ready to oviposit at the start of adult life) and often attack hosts that are smaller than themselves (Quicke, 1997). This dichotomy between idio- and koinobionts is also reflected in the parasitoids' host range: koinobionts usually have a narrower host range than idiobionts and are therefore typically considered specialists (Askew & Shaw, 1986; Sato, 1990; Sheehan & Hawkins, 1991; Hawkins, 1994; Shaw, 1994; Althoff, 2003; but see Mills, 1992). One reason for this may be that koinobionts have a more prolonged interaction with the immune system of their hosts, and adaptations to overcome this difficulty probably restrict the number of hosts that koinobionts can use successfully. On the contrary, idiobionts do not have to deal with the immune responses of their hosts, and consequently are able to adapt, at least potentially, to what they find within their searching niche and develop in a wider range of hosts (Hawkins, 1994; Shaw, 1994, 1997; Quicke, 1997). However, there is a complete spectrum between idiobiont and koinobiont strategies, and there are exceptions to virtually all the above mentioned generalizations. For example, many parasitoid Diptera species are koinobionts and still have a wide host range (Belshaw, 1994; Feener & Brown, 1997; Stireman *et al.*, 2006), although the generality of this pattern has been questioned (see Smith *et al.*, 2007).

1.1.3. Host range

The host range of a particular parasitoid species is the group of potential hosts that it can attack successfully, after exhibiting a pattern of searching behaviour that permits it to find hosts regularly (Shaw, 1994). In general, most herbivorous insect species are attacked by whole complexes of parasitoid species, typically varying between 2 and 8 parasitoid species per host, although this number can reach 100 species in some cases (Hawkins & Lawton, 1987; Hawkins, 1990; Hochberg & Hawkins, 1993; Lewis *et al*., 2002). Extra host species will only be recruited slowly into a parasitoid's host range, and the probability of expanding to a new host will be determined both by the frequency by which that host is encountered and, likely, by the relatedness of the potential new host to the existing one, since closely related hosts may require more similar adaptations in the parasitoid (Quicke, 1997). Therefore, the realised host range of a parasitoid may change over time and space, and, in fact, it has been demonstrated that individuals can exhibit behavioural plasticity that enables them to respond to an inconstant and uneven environment, in ways that help to maintain their chances of success (Cornell & Hawkins, 1993; Hawkins & Marino, 1997; Tanaka *et al.*, 2007). Predicting whether or not a parasitoid will attack non-target hosts requires understanding the full range of evolutionary and ecological factors influencing its host range. However, host range remains one of the less well understood aspects of parasitoid biology (Hawkins & Sheehan, 1994; Shaw, 1994), and published host records are frequently unreliable (Noyes, 1994; Shaw, 1994). In the absence of detailed rearing record, the koinobiont/idiobiont dichotomy represents a practical criterion for distinguishing between parasitoids that tend to be specialists (koinobionts) and parasitoids that are potentially more generalist (idiobionts) (Hawkins *et al*., 1990).

1.1.4. Diversity

Parasitoids are a key component of most terrestrial ecosystems, due to their numbers and ecological importance (LaSalle & Gauld, 1991, 1993). They are vitally important in maintaining the diversity of other animals and plants, being involved in a sheer number of trophic interactions (e.g. Hawkins & Lawton, 1987; Müller *et al.*, 1999; Lewis *et al.*, 2002)

and having a regulatory effect on arthropod populations (e.g. Hassell 2000a, b; Letourneau *et al.*, 2009).

Despite their ecological importance, relatively little is known about the diversity, distribution and biology of parasitoids. Although the Hymenoptera are one of the most species rich and abundant groups of organisms, with estimates of total species richness ranging from 130,000 to 2.5 million (Brown, 1982; Gauld & Bolton, 1988; Gaston, 1991a; LaSalle & Gauld, 1991; Stork *et al.*, 1996; Ulrich, 1999), the number of described species is only approximately 115.000 (LaSalle & Gauld, 1993), indicating that most species are still undescribed. The parasitic Hymenoptera are particularly poorly known; it is estimated that less than half of the species of one of the largest and better studied parasitic groups, the family Braconidae, have been formally described (Dolphin & Quicke, 2001; Jones *et al.*, 2009). Furthermore, taxonomical work on this group is biased against the description of tropical and small bodied species (Gaston, 1993; Jones *et al.*, 2009).

Several studies have examined the geographic distribution of some parasitic taxa. Most of these studies regarded the Ichneumonidae and suggested that this family is less species rich towards the tropics than on temperate regions, with such pattern being more evident for the koinobionts (Owen & Owen, 1974; Janzen & Pond, 1975; Janzen, 1981; Askew & Shaw, 1986; Gauld, 1986; Noyes, 1989; Askew, 1990; Hawkins & Compton, 1992; Hawkins, 1994). Quicke & Kruft (1995) found the same pattern for the Braconidae of North America, but such results might be misleading since their data did not include areas close to the equator, California was not placed in the correct latitudinal zone, and the southern latitudinal zone is very arid and therefore with expected depauperateness (D.L.J. Quicke, pers. com.). In contrast to these two taxa, there is little evidence for the existence of such pattern in some Chalcidoidea families (Askew, 1990).

In an attempt to understand the distribution patterns of the Ichneumonidae, some authors (Hawkins, 1990, 1994; Hawkins *et al.,* 1992) found that the observed latitudinal trends of species richness vary with the host feeding niche; exophytic hosts, i.e., those that are not protected by any plant tissues, support more parasitoids in the temperate zone than in the tropics, whereas endophytic hosts, i.e., those that live in concealed situations (e.g. wood borers, gallers, leaf miners), generally support at least as many parasitoids in the tropics as they do in temperate regions, with some types of host even supporting more. Host feeding

niche is also correlated with life history strategies, with idiobionts comprising more than half of all parasitoid species attacking endophytic hosts, and koinobionts dominating the parasitoid complexes on exophytic hosts.

A number of non-mutually exclusive explanations, mainly based on life history traits, have been put forward to explain parasitoid species richness patterns. (i) The *resource fragmentation hypothesis* (Janzen & Pond, 1975; Janzen, 1981) proposes that as the diversity of hosts rises towards the equator, the density of each host population drops until a point is reached when they are too rare to support specialist (i.e. koinobiont) species. (ii) The *predation on hosts hypothesis* (Rathcke & Price, 1976) states that, since predation on herbivores in the tropics is typically greater than in temperate regions, it can be expected that parasitized herbivores will be predated more often than healthy individuals, and thus tropical parasitoids may suffer high levels of juvenile mortality; this would force relatively more tropical parasitoids to exploit host stages that are less susceptible to predation (e.g. pupae) or hosts that are well hidden, and protected, by plant parts. (iii) The *predation on parasitoids hypothesis* (Gauld, 1987) is based on predation pressures being higher for adults rather than for immature parasitoids; as koinobionts are relatively slow flyers and must spend additional time searching for scarce hosts in the tropics, they will be more exposed to predation; on the other hand, since idiobionts have a wider host range, they do not need to spend so much time searching for suitable hosts, and hence they are less exposed to predation. (iv) The *interphyletic competition hypothesis* (Eggleton & Gaston, 1990) postulates that parasitoids have to compete for hosts with other parasitic organisms that are probably more diverse in the tropics, such as nematode and fungi, and so parasitoid diversity is reduced through competitive exclusion. Finally, (v) the *nasty hosts hypothesis* (Gauld *et al.,* 1992; Gauld & Gaston, 1994) is based on the tendency of tropical plants to have more chemical toxins than their temperate counterparts, which implies that tropical herbivores also tend to contain more toxins, requiring their parasitoids to have special adaptations to cope with these potentially harmful chemicals; this would restrict tropical parasitoid diversity, that in fact should be biased towards specialist species. None of these hypotheses has been formally confirmed to date, and in fact more recent studies suggest that tropical Ichneumonidae and Braconidae faunas might actually be highly diverse (e.g. Gauld *et al.*, 2000; Sääksjärvi *et al.*, 2004; Smith *et al.*, 2008). Due to this, to date it remains unclear whether the anomalous latitudinal

patterns described for parasitoids (and the related explanatory hypotheses) are actually real, or are just artefacts of taxonomic and sampling biases (e.g. Jones *et al.*, 2009).

1.1.5. Dispersal, colonization and islands

Much of what is known about the diversity of parasitoid communities at large geographical scales (i.e. above the landscape level) comes from reviews of the available literature on studies of parasitoids reared from their individual hosts (e.g. Cornell & Hawkins, 1993; Hawkins, 1994; Hawkins & Marino, 1997; but see Stone *et al*., 1995). So far, the studies on the dispersal, colonization and establishment of parasitoids in new areas have mainly focused on the landscape level, regarding fragmented habitats and some individual species. Most of these studies show that parasitoid populations tend to be more vulnerable to extinctions than their hosts due to stochastic processes (e.g. Kruess & Tscharntke, 1994, 2000; Nouhuys & Tay, 2001; Cronin, 2004). However, parasitoids can travel several kilometres, and sometimes even further than their host (Antolin & Strong, 1987; references in Godfray, 1994; Jones *et al.*, 1996; Nouhuys & Hanski, 2002; Elzinga *et al.*, 2007). Such high dispersal ability may result in high colonization rates, which could compensate local extinctions in sink or newly established populations. Unfortunately, the sporadic and local character of these works prevents from extracting conclusions about how dispersal and assembly processes determine the structure of parasitoid communities. Achieving such knowledge requires studies on the diversity of parasitoids in new habitats, that take into account different biologies and life history strategies. Here, island communities could be a particularly good study system (see section 1.2 below).

Very little is known about island parasitoid communities; most published works are limited to checklists (e.g. Gauld & Carter, 1983; Belokobylskij & Maetô, 2008; Bennet, 2008), and are often biased towards introduced species and agricultural habitats (e.g. Funasaki *et al.*, 1988; Peck *et al.*, 1998, 2008; Santos *et al*., 2005; Hoy *et al.*, 2007; Lozan *et al.*, 2008). In fact, very few studies explore the biogeography and community assembly of island parasitoid faunas (Maetô & Thorton, 1993; Schoener *et al.*, 1995; Hodkinson *et al.*, 2004), and almost nothing is known about the life history traits of parasitoids colonizing islands. The only exception comes from a study developed by Maetô & Thorton (1993) in Anak Krakatau island, 34 years after the self-devastating eruption of 1952 (see below).

As hosts on islands may be unusual or novel compared to those on the mainland, it might be expected that island faunas should be biased towards generalist species (i.e. idiobionts), at least in the initial stages of their colonization. Evidence from studies on host range revealed that either generalists are better in adapting to new habitats and are generally richer in new hosts than specialists (Cornell & Hawkins, 1993; Stone *et al.*, 1995), or that no biological or ecological trait of the parasitoids can predict changes in the host range (Godfray *et al.*, 1995; Hawkins & Marino, 1997). Contrary to expectation, Maetô & Thorton (1993) found that the early-phase parasitoid colonists were dominated by taxa that are koinobionts endoparasitoids of Lepidoptera. Nevertheless, these studies were carried out in very recent and probably unstable communities. Given that the time required for the evolution and full acquisition of parasitoids by some hosts may fall between 100 and 10,000 years (Cornell & Hawkins, 1993), it is difficult to extend these interpretations to other systems. It then remains unclear how biological and ecological traits influence the establishment of parasitoids on islands.

1.2. Islands and their communities

Islands have been used as natural laboratories since Darwin's studies in the Galapagos. Their discrete, isolated nature, small size, and simplified biotas provide excellent opportunities to study evolutionary and ecological patterns (e.g. MacArthur & Wilson, 1963, 1967; Diamond, 1969, 1970; MacArthur *et al.*, 1972; Emerson, 2002; Gillespie & Roderick, 2002; Ricklefs & Bermingham, 2008; Whittaker *et al.*, 2008).

1.2.1. Island types

Islands have different sizes, shapes, geology, environments, and history, which make each one of them unique entities (Whittaker & Fernández-Palacios, 2007). Within them, oceanic islands stand out for their generally discrete character; they are of volcanic or coralline formation and have never been connected to continental landmasses. These islands are usually short-lived, have a dynamic geological history, often have high mountains, and sometimes are very isolated (e.g. Hawaii). By contrast, continental islands are located in the

continental shelf, and many of them have been connected to mainland once or several times during the Quaternary ice ages, hence losing their discrete character. Continental fragment islands are an intermediate between these two island types, as they are long-isolated ancient fragments of continental rock stranded out in the oceans by plate tectonic processes (Whittaker & Fernández-Palacios, 2007).

1.2.2. Equilibrium model of island biogeography

In their original formulation of the "Theory of Island Biogeography", MacArthur & Wilson (1963, 1967) proposed that the number of species on an island tends to an equilibrium state resulting from the balance between immigration and/or speciation and extinction rates. Their model implies that these three fundamental processes should vary in a predictable way in relation to isolation and area. Immigration rate should decline with increasing isolation, and extinction rate should decline with increasing area (a general surrogate for the total carrying capacity of the island). So, considering the hypothetical example of a recently formed island, the immigration rate starts at its highest point and declines as a hollow exponential curve as the proportion of new species arriving on the island declines, while extinction rate rises as the space is occupied. With time, these rates intersect causing a dynamic equilibrium between immigration and extinction rates, with a turnover of species occurring from this point onwards. Evolution is included in the model with the assumption that in more isolated islands, new forms are increasingly likely to appear as a result of *in situ* radiation rather than immigration (Gillespie & Roderick, 2002; Gillespie, 2004; Whittaker & Fernández-Palacios, 2007; Whittaker *et al.*, 2008). Although many other factors can shape island diversity, the Theory of Island Biogeography is still one of the most supported bodies of theory in ecology.

In a recent work, Whittaker and colleagues (2008) presented a general dynamic model (GDM) of oceanic island biogeography that aims to explain biodiversity patterns in oceanic islands by considering the relationships of speciation, immigration and extinction through time and in relation to island ontogeny. The GDM includes an extra premise into the ideas behind MacArthur & Wilson's theory, assuming that each island has its own developmental life cycle that strongly influences the evolutionary dynamics shaping the biota of oceanic islands. According to the GDM, in a recently formed volcanic island, where catastrophic episodes of volcanism are still occurring, most of the species present result

directly from immigration processes. In its "immature" stage, during which area and altitude increase, speciation rate reaches its peak, as there are enough lineages present that can serve as a basis for this process and there are many adaptive opportunities in the form of empty niche space. During the "maturity" stage, the island reaches its maximum size and altitude (which might in fact be already slowly decreasing), species richness peaks, and speciation continues at a high rate. With time, the island erodes, decreasing in altitude, area, and habitat diversity, and becomes increasingly dissected. During this period, species richness declines with an increase in extinction rate, until the moment when the island finally subsides. This model seems to hold true for some archipelagos (e.g. Aeolian Islands, Canary Islands, Hawaii Islands; Whittaker *et al.,* 2008; Fattorini, 2009). However, its effectiveness and importance may vary between different groups, depending on their life histories and ecological characteristics (as shown by the diversification patterns of Azorean arthropods; Borges & Hortal, 2009), implying that the GDM still needs further development in order to be of wide applicability.

1.2.3. Island species–area relationship (ISAR)

The species–area relationship (SAR) is usually referred as one of ecology's few general rules (Schoener, 1976; Rosenzweig, 1995, 2003; Lawton, 1996, 1999), being one of the best documented pattern in biogeography and ecology. SAR has proved to be a useful tool in exploring and explaining other diversity patterns, like the latitudinal gradients in species diversity, elevational gradients in species richness, and in predicting future changes and losses in biological diversity (e.g. Rosenzweig, 1995; Brooks *et al.*, 1997; Lomolino, 2001a,b; Ewers & Didham, 2006), having also been applied in conservation biology (e.g. Rosenzweig, 2004; also see Lomolino, 2001b). According to this "rule", species richness increases with area, and the rate of accumulation of new species usually declines as area increases. There are many ways to quantify this relationship, although the power model developed by Arrhenius (1921), expressed in its log-log form, is the most often used:

$$\log S = \log c + z \log A,$$

where S is the number of species of a given taxon on an island, A is the area, and c and z are constants determined empirically from the data; z describes the slope of the log-log relationship and c describes its intercept. So, when z is low there is less sensitivity to island

area, while *c* varies with taxon, climate and biogeographical region (Whittaker & Fernández-Palacios, 2007).

As several authors have pointed out, it is important to consider scale factors when analyzing the SAR. There are in fact a number of classifications for the different types of species–area relationships, depending on the scale at which they are analyzed, or whether they are measured from nested areas or not (e.g. Rosenzweig, 2003; Scheiner, 2003; Gray *et al.*, 2004; Whittaker & Fernández-Palacios, 2007; Dengler, 2009). Rosenzweig (1995) argued that there are three main scales and types of SAR (or four, if the point scale, that depends on sampling effort, is also considered) that show distinct slope values (z): (i) archipelagic (or island species–area relationship, ISAR), which is the species–area relationship within a group of islands, usually presenting slope values that vary between 0.25 and 0.45; (ii) intraprovincial (or regional species accumulation curve), which is a species accumulation curve within a large continental area on a regional scale, with slopes typically ranging between 0.1 and 0.2; and (iii) interprovincial, which encompasses different biotic regions, and shows much steeper slopes (z ranges from 0.8 to 1) (see also Rosenzweig, 2004; Triantis *et al.*, 2008a).

MacArthur's & Wilson's seminal theory opened discussion on island biogeography, especially in what concerns the patterns of variation in island species richness (see review in Losos & Ricklefs, 2009). In fact, the form and slope of ISARs depend on the particular process(es) that dominate(s) the study system (immigration, speciation and extinction) (Rosenzweig, 1995; see also MacArthur & Wilson, 1963, 1967; Triantis *et al.,* 2008a; Whittaker *et al*., 2008; Borges & Hortal, 2009). However, many other alternative explanations for the patterns of variation in island species richness in relation to area have been proposed (see Whittaker & Fernández-Palacios, 2007 for more details): (i) *random placement* – this hypothesis regards islands as samples of a random community, without reference to particular patterns of turnover; large samples will simply contain more species (Connor & McCoy, 1979; Coleman *et al.,* 1982); (ii) *habitat diversity* - the number of species may be related to the number of habitats, which in turn increase with island area (e.g. Hart & Horwitz, 1991; Triantis *et al.*, 2003); (iii) *incidence functions* – some species only occur on large islands because they need big territories, while others only occur on small islands where they can escape from competition (e.g. Diamond, 1974); (iv) *species-energy theory* –

the capacity for richness is considered a function of the resource base of the island, which can be estimated using, for example, total primary productivity multiplied by area (Wright, 1983); (v) *small-island effect* - assumes that certain species cannot occur on islands below a certain size (e.g. Whitehead & Jones, 1969; Lomolino & Weiser, 2001, Triantis *et al.*, 2006); (vi) *small-island habitat effect* – it has been suggested that in some systems, small islands actually possess habitats that do not occur in larger islands, or may have a greater diversity of habitats than predicted by their area, hence influencing species richness; and (vii) *disturbance hypothesis* – small islands (or "habitat islands") suffer more disturbance, which removes species or makes them less suitable for the colonization by some of the species present in the species pool (e.g. McGuinness, 1984). This diversity of hypotheses evidences that, in spite of the universality of the relationship between island species richness and area, this relationship may be caused by a complex mixture of underlying mechanisms.

1.2.4. Dispersal and colonization

Island faunas, especially those of oceanic islands, tend to be species–poor and disharmonic (Williamson, 1981; Whittaker & Fernández-Palacios, 2007), meaning that there are often fewer species on an oceanic island than on a same-sized area of mainland, and that the structure of their communities is different from their continental counterparts. In most cases, an island biota is the product of oversea dispersal and local diversifications. Because of differential dispersal ability in the putative source biota, only a small portion of the mainland pool can actually colonize islands (e.g. Davis *et al.*, 1995; Gillespie & Roderick, 2002). Only a subset of those species that can disperse to an island will be able to establish and maintain populations, depending on the attributes of the species and the island. Factors such as island area, habitat diversity, isolation, geological age and pre-existing biota are all important in determining species maintenance on islands (e.g. MacArthur & Wilson, 1963, 1967; Simberloff, 1976; Borges & Brown, 1999; Triantis *et al.*, 2003, 2005, 2008a; Piechnik *et al.*, 2008; Whittaker *et al.*, 2008; Borges & Hortal, 2009; see review in Rosenzweig, 1995; Whittaker & Fernández-Palacios, 2007).

Once a species reaches a remote island, it will typically establish by means of a small founding population (founder principle *sensu* Mayr, 1954). These "founders" carry with them only a very small fraction of the genetic variability of the source population (Berry, 1998),

which immediately provides a bias on which other evolutionary processes can operate. The genetic variability of these populations can then be reduced by genetic drift, as small populations under sustained conditions are prone to random alternation of allele frequencies from one generation to the other (Whittaker & Fernández-Palacios, 2007). Such bottlenecks seem to be very important in the evolutionary divergence of mainland and island lineages, as new phenotypes might rise from subsequent natural selection operating on the genetic variability (e.g. Berry, 1998; Hinten *et al.*, 2003; Lampert *et al.*, 2007; Barrientos *et al.*, 2009; Hundertmark & Daele, 2010; see review in Whittaker & Fernández-Palacios, 2007).

1.2.5. Ecological consequences of empty niche space

After the founding event, several evolutionary and ecological processes usually take place, many times as a response to empty niche space. It is not uncommon that some trophic guilds are absent or misrepresented from island communities, thus providing the evolutionary opportunities for new colonizers to occupy such niches (e.g. Wilson, 1990; Olesen & Valido, 2003a; 2004).

The phenomenon of ecological release, typical in many island populations (e.g. Diamond, 1970; Olesen *et al.*, 2002; Scott *et al.*, 2003), occurs when a species colonizing an island encounters a new environment in which competitors and predators are missing (Whittaker & Fernández-Palacios, 2007). One of the consequences of this process is the expansion to empty or invasible niche space, leading to niche expansion and/or niche shifts (Diamond, 1970; Cox & Ricklefs, 1977). The classical example of increase in niche breadth comes from finch species from Hawaii and Galápagos, where species have diversified widely in terms of beak sizes when compared to the mainland counterparts (Schluter, 1988).

Taking this into account, it is not surprising that, in many cases, oceanic islands have a high representation of generalist species when compared to the mainland. For example, it is known that lizards can act as pollinators on islands, while on the mainland such behaviour is very rare (e.g. Elvers, 1977; Olesen & Valido, 2003b; 2004). Other examples come from bird species that feed on a wide variety of food sources (Diamond, 1970; Olesen & Valido, 2003a; see review in Olesen & Valido, 2004), or that exhibit diverse foraging ecologies (Scott *et al.*, 2003; Schlotfeldt & Kleindorfer, 2006). Many insects also display such patterns, as illustrated by the presence of endemic generalists on pollination networks (e.g. Olesen *et*

al., 2002) and from species that can utilize a wide range of host-plants and/or habitats (e.g. Kitahara & Fujii, 1997; Ribeiro *et al.*, 2005a). In addition, some evidence shows that generalist species may simply have an *a priori* advantage during the colonization process (Piechnik *et al.*, 2008).

Another consequence of ecological release is that species present on islands are often at higher densities compared to the mainland (i.e. there is density compensation). This effect is greater where a colonizing species finds "empty niche space", and when richness per unit area is low (Olesen *et al.*, 2002; Whittaker & Fernández-Palacios, 2007). The main explanations for this phenomenon are: (i) a species becomes more able to find more food per unit effort and therefore reaches higher abundance within the same habitat (Blondel & Aronson, 1999); and (ii) as a consequence of niche expansion, a species utilizes more habitats, foraging strata, foraging techniques, or dietary components, also reaching high abundance (MacArthur *et al.*, 1972; Blondel & Aronson, 1999). In turn, these mechanisms may be supported by the absence of certain guilds, such as some predator or competitor groups. However, ecological release, niche changes and density compensation are phenomena that do not apply to all island populations, even though there seems to be good evidence supporting their influence in many taxa (Whittaker & Fernández-Palacios, 2007).

1.2.6. A model island system: the Macaronesia

The Macaronesia concept was first used by Philip Baker Webb, in the 19th century, to include five North Atlantic archipelagos: Azores, Madeira, Salvage Islands, Canary Islands and Cape Verde Islands (cited in Fernández-Palacios & Dias, 2002). Some authors argue that this region should also include parts of the adjacent African mainland (Morocco and Mauritania) (Sunding, 1979), while others stress the inclusion of the southern part of the Iberian Peninsula (Kunkel, 1993). Although the concept of Macaronesia as a distinct region within the Palaearctic realm is widely used, some authors question its unity. In particular, the inclusion of the Cape Verde archipelago is highly controversial (Santos-Guerra, 1983; Nicolás *et al*., 1989), and the boundaries of the region are still under debate (see discussion in Whittaker & Fernández-Palacios, 2007). In this thesis I follow Sunding (1979) and Kunkel (1993), and consider that parts of both the Moroccan coast and the south-west of the Iberian Peninsula are integrated within this region (or at least highly related with it) (Fig.1.1).

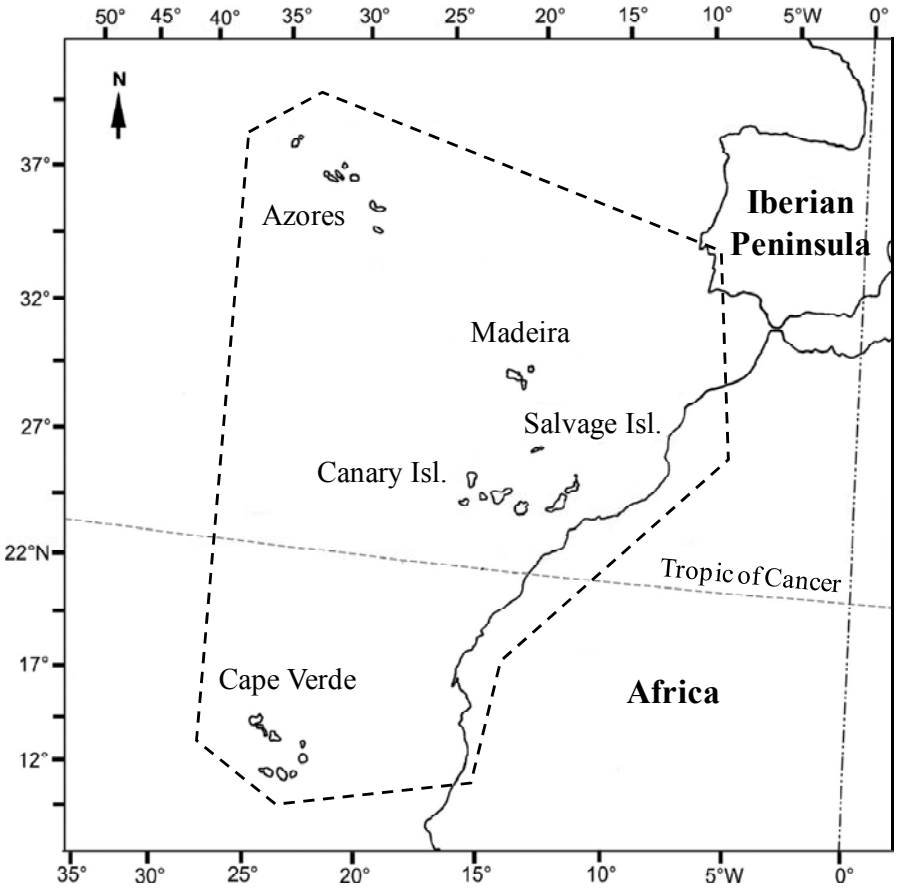

Figure 1.1. Location and boundaries of the Macaronesian region (following Sunding, 1979 and Kunkel, 1993; modified from Kim *et al.*, 2008; Whittaker & Fernández-Palacios, 2007)

The five archipelagos are situated between 15° to 40° N, with distances from the European or African continents varying from 96 to 1600 km. All are of volcanic origin, and the number of islands within each archipelago varies from two in the Salvage Islands to ten in the Cape Verde (Madeira – three islands; Canary Islands – seven islands; Azores – nine islands). Geological ages of individual islands vary from 0.25 million years for Pico (Azores) to 27 million years for Salvage Islands (Carvalho, 1991; Nunes, 1999; Ribeiro *et al.*, 2005b; Anchochea *et al.*, 2006; Kim *et al.,* 2008; Triantis *et al.*, 2010). There is a diversity of climates along this region, from the humid Atlantic climate in the Azores, to the tropical monsoon-drift climate in Cape Verde, and the arid Mediterranean-like climates in the archipelagos of Madeira, the Salvages and the Canary Islands (Fernández-Palacios & Dias, 2002).

Some of the islands from this region are very close to the potential continental source areas, particularly those from the Canary Islands. The eastern-most Canary Island, Fuerteventura, is currently less than 100 km from the west coast of Morocco and used to be less than 65 km during the most extreme glacial stages (see García-Talavera, 1999; Whittaker & Fernández-Palacios, 2007). This, together with their general lack of subsidence, the altitudinal gradient (e.g. Tenerife in the Canary Islands reaches more than 3,700 meters in altitude), and the comparatively old and broad range of geological ages, contribute to several patterns of colonization and diversification (see examples in Whittaker & Fernández-Palacios, 2007) .

The Macaronesian arthropod fauna displays a high degree of endemism, ranging from 19% in the Azores to 45% in the Canary Islands (28% in Madeira Islands, and 30% in Cape Verde; Izquierdo *et al.*, 2004; Arechavaleta *et al.*, 2005; Borges *et al.*, 2005a, 2008). Due to their high level of endemism, the Macaronesian islands have been widely studied in terms of evolutionary and speciation patterns, and arthropods have been the focus of intensive investigation in the last ten years (Triantis *et al*., 2010). In fact, the study of arthropod groups has already provided valuable insights into the colonization and evolutionary patterns of these islands, and also into the processes regulating species richness (e.g. Borges & Brown, 1999; Emerson *et al.*, 2000; 2006; Emerson & Oromí, 2005; Borges & Hortal, 2009; Hochkirch & Görzig, 2009). Such studies indicate that diversification has been higher in the Canary Islands and Madeira archipelagos than in the Azores and Cape Verde, and that the geomorphology and geological history of the islands and the particular characteristics of each taxon also shape diversification patterns within each archipelago.

1.3. Thesis aims and outline

The general aim of this thesis is to study the geographic patterns of generalism and specialism in island parasitoid faunas. Until now, the level of generalism of island faunas has been studied for several taxa (e.g. Olesen *et al.,* 2002; Olesen & Valido, 2004; Ribeiro *et al*., 2005a). There is however little knowledge on the structure of parasitoid communities, and this is especially true when it comes to island systems. In fact, most studies on parasitoid host ranges and host shifts have been developed in continental areas (e.g. Cornell & Hawkins, 1993; Hawkins & Marino, 1997). Following these studies, and given that the hosts of parasitoids on islands may be novel or unusual compared to those on the mainland, it can be expected that parasitoids arriving on islands are more likely to establish if they are able to cope with less preferred hosts, which will usually mean potentially having a wide host range. The only study available on host ranges of parasitoids on islands (Maetô & Thorton, 1993) indicates that at least some island faunas are biased towards specialists (koinobionts), contradicting initial expectations. Therefore, this thesis aims to test the following:

Hypothesis: Island parasitoid faunas are biased towards generalist species, when compared to the mainland faunas.

I analyse this hypothesis at two different geographical scales: a global scale, using data from islands worldwide, and a regional scale, where I study islands and continental areas from the Macaronesian region.

At the *global scale*, I evaluate whether island parasitoid faunas are biased towards idiobiont species when compared with the corresponding species pool. I also examine whether some of the factors that usually control the assembly of island faunas, such as isolation, area, environmental variations and composition of the regional pool, also have an affect on the ratio between idiobionts and koinobionts on islands. To investigate this I use Taxapad, a published database on the distribution of Braconidae and Ichneumonidae worldwide (Yu *et al.*, 2005). In this database the data on parasitoid inventories are many times grouped into archipelagos rather than into single islands. Due to this, I first examine whether there is a

consistency in the processes building up the biotas of single islands and entire archipelagos. To do this:

Chapter 2: I evaluate whether entire archipelagos follow the same species–area relationship as that defined by their constituent islands, and explore the factors that may explain departures from such relationship.

Data in Taxapad is a compilation of all available knowledge on the distribution of the studied families. Since taxonomic and geographic biases are common in biodiversity inventories (Brown & Lomolino, 1998; Lomolino, 2004; Whittaker *et al*., 2005), it would be expected that the quality and completeness of the data on Braconidae and Ichneumonidae faunas provided by Taxapad is also uneven. Therefore, in order to minimise the effects of taxonomic and geographic biases in the subsequent analyses:

Chapter 3: I develop a protocol for the identification of evenly inventoried islands from taxonomic databases.

Once I have identified islands with comparable inventories, I follow the main objectives of the analyses at the global scale:

Chapter 4: I test whether island parasitoid communities are more biased towards generalist species than in the mainland and their adjacent species pool, and examine which factors have an effect on the ratio between idiobionts and koinobionts on these islands.

At the *regional scale*, I study how the diversity and attack strategy of the parasitoid communities associated with a particular host system vary between the islands and adjacent mainland areas of the Macaronesian region. In particular, I study the community of parasitoids attacking the tortricid moth *Acroclita subsequana* that feeds on spurges (*Euphorbia spp.*, Euphorbiaceae). Based on the samples obtained during several field work campaigns carried out on different islands and mainland areas of the Macaronesia:

Chapter 5: I evaluate the usefulness of a protocol based on DNA barcoding for the study of the geographical variation of host-parasitoid relationships.

Using this protocol I assign both hosts and parasitoids to Molecular Operational Taxonomic Units (MOTUs; Floyd *et al.*, 2002; Blaxter *et al.*, 2005). The so-obtained data allowed to test whether (i) parasitoid species richness differs between island and mainland territories; (ii) the island parasitoid communities are biased towards generalist (i.e. idiobiont) species; and (iii) whether these changes in the composition and diversity of the parasitoid communities translate into variations in the parasitism rates. In other words, using the data collected in the Macaronesian islands and adjacent mainland:

Chapter 6: I test whether island parasitoid faunas are different from the ones in the mainland areas in terms of species richness, type of attack strategy (idiobionts vs. koinobionts) and parasitism rates.

For ease of exposition, each chapter is treated as an unitary essay. Overall conclusions are drawn in **Chapter 7**.

Chapter 2: Are species–area relationships from entire archipelagos congruent with those of their constituent islands?[1]

2.1. Abstract

Aim To establish the extent to which archipelagos follow the same species–area relationship as their constituent islands and to explore the factors that may explain departures from the relationship.

Location Thirty-eight archipelagos distributed worldwide.

Methods We used ninety-seven published datasets to create island species–area relationships (ISARs) using the Arrhenius logarithmic form of the power model. Observed and predicted species richness of the archipelago and of each of its islands were used to calculate two indices that determined whether the archipelago followed the ISAR. Archipelagic residuals (*ArcRes)* were calculated as the residual of the prediction provided by the ISAR using the total area of the archipelago, standardized by the total richness observed in the archipelago. We also tested whether any characteristic of the archipelago (geological origin and isolation) and/or taxon accounts for whether an archipelago fits into the ISAR or not. Finally, we explored the relationship between *ArcRes* and two metrics of nestedness.

Results The archipelago was close to the ISAR of its constituent islands in most of the cases analysed. Exceptions arose from archipelagos where i) the slopes of the ISAR are low, ii) observed species richness is higher than expected by the ISAR and/or iii) distance to the mainland is small. The archipelago's geological origin was also important; a higher percentage of oceanic archipelagos fit into their ISAR than continental ones. *ArcRes* indicated that the ISAR underpredicts archipelagic richness in the least isolated archipelagos.

[1]This chapter has been published as: Santos, A.M.C., Whittaker, R.J., Triantis, K.A., Borges, P.A.V., Jones, O.R., Quicke, D.L.J. & Hortal, J. (2010) Are species–area relationships from entire archipelagos congruent with those of their constituent islands? *Global Ecology and Biogeography*, in press, doi:10.1111/j.1466-8238.2010.00536.x

Different types of taxon showed no differences in *ArcRes*. Nestedness and *ArcRes* appear to be related, although the form of the relationship varies between metrics.

Main conclusions Archipelagos, as a rule, follow the same ISAR as their constituent islands. Therefore, they can be used as distinct units themselves in large-scale biogeographical and macroecological studies. Departure from the ISAR can be used as a crude indicator of richness-ordered nestedness, responsive to factors such as isolation, environmental heterogeneity, number and age of islands.

2.2. Introduction

The species–area relationship is one of the most studied patterns in ecology, often being referred to as one of ecology's few laws (Schoener, 1976; Rosenzweig, 1995, 2003; Lawton, 1996, 1999). According to this "rule" the number of species increases with area, and the rate of species richness increase usually declines as area increases. There are a number of classifications for the different types of species–area relationships, depending on the scale at which they are analyzed, or whether they are measured from nested areas or not (e.g. Rosenzweig, 2003; Scheiner, 2003; Gray *et al.*, 2004; Whittaker & Fernández-Palacios, 2007; Dengler, 2009). Rosenzweig (1995) described three main scales (and types) of species–area relationships (four, if the point scale, which depends on sampling effort, is included), that correspond to different spatial/temporal scales. Following Whittaker & Fernández-Palacios (2007) we may describe them as: (i) archipelagic (or island species–area relationship), which is the species–area relationship within a group of islands; (ii) intraprovincial (or regional species accumulation curve), which is a species accumulation curve within a large continental area on a regional scale; and (iii) interprovincial, which encompasses different biotic regions (see also Rosenzweig, 2004; Triantis *et al.*, 2008a). In the present work we focus on the archipelagic– or island–scale species–area relationship, henceforth termed the ISAR.

The form and slope of ISARs depend on the particular process(es) that dominate(s) the study system (immigration, speciation and extinction) (Rosenzweig, 1995; see also MacArthur & Wilson, 1963, 1967; Triantis *et al.*, 2008a; Whittaker *et al*., 2008; Borges &

Hortal, 2009). Some archipelagos (e.g. Azores, Galápagos, Hawaii,) are sufficiently isolated, in space or time, to host a distinctive ('disharmonic') species pool, often drawn from more than one source region but with many shared elements (e.g. species or lineages) among the islands of the archipelago. The small number of colonization events, a characteristic of isolated archipelagos, creates homogeneity in the species colonizing these islands, which could imply that the processes establishing island species richness would largely be a property of the archipelago rather than of each constituent island on its own. Consequently each archipelago – or at least each remote archipelago – may be regarded as a unique entity similar to a province (Triantis *et al.*, 2008a), regardless of the particularities of each island (see discussion in Whittaker *et al.,* 2008). The homogeneity in the processes that build up island biotas would only be broken in cases where local (i.e., within-island) idiosyncratic processes are predominant or the archipelago is composed by different subsets of islands that draw their components from significantly different species pools.

Regional factors acting on the whole of the archipelago (such as archipelago isolation, age, origin of the islands) are generally thought to have a consistent effect on the local diversity patterns at the island level. Therefore, archipelagos are usually considered to be homogeneous entities, and it is thus not surprising that many authors have used complete archipelagos as single data points in their analyses (e.g. Wilson, 1961; Scott, 1972; Schoener, 1976; Wright, 1983; Adler, 1992, 1994; Adler & Dudley, 1994; Adler *et al.*, 1995; Biber, 2002; Carvajal & Adler, 2005; Hamilton *et al.*, 2009). In fact, in his discussion of the so-called 'single large or several small' debate on the implications of island theory for reserve design, Rosenzweig (1995, p.382) argued that "the diversity and the area of whole archipelagos falls in the same species–area curve as the separate islands that constitute them", although stating that this hypothesis deserves further examination. However, formal tests of the assumption that archipelagos act as homogeneous entities in biogeographical terms are lacking. Should this assumption be rejected, either local ecological factors or the particular characteristics of the group studied (e.g. life history traits, physiological adaptations) would predominate over classical island biogeography processes, challenging the universality of regional processes as the main factor shaping the diversity of island biotas. Here, we evaluate whether entire archipelagos follow the same species–area relationship as that defined by their constituent islands. That is, we assess to what extent the total richness of

the archipelago departs from the extrapolation of the ISAR to the total area of the islands that compose it. By implication we therefore test the assumption that archipelagos act as single entities in biogeographical terms, and hence the reliability of using them as single units in large-scale biogeographical and macroecological studies. We then evaluate our findings with regard to the type of taxon (invertebrates, vertebrates and plants), the geological origin (continental or oceanic) and isolation (distance to the mainland) of each archipelago, and the possible biological interpretation of departures of the archipelago data point from the ISAR, including its relationship with the nestedness of island biotas.

2.3. Materials and Methods

Information on the species richness on islands was compiled from several sources for ninety-seven archipelago/taxon combinations, pertaining to thirty-eight island groups distributed worldwide. Our data include archipelagos of oceanic (i.e., both true oceanic islands and continental fragments *sensu* Whittaker & Fernández-Palacios, 2007, following Wallace, 1902), mixed, and continental origin and of varying size and degree of isolation from the closest mainland, and comprise data on several groups of vertebrates, invertebrates and plants. We excluded introduced species and subspecific taxa from all datasets. Total species richness for each archipelago was obtained by pooling the species lists of their constituent islands. We use the term "ISAR" to refer to the species–area relationship constructed from the islands that constitute the archipelago (following Whittaker & Fernández-Palacios, 2007). We also use "archipelagic point" to refer to the total area and richness of the corresponding island group (archipelago).

For each archipelago/taxon combination, an ISAR regression model, with observed species richness (S_{obs}) as the response variable and island area (A) as the predictor, was constructed on a log–log scale. This follows the same approach as Arrhenius' (1921) power model $\log S_{obs} = c + b \times \log A$, where c is the intercept and b the slope. In the particular case of the Canary Islands, ISARs were constructed for both (i) all seven main islands, and (ii) all islands with the exception of Fuerteventura and Lanzarote, because these two islands are known to deviate from the general ISAR of their archipelago, being environmentally

different from the younger islands located to the west and lacking mesic upland habitats (see discussion in Whittaker & Fernández-Palacios, 2007; Whittaker *et al*., 2008).

We were unable to find published protocols for evaluating the congruence of archipelagos and their ISARs. Logically, the archipelagic point in terms of species richness must fall somewhere between the species richness of the maximum individual island richness and the sum of the species richness of all islands in the archipelago, and archipelagic area is simply the sum of the area of all constituent islands. Therefore, the archipelagic point cannot be considered independent of the ISAR, and so we cannot formally test congruence using standard regression techniques. We therefore generated two simple indices to evaluate the departure of the archipelagic point from the richness predicted by extrapolating the ISAR to the total area for the whole archipelago (see below). These indices are based on an examination of the variation around the predicted ISAR but without any statistical probability being attached to them. However, having calculated the indices of fit, we do make use of inferential statistical tests to evaluate the strength of the relationships between these metrics and the properties of the archipelago and the type of taxon studied.

For each archipelago/taxon combination we estimated archipelagic (SA_{pred}) and constituent islands' (SI_{pred}) species richness from the ISAR regression model. Values of SI_{pred} were simply the fitted values of the regression model, while SA_{pred} was estimated from the model using the total land-surface area of the archipelago as the predictor. We then calculated the residuals of the regression model (i.e., observed species richness minus SI_{pred}) and identified their maximum absolute value (*MaxRes*). We expressed *MaxRes* as a proportion (*PropMaxRes*) of SI_{pred} for that particular observation (i.e. if the residual was 1 and the predicted log [species richness] for a given island's area was 3, then *PropMaxRes* would be 0.33). We used *PropMaxRes* as an aid to examine the amount of disparity between the observed whole-archipelago species richness (SA_{obs}) and its predicted species richness (SA_{pred}). If SA_{obs} was within the bounds of $SA_{pred} \pm (SA_{pred} \times PropMaxRes)$, then we assume that we are not able to reject the hypothesis that the archipelago follows the ISAR. Conversely, if SA_{obs} was outside these bounds, we assume that this hypothesis can be rejected, and the archipelago species richness is deemed to violate the ISAR. We conducted analogous analyses using the median of the residuals (*MedRes*) as a more conservative criterion, determining whether the archipelago falls into the interval defined by $SA_{pred} \pm$

(SA_{pred} x *PropMedRes)* or not. Where the archipelago had an even number of islands the *PropMedRes* was calculated using the median values of the absolute residuals and of all the SI_{pred}.

The above procedure can be illustrated using the vascular plants of Cape Verde as an example (Table 2.1). For this dataset, the ISAR equation (on a log–log scale) is log S = 1.385 + 0.291 × log A; SA_{pred} and SI_{pred} were obtained by applying this equation to the logarithm of the total land area of the archipelago (4,076 km^2), and to the logarithm of each island area, respectively (Table 2.1). The maximum residual was 0.157 (Santo Antão island) and the *PropMaxRes* was 0.074, which was obtained by calculating the proportion of *MaxRes* over its corresponding SI_{pred} (2.127). The value obtained for SA_{pred} x *PropMaxRes* was 2.436 × 0.074 = 0.179, so the interval defined by SA_{pred} ± (SA_{pred} x *PropMaxRes)* was 2.436 ± 0.179. Since the logarithm of the total richness of the archipelago (2.441) lies inside this interval, we cannot reject that the archipelago is following the ISAR. The same procedure was followed using the median residual (0.087) instead of *MaxRes*.

Table 2.1. Values used to calculate the interval that delimitates whether an archipelagic point is congruent with its island species–area relationship (ISAR) or not (for more details see text).

Islands	S_{obs}	A	log S_{obs}	log A	SI_{pred}	SA_{pred}	**Abs Resid**
Boa Vista	126	634.1	2.100	2.802	2.201		0.101
Brava	100	66.6	2.000	1.823	1.916		0.084
Fogo	154	474.8	2.188	2.677	2.164		0.023
Maio	117	279.0	2.068	2.446	2.097		0.029
Sal	92	221.5	1.964	2.345	2.068		0.104
Santa Lucia	61	36.7	1.785	1.565	1.841		0.055
Santiago	183	991.0	2.262	2.996	2.228		0.034
Santo Antão	192	787.3	2.283	2.896	2.127		0.157
São Nicolau	144	352.2	2.158	2.547	2.257		0.099
São Vincente	146	232.8	2.164	2.367	2.074		0.090
Cape Verde	276	4076.0	2.441	3.610	-	2.436	-

S_{obs} is the observed species richness of the vascular plants of Cape Verde, A is the island/archipelago area expressed in Km^2, log S_{obs} is the logarithm of S_{obs}, log A is the logarithm of A, SI_{pred} is the predicted value for the species richness of each island, SA_{pred} is the predicted value for the species richness of the archipelago, and Abs Resid is the absolute value of the residuals obtained by subtracting SI_{pred} from log S_{obs}.

We used the ratio between *MaxRes* and *MedRes* as a measure of the dispersion of the most distant island points within the archipelago for a preliminary evaluation of whether such dispersion would affect the results of our analyses. The cases in agreement with the ISAR showed similar *MaxRes*/*MedRes* ratios to those falling outside this relationship, for both the maximum and median residual criteria (not shown). The degree of dispersion of the distant island points was however higher for the cases meeting only the *MaxRes* criterion than for the cases meeting both criteria, as expected. We therefore assume that the degree of dispersion of the island points does not affect the probability of rejecting the congruence of an archipelagic point with its ISAR. Rather, it only affects the probability of meeting just the less restrictive or both criteria. Therefore, we expect differences in the criterion met to be mainly driven by the degree of dispersion of the islands, and not by factors causing the archipelagic point to depart from the ISAR. It follows that both criteria are equally reliable in terms of identifying whether an archipelago follows the ISAR of its constituent islands or not.

To determine if any archipelago- and/or taxon- characteristics account for the fit of an archipelago to its ISAR, we classified the datasets according to (a) the kind of taxon they belong to (invertebrates, vertebrates or plants), and (b) the origin of the archipelago (continental, mixed or oceanic). In addition, we measured (c) the isolation of the archipelago as the smallest distance between any of the islands and the nearest mainland.

To obtain a measure of how much the archipelago departs from the ISAR, and allow an exploration of potential causes of deviation, we calculated the archipelagic residual (*ArcRes*) as the residual of the prediction provided by the ISAR using the total area of the archipelago. To enable comparisons between different archipelagos, we standardised this residual by dividing it by the total richness observed in the archipelago. Using the above example of the vascular plants from Cape Verde, *ArcRes* would be calculated as (log SA_{obs} – SA_{pred}) / log SA_{obs}, that is (2.441 – 2.436) / 2.441 = 0.002. We used *ArcRes* as a response variable in regression models designed to explore the potential causes of deviation from the ISAR in the datasets that yielded significant regressions ($p < 0.05$). Potential explanatory variables included taxon-type, archipelago geological origin and isolation, as above.

Finally, we explored whether there is a relationship between the magnitude of *ArcRes* and the degree of nestedness of the island biotas within the archipelago. Detailed data on

species composition per island were not available for many of the datasets used for the former analyses. Due to this, and to avoid problems related with uneven sampling effort, we only analyzed a reduced number of arthropod groups in two archipelagos we are more familiar with: Azores and Canary Islands. These datasets, however, present an ample variation in *ArcRes* values (compared to the variation found in all studied datasets) and include cases that both enter and fail to enter in the median and maximum residual criteria (see Table 2.1). Given current debate on the most appropriate measure of nestedness (e.g. Almeida-Neto *et al.*, 2007; Ulrich *et al.*, 2009), we calculated two different measures: the Nestedness metric based on Overlap and Decreasing Fill (NODF; Almeida-Neto *et al.*, 2008), as recommended by Ulrich *et al.* (2009); and the original Temperature (T) measure proposed by Atmar & Patterson (1993). We compared these measures and *ArcRes* by simple correlations and visual examination. Nestedness measures were calculated using ANINHADO (Guimarães & Guimarães, 2006). All other statistical analyses were performed using STATISTICA 6.1 (StatSoft, 2003).

2.4. Results

Seventy-two (74%) out of the ninety-seven ISARs examined had slopes significantly different from zero (Table 2.2). Most of the non-significant ISARs came from the Canary Islands (18 out of 25), but most of these became statistically significant after excluding the two more xeric and older islands: Fuerteventura and Lanzarote (see example in Fig. 2.1a, b). All subsequent results are based on the significant ISARs only. In these archipelago/taxon combinations, slopes (i.e. *z*–values) ranged from 0.08 to 0.94, with the lower and upper quartiles being 0.22 and 0.52, respectively; the median was 0.33; and the overall mean was 0.38.

We could not reject the hypothesis that the archipelago species richness follows the ISAR in sixty-three cases (88%) when using the maximum residual criterion (Table 2.2; Fig. 2.1b, f, g, h). The nine cases where the archipelago did not follow the ISAR according to this criterion had significantly lower slopes (median = 0.21, lower and upper quartiles = 0.18 and 0.28) than those that did fit (median = 0.40, lower and upper quartiles = 0.27 and 0.53)

(Mann-Whitney $U = 156.5$, $Z = 2.162$, $n_1 = 9$, $n_2 = 63$, $p < 0.05$). Using the more conservative median residual criterion, only 45 out of 72 cases were congruent with their ISAR (63%) (Table 2.2; see examples in Fig. 2.1b, g, h). Again, most of the cases where the hypothesis of the archipelago following the ISAR was rejected showed lower slopes (median = 0.27, lower and upper quartiles = 0.19 and 0.33) than those where such hypothesis was not rejected (median = 0.40, lower and upper quartiles = 0.29 and 0.58) (Mann-Whitney $U = 301.5$, $Z = 3.559$, $n_1 = 27$, $n_2 = 45$, $p < 0.001$).

When the maximum residual interval was used, vertebrates had more archipelagos following their ISAR than invertebrates or plants (vertebrates 92%; invertebrates 88%; plants 78%; Table 2.2). However, these differences were not significant ($\chi^2 = 1.06$; $p = 0.59$). Furthermore, when considering the interval defined by the median residual, the proportion of cases that were congruent with the ISAR was almost the same for each one of the three groups (vertebrates and invertebrates 62%, and plants 67%; $\chi^2 = 0.08$; $p = 0.96$). In any case, differences seemed to be stronger between archipelagos than among taxa. Some evidence of this came from the archipelagos for which we have data on different taxonomic groups; whereas in several taxa of the Canary Islands the archipelagic point fell outside its ISAR, this was not the case for the Azores or Cape Verde (Table 2.2).

Oceanic archipelagos were congruent with their ISAR more often than continental ones, according to the *MaxRes* criterion (95%, vs. 76%; $\chi^2 = 5.43$; $p < 0.05$). This difference was more pronounced when the *MedRes* criterion was used; while most oceanic archipelagos remain within their ISAR (75%), only 41% of the continental archipelagos showed the same result ($\chi^2 = 7.98$; $p < 0.05$). Mixed archipelagos were not considered in these comparisons because of the small number of cases (n = 3). The distance from the archipelago to the mainland also had a significant effect on the probability of rejecting the hypothesis, since more isolated archipelagos were more congruent with their ISARs than less isolated ones (Mann-Whitney $U = 159$, $Z = -2.12$, $n_1 = 9$, $n_2 = 63$, $p < 0.05$, for the *MaxRes*; Mann-Whitney $U = 413$, $Z = -2.26$, $n_1 = 27$, $n_2 = 45$, $p < 0.05$, for the *MedRes*).

Table 2.2. Characteristics of the archipelago/taxon combinations studied, and results of the species–area regressions and the degree of departure of the archipelagic point from its island species–area relationship (ISAR).

	Archipelago	*I*	n	*A*	G	Taxon	S_{obs}	SA_{pred}	Slope	Inter.	R^2	Interval	R
Continental	Adriatic Islands	1	13	2586	V	Amphibians	7	9.8	0.50	-0.70	**0.52****	Max, Med	1
	Adriatic Islands	1	14	2638	V	Mammals	13	14.1	0.29	0.15	**0.69*****	Max, Med	1
	Adriatic Islands	1	14	2638	V	Reptiles	28	33.4	0.36	0.29	**0.79*****	Max, Med	1
	Adriatic Islands	1	14	2638	V	Vertebrates	48	57.8	0.36	0.52	**0.78*****	Max, Med	1
	Aegean Islands	2	44	3562	I	Isopods	69	49.6	0.20	0.97	**0.91*****	Max	2
	Aegean Islands	2	20	3371	I	Isopods	59	42.3	0.21	0.88	**0.59*****	-	3
	Aegean Islands	7	65	15853	I	Land Snails	264	72.5	0.19	1.08	**0.83*****	-	4
	Aegean Islands	7	64	7593	I	Land Snails[1]	196	59.4	0.18	1.08	0.83	-	4
	Aegean Islands	10	9	18	P	Plants	402	279.8	0.35	2.00	**0.78****	Max, Med	5
	Aegean Islands	0.1	32	20313	I	Tenebrionids	126	41.9	0.28	0.41	**0.41*****	Max	6
	Aegean Islands	8	26	369	I	Tenebrionids	59	30.5	0.28	0.78	**0.75*****	Max	7
	Åland Archipelago	0.25	5	1	I	Carabids	33	23.0	0.21	1.40	0.47	-	8
	Alexander Arch.	0.35	24	32707	V	Mammals	23	5.7	0.19	-0.10	**0.95*****	Max	9
	Baltic Islands	0.3	24	78	I	Carabids	61	30.8	0.11	1.28	**0.47*****	-	10
	Cyclades	13	24	2437	I	Land Snails	82	62.1	0.27	0.89	**0.64*****	Max	11
	Italian Islands	0.45	31	1234	I	Lepidoptera	86	32.6	0.13	1.11	**0.21***	Max	12
	Kalymnos Islands	8	12	132	I	Land Snails	47	49.9	0.20	1.28	**0.81*****	Max, Med	13
	Kornati Archipelago	16	5	34	P	Plants	634	363.3	0.28	2.13	**0.92***	-	14
	Lake Mamri Islands	0.4	15	51	I	Carabids	71	36.4	0.14	1.60	**0.66*****	-	15
	Peter the Great Bay	0.3	11	161	V	Mammals	19	10.1	0.31	0.31	**0.39***	Max, Med	16
	Pihlajavesi Arch.	2	13	1	I	Carabids	23	16.5	0.33	1.24	**0.37***	Max, Med	17
	Sardinian-Corsican	50	11	326	I	Lepidoptera	65	24.7	0.15	1.01	**0.49***	-	12
	Scilly Isles	45	7	14	I	Land Snails	51	54.6	0.36	1.34	**0.85****	Max, Med	18
	Shetland Islands	180	42	3	P	Plants	81	186.1	0.48	2.03	**0.73*****	Max	19
	Šibenik Archipelago	1	10	10	P	Plants	278	214.8	0.18	2.15	**0.94*****	-	20
	Sicilian Islands	22	10	525	I	Lepidoptera	30	20.1	0.09	1.07	0.17	Max	12
	Skyros Archipelago	90	12	221	I	Land Snails	42	40	0.18	1.19	**0.88*****	Max, Med	21
	Stockolm Arch.	10	12	4	I	Carabids	28	16	0.30	1.03	**0.52****	Max	17
	Tuscan Archipelago	9	7	290	I	Lepidoptera	67	54.6	0.35	0.88	**0.73***	Max	22
	Tvarminne Arch.	1	16	0	I	Carabids	19	8.8	0.28	1.08	**0.47****	Max	17
	Vargskar Arch.	20	13	2	I	Carabids	42	38.6	0.33	1.50	**0.74*****	Max, Med	17
	Wessel Islands	2	37	513	I	Ants	74	53.2	0.28	0.96	**0.68*****	Max, Med	23
Mixed	Dahlak Archipelago	1	26	75	V	Birds	38	18.8	0.31	0.70	**0.52*****	Max, Med	24
	Japan	175	10	367697	V	Mammals	55	34.6	0.23	0.28	**0.77*****	-	25
	Mollucas	400	15	58534	I	Sphingidae	83	68.7	0.55	-0.81	**0.42****	Max, Med	26
Oceanic	Azores	1584	9	2435	I	Arachnids	172	241.4	0.66	0.15	**0.71****	Max, Med	27
	Azores	1584	9	2435	I	Arthropods	1491	1569.4	0.48	1.56	**0.89*****	Max, Med	27
	Azores	1584	6	2051	I	Braconids	14	7.1	0.57	-1.04	0.29	Max, Med	27
	Azores	1584	9	2435	I	Coleoptera	217	264.1	0.53	0.64	**0.69****	Max, Med	27
	Azores	1584	9	2435	I	Hymenoptera	114	103.7	0.64	-0.14	**0.77****	Max, Med	27
	Azores	1584	7	2345	I	Ichneumonids	18	33.4	0.85	-1.33	0.55	Max	27
	Azores	1584	9	2435	I	Land Snails	111	89.1	0.21	1.25	**0.69****	Max	27
	Azores	1584	9	2435	I	Lepidoptera	104	93.1	0.19	1.33	**0.83*****	Max	27
	Azores	1584	9	2435	P	Plants	266	267.4	0.15	1.92	**0.64****	Max, Med	27

Table 2.2 (continued)

	Archipelago	*I*	n	*A*	G	Taxon	S_{obs}	SA_{pred}	Slope	Inter.	R^2	Interval	R
Oceanic	Azores	1584	9	2435	V	Vertebrates	78	65.4	0.08	1.55	**0.58***	Max	27
	Canary Islands	96	7	7301	I	Arachnids[2]	775	493.3	0.44	0.98	0.41	Max	28
	Canary Islands	96	5	4878	I	Arachnids[3]	683	618.4	0.55	0.75	**0.80***	Max, Med	28
	Canary Islands	96	7	7301	I	Arthropods[2]	6269	4222.7	0.37	2.21	0.34	Max	28
	Canary Islands	96	5	4878	I	Arthropods[3]	5679	5959.5	0.52	1.86	**0.86***	Max, Med	28
	Canary Islands	96	7	7301	I	Braconids[2]	55	33.8	0.63	-0.91	0.33	Max, Med	28
	Canary Islands	96	5	4878	I	Braconids[3]	51	42	0.78	-1.24	0.47	Max, Med	28
	Canary Islands	96	7	7301	I	Coleoptera[2]	1854	980.3	0.22	2.14	0.21	-	28
	Canary Islands	96	5	4878	I	Coleoptera[3]	1679	1404.4	0.37	1.80	**0.90***	-	28
	Canary Islands	96	7	7301	I	Diptera[2]	983	707.2	0.43	1.19	0.22	Max, Med	28
	Canary Islands	96	5	4878	I	Diptera[3]	912	1233.3	0.65	0.68	0.74	Max, Med	28
	Canary Islands	96	7	7301	I	Hemiptera[2]	488	378	0.35	1.22	0.41	Max, Med	28
	Canary Islands	96	5	4878	I	Hemiptera[3]	440	499.7	0.48	0.91	**0.91***	Max	28
	Canary Islands	96	7	7301	I	Hymenoptera[2]	932	799.6	0.56	0.73	0.47	Max, Med	28
	Canary Islands	96	5	4878	I	Hymenoptera[3]	847	1070.7	0.73	0.33	0.75	Max, Med	28
	Canary Islands	96	7	7301	I	Ichneumonids[2]	124	63.1	0.27	0.75	0.07	Max, Med	28
	Canary Islands	96	5	4878	I	Ichneumonids[3]	120	148.4	0.56	0.11	**0.86***	Max	28
	Canary Islands	96	7	7301	I	Insects[2]	5181	3602.7	0.36	2.15	0.33	Max	28
	Canary Islands	96	5	4878	I	Insects[3]	4702	5148.3	0.52	1.78	**0.86***	Max, Med	28
	Canary Islands	96	7	7301	I	Land Snails[2]	213	57.9	0.18	1.08	0.09	-	28
	Canary Islands	96	5	4878	I	Land Snails[3]	182	88	0.33	0.72	0.51	-	28
	Canary Islands	96	7	7301	I	Lepidoptera[2]	582	857.8	0.60	0.50	0.51	Max, Med	28
	Canary Islands	96	5	4878	I	Lepidoptera[3]	533	847.9	0.73	0.22	**0.88***	-	28
	Canary Islands	96	7	7301	P	Plants[2]	1360	957.5	0.18	2.28	0.32	-	28
	Canary Islands	96	5	4878	P	Plants[3]	1245	1169	0.27	2.07	**0.90***	Max, Med	28
	Canary Islands	96	7	7301	V	Vertebrates[2]	96	71.1	0.10	1.47	0.28	-	28
	Canary Islands	96	5	4878	V	Vertebrates[3]	84	77.9	0.14	1.37	0.65	Max	28
	Cape Verde	568	10	4076	I	Arachnids	144	188.9	0.94	-1.11	**0.68****	Max, Med	29
	Cape Verde	568	10	4076	I	Arthropods	1379	1474.2	0.62	0.91	**0.69****	Max, Med	29
	Cape Verde	568	10	4076	I	Braconids	36	22.9	0.49	-0.31	**0.46***	Max, Med	29
	Cape Verde	568	10	4076	I	Coleoptera	419	323.2	0.78	-0.32	**0.68****	Max, Med	29
	Cape Verde	568	10	4076	I	Diptera	196	212.9	0.64	0.02	**0.58****	Max, Med	29
	Cape Verde	568	10	4076	I	Hemiptera	260	208.8	0.39	0.92	**0.55***	Max, Med	29
	Cape Verde	568	10	4076	I	Hymenoptera	183	201.9	0.85	-0.77	**0.71****	Max, Med	29
	Cape Verde	568	10	4076	I	Insects	1174	1264.2	0.60	0.94	**0.69****	Max, Med	29
	Cape Verde	568	10	4076	I	Land Snails	24	29.2	0.45	-0.16	**0.53***	Max, Med	29
	Cape Verde	568	10	4076	I	Lepidoptera	139	153	0.66	-0.19	**0.44***	Max, Med	29
	Cape Verde	568	10	4076	P	Plants	276	273.1	0.29	1.39	**0.78*****	Max, Med	29
	Cape Verde	568	10	4076	V	Vertebrates	55	46.2	0.25	0.77	**0.59****	Max	29
	Chatman Islands	2800	5	975	V	Birds	26	27	0.13	1.05	**0.96****	Max, Med	30
	Cook Islands	4400	15	230	V	Birds	50	21.1	0.31	0.59	**0.36***	Max	31
	Cook Islands	4400	15	247	P	Plants	187	199.5	0.45	1.23	**0.82*****	Max, Med	32
	Fiji	2700	7	16993	I	Ants	113	76.8	0.33	0.50	**0.75***	Max	33
	Futuna & Wallis	3200	6	166	I	Ants	21	18.9	0.22	0.78	**0.71***	Max, Med	34
	Galápagos	850	19	7817	I	Oribatids	202	111.1	0.22	1.20	**0.54*****	Max, Med	35
	Hawaii	3650	8	16399	I	Braconids	40	27.1	0.34	0.02	**0.81****	Max, Med	36

Table 2.2 (continued)

	Archipelago	*I*	n	*A*	G	Taxon	S_{obs}	SA_{pred}	Slope	Inter.	R^2	Interval	R
Oceanic	Hawaii	3650	10	16582	I	Ichneumonids	53	41.1	0.40	-0.07	**0.77*** **	Max, Med	36
	Hawaii	3650	6	16392	I	Ophioninae	30	32.7	0.35	0.03	0.58	Max, Med	37
	Hawaii	3650	10	16397	I	Land Snails	752	462.2	0.58	0.21	**0.93*** **	Max, Med	38
	Hawaii	3650	8	16885	P	Lobeliads	76	62.9	0.73	-1.31	**0.67***	Max, Med	39
	New Zealand	1641	23	267039	V	Birds	60	76.3	0.19	0.87	**0.74*** **	Max, Med	30
	Ogasawara Is.	1000	16	71	I	Land Snails	92	102.8	0.64	0.82	**0.79*** **	Max, Med	40
	Solomon Is.	1500	12	23955	I	Sphingidae	38	21.6	0.38	-0.32	0.22	Max, Med	26

I is the smallest distance to the closest source of immigrants (in km), n is the number of islands considered, and *A* the sum of their areas (in Km^2). G is the kind of taxon studied (I stands for Invertebrates, V for Vertebrates, and P for Plants). The studied data usually refers to all the islands present in the respective reference (R), except when indicated ([1]all Aegean islands except Crete; [2]all Canary Islands; [3]all Canary Islands except Fuerteventura and Lanzarote). S_{obs} is the total species richness, and SA_{pred} *is* the richness for the whole archipelago predicted by the ISAR, according to the relationship defined by the slope and intercept (Inter.) of the regression equation given by the log-log form of the power model. R^2 is the variability explained by the equation (significant ISARs are in bold; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Finally, Interval describes whether the archipelago is congruent with its ISAR or not, according to two criteria, the maximum (Max) and median (Med) residual (see text for further details). The source references (R) for all datasets are as follows: 1) Kryštufek & Kletečki (2007); 2) Sfenthourakis (1996); 3) Sfenthourakis *et al.* (2004); 4) Welter-Schultes & Williams (1999); 5) Panitsa & Tzanoudakis (1998); 6) Fattorini (2002); 7) Trichas *et al.* (2008); 8) Niemelä (1988); 9) Conroy *et al.* (1999); 10) Kotze *et al*. (2000); 11) Mylonas (1982); 12) Dapporto & Dennis (2008); 13) Triantis *et al.* (2008b); 14) Pandža & Stančić (2004); 15) Zalewski & Ulrich (2006); 16) Sheremet'ev (2004); 17) Niemelä *et al.* (1987); 18) Holyoak *et al*. (2005); 19) Kohn & Walsh (1994); 20) Pandža *et al.* (2002); 21) Triantis *et al*. (2005); 22) Dapporto & Cini (2007); 23) Woinarski *et al.* (1998); 24) Azeria (2004); 25) Millien-Parra & Jaeger (1999); 26) Beck & Kitching (2004-2008); 27) Borges *et al.* (2005a); 28) Izquierdo *et al*. (2004); 29) Arechavaleta *et al*. (2005); 30) Williams (1981); 31) Blackburn *et al.* (2004); 32) McCormack (2007); 33) Ward & Wetterer (2006); 34) Wilson & Hunt (1967); 35) Schatz (1998); 36) Nishida (2002); 37) Bennett (2008); 38) Cowie (1995); 39) Givnish *et al.* (2009); (40) Tomiyama & Kurozumi (1992).

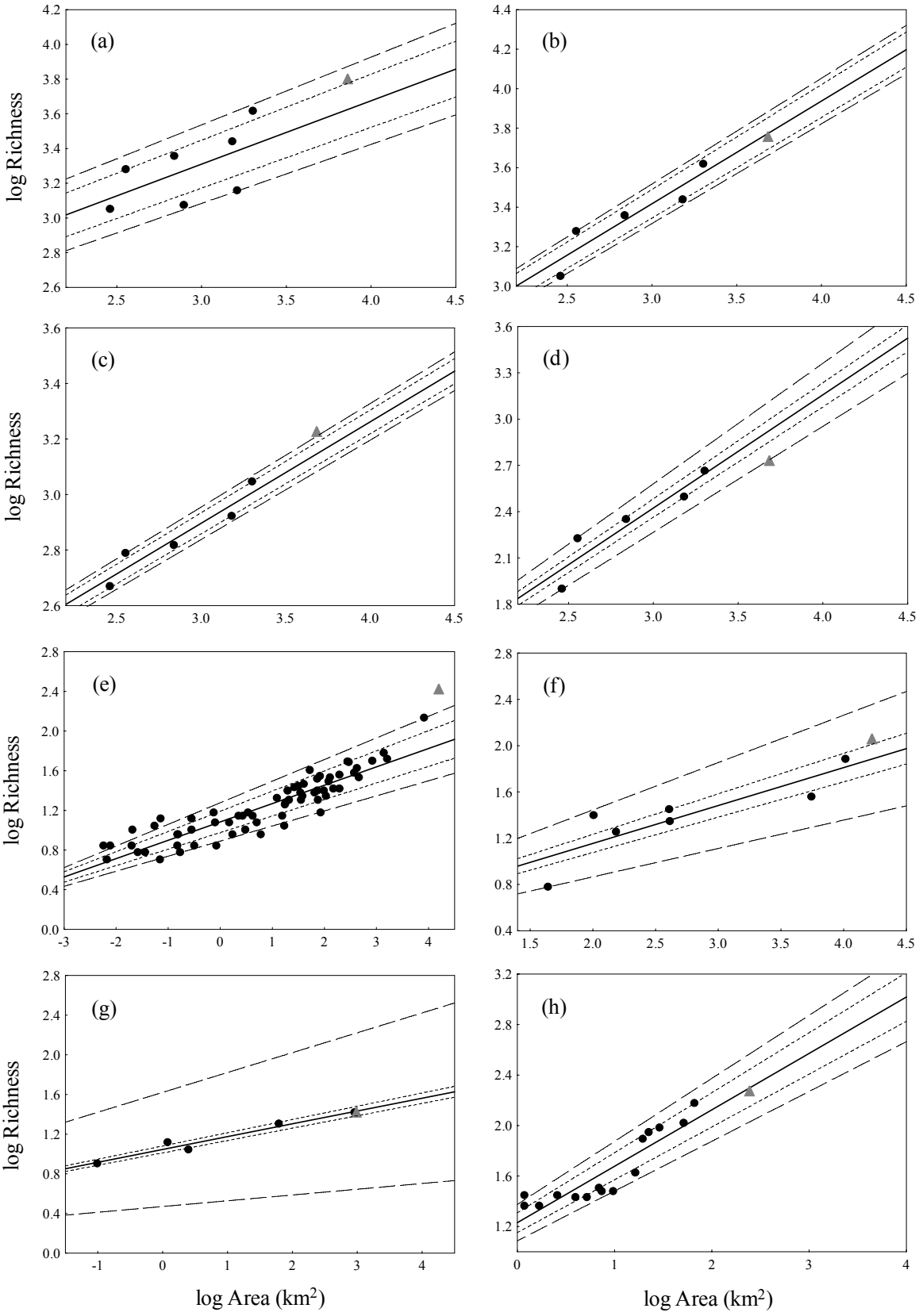
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
log Richness
log Area (km2)

Figure 2.1. Relationship between species richness and area for several archipelago/taxon combinations. Individual islands are represented by black circles and the archipelagos by grey triangles. The island species–area relationship (ISAR) predicted by the regression function is shown as a continuous line in each case. The intervals defined by the maximum and median residuals criteria (see text) are represented by the dashed and the dotted lines, respectively. a) Canary Islands – Arthropods (all islands); b) Canary Islands – Arthropods (without Fuerteventura and Lanzarote); c) Canary Islands – Coleoptera (without Fuerteventura and Lanzarote); d) Canary Islands – Lepidoptera (without Fuerteventura and Lanzarote); e) Aegean Islands – Land Snails; f) Fiji – Ants; g) Chatman Islands – Birds; h) Cook Islands – Plants. See data sources and regression statistics in Table 2.2.

In Fig. 2.2 we represented the *ArcRes* of the datasets with significant ISARs, against their respective distances to the mainland, indicating also the type of taxon and geological origin of the archipelago. For continental islands *ArcRes* values showed a marginally non-significant negative relationship with isolation (Spearman $R = -0.33$, $p = 0.08$), whereas for oceanic islands this relationship was significant and positive (Spearman $R = 0.39$, $p < 0.05$). *ArcRes* of continental archipelagos and vertebrates showed higher variation than in other categories (SD = 0.14 and 0.16 respectively, vs. 0.12 for plants, 0.09 for invertebrates, 0.08 for mixed archipelagos and 0.07 for oceanic archipelagos). In fact, there were significant differences between the *ArcRes* values as a function of the geological origin of the archipelagos (i.e. *ArcRes* values were bigger for continental archipelagos; Mann-Whitney $U = 344$, $Z = 2.87$, $p < 0.01$; mixed archipelagos were not considered for this analysis) but not between different taxa [Kruskal-Wallis H (2 d.f., n = 72) = 0.093; $p = 0.95$]. It is noteworthy that invertebrates from continental islands had more positive *ArcRes* values than negative ones indicating that, in such cases, the ISAR tends to under-predict archipelagic species richness, especially in the least-isolated islands. However, in the case of the invertebrates from oceanic islands the opposite relationship appears to occur: the least-isolated archipelagos typically had negative *ArcRes* values while the most distant ones exhibited positive residuals. For all the other archipelago/taxon combinations the few data points available were much more scattered and therefore showed no evident trend.

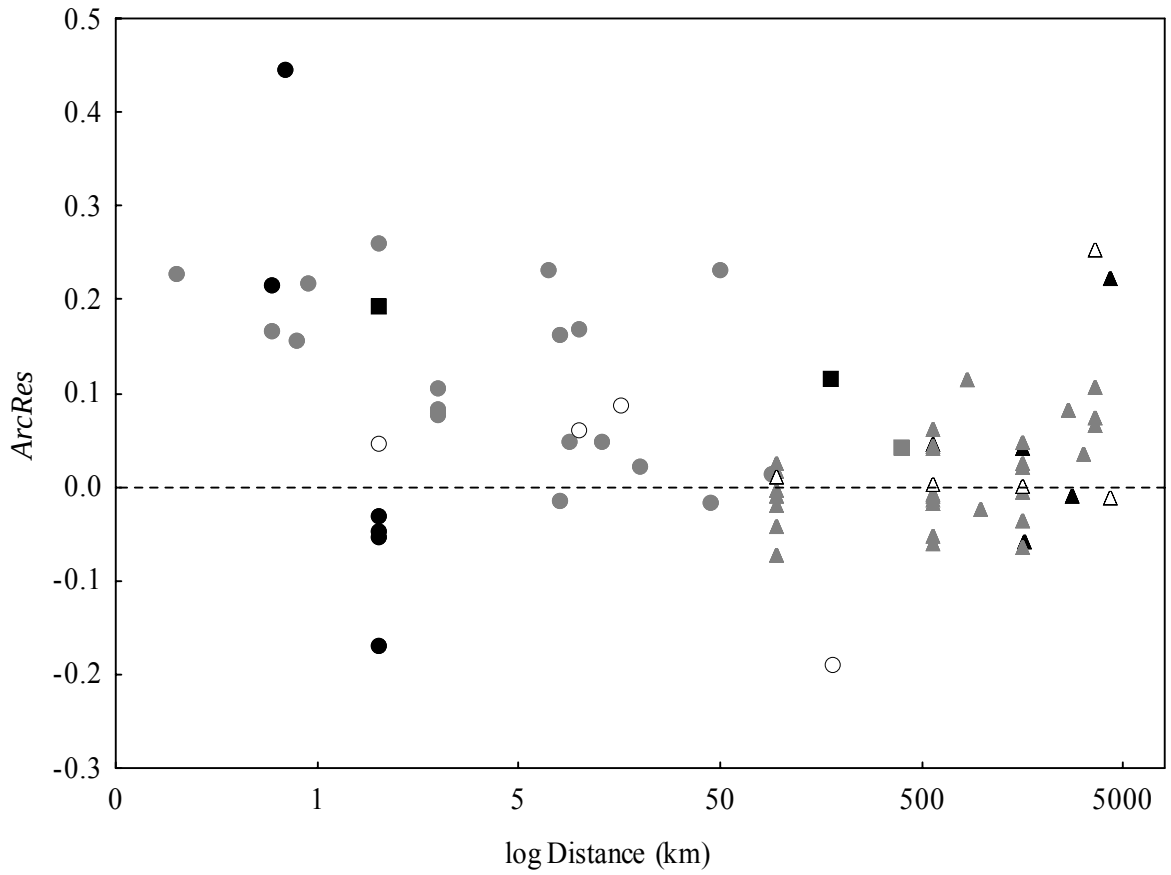

Figure 2.2. Distribution of the archipelagic residual (*ArcRes*) for the seventy–two significant archipelago/taxon combinations, according to the logarithm of the distance to the mainland (in Km). *ArcRes* was calculated as the residual of the prediction provided by the island species–area relationship (ISAR) using the total area of the archipelago, standardized by the total richness observed in the archipelago. Symbol colour represents the type of taxon (black – vertebrates; grey – invertebrates; white – plants), and their shapes represent the type of archipelago (circles – continental; triangles – oceanic; squares – mixed archipelagos). Horizontal line serves only as a guide line to *ArcRes* = 0.

The degree of nestedness of island biotas showed a clear relationship with *ArcRes*: the more nested a dataset, the lower (and negative) the archipelagic residual (Table 2.3, Fig. 2.3). In the cases analyzed this pattern is more evident using the Temperature index [Spearman $R = 0.83$, n = 10, t (N – 2) = 4.21, $p < 0.01$] than for NODF [Spearman $R = -0.48$, n = 10, t (N – 2) = -1.54, $p = 0.16$].

Table 2.3. Results of the nestedness analyses for several arthropod groups at the Azores and Canary Islands (data from Borges *et al.*, 2005a and Izquierdo *et al.,* 2004, respectively).

Archipelago	N	Taxon	*ArchRes*	T	NODF
Azores	9	All Arthropods	-0.701×10^{-2}	19.38	31.53
	9	Arachnids	-6.585×10^{-2}	20.87	31.04
	9	Coleoptera	-3.653×10^{-2}	18.29	23.35
	9	Lepidoptera	2.376×10^{-2}	28.20	34.55
Canary Islands	7	Arachnids[1]	6.791×10^{-2}	33.62	14.49
	5	Arachnids[2]	1.522×10^{-2}	34.72	16.92
	7	Coleoptera[1]	8.468×10^{-2}	40.83	23.05
	5	Coleoptera[2]	2.405×10^{-2}	40.12	26.20
	7	Lepidoptera[1]	-6.093×10^{-2}	20.64	26.45
	5	Lepidoptera[2]	-7.394×10^{-2}	15.57	30.98

[1] refers to all Canary Islands, and [2] to all Canary Islands except Fuerteventura and Lanzarote (see text). *ArchRes* is the archipelagic residual (the residual of the prediction provided by the island species–area relationship (ISAR) using the total area of the archipelago, divided by the total richness observed in the archipelago), T is the original Temperature measure of nestedness (Atmar & Patterson, 1993), and NODF is the nestedness metric based on overlap and decreasing fill proposed by Almeida-Neto *et al.* (2008). Analyses for all arthropods in the Canary Islands were not performed due to the limit of 3,000 lines (i.e. species) of the program used to compute the nestedness measure (ANINHADO; Guimarães & Guimarães, 2006).

2.5. Discussion

It is often commented that community ecology has few general rules or laws (Lawton, 1996, 1999, 2000; but see Gaston & Blackburn, 2000; Simberloff, 2004; Ricklefs, 2008). One of the few exceptions is held to be the species–area relationship, which is widely applicable at all scales and types of organisms, from bacteria to vertebrates (Rosenzweig, 1995). The species–area relationship has commonly been described for discrete geographic units, such as islands within an archipelago (Rosenzweig, 1995; Whittaker & Fernández-Palacios, 2007). However, it is not unusual to lump data on the constituent islands of archipelagos together by adding island areas and combining island species lists to obtain the overall area and richness of the archipelagos (e.g. Wilson, 1961; Scott, 1972; Wright, 1983; Adler *et al.*, 1995; Carvajal & Adler, 2005; among others). Although this allows using these data in large-scale analyses, it also implies that the archipelagos as a whole follow the same relationship with area that their constituent islands do, an assumption that was never evaluated before.

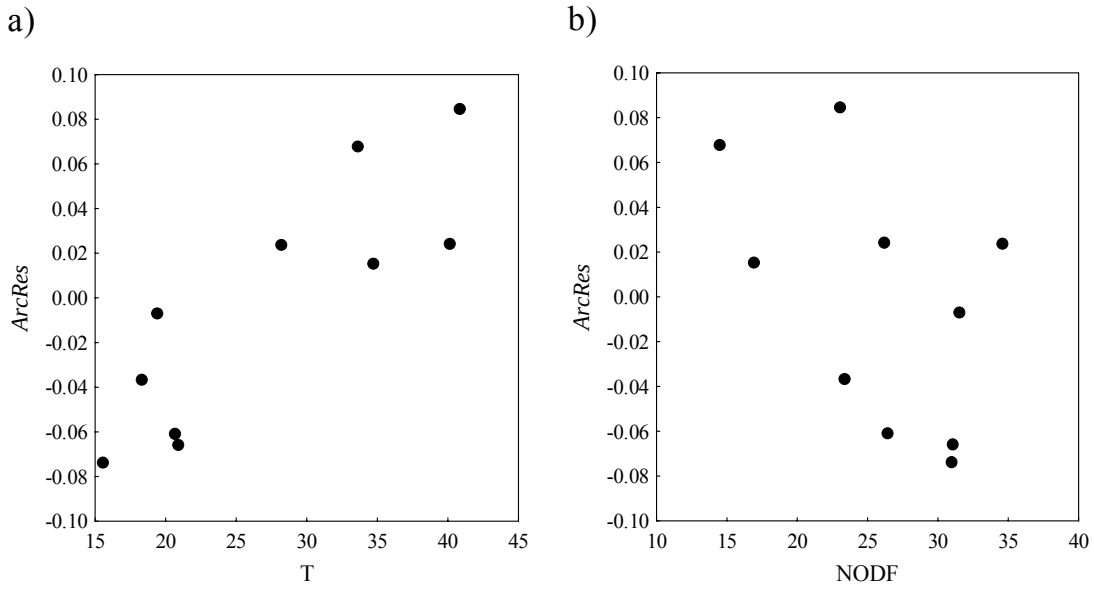

Figure 2.3. Relationship between the archipelagic residual (*ArchRes*) and two nestedness measures: (a) Temperature (T), the original measure proposed by Atmar & Patterson (1993), and (b) the overlap and decreasing fill metric (NODF) proposed by Almeida-Neto *et al.* (2008). Note that the higher NODF, the more nested the archipelago, which is the converse of the ordering of the T metric. Data correspond to several arthropod groups of the Azores and the Canary Islands (see Table 2.3).

We have shown that archipelagos do often follow the same ISAR of their constituent islands. In the majority of the cases studied, the archipelagic point is congruent with its ISAR, which begs the question as to why should whole archipelagos follow the same species–area relationship as their constituent islands? The answer must be related to the endogenous dynamics of the system (speciation, immigration and extinction), which are determined by a number of regional factors such as total area of the archipelago, number of islands, environmental heterogeneity, isolation and geological age. These factors act as local filters of the regional processes acting over the species pool of the archipelago (see Ricklefs, 2007, 2008). Given the importance of regional processes common to all their constituent islands, many archipelagos can be considered to behave as a coherent entity for the different processes establishing species diversity. Interestingly, as a consequence of source pool effects there is a close association between species–area and local–regional richness relationships (see Srivastava, 1999; He *et al.*, 2005), so species richness on individual islands is to some extent a reflection of the species pool of the archipelago.

Given that area is one of the best macroecological descriptors of island species richness (see, e.g., Rosenzweig, 1995; Whittaker & Fernández-Palacios, 2007; Triantis *et al.*, 2008a), the island group as a whole should also be expected to follow its endogenous species–area dynamics. We thus argue that if the archipelago is isolated enough for all the islands to have an equivalent species pool, and the geological characteristics and evolutionary processes are coherent from island to island, it is unsurprising that the biota of the whole of the archipelago would follow the same relationship with area as the one operating within the constituent islands. In other words, the accumulation of new species with additional islands will show a consistent relationship with their area. It follows from our rationale that the departure of the archipelago from the ISAR will be related to some extent with the degree of nestedness of the island biotas (see Wright *et al.*, 1998).

The additional analyses carried out on several arthropod groups of the Canary Islands and the Azores show that the magnitude of the departure of the archipelago from the ISAR is related to nestedness. The more nested the biota of the archipelago is, the lower the archipelagic residual, a trend that is especially evident when using the Temperature metric. The sensitivity to the choice of nestedness metric [Temperature metric of Atmar & Patterson (1993) versus NODF metric of Almeida-Neto *et al.* (2008)] might reflect the nature of the nestedness patterns. While traditional 'gap-counting' nestedness metrics such as Temperature are biased towards the loss of species among islands, NODF also accounts for the degree of coincidence of species presences in the poorer sites (see Almeida-Neto *et al.*, 2008; Ulrich *et al.,* 2009). In other words, while Temperature values reflect how widespread species are distributed in progressively less rich islands, NODF also takes into account whether poor islands host rare species or not. These rare species are species present in just one or a few islands, so NODF would be expected to be more sensitive when the patterns of nestedness within the archipelago are driven by the numbers of single island endemics (SIEs). Within this framework, the less tight relationship between the archipelagic residual and NODF compared to its relationship with Temperature allows to postulate that the number of SIEs *per se* does not necessarily have an effect on the departure of the archipelago from the ISAR. In fact, many cases with disproportionately high numbers of SIEs (and therefore highly non-nested biotas) fall into the confidence intervals we used in this work [e.g. Hawaiian land snails (Cowie, 1995) and lobeliads (Givnish *et al.*, 2009)].

The residual variation of the archipelagic data point seems thus to reflect a particular aspect of nestedness: the absence of species present in the richer islands in progressively poorer islands (i.e., richness-ordered nestedness *sensu* Whittaker & Fernández-Palacios, 2007). Departures from the ISAR are thus expected in systems that are either highly nested or not nested at all (Fig. 2.4), independently of the number of SIEs. In the case of highly–nested systems, the richness of the archipelago will scarcely exceed that of the largest island and will be fairly insensitive to the number and area of smaller islands. Thus, the predicted number of species for the total area of the archipelago will be higher than the observed species richness (e.g. Lepidoptera from the Canary Islands, Fig. 2.1d). Conversely, in highly non–nested systems there is a high rate of accumulation of new species with the addition of each island. Hence, the observed archipelagic species richness (a cumulative total) should be higher than that predicted by the non-cumulative series provided by the ISAR (e.g. Coleoptera of the Canary Islands or land snails of the Aegean Islands, Figs. 2.1c,e). However, as discussed above high overall numbers of SIE in the archipelago are not enough to cause significant departures from the ISAR (e.g. the highly species rich land snails and lobeliads of Hawaii mentioned above). Rather, departures will appear when the processes leading to the appearance of high numbers of SIE differ within the set of islands collated together for an analysis. Where an archipelago is composed of different groups of islands with differing characteristics, the processes building up island biotas might vary amongst the constituent islands. This will happen in archipelagos where: (i) the proximity to the source(s) of colonizers allows inter-island variation in colonization rates and/or the arrival probability of particular species or lineages (thus different sets of widespread species will be found in different clusters of islands); (ii) one or some of the islands show higher speciation rates (e.g. because they are significantly larger; see Losos & Schluter, 2000); and also (iii) some islands suffer anomalous pulses of extinction (e.g. island sterilization processes; see Whittaker & Fernández-Palacios, 2007). All these cases will produce anomalous patterns of species accumulation with area, and the departure of the overall richness of the archipelago from the ISAR of its constituent islands.

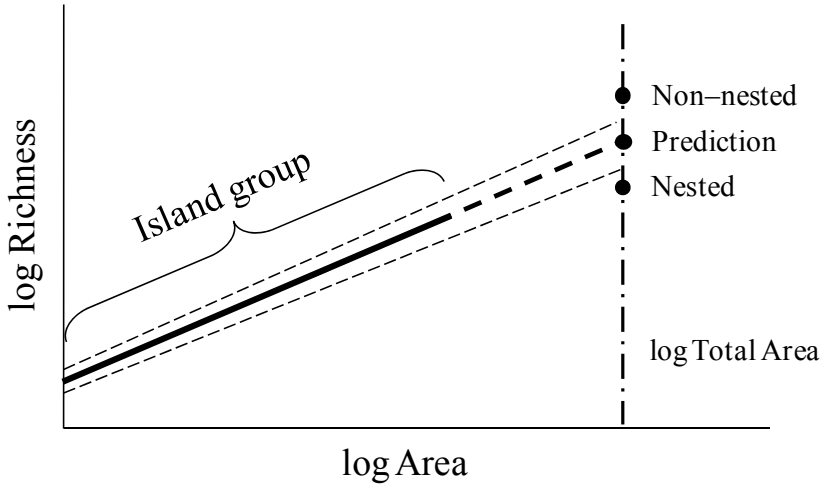

Figure 2.4. Hypothetical relationships between different degrees of nestedness and the departure of the archipelago point from the island species–area relationship (ISAR), in a log-log species–area plot. Here, nestedness is a by-product of the rate of accumulation of new species to the total list of the archipelago with the addition of new islands (i.e. richness-ordered nestedness *sensu* Whittaker & Fernández-Palacios, 2007). Where a system tends towards perfect nestedness, the archipelago richness will be the same as that of the largest island (or only a little higher), while for completely unnested systems the archipelago richness is the sum of the richness of each constituent island.

This raises a more general point: almost all situations where the archipelagic point deviates significantly from the ISAR came from cases where both the slope of the ISAR and degree of isolation were low, and the total species richness was higher than expected by the ISAR. Given that the ISAR slopes of these exceptional cases are low, it is not surprising that the total richness of the archipelago falls above the relationship observed for the islands, as seen for the Coleoptera of the Canary Islands or the land snails of the Aegean Islands (Figs. 2.1c,e, respectively). The reasons for such non–nested pattern could be: (i) a particularly high speciation rate and/or particular patterns in clusters of islands (i.e., limitations to dispersal and availability of ecological space that allow a higher number of speciation events and thus the generation of large numbers of species over the whole archipelago); (ii) an heterogeneous geological history among the individual islands, enough to differentiate sets of islands with particular dynamics (e.g. Canary Islands; see Whittaker *et al.*, 2008); or (iii) multiple sources for the arrival of new species (which is the case for the Aegean islands). Conversely, highly nested systems might arise from several circumstances, including: (iv) a low rate of

colonisation from the continent, which will result in a low number of lineages inhabiting the archipelago, and thus lower compositional replacement; and (v) high rates of dispersal between islands, which will also result in low compositional replacement from island to island. Canarian Lepidoptera provided the only example in which the overall richness of the archipelagic point falls significantly below the ISAR according to our maximum residual criterion, indicating a low degree of dissimilarity for this group (see Fig. 2.1d). Butterflies and moths are in general very good dispersers (e.g. Borges & Hortal, 2009), which results in low compositional differences between island faunas (our reason v). Hence, the total species richness of the archipelago does not increase significantly with the addition of new islands.

Our analytical approach presents several limitations that reflect the exploratory nature of our study. For example, many of the cases we studied pertain to just five island groups (Aegean Islands, Azores, Canary Islands, Cape Verde and Hawaii) for which relatively comprehensive data are available. As a consequence, although the results from these archipelagos reassure us that our conclusions are reliable in broad qualitative terms, we cannot be sure that these results will also turn out to be reliable in quantitative terms. Given the relationship between the degree of departure of the ISAR and nestedness found here, we recommend that further research on this topic should rely on the development of null models of the relationship between area and species assembly in a presence/absence matrix. The assumptions and development of these models are currently under debate, and several null hypotheses for random assembly have been proposed so far (see, e.g., Wright *et al.*, 1998; Rodríguez-Gironés & Santamaría, 2006; Almeida-Neto *et al.*, 2007, 2008; Ulrich *et al.*, 2009). In fact, these null hypotheses correspond to different aspects of nestedness: richness-ordered or area-ordered (see also Whittaker & Fernández-Palacios, 2007; Ulrich *et al.*, 2009). We anticipate that departures from the null expectations of these models would depend on the disparity in the presence of widespread species among islands, rather than on the number of rare species (e.g. SIE; see above). Therefore, we hypothesize that these departures would provide insight into the processes determining the assembly of island biotas within the archipelago, such as varying geological histories, island isolation, or habitat diversity (see, e.g., Roughgarden, 1989; Lomolino & Davis, 1997; Hortal *et al.*, 2009), but they will be relatively independent of differences in the evolutionary processes among islands.

To summarize, we have shown that archipelagos usually follow the same species–area relationship as their constituent islands. A straightforward implication of our results is that archipelagos can, in most cases, be considered as distinct entities. Hence, researchers would be justified in lumping species lists from their constituent islands when conducting biogeographical and/or macroecological studies. It is also important to note that most of the archipelagos studied are in fact 'SLOSS-neutral' (*sensu* Rosenzweig, 2004), and thus that at this large scale whether conservation efforts are devoted to a single large island or to several small ones may be of limited relevance (see also Rosenzweig, 2004). Importantly, the degree of departure from the ISAR (i.e., the archipelagic residual) is related to a particular aspect of nestedness, the loss of species present in the richest islands from the poorer ones, and can therefore be used as a crude index of richness-ordered nestedness when detailed island checklists are lacking. Given that area is just one of a number of factors determining the species richness on islands, within this framework the departure of some archipelagos from their ISAR would be caused by other factors affecting the assembly of island faunas, and therefore nestedness patterns (see Wright *et al.*, 1998). Further studies are required to understand the complexities of the influence of these factors on the degree of departure of the archipelagic point from the ISAR and the exact nature of the relationship between such departure and nestedness, and also to establish the pattern of departure of archipelagic data points from their constituent ISARs for other types of insular system, including anthropogenic habitat islands in fragmented landscapes.

Chapter 3: Assessing the reliability of biodiversity databases: identifying evenly inventoried island parasitoid faunas (Hymenoptera: Ichneumonoidea) worldwide[2]

3.1. Abstract

1. Taxonomic and geographic biases are common in biodiversity inventories, especially in hyperdiverse taxa, such as the Ichneumonoidea. Despite these problems, biodiversity databases could be a valuable source of information if their reliability is carefully assessed.

2. One major problem of using these data for large-scale analyses is the unevenness of data quality from different areas, which makes them difficult to compare. One way of surpassing such problem would be to identify sets of areas that are evenly inventoried.

3. Here we propose a scoring protocol for the identification of sets of evenly inventoried areas from taxonomic databases, based on three criteria: (i) completeness at high taxonomic levels, (ii) congruence with well-established ecological relationships (such as species–area relationship), and (iii) publication effort received. We apply this protocol to the selection of a set of evenly inventoried islands worldwide for two Ichneumonoidea families (Braconidae and Ichneumonidae) from the data gathered in Taxapad database.

4. From the 118 islands included in Taxapad, 53 and 70 can be considered sufficiently inventoried for Braconidae and Ichneumonidae, respectively. The publication effort criterion was more restrictive than the other two criteria. The Indomalayan, Nearctic and Palaearctic regions had more than half of their islands identified as evenly inventoried, for both families.

5. We discuss the generality of the biases and incompleteness of most biodiversity data, and also how the basic principles of the protocol proposed here can be applied to taxonomic databases devoted to other taxa. Also, the islands identified here can serve as the basis for large-scale analyses of the poorly known biogeography of the Ichneumonoidea.

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3.2. Introduction

The number of studies on large-scale diversity patterns has rapidly increased in the last two decades, in part due to the compilation of extensive databases on the distribution of biodiversity (herein, biodiversity databases) and, lately, due to the development of biodiversity information networks, such as the Global Biodiversity Information Facility (GBIF, http://www.gbif.org/) (see, e.g., Soberón & Peterson, 2004; Guralnick *et al.*, 2007). Although there are numerous approaches to the creation of biodiversity databases, most of them aim to gather the scattered information available from museums and herbaria, private collections, and the literature. Thus, in practice, these databases include data from a heterogeneous range of different inventories, which have been developed either with or without standardised surveys, and with varying amounts of effort (e.g. Soberón *et al*., 1996, 2000; Hortal *et al.*, 2007).

It is well known that our knowledge of the geographical distribution of biodiversity is, in general, taxonomically and geographically biased (the so-called Linnaean and Wallacean Shorfalls; Brown & Lomolino, 1998; Lomolino, 2004; Whittaker *et al*., 2005). If these shortfalls have a direct effect on the data included in the databases, then the description of biodiversity patterns will be compromised (Prendergast *et al*., 1993; Stockwell & Peterson, 2002; Hortal *et al.,* 2007). Unfortunately, distributional data of outstanding quality (e.g. some of the data available for the British Isles; Griffiths *et al.*, 1999) are the exception and not the rule. Rather, the information gathered in biodiversity databases is usually biased, scarce, or otherwise of poor quality (see Hortal *et al.*, 2007, 2008a; Lobo *et al.*, 2007; Rocchini *et al.*, in press and references therein).

Although limited data quality can affect all taxa, these problems are paramount for hyperdiverse groups, such as insects (see, e.g., Gaston, 1994; Godfray *et al.*, 1999; Martín-Piera & Lobo, 2000; Baselga *et al.*, 2010). This is certainly the case in the Ichneumonoidea (Hymenoptera), a superfamily that includes two of the largest families of Hymenoptera, the Braconidae and the Ichneumonidae. These families mainly include parasitoid species that develop as larvae by feeding on or in the bodies of other arthropods, usually killing their host (Godfray, 1994; Quicke, 1997). Although approximately 17,000 braconid species and 23,000 ichneumonid species have been described so far (Yu *et al*., 2005), these two families are still

taxonomically poorly known (Quicke, 1997). Recent estimates suggest that less than one-half of the total number of species of braconids and ichneumonids have been formally described (Dolphin & Quicke, 2001; Jones *et al.*, 2009). Furthermore, taxonomical work on these families is biased against the description of tropical and small bodied species (Gaston, 1993; Jones *et al.*, 2009). These biases result in an uneven description of the parasitoid faunas in different regions of the world; while the faunas of some areas are poorly known (i.e., underdescription due to poor sampling), others are so extensively studied that they cannot be readily compared with most of the less-well inventoried areas (i.e., taxonomic inflation or overdescription; see, e.g., Lobo & Martín-Piera, 2002).

Despite their collection biases and lack of completeness, natural history collections and taxonomic works are a highly valuable resource, often providing the only essential biological information for ecological, conservation and biogeographical studies. Databases compiling data from these sources contain massive amounts of distributional information gathered over decades or even centuries of survey work. Discarding such information because of perceived quality data issues would mean failing to take advantage of the work of several generations of naturalists. Instead, an assessment of the data quality of biodiversity databases could bridge the gap between the need for data on the distribution of biodiversity and limited investment in taxonomic and inventory work (Soberón *et al.*, 2000, 2007; Hortal *et al.*, 2007, 2008a; Lobo, 2008). Where these databases provide exhaustive data on the distributional information gathered from field records and natural history collections, comprehensive sampling effort assessments can indicate which areas have been surveyed sufficiently well for their inventories to be reliable (e.g. Garcillán *et al.*, 2003; Hortal & Lobo, 2005). However, many biodiversity databases only include partial compilations of survey effort (see Hortal *et al.*, 2007), or are reduced to the output of these efforts, the inventories of particular areas (i.e. checklists). This is the case for a particular type of biodiversity databases, those that compile the information that has traditionally featured in taxonomic monographs, henceforth termed taxonomic databases. Like monographs, taxonomic databases are usually based on extensive revisionary work (i.e., beta taxonomy; see Baselga *et al.*, 2010). Despite being taxonomically exhaustive, taxonomic databases lack comprehensive information on survey effort, making it difficult to determine which territories have reliable species inventories.

In this work we develop a protocol for the identification of evenly inventoried areas from taxonomic databases. We describe the practical application of this conceptual protocol to determine, as an example, the islands that host comparable (but not necessarily well-sampled) Braconidae and Ichneumonidae inventories, based on a database on the taxonomy and worldwide distribution of Ichneumonoidea (Yu *et al*., 2005). The method we propose is a simple scoring protocol based on three criteria: (i) the completeness of the inventory of higher taxa (subfamily level); (ii) congruence with a realistic species–area relationship (SAR); and (iii) an indirect measurement of survey effort (measured as the number of published pages). Although we apply this protocol to the diversity of parasitoids on islands, we discuss the potential advantages and limitations of the application of these three criteria in other areas. Our goal is to provide the basis for similar assessments of other taxonomic databases, which will eventually help workers to use the taxonomic and distributional information stored within them, while minimising problems caused by variable data quality.

3.3. Data and Methods

Data on Braconidae and Ichneumonidae species distribution on islands worldwide were obtained from Taxapad (Yu *et al*., 2005). Taxapad is an interactive digital catalogue that includes information from all literature published on these two families until 2004 (see http://www.taxapad.com/ for more information). The distribution of island species in Taxapad is organised by archipelagos, single island nations, or other administrative units. Given that archipelagos usually follow the same species–area relationship (SAR) as their constituent islands (Chapter 2), both archipelagos and islands were considered to be comparable units. Thus we used both types of data together in our analyses, referring them all as *islands* for simplicity. In addition, islands or archipelagos that are divided into political subregions and that are not true islands (e.g. Haiti and Dominican Republic, Brunei, Indonesia and Malaysia, and Papua New Guinea and Indonesia), were combined to give single data points, by considering the species list and island area as the sum of those of the territories included in the island (e.g. Hispaniola, Borneo, New Guinea). Introduced species, subspecies and synonyms were excluded.

Up-to-date data on the area and location of all islands were obtained from several sources, including the UNEP Island Directory (http://islands.unep.ch/isldir.htm), Wikipedia (http://en.wikipedia.org/), GPS visualizer (http://www.gpsvisualizer.com/geocode), and a number of literature sources (e.g. Heaney, 1978, 1986; Lawlor, 1986; Juste & Perez del Val, 1995; Millien-Parra & Jaeger, 1999; Michaux *et al.*, 2002; Borges & Wunderlich, 2008; for more details see Appendix A1.1 and A1.2). The total land area of archipelagos was defined as the sum of the areas of their constituent islands.

Determining which island inventories are relatively complete using commonly used methodologies such as collector's curves (e.g. Hortal & Lobo, 2005) is not possible due to the lack of information on sampling effort in Taxapad. However, we argue that these data can still be used to identify those islands which harbour sufficiently reliable (and thus comparable) inventories according to three criteria: (i) completeness at higher taxonomic levels; (ii) congruence with the species–area relationship (SAR) (i.e., which islands follow a realistic SAR); and (iii) publication effort (i.e., the amount of published information). Although some of the islands might not have complete or nearly complete checklists, we assume that their observed inventories will be sufficiently complete when most or all the former criteria are met.

Criterion 1: Completeness at higher taxonomic levels

Two obvious characteristics of sufficiently inventoried areas are that at least some species from most higher level taxa that are present have been recorded, and that there is no obvious bias towards recording (or not recording) any particular higher taxon. This could be assessed by determining whether the inventories include a realistic range of higher taxa. We selected subfamilies as the adequate higher level taxon because they have broad geographic distributions and are thus present on many islands. Tribe was not used because not every Ichneumonoidea species recorded in Taxapad have been assigned to this taxonomic level. We also dismissed genera because, for the Ichneumonoidea, their distributions are often geographically restricted.

Given that the number of subfamilies that are present on each island is unknown, we require an indicator of the completeness of the inventory at higher taxonomic levels that does not involve knowing their true number. So, we opted to determine if the islands host a

realistic number of the most geographically widespread subfamilies within each biogeographic region. We first identified the most ubiquitous subfamilies on the islands of each biogeographic region (as defined by Moss & Wilson, 1998 and Cox, 2001), by counting the islands where each subfamily was found. Subfamilies in the upper quartiles of this distribution were considered widespread, and hence likely to be present in most island faunas. In a second step, we identified the minimum number of subfamilies that an inventory should host to be considered potentially reliable. We plotted the accumulated number of islands in relation to the number of widespread subfamilies that were recorded there. This plot includes information from two kinds of islands; those where the observed number of subfamilies is underestimated as a direct consequence of the lack of survey effort, and those where the number recorded accurately reflects the real number of existent subfamilies (Fig. 3.1).

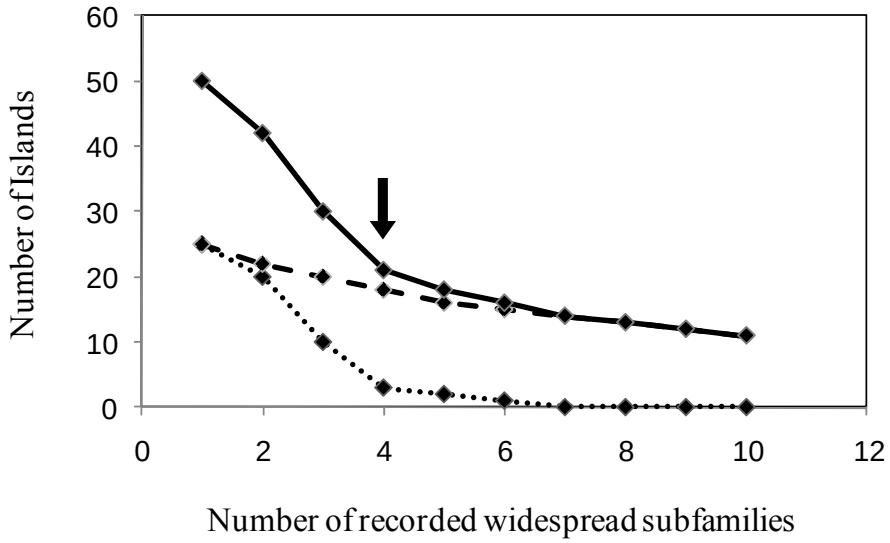


Figure 3.1. The hypothetical relationship between the number of widespread subfamilies and the accumulated number of islands where these subfamilies can be found. The dotted line represents the hypothetical case of all islands being poorly–inventoried, while the dashed line represents only well-inventoried islands. The unbroken line depicts a case where both poorly– and well–inventoried islands are present. The arrow indicates the threshold value that establishes the number of widespread subfamilies that the inventory of a well-studied island should include.

It seems logical to assume that the number of poorly inventoried islands that host progressively more widespread subfamilies decreases steeply, and that this relationship is substantially shallower in well-inventoried islands. Hence, the slope of the plot of accumulated number of widespread subfamilies will show a significant change (i.e., an inflection point). We thus selected the threshold from which the effect of undersampling on the number of widespread subfamilies would be negligible as the point at which this distribution curve changes its slope (see Fig. 3.1). This point can be identified visually as the last point on this relationship where the number of subfamilies stops decreasing steeply. Islands with a total number of widespread subfamilies equal or higher than this value were considered to fulfil this criterion.

Criterion 2: Congruence with established species–area relationship patterns

The departure of the observed richness values from well-established ecological and/or inventory effort models can be used to determine which inventories might be reliable (e.g. Hortal *et al.*, 2001, 2007; Lobo & Martín-Piera, 2002; Garcillán *et al.*, 2003; Soberón *et al.*, 2007). The increase in species richness with increasing area (i.e. species–area relationship, SAR) is one of the most studied patterns in ecology (Schoener, 1976; Rosenzweig, 1995, 2003; Lawton, 1996, 1999). Its generality makes it appropriate to identify areas with abnormally low recorded numbers of species (see Garcillán *et al.*, 2003).

The slopes of the SAR for islands within archipelagos (herein, ISAR) are usually between 0.25 and 0.35, although values between 0.2 and 0.45 are not uncommon (see reviews in, e.g., Rosenzweig, 1995; Whittaker & Fernández-Palácios, 2007). However, the slopes of the ISARs vary depending on the dispersal abilities and life histories of each particular group (e.g. Ricklefs & Lovette, 1999). ISARs recently reported for parasitoid faunas show slopes ranging from 0.3 to 0.6 (see Table 2.2 in Chapter 2). Based on these results and the review by Rosenzweig (1995), we assumed that the inventory from any island with a SAR ratio (log species richness / log island area) lower than 0.2 is evidently incomplete and does not pass this criterion. Given that the range of ISAR slopes reported in the literature has also an upper limit, we also used SAR ratios to identify which islands might have been so intensively inventoried that could be unsuitable for comparison with the rest of

the studied areas (i.e., oversampled *sensu* Lobo & Martín-Piera, 2002). All islands with a SAR ratio greater than 0.65 were thus regarded as being potentially oversampled.

Criterion 3: Publication effort

Detailed descriptions of the sampling effort, including direct (e.g. number of traps or field days), and indirect measures (e.g. accumulated number of records or captured specimens) are often used to determine the completeness of inventories (see, e.g., Garcillán *et al.*, 2003; Hortal & Lobo, 2005; Lobo, 2008). Like most taxonomic databases, Taxapad does not include information on the number of times each species has been recorded. A proxy measure for sampling effort could be the number of taxonomic publications devoted to the inventory of each area, under the assumption that it is correlated with sampling effort. We evaluated the capacity of the total number of pages of the publications to represent the sampling effort devoted to each island. We represented this measure against species richness in a log-log plot to identify whether the rate of accumulation of new species in the inventory with additional published pages shows a decreasing trend, similar to species accumulation curves (Soberón & Llorente, 1993; Hortal & Lobo, 2005). When the accumulation of new published pages does not relate with an increase in the number of species inventoried, we will assume that the completeness of the inventory is high (see Hortal *et al.*, 2007). To avoid the spurious effects due to the disparity in size of the islands, we standardized all variables by area. We chose not to use the number of publications alone because short notes would contribute just as much as detailed monographs, thereby inflating the effort estimates. In contrast, using the number of pages provides a natural weighting in favour of more exhaustive works.

Categorisation of inventories according to different criteria

Islands were assigned a score of 0, 1, 2 or 3, depending on how many of the aforementioned criteria were fulfilled. Islands that passed all criteria were given the maximum score of 3. Similarly, islands that fulfilled any two, only one or none of the criteria were given scores of 2, 1 or 0, respectively. Only islands assigned with the two highest scores (2 and 3) were considered to be evenly inventoried, and therefore suitable for future large-scale analyses of their parasitoid faunas. Data from islands with lower scores (1) could be suitable for these

analyses too, but should be discarded if they appear as outliers. Islands with a score of zero should be discarded from any future analyses.

All analyses were carried out using STATISTICA 6.1 (StatSoft, 2003). Maps were drawn using Idrisi Kilimanjaro GIS software (Clark Labs, 2004).

3.4. Results

Braconidae

Of the 118 islands represented in Taxapad, 105 include records of braconid species. A total of 41 subfamilies and 5,255 species have been recorded for these islands. The number of common subfamilies used in the first criterion varied according to the biogeographic region, ranging from eight in both Indomalaya and the Neotropics, to 11 in the Palaearctic, with the Agathidinae, Cheloninae and Microgastrinae being the only widespread subfamilies present in every biogeographic region. The threshold used in criterion 1 to establish the minimum number of common subfamilies that a sufficiently inventoried island should include in each region ranged from three to eight (see Figs. 3.2c to 3.2f). In total, 48 islands fulfilled this criterion: three from the Afrotropics (30% of all islands in this region), eight from Australasia (30%), 13 from Indomalaya (62%), two from the Nearctic (67%), eight from the Neotropics (33%) and 14 from the Palaearctic (70%).

Regarding the second criterion, 14 out of the 105 islands were excluded *a priori* because only one species was recorded from them. From the rest, 18 had a SAR ratio lower than the threshold of 0.2 (dashed line in Fig. 3.3a), and four (Bermuda, Grenada, Saint Vincent and Singapore) higher than the upper threshold of 0.65 (dotted line in Fig. 3.3a), leaving 69 that were neither insufficiently inventoried, nor oversampled. The number of published pages was highly positively correlated with the number of species inventoried (Spearman $R = 0.91$, $p < 0.001$). However, the plots show no consistent pattern of decrease in the rate of accumulation of new species with new published pages, except for a small number of islands (Fig. 3.4a). Only thirteen islands complied with the publication effort criterion (see Appendix A1.1).

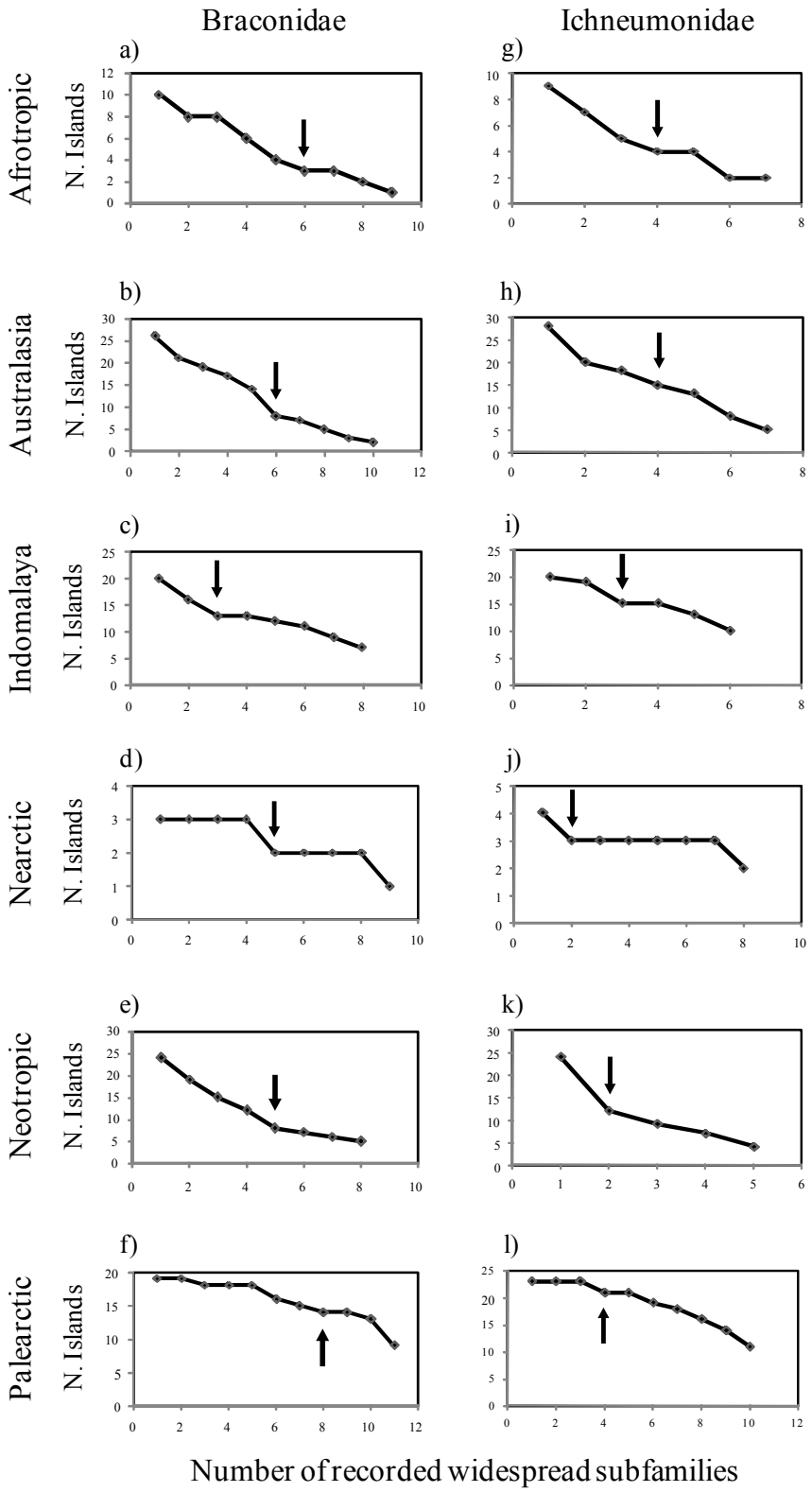


Figure 3.2. The number of widespread subfamilies per accumulated number of islands. The arrow indicates the threshold value used to establish the minimum number of widespread subfamilies an island should harbour to pass the completeness at higher taxonomic level criterion.

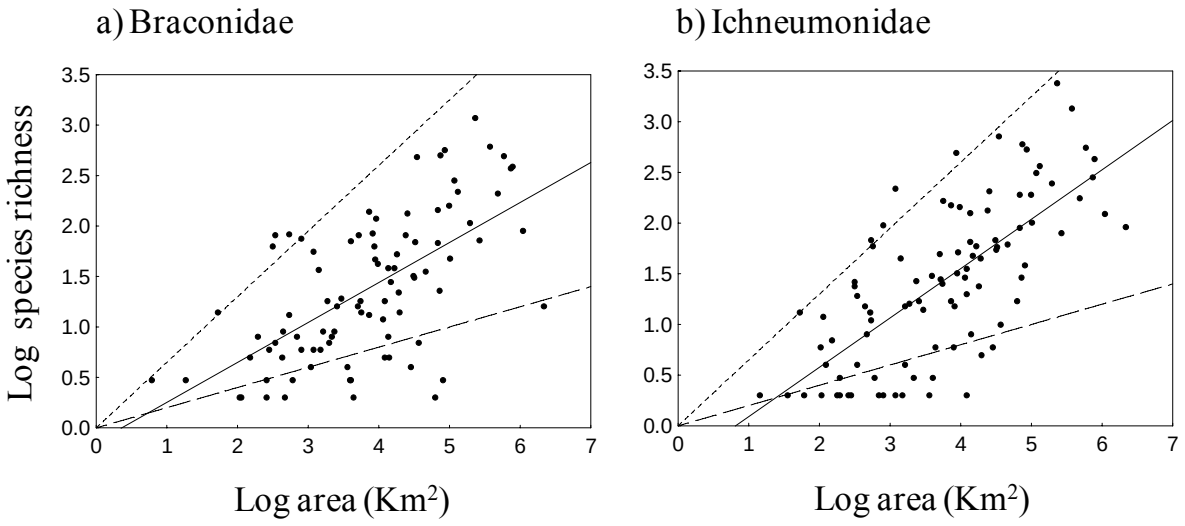


Figure 3.3. Observed (continuous line) and theoretical (dotted and dashed lines) species–area relationships for a) the Braconidae and b) the Ichneumonidae inventories of islands worldwide. Each black point represents an island. The dotted line has a slope of 0.65 while the dashed line has a slope of 0.2. Islands over the lower line are considered sufficiently inventoried, and those over the upper threshold as potentially oversampled (see text).

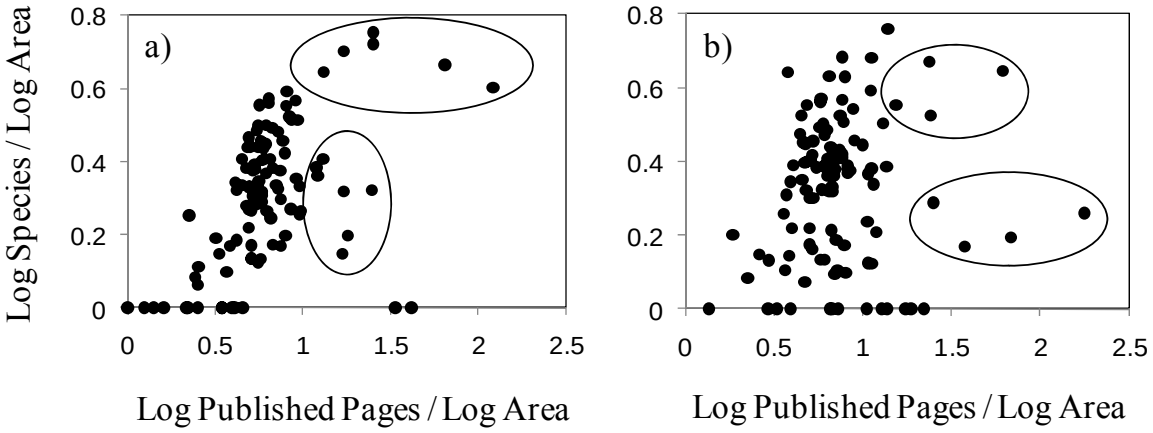
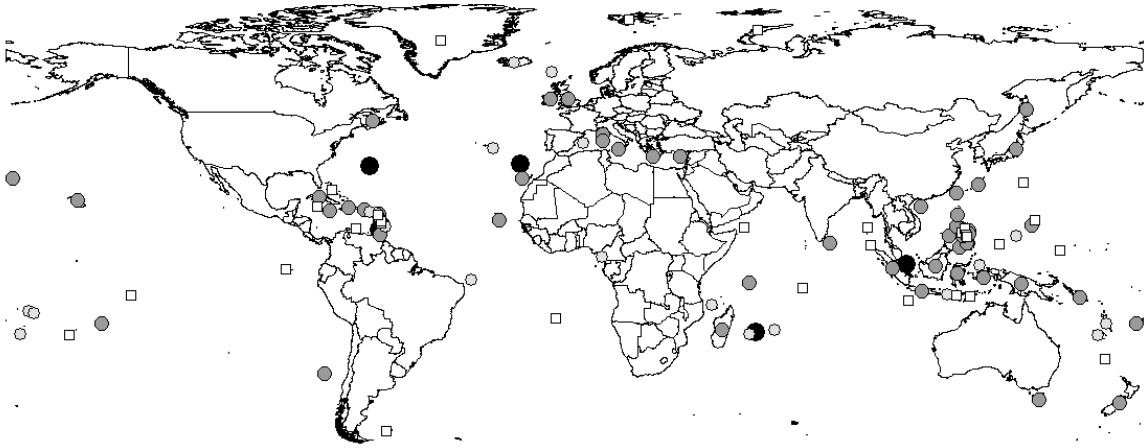


Figure 3.4. The relationship between the observed number of species and the number of published pages from each island on a log-log scale standardised by island area, for a) the Braconidae and b) the Ichneumonidae. The circles indicate those islands that have received an important amount of effort in relation to their area.

After applying the three criteria only 53 islands (50% of the islands with records of braconid species) were scored with the two highest levels (Fig. 3.5a) (see Appendix A1.1). While the Indomalayan, Nearctic and Palaearctic regions had more than half of their islands scored with one of these two high levels (62%, 67% and 70%, respectively), the other three regions only had around 40% of their islands ranked within these levels. Twenty-two islands were scored as level 1, and 30 failed to pass any of the criteria (Fig. 3.5a; see also Appendix A1.1).

a) Braconidae



b) Ichneumonidae

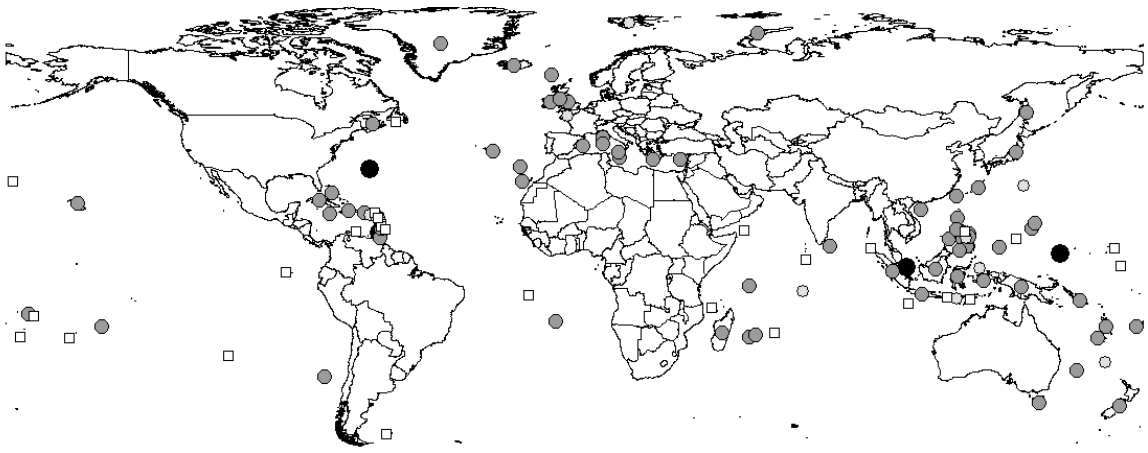


Figure 3.5. The geographical distribution and scoring level of the islands that have a) braconid species (Braconidae) and b) ichneumonid species (Ichneumonidae). Each point represents an island, and the symbols and shades of grey indicate the scoring value. These are as follows: White squares = islands with no score; small light grey circles = islands with score 1; medium grey circles = islands with score 2; black circles = islands with score 3. Islands with scores 2 and 3 can be considered sufficiently inventoried.

Ichneumonidae

One hundred and ten islands have records of ichneumonids, comprising 36 subfamilies and 7,406 species. The number of widespread subfamilies in each biogeographic region ranged from five (in the Neotropics) to ten (in the Palaearctic) and Campopleginae and Pimplinae were the only subfamilies present in every biogeographic region. Figures 3.2g to 3.2l show the decline in the number of islands that host progressively more widespread subfamilies. The thresholds identified here to determine the minimum number of widespread subfamilies that an evenly inventoried island should include varied from two to four. However, the threshold was not always easily established, because the slope of the relationship between the number of accumulated widespread subfamilies and the number of islands did not always reach an evident plateau (e.g. for Australasia and Palaearctic regions; see Figs. 3.2h and 3.2l). Nevertheless, 70 islands fulfilled this criterion: four from the Afrotropics (40% of all islands in this region), 15 from Australasia (52%), 15 from the Indomalayan region (75%), three from the Nearctic (75%), 12 from the Neotropics (50%) and 21 from the Palaearctic (91%).

Thirteen islands were discarded because only one icheumonid species had been recorded there. Twenty out of the remaining 97 islands had SAR ratios that fell below the 0.2 criterion (dashed line in Fig. 3.3b), and were thus discarded. In total 77 islands fulfilled the SAR criterion, from which Corsica, Madeira, Okinawa and Singapore fell above the 0.65 SAR ratio threshold (dotted line in Fig. 3b), indicating that they might be outliers due to oversampling. As with the braconids, the number of published pages was highly positively correlated with the number of species inventoried (Spearman $R = 0.85$, $p < 0.001$). Again, except for a small subset of islands (Fig. 3.4b), the plots show no consistent decrease in the rate of new species accumulation with new published pages. Only eight islands complied with the publication effort criterion (see Appendix A1.2).

Considering all criteria, 70 islands (64% of the total number of islands with ichneumonid species) were scored with the two highest levels, and were considered evenly inventoried, and thus comparable as a group (see Fig. 3.5b and Appendix A1.2). All regions except the Afrotropics and the Neotropics (50% and 42%, respectively) had more than half of their islands scored with one of these two levels (Australasia – 55%; Indomalayan – 68%; Nearctic – 75%; Palaearctic – 91%). Eleven islands were scored as level 1 and 29 did not pass any criteria (see Fig. 3.5b; Appendix A1.2).

3.5. Discussion

Bias and incompleteness in biodiversity inventories

Although parasitic wasps are key components of nearly all terrestrial ecosystems (LaSalle & Gauld, 1993), their macroecological and evolutionary patterns have been scarcely studied outside of a few temperate and tropical areas, mainly because of the inherent difficulty of working with an hyperdiverse group with complex biological interactions and whose taxonomy is far from complete. Further, it is likely that unevenness in the effort devoted to their inventory and systematics (see, e.g., Gaston, 1993; Jones *et al.*, 2009; Baselga *et al.*, 2010) has prevented from developing large-scale analyses of their diversity patterns (but see, e.g., Hawkins, 1994, and references therein).

Many factors can affect the process of inventorying and describing species, and therefore the quality of taxonomic databases. The characteristics of the species affect their probability of being inventoried. For example, body size, abundance, geographical range and ecological requirements (e.g. trophic and habitat ranges) are all known to influence species discovery (Gaston, 1991b, 1993; Gaston & Blackburn, 1994; Patterson, 1994; Blackburn & Gaston, 1995; Gaston *et al.*, 1995; Cabrero-Sañudo & Lobo, 2003; Collen *et al.* 2004; Adamowicz & Purvis, 2005; Baselga *et al.*, 2007, 2010; Guil & Cabrero-Sañudo, 2007; Jiménez-Valverde & Ortuño, 2007; Jones *et al.*, 2009). In addition, geographical biases in survey effort are the rule rather than the exception (see, e.g., Dennis *et al.*, 1999; Dennis & Thomas, 2000; Hortal *et al.*, 2007, 2008a; Lobo *et al.*, 2007; Baselga *et al.*, 2010). In general, northern temperate areas have been more thoroughly studied than the tropics or south temperate regions (Gaston, 1994; Allsop, 1997; Medellín & Soberón, 1999; Cabrero-Sañudo & Lobo, 2003; Collen *et al.*, 2004; Adamowicz & Purvis, 2005; Gibbons *et al.*, 2005; Baselga *et al.*, 2007; Guil & Cabrero-Sañudo, 2007). This bias also seems to be common to the parasitoids (e.g. Gaston, 1993; Jones *et al.*, 2009; Baselga *et al.*, 2010), and is further confirmed by our results (see Fig. 3.5 and Appendix A1.1 and A1.2). Surveys may also be biased at smaller spatial scales. Survey effort is usually higher near recorders' home ranges, work centres, roads and railway stations, or simply in more accessible natural areas (Prendergast *et al.*, 1993; Allsop, 1997; Dennis *et al.*, 1999; Dennis & Thomas, 2000; Kadmon *et al.*, 2004; Diniz-Filho *et al.*, 2005; Jiménez-Valverde & Ortuño, 2007; Sánchez-

Fernández *et al.,* 2008; Baselga *et al.*, 2010). These biases seriously compromise the description of species distributions, as well as the representation of their environmental responses (Lobo *et al.*, 2007; Hortal *et al.*, 2008a; Jiménez-Valverde *et al.*, 2008; D. Rocchini *et al.*, in press).

Identifying evenly inventoried areas

Several methods have already been developed to identify and account for different types of bias and limitations of biodiversity data. The most developed ones make use of several measures of sampling effort, such as the number of survey records, individuals or traps, in combination with species accumulation curves (e.g. Soberón & Llorente, 1993; Lobo & Martín-Piera, 2002; Hortal *et al.*, 2004, 2008a; Hortal & Lobo, 2005), or other relationships with survey effort (Hortal *et al.*, 2001, 2007; Lobo & Martín-Piera, 2002; Garcillán *et al.*, 2003), including species richness estimators (Petersen *et al.*, 2003; Soberón *et al.*, 2007; Lobo, 2008). However, these methodologies usually involve the use of detailed data on the surveys, which is not always accessible, especially in taxonomic databases, such as in the case study presented here. This hampers analyses of survey completeness, thereby limiting the reliability and usefulness of some databases for macroecological studies. In such cases, it is necessary to develop new methods that allow meaningful comparisons of species inventories from different areas without the need for detailed information on the recording process.

Here we presented a protocol based in three criteria, covering the three main aspects that we believe that, ideally, characterize a reliable inventory: (i) lack of evident biases towards particular taxa, (ii) congruence with well-established ecological relationships, and (iii) origination from works involving enough sampling effort to be potentially complete. The criterion of completeness at higher taxonomic levels accounts for the effort made in describing and inventorying species from different high-level taxa (in this case, subfamilies), taking into consideration that each region has its own colonization and evolutionary history, and therefore its own taxonomic composition (see, e.g., Ricklefs, 2007). The most important drawback in the use of this criterion relates to how we determine which particular components an inventory must have to be considered reliable. Our sequential approach of first determining how many subfamilies are widespread in the island faunas of the region,

and then establishing the minimum number of widespread subfamilies an island should have to be considered as evenly inventoried from the decay in their recorded numbers (see Fig. 3.1) is a plausible and easy-to-implement approach. However, identifying the point at which this decay pattern changes from being the outcome of biogeographical processes to being a consequence of undersampling can prove difficult sometimes (as evidenced by, e.g., the case of the ichneumonids from Australasia and Palaearctic, Figs. 3.2h and 3.2l). This has the unfortunate effect of adding some undesired subjectivity to this criterion. Also, exceptionally, some islands might truly host less widespread subfamilies due to other causes than being poorly inventoried (e.g. biogeographical factors), and therefore fail to comply with this criterion despite being, in fact, well–inventoried. Nevertheless, we believe these cases are uncommon; the consistency with the islands selected with the SAR criterion provides some support to the adequacy of the choices made.

The rationale for our second criterion comes from the assumption that obvious outliers in well-established ecological relationships are unlikely to have been completely inventoried or nearly so. Perhaps the most adequate of these relationships is the species–area relationship, due to its generality. Several authors have used the SAR to determine the reliability of the observed species richness from a territory by comparing it with the general relationship found for other areas or well-sampled territories (e.g. Garcillán *et al.*, 2003; Petersen *et al.*, 2003; Roos *et al.*, 2004; Adamowicz & Purvis, 2005; Nikolić *et al.*, 2008). This seems especially appropriate for islands, where land area is known to be one of the most important, although not universal, determinants of species richness (reviewed in, e.g., Whittaker & Fernández-Palacios, 2007). However, this method requires that observed species richness is compared with the extrapolation from the SAR of a well-studied area. Since in our case study there was no *a priori* knowledge of which areas are well sampled, it was not possible to extrapolate the number of species that might be *missing* from a particular island. Given the large body of knowledge on ISARs, our alternative solution is to use theoretical thresholds (e.g. lower and upper SAR ratio thresholds of 0.2 and 0.65, respectively) to determine when the inventory from any island is poorer, or richer, than should be expected given its area. We use an upper threshold to give cautionary advice about oversampled areas, which might not be comparable to the rest of the less-well (but sufficiently) inventoried ones (see Lobo & Martín-Piera, 2002). Thus, although we

recommend discarding data from areas with a SAR ratio of <0.2, we also flag those that have a SAR ratio of >0.65 and would recommend that, rather than omitting them entirely, they should only be discarded if they appear as outliers in other analyses. Islands that are truly species–poor could be incorrectly excluded by this criterion. However, since parasitoids typically show ISAR slopes higher than 0.3 (see, e.g., Chapter 2), such incorrect exclusions should be rare or nonexistent.

The publication effort criterion is intended to act as a proxy for sampling effort (see, e.g., Hortal *et al.*, 2007; Soberón *et al.*, 2007). However, implementing this kind of criterion using taxonomic databases can be more difficult than expected. In our case, Taxapad only provides information on the total number of pages per publication, but no detailed record on the specific number of pages that refer to a particular island or territory. This could explain why we were unable to identify any patterns of decreasing rate of species accumulation with increasing number of published pages, except for a few islands that have received an important amount of effort in relation to their area. These problems are probably common to many databases and evidence that the implementation of a criterion based on the intensity of inventory effort needs more detailed information on the surveys than that available in most taxonomic databases (see Discussion in Hortal *et al.*, 2007).

Although we have specifically applied our protocol to islands, the generality of its principles may make it easy to adapt to mainland areas, such as countries or biogeographical provinces, and/or to other taxa. Its importance lies in the fact that only requires information on the species inventory and a few general characteristics of the areas, allowing the use of checklists that normally would be considered unsuitable for macroecological studies. Furthermore, by scoring areas instead of simply discarding some of them, this protocol can be useful for identifying different levels of uncertainty, that could be used to weight the areas in regressions or other analyses. Such scoring could also be used to allocate field and taxonomic resources. Of course, our method, like any other, has its limitations. It only allows the identification of which inventories are comparable in terms of taxonomic effort, rather than identifying well-surveyed areas. Therefore, its use within large-scale conservation assessments should be discarded (or used with caution), because these analyses need detailed and accurate results if they are to be used for decision-making. Nevertheless, we believe this

protocol might be adequate as a previous step for many analyses of macroecological patterns, as evenly inventoried areas identified this way can be reliably used for large-scale analyses.

Chapter 4: Species pool structure determines the level of generalism of island parasitoid faunas[3]

4.1. Abstract

Although ecological relationships may play a determinant role in shaping diversity gradients, geographical variations in community structure are poorly studied. Island biotas are useful for identifying and understanding the factors shaping community structure. Here we examine whether island parasitoid faunas are biased towards generalists, and evaluate the effects of different environmental, physiographic and regional factors on the relative proportions of idiobionts (i.e. generalists) and koinobionts (i.e. specialists) of two parasitic wasp families, Braconidae and Ichneumonidae. Islands host comparatively more idiobionts than continental areas. However, although there is a latitudinal gradient in the level of generalism of island faunas correlating with both environmental factors and island characteristics, the most important determinant of island community structure for both families is their source pool. This effect is stronger for ichneumonids, and is probably associated with the large rainforests of the Indomalayan region, arguably due to the significant utilization of endophytic hosts by idiobionts, highlighting the complex nature of geographical gradients in community structure.

[3]This chapter is the basis of: Santos, A.M.C., Quicke, D.L.J., Borges, P.A.V. & Hortal, J., which is a manuscript that has been submitted for publication.

4.2. Introduction

Geographical variations in biological diversity are known to be driven by a number of biotic and abiotic factors. These include environmental gradients (climate and habitat) and the physical characteristics of each site or region (e.g. area, isolation, habitat diversity and topographic and landscape heterogeneity), in addition to regional processes and historical events, that determine the characteristics and evolutionary history of the species present in the regional pool (e.g. Ricklefs, 1987, 2004, 2007; Rahbek & Graves, 2001; Hawkins *et al.*, 2003; Hortal *et al*., 2008b). However, most current knowledge on diversity gradients is based on the study of variations in species richness and, to a lesser extent, a few morphological and ecological traits (e.g. Traynor & Mayhew, 2005; Diniz-Filho *et al*., 2009). In fact, relatively little is known about the determinants of the spatial and temporal distributions of other aspects of diversity, such as the functional structure of communities or ecological interactions (Roy *et al.*, 2004; but see, e.g., Cardillo, 2002; Rodríguez *et al.*, 2006; Heino *et al.*, 2007; Schemske *et al.*, 2009; Warren *et al.*, 2010). This is especially true for invertebrates and particularly for many insect groups, including parasitoids (but see, e.g., Hawkins, 1994).

Parasitoids are insects that develop to adulthood by feeding on the body of an arthropod host, eventually killing it (Quicke, 1997). Their high diversity, coupled with a large variation in life history traits, makes them a key component of nearly all terrestrial ecosystems (LaSalle & Gauld, 1991, 1993; Hassell, 2000b). Surprisingly, several studies suggested that the species richness of some parasitoid groups does not increase towards the tropics (Owen & Owen, 1974; Janzen & Pond, 1975; Janzen, 1981; Gauld, 1986; Hawkins *et al.*, 1992; Quicke & Kruft, 1995; Bartlett *et al.*, 1999; but see Noyes, 1989; Askew, 1990), contrary to the geographical gradients observed in many other taxa (e.g. Stevens, 1989; Rosenzweig, 1995; Hawkins, 2001; Hillebrand, 2004). However, the possibility that these findings represent artefacts of the limited sampling effort and/or the level of taxonomic treatment received cannot be excluded (see Jones *et al.*, 2009; Baselga *et al.*, 2010). In an attempt to understand this possible pattern, Hawkins (1990, 1994) and Hawkins *et al.* (1992) showed that the latitudinal trends of parasitoid species richness are influenced by the host feeding niche and by the variation in a particular life history trait, the dichotomy between

idiobiosis and koinobiosis. This dichotomy largely determines the trophic width (i.e., generalism) of each species: while idiobionts are usually ectoparasitic, have broader host ranges (i.e. they are generalists) and attack concealed hosts, koinobionts, in contrast, are typically endoparasitic, have narrower host ranges (i.e. they are specialists) and tend to attack hosts in a more exposed situation (Askew & Shaw, 1986).

In this work we investigate the geographical variation in the relative proportions of idiobionts and koinobionts on island parasitoid communities. Island biotas are known to be species–poor and disharmonic when compared to the mainland (Williamson, 1981; Whittaker & Fernández-Palacios, 2007). Typically, interspecific competition tends to be low on islands, and entire groups of predators, parasitoids or pathogens are absent from their biotas, causing the ecological space to be often not fully saturated. Consequently, colonising species are subject to different evolutionary and ecological processes (e.g. ecological release, density compensation, niche expansion and niche shifts) that result in the species from island assemblages often using a wider range of resources than their counterparts from the source mainland (Whittaker & Fernández-Palacios, 2007), in what seems to be a common pattern (e.g. Diamond, 1970; Kitahara & Fujii, 1997; Olesen *et al*., 2002; Olesen & Valido, 2003b; Scott *et al.*, 2003; Ribeiro *et al.*, 2005a). It is likely that colonising parasitoids are subject to these same processes, often being forced to use unusual or novel hosts due to the lack of preferred ones. Therefore, it can be expected that island parasitoid faunas include a comparatively high proportion of generalist species (i.e. idiobionts), when compared to their mainland counterparts.

Here we examine whether island parasitoid communities are biased towards generalist species in comparison to the mainland and their adjacent species pool. To do so, we use a database on the taxonomy and worldwide distribution of two parasitoid families, the Braconidae and Ichneumonidae, and the ratio between the number of idiobiont and koinobiont species as a proxy for the level of generalism. We also examine whether some of the factors that usually control the assembly of island faunas, such as isolation, area, environmental variations and composition of the species pool, also have an affect on the ratio between idiobionts and koinobionts on islands.

4.3. Methods

Data source

Data on the distribution of braconid and ichneumonid species were obtained from Taxapad (Yu *et al.*, 2005), a digital catalogue that includes information from all literature published on these two families until 2004 (see http://www.taxapad.com/ for more details). Island species checklists in Taxapad are organised by archipelagos, single island nations or other administrative units. Following the results of Chapter 2, we will consider both archipelagos and islands to be comparable units (herein called islands for simplicity). The checklists from islands with several political subdivisions (e.g. Borneo, Hispaniola, New Guinea) were combined to give single data points. Since the data in Taxapad may provide incomplete inventories for some areas, in a former work we identified the islands with comparable inventories (Chapter 3). Only 53 and 70 islands have comparable inventories of Braconidae and Ichneumonidae species, respectively, and were therefore used for the analyses.

After examining several ways of identifying the territories that conform the potential species pool of a given island (varying the geographic extent of the pool and/or including only mainland areas), a distance radius of 1,000 km that included both islands and mainland provided the most realistic description, according to the geographical location of most islands. We defined the species pool for each island as the species found in all territories occurring within 1,000 km of each island; if an island was located more than 1,000 km from the mainland, we also included the species from the most likely source mainland area in the species pool (see Appendix A2.1).

The level of generalism of the parasitoid faunas (i.e. our response variable) was measured as the ratio between the number of idiobiont and koinobiont species (herein *I/K ratio*); the higher the value of this ratio, the higher the level of generalism of the parasitoid community. Species from both islands and species pools were classified as either idiobionts or koinobionts, and also as ectoparasitoids or endoparasitoids (Appendices A2.2 and A2.3). This classification was based on the life history data available from a number of literature sources (see Appendices A2.2 and A2.3), and was also reviewed by DLJQ, M.R. Shaw and G.R. Broad. In most cases, such classification was made at the subfamily level, as only a few subfamilies contain both idiobionts and koinobionts or ectoparasitoids and endoparasitoids

(Hawkins *et al.*, 1992). In these cases, this classification was applied to tribe or genus level as appropriate. Introduced species, subspecies and synonyms were excluded from all analyses.

We used several climatic, physiographic and regional factors as predictors of the level of generalism. Climate was described by means of average temperature (*Temp*) and annual precipitation (*Prec*), obtained from Worldclim (Hijmans *et al.*, 2005) in a GIS environment. The physiographic factors included two categorical and four continuous variables: (i) whether an "island" was composed of only one island or was an archipelago (*Archipelago*); (ii) the geological origin of the island (*IslType*), namely oceanic (i.e., both true oceanic islands and continental fragments *sensu* Whittaker & Fernández-Palacios, 2007, following Wallace, 1902), mixed or continental; (iii) island area (*Area*); (iv) highest altitude, measured from sea level (*Alt*); (v) distance (in km) to the closest larger territory (either island or mainland; *DistArea*); (vi) distance (in km) to the closest mainland (*DistMainl*). *Area* was obtained as in Chapter 3, *Alt* was obtained from several sources, including the UNEP Island Directory (http://islands.unep.ch/isldir.htm), Wikipedia (http://en.wikipedia.org/) and GPS visualizer (http://www.gpsvisualizer.com/geocode/), and *DistArea* and *DistMainl* were obtained from Google Earth (http://earth.google.co.uk/). We accounted for regional factors by means of one categorical variable, the biogeographic realm (as defined by Moss & Wilson, 1998 and Cox, 2001) where the island is located (*Region*), and two continuous variables, the island species richness (*RichIsl*) and the level of generalism (i.e. *I/K ratio*) of its species pool (*SpeciesPool*). Finally, we used the absolute value of latitude (*AbsLat*) to evaluate the potential existence of a latitudinal structure in the response variable. All these variables are presented in Appendices A2.4 and A2.5.

Analyses

The *I/K ratio* and the ratio ectoparasitoids/endoparasitoids per island were highly correlated in both families (Braconidae: Spearman $R = 0.999$, $p < 0.001$; Ichneumonidae: Spearman $R = 0.656$, $p < 0.001$). Given that the idiobiont/koinobiont dichotomy is more useful in explaining the level of generalism of parasitoids than ecto versus endoparasitism (Askew & Shaw, 1986), the subsequent analyses refer only to the *I/K ratio*.

Chi-square tests were used to evaluate whether the relative proportions of idiobiont and koinobiont species differed between islands and mainland as a whole. Island faunas were also compared to their species pool using a Wilcoxon matched pairs test.

The effects of the environmental, physical and regional predictors on *I/K ratio* were assessed using regression analyses. Both the response variable and *SpeciesPool* were transformed into log(idiobionts+1/koinobionts+1) in order to normalize model residuals. Preliminary analyses using other transformations (logarithm of *I/K ratio* + 1, and arcsin of the proportion of generalists) gave conspicuously non-normal residuals, and therefore were discarded. The remaining continuous variables were standardized to mean = 0 and standard deviation = 1. Level of generalism was regressed against each independent variable individually using generalized linear models (GLMs). The quadratic function of each continuous variable was also examined in order to account for possible curvilinear relationships. All significant variables (with the exception of *AbsLat*) were submitted to a two-fold model selection process. First, all possible models based on continuous variables were compared by means of their partial Akaike weighting (using the small sample size-corrected Akaike index, AICc; see Burnham & Anderson, 2002; Diniz-Filho *et al.*, 2008). The model with the lowest value of partial Akaike weighting was retained, in order to select the most parsimonious model in a trade-off between complexity and information. The final model was chosen by submitting the selected model and the significant categorical variables into a backwards step-wise analysis.

We evaluated whether the variables chosen in the final model account for the spatial structure in the variations of level of generalism by comparing the pattern of spatial autocorrelation in the original data with that of the residuals of the final model (Diniz-Filho *et al.*, 2003). To do this, we generated correlograms based on Moran's *I* coefficient. The absence of significant levels of spatial autocorrelation in the residuals indicated that all spatial structure in the data is explained by the variables included in the final model (Diniz-Filho *et al*., 2003).

Given that many geographical gradients in diversity are known to be latitudinally structured, we used partial regression analyses (Legendre & Legendre, 1998) to determine whether the final model obtained in the former analyses accounts for all the latitudinal structure in *I/K ratio*. Briefly, all the variables in this model were regressed against *AbsLat*

using GLMs; where appropriate, *Region* was added as a set of dummy variables (i.e. one dummy variable per region minus one). The residuals of these regressions were retained to account for the part of the variability of the predictors of the final model that is unrelated to *AbsLat*. Conversely, *AbsLat* was regressed against the final model and the residuals were kept to account for the latitudinal variation not explained by such model. Then, these residual variables were used as predictors of *I/K ratio*, using separately *AbsLat* and the variables from the final model to estimate their separate influences. Finally, we calculated the magnitude of the interaction between *AbsLat* and the final model using a simple system of equations (see full description and examples in Hawkins *et al.*, 2003; Hortal *et al.*, 2008b).

Apart from these general analyses, we identified which island faunas depart from the level of generalism of their respective species pools, by means of Chi-square tests. We evaluated whether any of the abovementioned factors determines that some islands have significantly higher or lower *I/K ratio* than their pools, using t-tests (for continuous variables) and Chi-square tests (for categorical variables).

All analyses were performed in STATISTICA 6.1 (StatSoft, 2003), except for the model comparisons with continuous variables and the correlograms, that were carried out in SAM 3.0 (Rangel *et al.*, 2010).

4.4. Results

The level of generalism of each island braconid and ichneumonid fauna is illustrated in Figure 4.1 (see also Appendix A2.5). When all territories are considered altogether, the proportion of generalists is greater in islands than in continental areas (Braconidae: χ^2 = 17.658, 1 d.f., $p < 0.001$; Ichneumonidae: $\chi^2 = 48.672$, 1 d.f., $p < 0.001$). However, the *I/K ratio* of island faunas was not significantly greater than that of their species pool (Braconidae: t = 511, $Z = 1.81$, $p = 0.07$; Ichneumonidae: t = 1050, $Z = 1.127$, $p = 0.26$). For the braconids, eight islands showed a significantly higher *I/K ratio* than their species pools, while in 12 islands it was significantly lower than on the relevant pool (Fig. 4.2a; Appendix A2.5). Similarly, nine islands showed significantly higher *I/K ratio* than their species pool for the ichneumonids, and nine other islands displayed the opposite trend (Fig. 4.2b; Appendix A2.5).

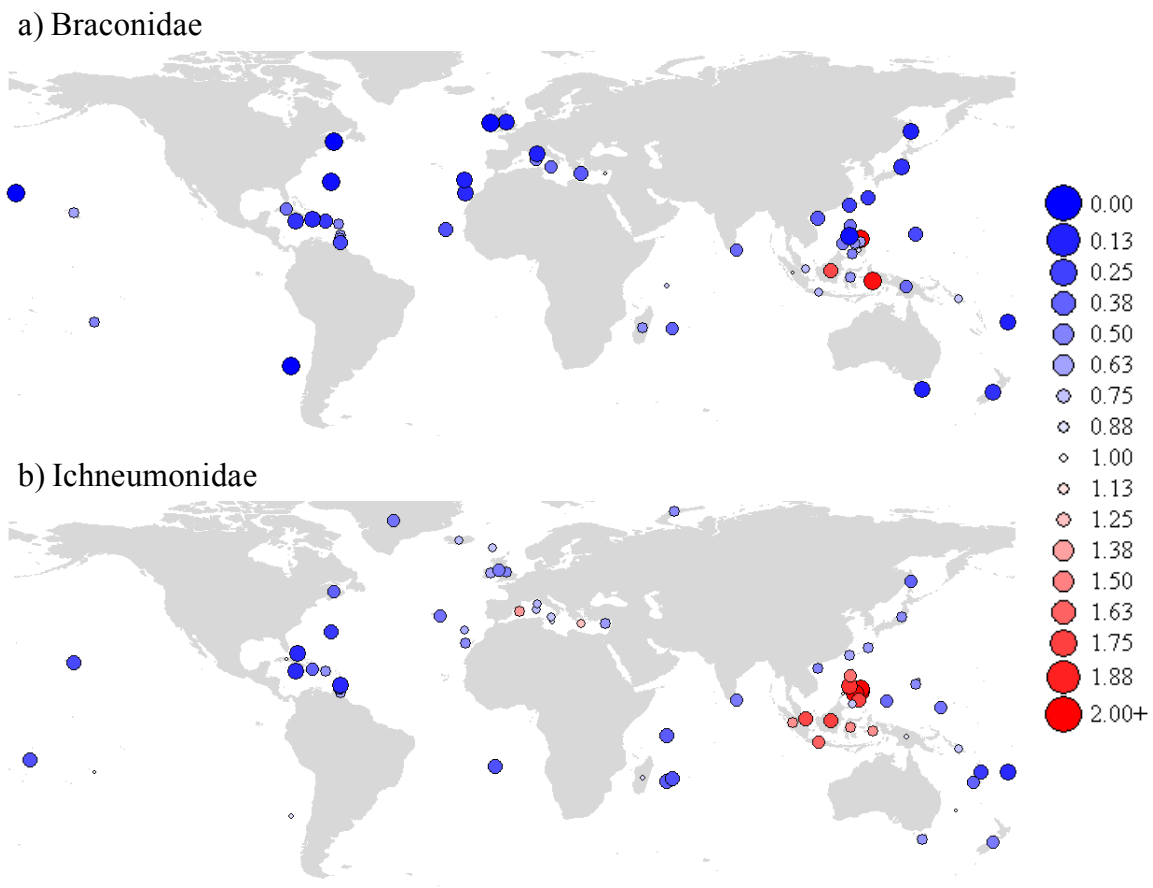


Figure 4.1. Level of generalism (measured as the ratio of idiobiont over koinobiont species, *I/K ratio*) of the island faunas of two parasitoid families: braconids and ichneumonids. The size and colour of the circles represent the level of generalism (blue – islands that have more specialist species; red – islands that have more generalist species).

Temp and *Prec* had significant positive effects on braconid *I/K ratio*, but not for ichneumonid *I/K ratio* (Table 4.1). Rather, ichneumonids were influenced by *DistArea* and *IslType*, with mixed islands showing a higher *I/K ratio*, followed by continental ones (Table 4.1). The level of generalism was influenced in both families by *AbsLat*, *Region* and *SpeciesPool*; *AbsLat* had a significant negative effect (Fig. 4.3), while *SpeciesPool* had a positive influence (Table 4.1). Indomalaya was the region where islands displayed higher levels of *I/K ratio* for braconids, followed by the Afrotropics, Australasia, Nearctic, Neotropics and Palaearctic; for ichneumonids, Indomalaya was also the region where islands show higher *I/K ratio*, followed by Australasia, Palaearctic, Neotropics, Afrotropics and Nearctic.

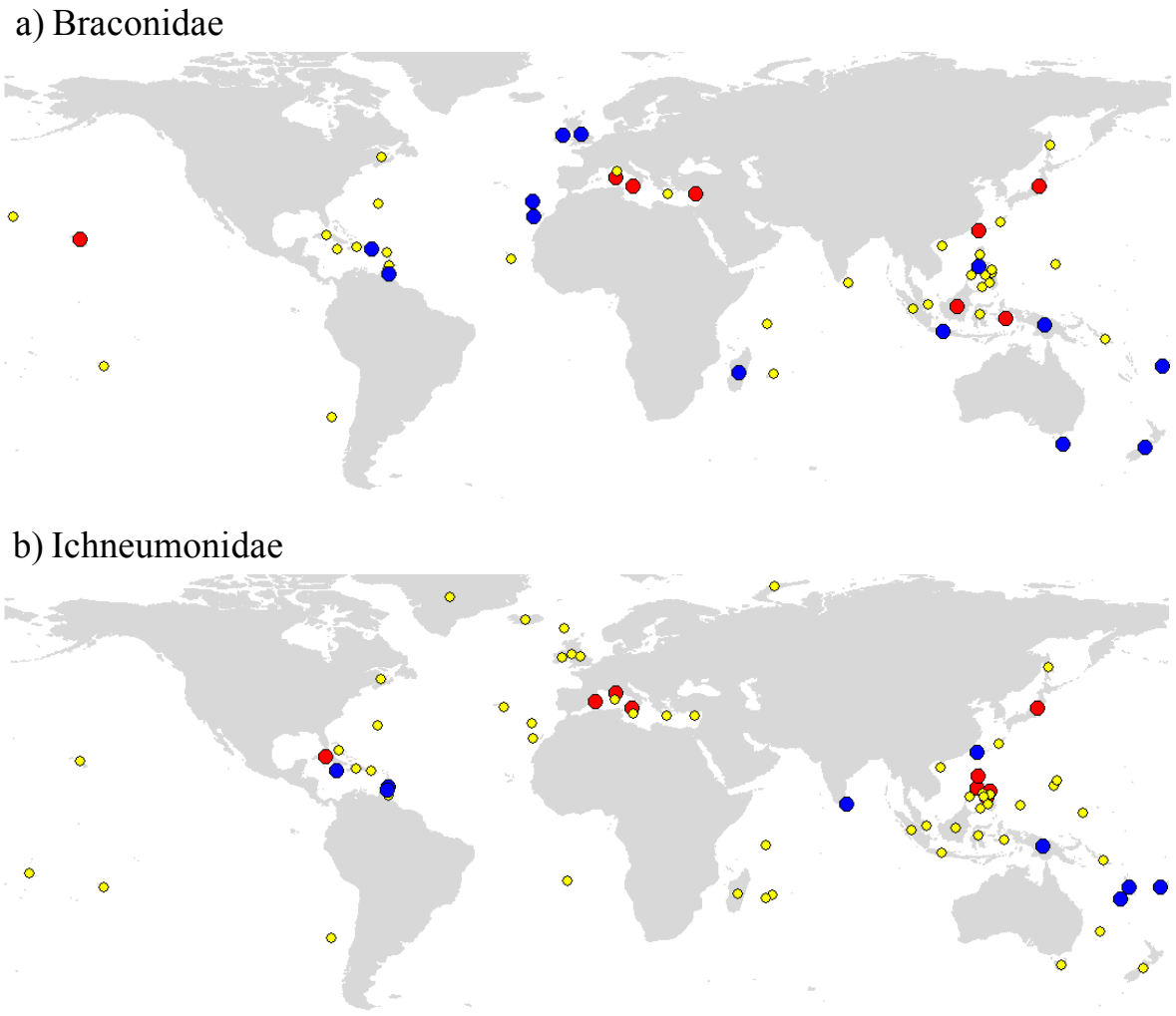


Figure 4.2. Departure of the level of generalism (*I/K ratio*) of island faunas from their correspondent species pool for both braconids and ichneumonids. Red circles represent islands with significantly higher level of generalism than their species pool; blue circles islands with significantly lower level of generalism than their pool; and yellow circles islands that not differ significantly from the level of generalism of their species pool.

For braconids, the final model included only *Temp* and *SpeciesPool* and explained 43.2% of the variance of *I/K ratio* on islands, while for ichneumonids, it comprised *Region* and *SpeciesPool*, which explained 53.2% of the variance (Table 4.1).

Table 4.1. Results of the regression analyses assessing the relationship between level of generalism (i.e., *I/K ratio*) and several factors for Braconidae and Ichneumonidae.

	Braconidae				Ichneumonidae			
Variable	**d.f.**	***F***	**Adj R^2**	**slope**	**d.f.**	***F***	**Adj R^2**	**slope**
Temp	51	38.382***	0.418	+	68	3.521	0.035	+
Temp+Temp²	50	18.876***	0.407	+ +	67	2.222	0.034	+
Prec	51	8.123**	0.120	+	68	3.108	0.030	+
Prec+Prec²	50	4.496*	0.119	+ -	67	1.683	0.019	+ -
Archipelago	51	0.020	-0.019		68	3.016	0.028	
IslType	50	0.953	-0.002		67	10.741***	0.220	
Area	51	1.570	0.011	+	68	0.159	-0.012	+
Alt	51	2.482	0.028	+	68	1.744	0.011	+
DistArea	51	0.032	-0.019	+	68	8.173**	0.094	-
DistMainl	51	0.862	-0.003	+	68	0.171	-0.012	-
Region	47	3.257*	0.178		64	14.430***	0.493	
RichIsl	51	3.139	0.040	-	68	0.006	-0.015	-
SpeciesPool	51	23.037***	0.298	+	68	28.376***	0.284	+
AbsLat	51	52.997***	0.500	-	68	5.962*	0.067	-
Final model								
Temp, SpeciesPool	50	20.741***	0.432					
Region, SpeciesPool					63	14.071***	0.532	

d.f. are the degrees of freedom; *F* is Fisher's *F* statistic; Adj R^2 is the adjusted R^2; slope is the slope of the relationship between level of generalism and the explanatory variables (+ indicates a positive relationship; - a negative relationship; and +- a hump-shaped relationship). * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Variable codes as in text.

Partial regressions showed the existence of strong covariance between the final models and latitude (*AbsLat*), indicating that these models account for the latitudinal gradient in *I/K ratio* (Fig. 4.4). The strong covariation of the predictors of *I/K ratio* and latitude was more evident for the braconids, for which the independent effect of latitude explained only 3.8% of the variation, and most of the variation could not be attributed either to the final model or to latitude. In contrast, the final model for ichneumonids showed a larger independence from latitude, and the independent effect of the model explained 39.3% of the variation. The final models also removed all significant spatial autocorrelation in short distance classes for both families (Fig. 4.5), indicating that no spatially structured variation in island *I/K ratio* remains unexplained.

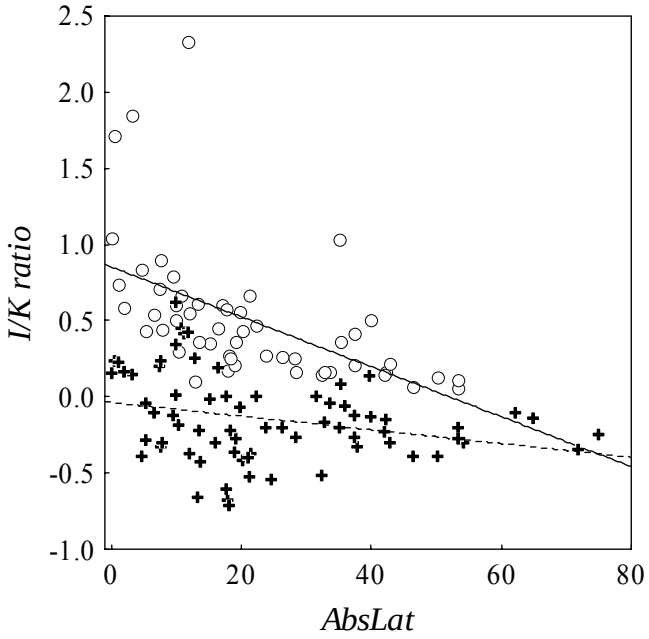


Figure 4.3. Relationship between the absolute value of latitude (*AbsLat*) and level of generalism (*I/K ratio*) for braconids (circles; continuous line) and ichneumonids (crosses; dashed line). Level of generalism is calculated as log(idiobionts+1/ koinobionts+1).

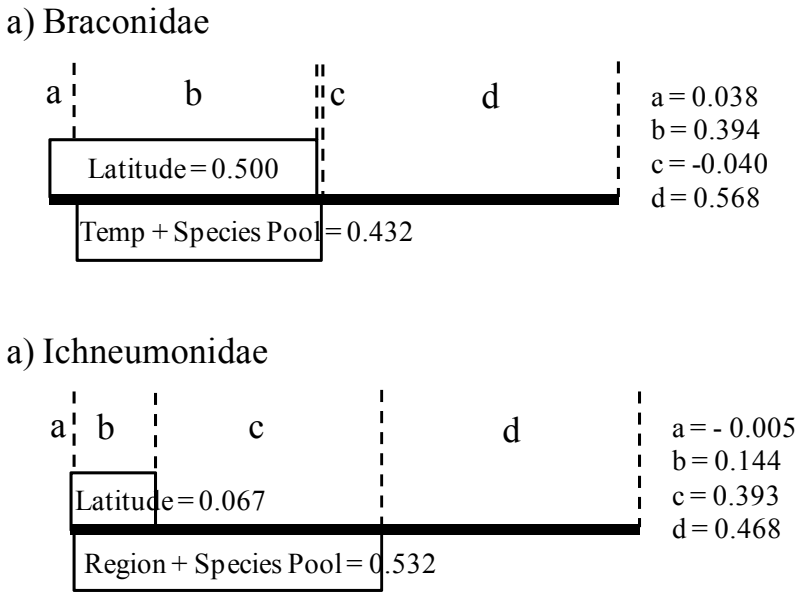


Figure 4.4. Results of the partial regression analyses relating the worldwide patterns of level of generalism on island parasitoids with the independent contributions of (a) latitude (absolute value of latitude) and (c) the final model (see Table 4.1), as well as their shared contribution (b). The unexplained variation d is 1 – adjusted R^2 of a GLM including latitude and the model. GLM results are listed in Table 4.1.

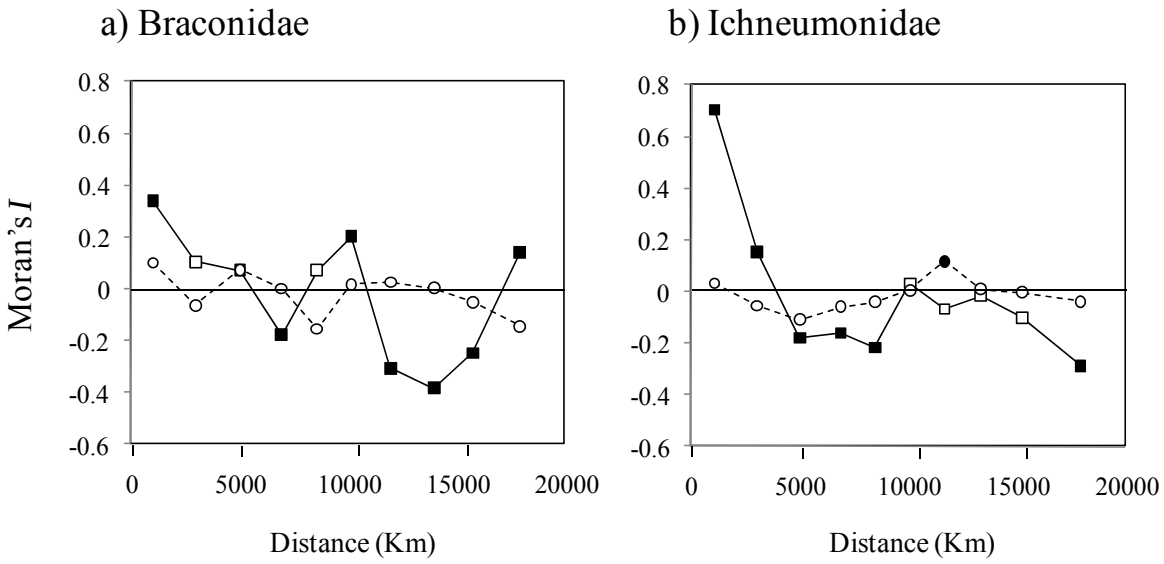


Figure 4.5. Correlograms for the level of generalism (squares, continuous line) and the residuals of the final model (circles, dashed line, see Table 4.1). Significant Moran's *I* scores are marked as filled symbols.

Islands with parasitoid faunas with significantly higher *I/K ratio* than their respective species pool had higher altitudes in the case of braconids, and were of mixed and continental origins in the case of ichneumonids (Appendix A2.6). In contrast, island faunas with a significantly lower *I/K ratio* than their respective species pool showed higher island species richness for braconids, and higher mean precipitation for ichneumonids (Appendix A2.7).

4.5. Discussion

Our results show that overall, island parasitoid faunas are more biased towards generalist species than mainland ones. However, this pattern is far from general, as many islands show the opposite trend. In fact, the little information available from field studies is also inconclusive. While Maetô & Thorton (1993) found a higher proportion of koinobiont species (i.e. specialists) in the recently colonized Anak Krakatau island, in Chapter 6 we found a higher proportion of generalists attacking the tortricid moth *Acroclita subsequana* on Macaronesian islands compared to the mainland.

The interaction between species throughout their distributions within a region is one of the most influential determinants of the species occurring locally (see Ricklefs, 2004, 2007). Although a connection between local and regional diversity has been largely acknowledged (e.g. Graves & Gotelli, 1983; Hortal *et al*., 2008b), few studies have explicitly analysed the effect of the regional pool on the structure of local communities (see Rodríguez *et al.*, 2006). According to our results, only a few island faunas depart from the level of generalism of their species pool, indicating a large influence of the composition of the pool in the structure of most island parasitoid communities. In braconids, islands with higher level of generalism than their corresponding species pool are also of higher altitude. Mountain habitats are less common in many island systems than other habitat types, virtually constituting "islands" within islands, and often being very isolated from their nearest similar habitats. Both insect species richness (e.g. Noyes, 1989) and parasitism levels (Hodkinson, 2005, and references therein) decrease with altitude. Therefore, it can be expected that comparatively fewer host species actually colonize high-altitude areas, favouring an imbalance towards parasitoids with wide host ranges due to the low diversity of hosts. Also, altitude regulates island climate, so this variable may be also capturing the departure of each island system from the general gradients in temperature and precipitation that the global climate models we used (Hijmans *et al.*, 2005) may not be able to capture accurately. The final model for braconid generalism included temperature alongside with species pool, indicating the particular importance of climatic factors for this family. Interestingly, the islands with lower level of generalism than their pool show particularly high species richness figures. The positive relationship between ecological specialization and species richness is well known (Hutchinson, 1959); increased specialisation reduces interspecific competition, facilitating species coexistence by a higher partitioning of the niche space (e.g. Dyer *et al.*, 2007). In contrast to braconids, the departure of some ichneumonid island faunas from the structure of their pool is more difficult to interpret since those with higher levels of generalism are mostly from non-oceanic islands, while those with lower levels of generalism are from islands with higher precipitation.

The most striking of our results is that the level of generalism of island parasitoid faunas is largely constrained by regional factors. In both families, the particular species pool of each island is one of the two factors remaining in the final model. For the ichneumonids,

the model also includes the biogeographic realm, which is also a significant (though less important) predictor of braconid generalism. Regional differences are known to determine community structure (e.g. Rodríguez *et al.*, 2006), but their interpretation is not straightforward. The construction of regional biotas depends largely on the evolutionary history and selection through time of the species and lineages present in the species pool (Ricklefs, 1987, 2004, 2007), as well as on the geomorphological and environmental characteristics of the region (Jetz & Rahbek, 2001; Rahbek & Graves, 2001), and on their variation through time (e.g. Hawkins *et al.*, 2005; Diniz-Filho *et al.*, 2009). Certainly, island community structure is also influenced by the local factors that build up their biotas, such as habitat diversity, colonization or immigration (see Whittaker & Fernández-Palacios, 2007 for a review), that filter the species present in the source pool. However, the relative contribution of local and regional factors to community structure depends on the scale considered (Ricklefs, 2007; Hortal *et al.*, 2008b), and separating such processes goes beyond the scope of this work.

For both families, the level of generalism of island parasitoids is higher in the Indomalayan region (see Fig. 4.1). The islands in this region share some characteristics that distinguish them from other island systems; most experience high temperature and precipitation, but many islands are also of mixed geological origins, with high altitudes and large size. In addition, they are either placed near the potential colonization sources, or were even connected to Southeast Asia during Pleistocene glacial maxima. These characteristics not only enhance their diversity, but also result in Indomalayan islands hosting some of the largest patches of rainforest still found on islands (Corlett & Primack, 2008). Plant architecture influences not only parasitoid species richness, but also the relative diversities of idio- and koinobionts (Hawkins, 1994). While the communities of idiobionts attacking hosts on trees are consistently richer than those on herbs, this pattern is more complex for koinobionts; those attacking endophytic hosts (i.e., concealed, such as wood borers and leaf miners) are as rich on herbs as on trees, whereas those attacking exophytic hosts (i.e., exposed, such as folivores) are richest on trees. Therefore, it can be expected that there will be a relatively higher proportion of idiobiont species in rainforests when compared to other habitats. This particular effect is stronger for ichneumonids (see Fig. 4.1), which are those with proportionally more idiobiont species overall. In fact, the continental rainforest areas

surrounding the Indomalayan islands (e.g. peninsular Malaysia, Thailand) also have higher recorded numbers of idiobiont than koinobiont species. In comparison, the level of generalism of Indomalayan braconid faunas is much lower both on island and mainland areas (data extracted from Yu *et al.*, 2005; not shown). This reinforces the reliability of the hypothesized importance of the species pool, with island faunas being consistently similar in structure to the faunas of their surrounding areas.

Latitudinal gradients of parasitoid species richness also provide indirect proof for the predominance of generalists on rainforests. The combined effects of the species pool and either temperature (for the braconids) or biogeographic realm (for the ichneumonids) largely recovered the latitudinal variations in the level of generalism on islands. In fact, the *I/K ratio* of the species pools is also correlated with latitude (Braconidae: Spearman $R = -0.791$, $p < 0.001$; Ichneumonidae: Spearman $R = -0.836$, $p < 0.001$), indicating that the latitudinal gradient is common to both islands and mainland. This agrees with former evidence on the latitudinal gradient in the distribution of koino- and idiobionts, which suggests that while koinobionts decrease in richness towards the tropics, idiobionts do not, or do less severely (e.g. Gauld, 1986; Askew & Shaw, 1986; Askew, 1990; Quicke & Kruft, 1995).

The richness of parasitoids feeding on exophytic hosts falls towards the tropics, remaining the same or actually increasing towards the tropics in endophytic hosts (Hawkins, 1990; 1994). If latitudinal gradients alone were responsible for the geographical patterns of level of generalism, one would expect all areas close to the equator to have high proportions of generalist species. However, our results show that this is not true for all islands in the tropics (e.g. Caribbean islands), but rather only those holding large rainforests. We therefore hypothesize that the trend for parasitoid faunas to be biased towards generalists in the tropics is mainly due to the location of tropical rainforests, both on islands and continental areas. Since tree species richness is higher in these ecosystems than in temperate forests, they likely provide a higher diversity of microhabitats for endophytic species. This, in turn, would increase the relative proportion of idiobionts, which are more successful in attacking endophytic hosts (Hawkins, 1990, 1994), ultimately resulting in a higher proportion of idiobionts in the tropics than in temperate areas.

Although the knowledge on the geographical distribution of parasitic wasps is taxonomically and geographically biased (Gaston, 1993; Jones *et al.*, 2009; Baselga *et al.*,

2010), we believe that our results are not affected by data quality issues, since we considered only the islands with comparable inventories previously identified in Chapter 3. Therefore, we can conclude that although island parasitoid faunas have comparatively higher proportion of generalists than the mainland, they rarely depart from the proportions observed in their species pools. Rather, regional factors, and in particular the structure of the species pool, seem to play an important role in the structure of island communities. Generalist species are more predominant in islands with a large cover of rainforests, highlighting the complexity of factors shaping the diversity and structure of parasitoid communities. Further studies on continental areas are necessary to determine whether there are consistently larger proportions of idiobionts on tropical forests, as well as to unveil the mechanisms causing this seemly general trend.

Chapter 5: Applying DNA barcoding for the study of geographical variation in host-parasitoid interactions[4]

5.1. Abstract

Studies on the biogeography of host-parasitoid interactions are scarce, mainly due to technical difficulties such as problems associated with rearing and species identification. DNA barcoding is increasingly recognized as a valuable tool for taxon identification, allowing to link different life history stages of a species. We evaluate the usefulness of a protocol based on COI sequencing for the study of geographical variation of host-parasitoid interactions. Larvae of *Acroclita subsequana* (Lepidoptera: Tortricidae) were collected in Macaronesia, and dissected to search for parasitoid larvae. Both hosts and parasitoids were sequenced and assigned to molecular operational taxonomic units (MOTUs) based on pairwise genetic distances, tree-based and similarity-based methods. Hosts were grouped into six MOTUs, usually with an allopatric distribution, while parasitoids clustered into 12 MOTUs, each of which was mostly found attacking a single host MOTU. Available COI sequence databases failed to provide identification to species level for these MOTUs. Three challenges related to the applicability of DNA barcoding in this type of studies are identified and discussed: *(i)* more suitable primers need to be developed for both parasitoids and hosts; *(ii)* the most commonly used approaches for inferring MOTUs have different limitations (e.g. arbitrary nature of defining a threshold to separate MOTUs) and need to be improved or replaced by other techniques; and *(iii)* for the identification of MOTUs, it is imperative to increase the range of sequenced taxa in the currently available reference databases. Finally, in spite of these difficulties, we discuss how DNA barcoding will help ecological and biogeographical studies of host-parasitoid interactions.

[4]This chapter is the basis of: Santos, A.M.C., Besnard, G. & Quicke, D.L.J. (2010) Applying DNA barcoding for the study of geographical variation in host-parasitoid interactions, *Molecular Ecology Resources,* in press, doi: 10.1111/j.1755-0998.2010.02889.x .

5.2. Introduction

Parasitoids are insects that undergo their larval development by feeding either internally (endoparasitoids) or externally (ectoparasitoids) on arthropod hosts (Godfray, 1997; Quicke, 1997). Almost invariably the individual host is killed as a result of parasitoid larvae development. Because of their life strategies, parasitoids constitute a key component of nearly all terrestrial ecosystems, contributing to the regulation of arthropod populations (LaSalle & Gauld, 1993; Hassell, 2000b).

Despite their ecological and economic importance, relatively little is known about the diversity, distribution and biology of parasitoids. Their study is challenged by their typical small size, high number of species, the complexity of their life cycle, and the difficulties in their taxonomy due to slight morphological differences between species. Much of what is known about the diversity of parasitoid communities at large geographical scales (i.e. above the landscape level) comes from reviews of the available literature on studies of parasitoids reared from their individual hosts (e.g. Hawkins, 1994). However, most of this literature is of limited value since it comes from incompatible sources that have no standard design, and is generally biased towards agricultural habitats, making it difficult to translate their results to other systems (Askew & Shaw, 1986). Moreover, host range, which has a central role in understanding host-parasitoid interactions, remains one of the less understood aspects of parasitoid biology (Shaw, 1994; Quicke, 1997). One key reason for this problem is due to frequent unreliable records, especially because of errors like misidentification of the host and/or parasitoid, and the wrong association of a parasitoid with the host due to contamination of the rearing system (Noyes, 1994; Shaw, 1997). Although rearing techniques have been commonly used for identifying host-parasitoid relationships, these methods bring other problems. The procedures are usually labour intensive, time consuming, and require much experience (Laurenne *et al.*, 2000; Tilmon *et al.*, 2000). In addition, a significant proportion of the larvae die under laboratory conditions (Agustí *et al*., 2005). An alternative could be host dissection, but, in this case, the identification of the host larvae based on morphology may be difficult and the identification of the parasitoid is often possible only to the family level (Quicke, 2002; Greenstone, 2003; Persad *et al*., 2004). All these drawbacks make these procedures impracticable when studying host-parasitoid interactions on large

geographical scales. It is therefore necessary to develop new methodologies and protocols applicable to the study of host-parasitoid interactions in ecological and/or biogeographical studies.

Molecular techniques, such as enzyme electrophoresis, immunoassays and methods based on polymerase chain reaction (PCR), have helped solve some of the abovementioned problems (Greenstone, 2006; Gariepy *et al.*, 2007). DNA-based techniques have been used to detect, identify and assess parasitism inside the hosts (e.g. Greenstone & Edwards, 1998; Laurenne *et al.*, 2000; Tilmon *et al.*, 2000; Agustí *et al.*, 2005; Traugott *et al.*, 2006, 2008; Gariepy *et al.*, 2007). However, most of these studies rely on the use of species-specific primers, and therefore have been limited to a small number of species from well studied host-parasitoid associations usually related to biological control.

A fairly new DNA-based concept, DNA barcoding, could help the study of host-parasitoid interactions. This technique has recently received much attention, as it has been argued to be a valuable tool for delimiting and identifying species, as well as linking different life history stages of a species (e.g. Blaxter, 2003; Hebert *et al.*, 2003a, b; Miller *et al.*, 2005; Pfenninger *et al.*, 2007; Emery *et al.*, 2009; Packer *et al.*, 2009). The notion of DNA barcoding was first proposed by Hebert *et al.* (2003a), who suggested that a sequence of approximately 650 bp of the mitochondrial cytochrome oxidase I gene (COI) could be used as a taxonomic tool for animal groups. Another acclaimed outcome of DNA barcoding is the possibility of defining molecular operational taxonomic units (MOTUs; Floyd *et al.*, 2002; Blaxter *et al.*, 2005). MOTUs are groups of organisms that can be used in taxonomic studies without necessarily being assigned to a taxonomic rank, making possible the study of biological diversity in poorly known regions, habitats and taxa (e.g. Blaxter *et al.*, 2005; Smith *et al.*, 2005, 2009; Puillandre *et al.*, 2009). DNA barcoding has proven to be useful and accurate in a number of studies covering a range of different taxa (e.g. amphibians: Vences *et al.*, 2005; bees: Sheffield *et al.*, 2009; birds: Herbert *et al.*, 2004a; butterflies and moths: Hebert *et al.*, 2003a; Janzen *et al.*, 2005; fishes: Steinke *et al.*, 2009), and has already been used to study host-parasitoid interactions, but never in a biogeographical perspective (Smith *et al.*, 2006, 2007, 2008; Janzen *et al.*, 2009).

Our goal here is to propose a DNA barcoding protocol for studying host-parasitoid relationships that can be used by non-taxonomists and that can be reproducible in different regions. We evaluate the usefulness of this protocol in a study of the geographical variability of host-parasitoid interactions. We focused on a particular ecological system composed of *Euphorbia* spp. (Euphorbiaceae) spurges (herein *Euphorbia* for short), their herbivores and parasitoids, from the Macaronesian islands and adjacent mainland. DNA barcoding was used to delineate MOTUs and, when possible, to link each MOTU to a recognized species or supraspecific taxa, thus avoiding the vagaries of rearing. We discuss the challenges this approach poses in order to be used successfully for ecological and biogeographical studies.

5.3. Materials and Methods

Study area and sampling

Our study focused on different islands and adjacent mainland of the Macaronesian region. Fifty-five sites mostly dominated by *Euphorbia* spp. were sampled in the islands of Madeira, La Gomera, La Palma and Tenerife, and in Morocco (western and northern regions) and the Portuguese mainland (Fig. 5.1; for more details see Appendix A3.1). Other Macaronesian archipelagos (i.e., Cape Verde and Azores) were not studied due to time and resource limitations. Island sites were sampled twice, in May-June 2006 and 2007, and mainland sites were sampled once (western part of Morocco in March 2007, northern part of Morocco and the Portuguese mainland in March-April 2008 and May 2008, respectively). On each site, approximately two hours were spent collecting both exposed and concealed Lepidoptera larvae from *Euphorbia* spp. Specimens were preserved in 100% ethanol and stored below 5 ºC in the laboratory. A total of 1473 larvae were collected and identified to family level based on the identification keys by Carter & Kristensen (1999) and Dias (2006). Most of the specimens belonged to Tortricidae (96.1%), while 2.4% corresponded to Sphingidae, 1% to other families, and 0.5% remain unidentified. Consequently, only Tortricidae were considered in further analyses. According to several sources (Aguiar & Karsholt, 2006; J. Baixeras and O. Karsholt, pers. com.), the only tortricid species that feeds on *Euphorbia* within the Macaronesia is *Acroclita subsequana* (Herrich-Schäffer, 1851). This was

corroborated by careful observation of the morphological characters of the larvae (J. Baixeras, pers. com.), but adult specimens of this species from museum and private collections - sampled in the Madeira Archipelago (Madeira and Porto Santo), the Canary Islands (Fuerteventura and Tenerife), and the Spanish mainland - were also sequenced to confirm this identification (see below).

The tortricid larvae (hereafter "tortricids") were carefully examined in order to find ectoparasitoid and endoparasitoid larvae. Tortricids were transferred individually to petri dishes with fresh tap water, left there for one hour to soften, and then dissected. Both parasitoid larvae and their tortricid hosts were prepared for molecular analysis, together with a subsample of non-parasitized tortricids.

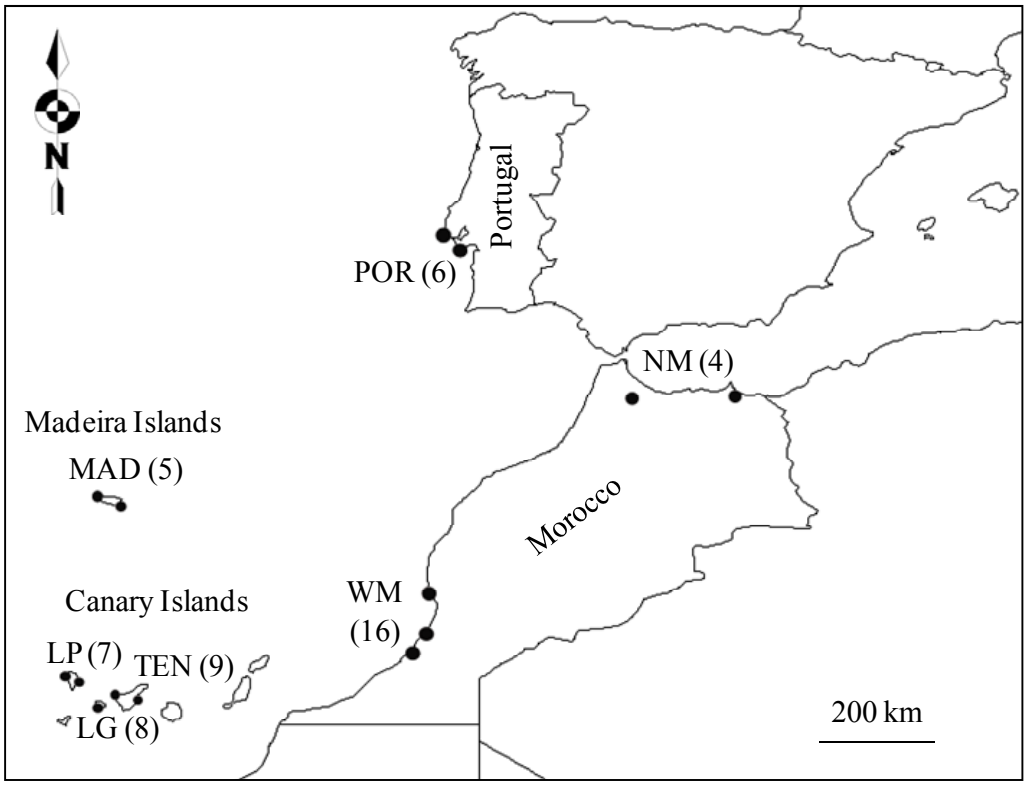


Figure 5.1. Geographical distribution of the study sites in the different island and mainland areas of Macaronesia. MAD – Madeira Island; LG – La Gomera; LP – La Palma; TEN – Tenerife; WM – Western Morocco; NM – Northern Morocco; POR – Portuguese mainland. Black dots indicate the location of the sites and the numbers inside brackets correspond to the number of studied sites from each area. More information is available in Appendix A3.1.

DNA extraction, PCR amplification and sequencing

DNA was extracted from the posterior portion of the abdomen of large larvae and the entire body of small larvae (some ~ 1 mm long), using the QIAGEN DNeasy kit. The manufacturer's protocol was followed, and DNA extracts were resuspended in 30-80 µl of elution buffer, depending on sample size. Primers used for PCR and sequencing reactions are listed in Table 5.1. For parasitoids we used the universal invertebrate primers LCO1490 and HCO2198 (primer pair A) to amplify the barcoding region of the mithocondrial gene cytochrome oxidase 1 (COI). When these primers were not successful in generating this product, we used customized primers for Hymenoptera (primer pair B). For the tortricids, primer pair A was also used. In cases when this primer pair failed, primer pair C was employed. Regarding the specimens from collections (some of them were more than 15 years old), DNA was extracted from the hind leg, and it was necessary to use internal primers to generate two shorter overlapping segments (with primer pairs D and E).

For the parasitoid samples, the PCR mixes contained 15.9 µl of ultrapure water, 0.5 U of *Taq* DNA polymerase (BIOTAQ DNA Polymerase; Bioline), 2 µl $MgCl_2$ (50 mM), 2.5 µl 10x reaction buffer (160 mM $(NH_4)_2SO_4$, 670 mM Tris-HCl, 0.1% stabilizer; Bioline), 1.25 µl of each primer (10 µM), 0.25 µl of each dNTP (100 mM), and 1 µl of template DNA, in a total volume of 25 µl. For the tortricid samples, the PCR reaction was performed in a total volume of 24 µl, containing 20 µl of 1.1x ReddyMix PCR Master Mix (2.5 mM $MgCl_2$; Thermo Scientific), 1 µl of each primer (10 µM) and 2 µl of template DNA. Amplification was carried out using a thermocycling profile consisting of 1 min at 94 ºC followed by 5 cycles of 30 s at 94 ºC, 40 s at 45 ºC, and 1.5 min at 72 ºC, then by 35 cycles of 30 s at 94 ºC, 40 s at 47 ºC, and 1.5 min at 72 ºC, and a final step of 10 min at 72 ºC. PCR products were visualized in a 1.5% agarose gel and samples containing clean single bands were purified using ExoSAP-IT (USB Corporation) and sequenced commercially using the same primers (both directions). All sequences were deposited in GenBank (Accession nos. FN665423 to FN665648, and FN662352 to FN662416; see Appendix A3.2 and A3.3 for more details).

Table 5.1. Primer pairs used for PCR and sequencing. (1) Folmer *et al*. (1994); (2) Smith *et al.* (2005); (3) Wahlberg (2009).

Primer pair code	Primer Name	Primer sequence, 5'-3'	Product length (bp)	Primer source
A	LCO1490	GGTCAACAAATCATAAAGATATTG	658	(1)
	HCO2198	TAAACTTCAGGGTGACCAAAAAATCA		(1)
B	NewParF	TAAGWTTAATTATTCGRTTAGAATTARG	580	this study
	NewParR	TAAACTTCWGGATGACCAAAAAATCA		this study
C	LepF1	ATTCAACCAATCATAAAGATATTGG	658	(2)
	LepR1	TAAACTTCTGGATGTCCAAAAAATCA		(2)
D	LCO1490	(see above)	325	(1)
	K699	WGGGGGGTAAACTGTTCATCC		(3)
E	Ron	GGAGCYCCWGATATAGCTTTCCC	376	(3)
	HCO2198	(see above)		(1)

Data analyses

Alignment of COI sequences was unambiguously established by examining the translated amino acids using MEGA 4 (Tamura *et al.*, 2007). However, 16 sequences displayed three 1-bp indels causing stop codons in the reading frame. These sequences were not removed from our dataset and clustered within Agathidinae in our phylogenetic reconstructions (pMOTU3; see below). The same indels were also observed on other members of this subfamily (DLJQ, personal observations). These COI sequences possibly correspond to nuclear DNA peudogenes of mitochondrial origin (or NUMTs; Lopez *et al.*, 1994) and additional analyses are necessary to determine the exact origin of this phenomenon.

MOTUs were delimited and tentatively identified using a combination of three different approaches that were considered *a priori* equally important: *(i)* genetic distances, *(ii)* tree-based methods, and *(iii)* similarity-based methods. We used MEGA 4 (Tamura *et al.*, 2007) to calculate genetic distances between each sequence pair by applying the Kimura-two-parameter model (K2P; pairwise deletion of missing data). When the genetic distance

between two sequences was lower than 3%, we assigned these sequences to the same MOTU (see Hebert *et al.,* 2003a). For the other approaches we merged redundant sequences to distinct haplotypes using DNASP v5 (Librado & Rozas, 2009) (see Table 5.2 and Appendix A3.5 for details). For the tree-based methods we used two clustering methods to infer the relationships within our sequences (Appendix A3.2) and also between our sequences and other available sequences from GenBank and from specimens collected outside our study sites (Appendix A3.3; new GenBank accessions: FN662417 to FN662473). For the parasitoids these sequences corresponded to specimens from subfamilies of Ichneumonoidea, from Bethylidae, and from various families of Chalcidoidea and Diptera, all known to be parasitoids of Lepidoptera. Tortricid sequences were compared with those of the *A. subsequana* specimens obtained from museum and private collections (GenBank accession nos. FN665423 to FN665430), and with sequences of other genera of Tortricidae available on GenBank (see Appendix A3.3). A neighbor-joining (NJ) tree based on K2P distances was computed using MEGA 4 (Tamura *et al.*, 2007), and branch support was calculated with 1,000 bootstrap replicates. The best sequence evolution model was determined using JMODELTEST 0.1.1 (Posada, 2008). For both parasitoids and tortricids, the best substitution model was GTR+I+Γ (generalized time reversible with a gamma distribution with a proportion of invariant sites). This model was then used to generate a maximum likelihood (ML) tree in PHYML 3.0 (Guindon & Gascuel, 2003). Branch support was assessed with 100 bootstrap replicates. In both NJ and ML trees, sequences that formed a terminal cluster with high node support values (≥ 98%) were considered as belonging to the same MOTU. Lastly, we compared our sequences with all available barcode records in BOLD (Ratnasingham & Hebert, 2007), using the identification engine BOLD-IDS (last accessed on 29th January 2010). We also performed a Basic Local Alignment Search Tool (BLAST) search to compare our sequences with available nucleotide sequences on GenBank (last accessed on 29th January 2010), based on the percentage of maximum sequence identity. For both similarity-based methods the genetic distance threshold of 3% (97% of similarity) was used to determine if sequences were conspecific or not (see Hebert *et al.,* 2003a). Based on the results of these three approaches, we proposed a tentative taxonomic identification for each sequence.

Sampling effort assessment

To determine whether or not the parasitoid community attacking tortricids had been well characterized, we examined species accumulation curves for each territory (i.e., each island or mainland area), and for all mainland territories and all islands as a whole. Species accumulation curves are commonly used to describe the probability of finding new species with additional sampling effort (e.g. Soberón & Llorente, 1993; Hortal & Lobo, 2005). Here, we measured sampling effort as the number of tortricids captured in each sampled area (i.e., Madeira, La Gomera, La Palma, Tenerife, Western Morocco, Northern Morocco, and Portuguese mainland), and the inventoried species as the number of parasitoid MOTUs collected from these larvae. The degree of completeness of the inventories was estimated using the ratio of accumulation of new MOTUs at the end of the inventory; i.e., the final slope of the curve that describes the accumulation of newly observed MOTUs with the addition of new samples (in this case tortricid larvae). We obtained such slope by first randomizing 1,000 times the order of entrance of the samples in ESTIMATES 8.2.0 (Colwell, 2009), and then calculating the rate of accumulation of new MOTUs in the last ten samples of such randomized curve (see Hortal & Lobo, 2005; Hortal *et al.*, 2008a). Following Hortal & Lobo (2005), areas with ratios of MOTUs accumulation lower than 0.05 (i.e. one new parasitoid MOTU is found every 20 new tortricid larvae sampled) were considered as well sampled.

5.4. Results

Seventy-nine of the 1415 tortricid larvae (5.6%) were found to be parasitized (Table 5.3), with parasitism being detected in 27 sites. In total, 234 tortricids (79 parasitized, 146 unparasitized and nine *A. subsequana* specimens from collections) and 78 parasitoids were prepared for barcoding. Two hundred and twenty six tortricids (including eight specimens from collections) and 65 parasitoids were successfully sequenced (97% and 83% of success, respectively). In the case of the parasitoids, 36 sequences were generated using primer pair A and 29 using primer pair B, while of the 226 tortricid sequences, 125 were generated using primer pair A, 94 using primer pair C and seven (from museum and private collections) using primer pairs D and E.

Table 5.2. Tentative identification (ID) of the parasitoid specimens using genetic distances, tree- and similarity-based methods.

Code	Area	Haplotype	MOTU	BOLD		GenBank		NJ tree ID	ML tree ID	Final ID	
				ID	%	ID	%			Higher Taxa	ID
PAR230	MAD	-	4	Braconidae	95	Braconinae	89	BraconinaeA	BraconinaeA	Braconidae	BraconinaeA
PAR264	MAD	-	4	Braconidae	95	Braconinae	89	BraconinaeA	BraconinaeA	Braconidae	BraconinaeA
PAR265	MAD	-	4	Braconidae	95	Braconinae	89	BraconinaeA	BraconinaeA	Braconidae	BraconinaeA
PAR266	MAD	-	4	Braconidae	95	Braconinae	89	BraconinaeA	BraconinaeA	Braconidae	BraconinaeA
PAR267	MAD	-	4	Braconidae	95	Braconinae	89	BraconinaeA	BraconinaeA	Braconidae	BraconinaeA
PAR334	MAD	-	4	Braconidae	95	Braconinae	88	BraconinaeA	BraconinaeA	Braconidae	BraconinaeA
PAR333	MAD	-	11	*Braunsia* sp.	93	Agathidinae	91	AgathidinaeA	AgathidinaeA	Braconidae	AgathidinaeA
PAR268	LG	3	3	*Cincta* sp.	94	Agathidinae	90	AgathidinaeB	AgathidinaeB	Braconidae	AgathidinaeB
PAR273	LG	-	3	*Bassus dimidiator**	94	Agathidinae	90	AgathidinaeB	AgathidinaeB	Braconidae	AgathidinaeB
PAR336	LG	3	3	*Cincta* sp.	94	Agathidinae	90	AgathidinaeB	AgathidinaeB	Braconidae	AgathidinaeB
PAR270	LG	-	5	Bethylidae	90	*Memphis appias*	81	BethylidaeB	BethylidaeB	Bethylidae	BethylidaeB
PAR126	LP	-	1	Chalcidoidea	91	*Diglyphus isaea*	90	ChalcidoideaA	ChalcidoideaA	Chalcidoidea	ChalcidoideaA
PAR190	LP	-	1	Chalcidoidea	91	*Diglyphus isaea*	90	ChalcidoideaA	ChalcidoideaA	Chalcidoidea	ChalcidoideaA
PAR203	LP	-	1	Chalcidoidea	91	*Diglyphus isaea*	90	ChalcidoideaA	ChalcidoideaA	Chalcidoidea	ChalcidoideaA
PAR277	LP	-	1	Chalcidoidea	91	*Diglyphus isaea*	90	ChalcidoideaA	ChalcidoideaA	Chalcidoidea	ChalcidoideaA
PAR163	LP	-	2	*Nemorilla* sp.	96	*Belvosia* sp.	90	TachinidaeA	TachinidaeA	Tachinidae	TachinidaeA
PAR165	LP	-	3	*Bassus dimidiator**	94	Agathidinae	91	AgathidinaeB	AgathidinaeB	Braconidae	AgathidinaeB
PAR274	LP	-	3	*Bassus dimidiator**	94	Agathidinae	90	AgathidinaeB	AgathidinaeB	Braconidae	AgathidinaeB
PAR275	LP	-	7	Bethylidae	90	*Helicopha einap*	80	BethylidaeA	BethylidaeA	Bethylidae	BethylidaeA
PAR276	LP	-	7	Bethylidae	91	*Mompha* sp.	80	BethylidaeA	BethylidaeA	Bethylidae	BethylidaeA
PAR332	TEN	5	3	*Bassus dimidiator**	95	Agathidinae	91	AgathidinaeB	AgathidinaeB	Braconidae	AgathidinaeB
PAR243	TEN	-	5	Bethylidae	89	*Nicolaea ophia*	79	BethylidaeB	BethylidaeB	Bethylidae	BethylidaeB
PAR253	TEN	-	5	Bethylidae	92	*Colletes annejohnae*	79	BethylidaeB	BethylidaeB	Bethylidae	BethylidaeB

Table 5.2 (continued)

Code	Area	Haplotype	MOTU	BOLD		GenBank		NJ tree ID	ML tree ID	Final ID	
				ID	%	ID	%			Higher Taxa	ID
PAR254	TEN	-	5	Bethylidae	91	*Colletes annejohnae*	79	BethylidaeB	BethylidaeB	Bethylidae	BethylidaeB
PAR245	TEN	-	6	Braconidae	90	Braconinae	89	BraconinaeB	BraconinaeB	Braconidae	BraconinaeB
PAR246	TEN	-	6	Braconidae	90	Braconinae	89	BraconinaeB	BraconinaeB	Braconidae	BraconinaeB
PAR252	TEN	-	6	Braconidae	90	Braconinae	89	BraconinaeB	BraconinaeB	Braconidae	BraconinaeB
PAR258	TEN	6	6	Braconinae	90	Braconinae	89	BraconinaeB	BraconinaeB	Braconidae	BraconinaeB
PAR280	TEN	6	6	Braconidae	90	Braconinae	89	BraconinaeB	BraconinaeB	Braconidae	BraconinaeB
PAR281	TEN	-	8	*Dolichogenidea* sp.	95	*Dolichogenidea* sp.	93	MicrogastrinaeA	MicrogastrinaeA	Braconidae	MicrogastrinaeA
PAR282	TEN	-	8	*Apanteles* sp.	94	*Dolichogenidea* sp.	93	MicrogastrinaeA	MicrogastrinaeA	Braconidae	MicrogastrinaeA
PAR284	TEN	-	9	*Dasineura mali*	90	*Asteromyia carbonifera*	89	CecidomyiidaeA	CecidomyiidaeA	Cecidomyiidae	CecidomyiidaeA
PAR285	WM	4	3	*Bassus dimidiator**	95	Agathidinae	91	AgathidinaeB	AgathidinaeB	Braconidae	AgathidinaeB
PAR286	WM	4	3	*Bassus dimidiator**	95	Agathidinae	91	AgathidinaeB	AgathidinaeB	Braconidae	AgathidinaeB
PAR287	WM	-	3	*Bassus dimidiator**	94	Agathidinae	91	AgathidinaeB	AgathidinaeB	Braconidae	AgathidinaeB
PAR288	WM	4	3	*Bassus dimidiator**	95	Agathidinae	91	AgathidinaeB	AgathidinaeB	Braconidae	AgathidinaeB
PAR289	WM	4	3	*Bassus dimidiator**	95	Agathidinae	91	AgathidinaeB	AgathidinaeB	Braconidae	AgathidinaeB
PAR290	WM	-	3	*Bassus dimidiator**	95	Agathidinae	91	AgathidinaeB	AgathidinaeB	Braconidae	AgathidinaeB
PAR291	WM	4	3	*Bassus dimidiator**	95	Agathidinae	91	AgathidinaeB	AgathidinaeB	Braconidae	AgathidinaeB
PAR292	WM	4	3	*Bassus dimidiator**	95	Agathidinae	91	AgathidinaeB	AgathidinaeB	Braconidae	AgathidinaeB
PAR297	WM	5	3	*Bassus dimidiator**	95	Agathidinae	91	AgathidinaeB	AgathidinaeB	Braconidae	AgathidinaeB
PAR301	WM	5	3	*Bassus dimidiator**	95	Agathidinae	91	AgathidinaeB	AgathidinaeB	Braconidae	AgathidinaeB
PAR296	WM	7	10	Braconidae	91	Braconinae	86	BraconinaeC	BraconinaeC	Braconidae	BraconinaeC
PAR298	WM	7	10	Braconidae	91	Braconinae	86	BraconinaeC	BraconinaeC	Braconidae	BraconinaeC
PAR300	WM	8	10	Braconidae	91	Braconinae	86	BraconinaeC	BraconinaeC	Braconidae	BraconinaeC
PAR303	WM	8	10	Braconidae	91	Braconinae	86	BraconinaeC	BraconinaeC	Braconidae	BraconinaeC
PAR304	WM	8	10	Braconidae	91	Braconinae	83	BraconinaeC	BraconinaeC	Braconidae	BraconinaeC

Table 5.2 (continued)

Code	Area	Haplotype	MOTU	BOLD		GenBank		NJ tree ID	ML tree ID	Final ID	
				ID	%	ID	%			Higher Taxa	ID
PAR309	WM	7	10	Braconidae	91	Braconinae	86	BraconinaeC	BraconinaeC	Braconidae	BraconinaeC
PAR299	WM	-	11	*Bassus* sp.	94	Agathidinae	92	AgathidinaeA	AgathidinaeA	Braconidae	AgathidinaeA
PAR305	WM	-	11	Braconidae	94	Agathidinae	92	AgathidinaeA	AgathidinaeA	Braconidae	AgathidinaeA
PAR306	WM	-	11	*Agathis* sp.	93	Agathidinae	92	AgathidinaeA	AgathidinaeA	Braconidae	AgathidinaeA
PAR307	WM	-	11	*Agathis* sp.	93	Agathidinae	91	AgathidinaeA	AgathidinaeA	Braconidae	AgathidinaeA
PAR308	WM	-	11	*Agathis* sp.	93	Agathidinae	91	AgathidinaeA	AgathidinaeA	Braconidae	AgathidinaeA
PAR310	WM	-	11	Braconidae	94	Agathidinae	92	AgathidinaeA	AgathidinaeA	Braconidae	AgathidinaeA
PAR311	WM	-	11	*Austroearinus* sp.	93	Agathidinae	91	AgathidinaeA	AgathidinaeA	Braconidae	AgathidinaeA
PAR302	WM	-	12	Ichneumonidae	95	Campopleginae	94	CampopleginaeA	CampopleginaeA	Ichneumonidae	CampopleginaeA
PAR312	POR	1	11	*Braunsia* sp.	94	Agathidinae	91	AgathidinaeA	AgathidinaeA	Braconidae	AgathidinaeA
PAR313	POR	-	11	Braconidae	94	Agathidinae	91	AgathidinaeA	AgathidinaeA	Braconidae	AgathidinaeA
PAR314	POR	2	11	*Braunsia* sp.	93	Agathidinae	91	AgathidinaeA	AgathidinaeA	Braconidae	AgathidinaeA
PAR315	POR	1	11	*Braunsia* sp.	94	Agathidinae	91	AgathidinaeA	AgathidinaeA	Braconidae	AgathidinaeA
PAR316	POR	-	11	*Braunsia* sp.	93	Agathidinae	91	AgathidinaeA	AgathidinaeA	Braconidae	AgathidinaeA
PAR317	POR	-	11	*Braunsia* sp.	94	Agathidinae	91	AgathidinaeA	AgathidinaeA	Braconidae	AgathidinaeA
PAR318	POR	1	11	*Braunsia* sp.	94	Agathidinae	91	AgathidinaeA	AgathidinaeA	Braconidae	AgathidinaeA
PAR319	POR	-	11	*Braunsia* sp.	94	Agathidinae	92	AgathidinaeA	AgathidinaeA	Braconidae	AgathidinaeA
PAR320	POR	2	11	*Braunsia* sp.	93	Agathidinae	91	AgathidinaeA	AgathidinaeA	Braconidae	AgathidinaeA

Area is the region where the specimens were collected (MAD – Madeira, LG – La Gomera, LP – La Palma, TEN – Tenerife, WM – Western Morocco, POR – Portugal); see Fig. 5.1 for more details. MOTU is the molecular taxonomic unit, as defined by the percentage of sequence divergence given by the K2P model, and by the tree-based methods (Fig. 5.2; Appendix A3.4). % is the percentage of maximum sequence identity given by BOLD and BLAST. NJ tree ID and ML tree ID are the identifications given by the neighbor-joining tree and the maximum likelihood tree, respectively. A final identification (Final ID) is given incorporating results from the different approaches. *The name given by BOLD to this specimen (*Laticinctus* sp.) is not a genus level name and should be referred to as *Bassus dimidiator*.

Table 5.3. Specimens collected from each sampling area (see Fig 5.1).

Area	Number of tortricids collected	Number of parasitized tortricids	Number of parasitoid MOTUs	Slope
Madeira	57	8	2	0.016
La Gomera	180	12	2	0.005
La Palma	187	11	4	0.005
Tenerife	240	13	5	0.008
Western Morocco	472	26	4	0.002
Northern Morocco	92	0	0	-
Portugal	187	9	1	0
Islands	664	44	10	0.004
Mainland	751	35	4	0.001
All areas	1415	79	12	0.002

Slope corresponds to final slope of the species accumulation curve, calculated from the accumulation of observed MOTUs in the last ten samples (i.e., larvae) of the randomized species accumulation curve (see Materials and Methods).

Barcoding analyses of parasitoid specimens

Twelve parasitoid MOTUs were delimited using genetic distances (Table 5.2), each with a within-group sequence divergence ranging from 0 to 0.7%. The tree-based identification also recognized the same number of MOTUs (Fig. 5.2; see ML tree in Appendix A3.4). Parasitoid MOTUs could not be identified to species level due to the lack of conspecific sequences in the dataset. Regarding the similarity-based methods, both BOLD and BLAST taxon identification engines were unable to identify the specimens to species or genus level, since the percentage of sequence similarity was always lower than the 97% threshold (Table 5.2).

Noteworthy are the specimens PAR243, PAR253, PAR254, PAR270, PAR275 and PAR276 (i.e., pMOTU5 and pMOTU7), that showed the lowest percentages of similarity to the sequences available in BOLD and GenBank (89 to 92% in BOLD and 79 to 81% in GenBank). BOLD identified these MOTUs as Bethylidae (Hymenoptera), but according to BLAST these specimens belong to taxa that either are non-parasitic Hymenoptera (Colletidae) or are Lepidoptera families that do not correspond to the host's family (Helicophidae, Lycaenidae, Momphidae and Nymphalidae).

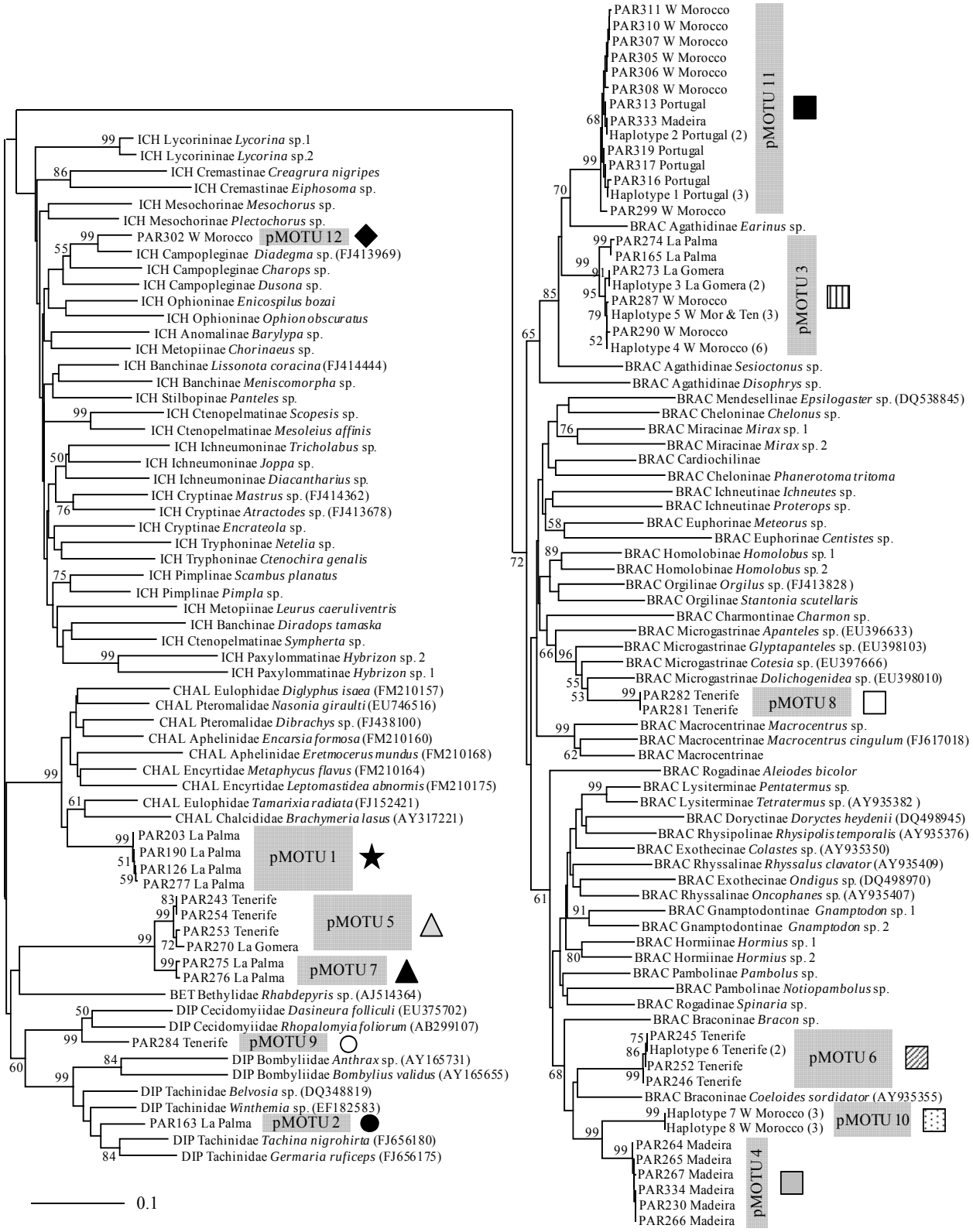

ICH Lycorininae Lycorina sp.1
ICH Lycorininae Lycorina sp.2
ICH Cremastinae Creagrura nigripes
ICH Cremastinae Eiphosoma sp.
ICH Mesochorinae Mesochorus sp.
ICH Mesochorinae Plectochorus sp.
PAR302 W Morocco
pMOTU 12
ICH Campopleginae Diadegma sp. (FJ413969)
ICH Campopleginae Charops sp.
ICH Campopleginae Dusona sp.
ICH Ophioninae Enicospilus bozai
ICH Ophioninae Ophion obscuratus
ICH Anomalinae Barylypa sp.
ICH Metopiinae Chorinaeus sp.
ICH Banchinae Lissonota coracina (FJ414444)
ICH Banchinae Meniscomorpha sp.
ICH Stilbopinae Panteles sp.
ICH Ctenopelmatinae Scopesis sp.
ICH Ctenopelmatinae Mesoleius affinis
ICH Ichneumoninae Tricholabus sp.
ICH Ichneumoninae Joppa sp.
ICH Ichneumoninae Diacantharius sp.
ICH Cryptinae Mastrus sp. (FJ414362)
ICH Cryptinae Atractodes sp. (FJ413678)
ICH Cryptinae Encrateola sp.
ICH Tryphoninae Netelia sp.
ICH Tryphoninae Ctenochira genalis
ICH Pimplinae Scambus planatus
ICH Pimplinae Pimpla sp.
ICH Metopiinae Leurus caeruliventris
ICH Banchinae Diradops tamaska
ICH Ctenopelmatinae Sympherta sp.
ICH Paxylommatinae Hybrizon sp. 2
ICH Paxylommatinae Hybrizon sp. 1
CHAL Eulophidae Diglyphus isaea (FM210157)
CHAL Pteromalidae Nasonia girault (EU746516)
CHAL Pteromalidae Dibrachys sp. (FJ438100)
CHAL Aphelinidae Encarsia formosa (FM210160)
CHAL Aphelinidae Eretmocerus mundus (FM210168)
CHAL Encyrtidae Metaphycus flavus (FM210164)
CHAL Encyrtidae Leptomastidea abnormis (FM210175)
CHAL Eulophidae Tamarixia radiata (FJ152421)
CHAL Chalcididae Brachymeria lasus (AY317221)
PAR203 La Palma
PAR190 La Palma
PAR126 La Palma
PAR277 La Palma
pMOTU 1
PAR243 Tenerife
PAR254 Tenerife
PAR253 Tenerife
PAR270 La Gomera
pMOTU 5
PAR275 La Palma
PAR276 La Palma
pMOTU 7
BET Bethylidae Rhabdepyris sp. (AJ514364)
DIP Cecidomyiidae Dasineura folliculi (EU375702)
DIP Cecidomyiidae Rhopalomyia foliorum (AB299107)
PAR284 Tenerife
pMOTU 9
DIP Bombyliidae Anthrax sp. (AY165731)
DIP Bombyliidae Bombylius validus (AY165655)
DIP Tachinidae Belvosia sp. (DQ348819)
DIP Tachinidae Winthemia sp. (EF182583)
PAR163 La Palma
pMOTU 2
DIP Tachinidae Tachina nigrohirta (FJ656180)
DIP Tachinidae Germaria ruficeps (FJ656175)
0.1
PAR311 W Morocco
PAR310 W Morocco
PAR307 W Morocco
PAR305 W Morocco
PAR306 W Morocco
PAR308 W Morocco
PAR313 Portugal
PAR333 Madeira
Haplotype 2 Portugal (2)
PAR319 Portugal
PAR317 Portugal
PAR316 Portugal
Haplotype 1 Portugal (3)
PAR299 W Morocco
pMOTU 11
BRAC Agathidinae Earinus sp.
PAR274 La Palma
PAR165 La Palma
PAR273 La Gomera
Haplotype 3 La Gomera (2)
PAR287 W Morocco
Haplotype 5 W Mor & Ten (3)
PAR290 W Morocco
Haplotype 4 W Morocco (6)
pMOTU 3
BRAC Agathidinae Sesioctonus sp.
BRAC Agathidinae Disophrys sp.
BRAC Mendesellinae Epsilogaster sp. (DQ538845)
BRAC Cheloninae Chelonus sp.
BRAC Miracinae Mirax sp. 1
BRAC Miracinae Mirax sp. 2
BRAC Cardiochilinae
BRAC Cheloninae Phanerotoma tritoma
BRAC Ichneutinae Ichneutes sp.
BRAC Ichneutinae Proterops sp.
BRAC Euphorinae Meteorus sp.
BRAC Euphorinae Centistes sp.
BRAC Homolobinae Homolobus sp. 1
BRAC Homolobinae Homolobus sp. 2
BRAC Orgilinae Orgilus sp. (FJ413828)
BRAC Orgilinae Stantonia scutellaris
BRAC Charmontinae Charmon sp.
BRAC Microgastrinae Apanteles sp. (EU396633)
BRAC Microgastrinae Glyptapanteles sp. (EU398103)
BRAC Microgastrinae Cotesia sp. (EU397666)
BRAC Microgastrinae Dolichogenidea sp. (EU398010)
PAR282 Tenerife
PAR281 Tenerife
pMOTU 8
BRAC Macrocentrinae Macrocentrus sp.
BRAC Macrocentrinae Macrocentrus cingulum (FJ617018)
BRAC Macrocentrinae
BRAC Rogadinae Aleiodes bicolor
BRAC Lysiterminae Pentatermus sp.
BRAC Lysiterminae Tetratermus sp. (AY935382)
BRAC Doryctinae Doryctes heydenii (DQ498945)
BRAC Rhysipolinae Rhysipolis temporalis (AY935376)
BRAC Exothecinae Colastes sp. (AY935350)
BRAC Rhyssalinae Rhyssalus clavator (AY935409)
BRAC Exothecinae Ondigus sp. (DQ498970)
BRAC Rhyssalinae Oncophanes sp. (AY935407)
BRAC Gnamptodontinae Gnamptodon sp. 1
BRAC Gnamptodontinae Gnamptodon sp. 2
BRAC Hormiinae Hormius sp. 1
BRAC Hormiinae Hormius sp. 2
BRAC Pambolinae Pambolus sp.
BRAC Pambolinae Notiopambolus sp.
BRAC Rogadinae Spinaria sp.
BRAC Braconinae Bracon sp.
PAR245 Tenerife
Haplotype 6 Tenerife (2)
PAR252 Tenerife
PAR246 Tenerife
pMOTU 6
BRAC Braconinae Coeloides sordidator (AY935355)
Haplotype 7 W Morocco (3)
Haplotype 8 W Morocco (3)
pMOTU 10
PAR264 Madeira
PAR265 Madeira
PAR267 Madeira
PAR334 Madeira
PAR230 Madeira
PAR266 Madeira
pMOTU 4

Figure 5.2. Neighbor-joining tree of the parasitoid barcode sequences (based on K2P genetic distances) showing the existence of 12 MOTUs (in grey). Symbols represented next to the sequence name correspond to the same symbols of Fig. 5.3, and indicate which parasitoid MOTU was found to parasitize which host MOTU (squares – Braconidae, diamond – Ichneumonidae, star – Chalcidoidea, triangle – Bethylidae, circle – Diptera). Accession numbers of sequences obtained from GenBank are also represented. Numbers next to branches represent the bootstrap values obtained after 1,000 replications. Values lower than 50 are not represented. Scale bar indicates 10% sequence divergence. The tree obtained with Maximum Likelihood method is available in Appendix A3.4.

Barcoding analyses of host specimens

In the case of the hosts, the similarity-based methods identified all specimens as belonging to the Tortricidae family, but failed to give identification to one single genus (see Appendix A3.5). However, all museum and collection specimens of *A. subsequana* were closely related to the samples we collected in the field (see below), confirming that all host individuals analysed belong to this taxon.

In our study area, the genetic distances obtained with K2P revealed six MOTUs (Appendix A3.5) with little internal sequence divergence (range from 0.1 to 0.7%), that are each restricted to a single sampling region. The NJ and ML tree topologies also strongly support these results (Fig. 5.3; see ML tree in Appendix A3.6). hMOTU13 is restricted to the Madeira Island, hMOTU14 to La Gomera, hMOTU15 to La Palma, hMOTU16 to Tenerife, hMOTU17 to the western part of Morocco and hMOTU18 to the northern part of Morocco and to the Portuguese mainland. The MOTU clusters from both NJ and ML trees were highly supported (98-100% bootstrap support in most cases), reflecting that sequence divergences were greater between MOTUs than within them. The adult specimens usually clustered with sequences from the same region, but samples from Fuerteventura and the Spanish mainland grouped with hMOTU18 that also includes specimens from Northern Morocco and mainland Portugal. The two museum specimens from Porto Santo formed a seventh *A. subsequana* cluster.

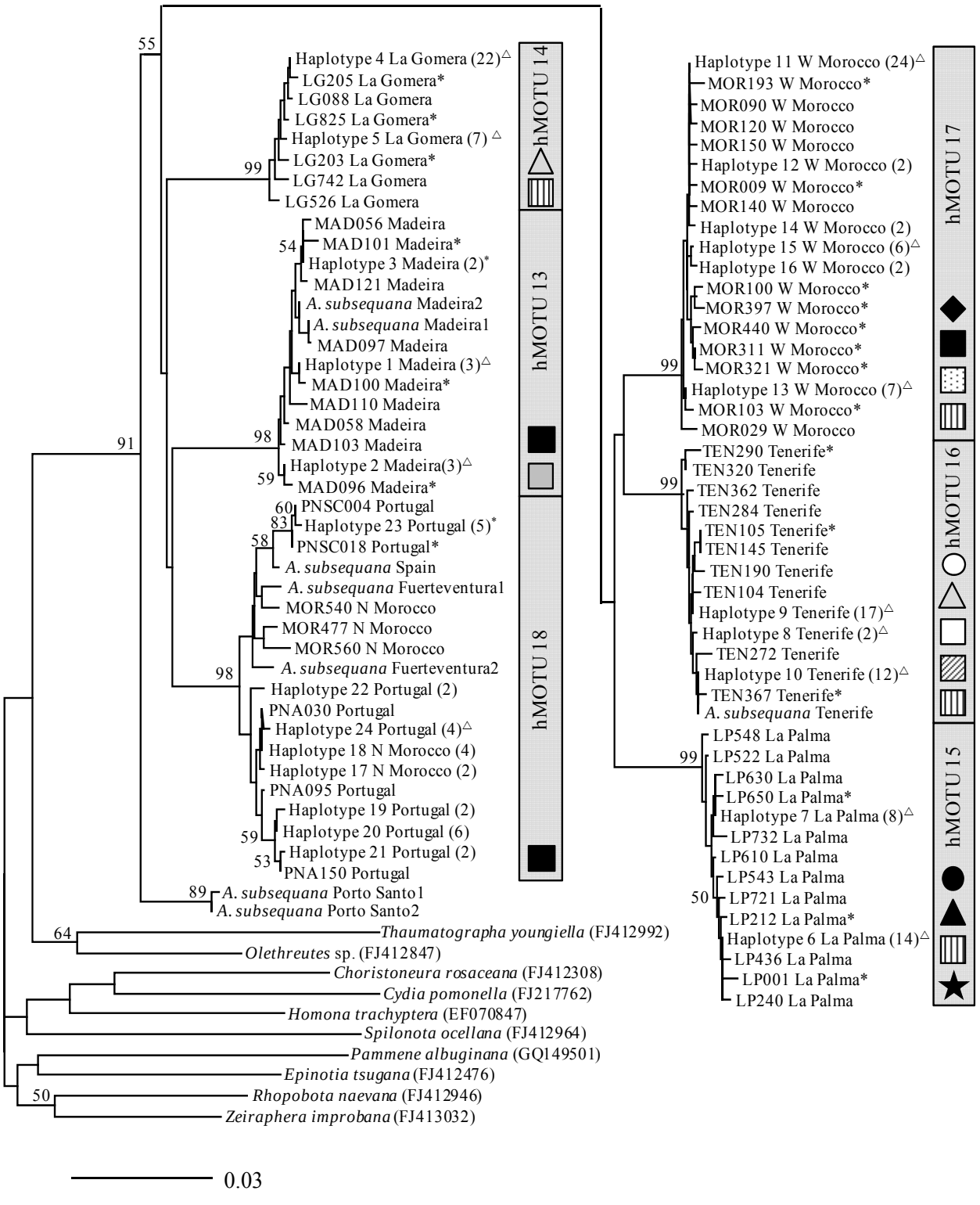

Haplotype 4 La Gomera (22)△
LG205 La Gomera*
LG088 La Gomera
LG825 La Gomera*
Haplotype 5 La Gomera (7) △
LG203 La Gomera*
LG742 La Gomera
LG526 La Gomera
MAD056 Madeira
MAD101 Madeira*
Haplotype 3 Madeira (2)*
MAD121 Madeira
A. subsequana Madeira2
A. subsequana Madeira1
MAD097 Madeira
Haplotype 1 Madeira (3)△
MAD100 Madeira*
MAD110 Madeira
MAD058 Madeira
MAD103 Madeira
Haplotype 2 Madeira(3)△
MAD096 Madeira*
PNSC004 Portugal
Haplotype 23 Portugal (5)*
PNSC018 Portugal*
A. subsequana Spain
A. subsequana Fuerteventura1
MOR540 N Morocco
MOR477 N Morocco
MOR560 N Morocco
A. subsequana Fuerteventura2
Haplotype 22 Portugal (2)
PNA030 Portugal
Haplotype 24 Portugal (4)△
Haplotype 18 N Morocco (4)
Haplotype 17 N Morocco (2)
PNA095 Portugal
Haplotype 19 Portugal (2)
Haplotype 20 Portugal (6)
Haplotype 21 Portugal (2)
PNA150 Portugal
A. subsequana Porto Santo1
A. subsequana Porto Santo2
hMOTU 14
hMOTU 13
hMOTU 18
Haplotype 11 W Morocco (24)△
MOR193 W Morocco*
MOR090 W Morocco
MOR120 W Morocco
MOR150 W Morocco
Haplotype 12 W Morocco (2)
MOR009 W Morocco*
MOR140 W Morocco
Haplotype 14 W Morocco (2)
Haplotype 15 W Morocco (6)△
Haplotype 16 W Morocco (2)
MOR100 W Morocco*
MOR397 W Morocco*
MOR440 W Morocco*
MOR311 W Morocco*
MOR321 W Morocco*
Haplotype 13 W Morocco (7)△
MOR103 W Morocco*
MOR029 W Morocco
TEN290 Tenerife*
TEN320 Tenerife
TEN362 Tenerife
TEN284 Tenerife
TEN105 Tenerife*
TEN145 Tenerife
TEN190 Tenerife
TEN104 Tenerife
Haplotype 9 Tenerife (17)△
Haplotype 8 Tenerife (2)△
TEN272 Tenerife
Haplotype 10 Tenerife (12)△
TEN367 Tenerife*
A. subsequana Tenerife
LP548 La Palma
LP522 La Palma
LP630 La Palma
LP650 La Palma*
Haplotype 7 La Palma (8)△
LP732 La Palma
LP610 La Palma
LP543 La Palma
LP721 La Palma
LP212 La Palma*
Haplotype 6 La Palma (14)△
LP436 La Palma
LP001 La Palma*
LP240 La Palma
hMOTU 17
hMOTU 16
hMOTU 15
Thaumatographa youngiella (FJ412992)
Olethreutes sp. (FJ412847)
Choristoneura rosaceana (FJ412308)
Cydia pomonella (FJ217762)
Homona trachyptera (EF070847)
Spilonota ocellana (FJ412964)
Pammene albuginana (GQ149501)
Epinotia tsugana (FJ412476)
Rhopobota naevana (FJ412946)
Zeiraphera improbana (FJ413032)
0.03

Figure 5.3. Neighbor-joining tree of the tortricid barcode sequences (based on K2P genetic distances) showing the existence of six MOTUs from our study area (in grey). * indicates specimens that were parasitized; △ indicates haplotypes with both parasitized and non-parasitized specimens. Symbols represented next to the sequence name correspond to the same symbols of Fig. 5.2, and indicate which tortricid MOTU was attacked by which parasitoid MOTU (squares – Braconidae, diamond – Ichneumonidae, star – Chalcidoidea, triangle – Bethylidae, circle – Diptera). Accession numbers of sequences obtained from GenBank are also represented. Numbers next to branches represent the bootstrap values obtained after 1,000 replications. Values lower than 50 are not represented. Scale bar indicates 3% sequence divergence. The tree obtained with Maximum Likelihood method is available in Appendix A3.6.

Sampling completeness and trophic relationships

The slopes of species accumulation curves fell below the 0.05 threshold, indicating that all areas were well sampled (Table 5.3). The slope of the overall species accumulation curve was 0.002, meaning that it would be necessary to collect 500 more tortricids in order to find one more parasitoid MOTU.

The trophic relationships between the parasitoids and their host larvae are shown in both Figs. 5.2 and 5.3, and are indicated by the symbols given to each MOTU. Nine out of 12 parasitoid MOTUs attacked only one provisional host species. pMOTU3 and pMOTU11, both identified as belonging to the subfamily Agathidinae, were the only clusters that were found in hosts from both island and mainland areas. Finally, pMOTU5 attacked both hMOTU14 (La Gomera) and hMOTU16 (La Palma).

5.5. Discussion

It has been argued that DNA barcodes can be used as a surrogate method for identifying and delimiting units of diversity, providing a rapid and accurate tool for ecological studies (e.g. Blaxter *et al.*, 2005; Sheffield *et al.*, 2009; Valentini *et al.*, 2009). While DNA barcoding has been used to describe general ecological patterns (see, e.g., Smith *et al.*, 2005, 2006, 2007, 2008, 2009; Pfenninger *et al.*, 2007; Emery *et al.*, 2009; Janzen *et al.*, 2009; Jurado-Rivera *et al.*, 2009), its application in ecological and biogeographical studies of parasitoids is far from routine, and, as far as we know, has rarely been used for ecological hypothesis-testing. Here

we present and evaluate a barcoding protocol for studying geographical variation in host-parasitoid interactions. Although our results indicate the potential utility of this approach, they also point to three potential challenges that need to be addressed for its future successful application.

Challenge 1: Potential methodological problems

Rearing collected hosts requires provisioning suitable artificial diet or living plant material to sustain the hosts until parasitoid emergence. This is a difficult, time-consuming and often unreliable procedure (Noyes, 1994; Shaw, 1997; Laurenne *et al.*, 2000; Tilmon *et al.*, 2000; Agustí *et al.*, 2005), which is also unsuitable for studies involving broad geographical scales, as it is often required in biogeographical and ecological studies. In the dissection method the host larvae are dissected to detect the presence of parasitoids, with both host and parasitoids classically being identified based on morphology. Although this method is more accurate than rearing (Day, 1994), it has also been criticized for the complexity of assigning a larva to a particular species based on morphology (Quicke, 2002; Greenstone, 2003; Persad *et al.*, 2004). A third alternative would be to use DNA techniques based on species-specific primers (singleplex and multiplex PCR; e.g. Tilmon *et al.*, 2000; Agustí *et al.*, 2005; Gariepy *et al.*, 2007; Traugott *et al.*, 2006, 2008). However, this approach gives similar parasitism rates as dissections (Tilmon *et al*., 2000), and can only be applied to small sets of parasitoids already well known (reared, identified and sequenced). Therefore, we believe that combining dissections and DNA barcoding is the most appropriate way to analyse understudied communities from a large geographical range.

Dissection methods can underestimate parasitism rates due to the difficulty in finding early instars and eggs (Symondson & Hemingway, 1997). Such problem is minimized if the same protocol is applied in the different areas being compared (provided that all of them are subject to the same sampling effort). The overall parasitism rate found in this study (5.6%) does not differ much from those obtained from long-term rearing projects (Smith *et al*., 2007, 2008). In addition, the shallow slopes of the species accumulation curves indicate that the sampling effort is appropriate. However, in spite of the apparently good knowledge of our host-parasitoid community, the total number of parasitoids discovered at each area is still

small, especially when the final goal is to use this protocol for ecological and/or biogeographical studies (Chapter 6).

One of the goals of the "DNA Barcoding of Life" project is to develop a standardized, rapid and accurate species identification method that is accessible to non-taxonomists. To achieve this, it will be necessary to develop a single pair of universal primers that can amplify the DNA barcode locus in any animal species. Although some studies showed the efficacy of using universal primers (e.g. Folmer *et al.*, 1994) in a variety of taxa from different phyla (e.g. Hebert *et al.*, 2003a, 2004a, b; Ekrem *et al.*, 2007), its applicability is not general (e.g. Blaxter *et al.*, 2005; Lorenz *et al.*, 2005; Vences *et al.*, 2005). In this study the "Folmer's universal primers" (LCO1490 / HCO2198; Folmer *et al.*, 1994) failed to amplify a large number of samples, so alternative primers had to be applied. Taking this into consideration, it is advisable to adjust and optimize primer sequences and PCR conditions prior to the use of DNA barcoding on arthropods.

Challenge 2: Delimiting MOTUs

DNA barcoding can be used to delimit MOTUs (Floyd *et al.*, 2002; Blaxter *et al.*, 2005) that serve as surrogate units for the assessment of richness and turnover across different scales (e.g. Smith *et al.*, 2005; Valentini *et al.*, 2009). In fact, the use of surrogates of true species is not new, and has already been successfully applied to arthropod surveys, where morphospecies were used as taxonomic units (e.g. Oliver & Beattie, 1996a, b; Borges *et al.*, 2005b).

MOTUs are usually defined as clusters of sequences with pairwise distances below a certain threshold (e.g. Hebert *et al.*, 2003a; Smith *et al.*, 2005, 2009; Pfenninger *et al.*, 2007; Puillandre *et al.*, 2009). Hebert and colleagues (2003a) initially proposed 3% pairwise sequence divergence (normally measured with the K2P model) as the threshold to distinguish between two MOTUs. Alternatively, a threshold may be set such that inter-MOTU variability is 10 times the value of the intraspecific variability (Hebert *et al.*, 2004a). The arbitrary nature of both approaches has been criticized, because the overlap between intra- and interspecific variability is likely to be significant in many taxa (Meyer & Paulay, 2005; Vences *et al.*, 2005; Hickerson *et al.*, 2006; Meier *et al.*, 2006). Indeed, a range of threshold

values has been applied to different taxa (e.g. Floyd *et al.*, 2002; Hebert *et al.*, 2004a; Puillandre *et al.*, 2009; Smith *et al*., 2009).

In our case, determining the correct threshold value was difficult because we aimed to define MOTUs belonging to three different higher taxa (Hymenoptera, Diptera and Lepidoptera). Therefore we used the less restrictive 3% sequence divergence threshold. After applying this we recognized 12 parasitoid MOTUs and six tortricid MOTUs, each displaying low levels of intra-unit sequence divergence. Lack of *a priori* knowledge of the parasitoid species associated with *A. subsequana* in Macaronesia prevented the application of the "10 times average intraspecific difference" threshold (Hebert *et al.*, 2004a).

MOTU boundaries can also be delimited by using tree-based methods (e.g. Hebert *et al.*, 2003a; Pons *et al.*, 2006; Elias *et al*., 2007; Pfenninger *et al*., 2007; Sheffield *et al.*, 2009). Since NJ trees have been considered unreliable by some authors (DeSalle *et al.*, 2005; Meier *et al.*, 2006; Little & Stevenson, 2007; but see Elias *et al.*, 2007; Pfenninger *et al*., 2007), we also computed ML trees. Both NJ and ML trees assigned all specimens to the same MOTUs previously defined by the sequence divergence approach, with clusters usually strongly supported by high bootstrap values (Figs. 5.2 and 5.3; Appendices A3.4 and A3.6). This congruence in our own results reinforces confidence in the defined MOTUs. Therefore, we advise the use of a combination of sequence divergence measures (with a 3% threshold, or another threshold if the community being studied is already known) and tree-based methods for the delimitation of MOTUs.

Challenge 3: Identification of the MOTUs

Similarity-based methods (e.g. BLAST, BOLD) provide a fast way for identifying a query sequence against a database. The accuracy of the given identification will depend on the completeness and correctness of the existing data (such as GenBank) (Blaxter *et al.*, 2005; Meyer & Paulay, 2005; Meier *et al.*, 2006; Ekrem *et al.*, 2007; Puillandre *et al.*, 2009). Based on these two similarity-based methods, none of the sequences obtained in this study could be assigned confidently to a genus (Table 5.2, Appendix A3.5). Regarding the tortricids all sequences were correctly identified to family level, but no method gave the correct genus. This shows that the available databases are far from complete, and are not yet reliable to be

used for the identification of poorly studied hyperdiverse taxa, such as parasitic Hymenoptera, Diptera and Microlepidoptera.

In tree-based methods, queries are considered successfully identified when they form clusters with conspecific barcodes. However this approach assumes that species are monophyletic, ignoring the evidence indicating that some recognized species are "paraphyletic" on trees (Crisp & Chandler, 1996; Funk & Omland, 2003). In spite of the consistency of the results obtained with NJ and ML trees, this approach failed to give a reliable identification to the species level, or even genus level. Like similarity methods, the usefulness of this approach strongly depends on the existence of a comprehensive database, which clearly is not the case. An alternative to overcome this problem would be either to build trees using sequences from identifiable adult specimens obtained from rearing, or to construct large sequence databases. But in most studies both options are unsuitable because rearing presents several limitations (see above), and building these large databases requires an amount of time and resources that are beyond the scope of many research projects. In addition, we had the opportunity to compare our sequences with a large unpublished database (with approx. 4200 sequences of almost all subfamilies of the Ichneumonoidea; Chesters *et al*. in prep), and even with such a large amount of data, success of identification to the genus level is not assured (results not shown).

Insights from the protocol

The efficiency of DNA barcoding in the detection of cryptic species is well documented in the literature (e.g. Hebert *et al.*, 2004a,b; Janzen *et al.*, 2005; Smith *et al.*, 2006; but see Hickerson *et al.*, 2006), especially in the case of insects, where a high percentage of the currently recognized species are estimated to comprise cryptic species complexes (Quicke, 2004). In our study, DNA barcoding also allowed us to discover several potential cryptic species. Our sequencing results indicate that *A. subsequana* is probably a complex of at least seven species or subspecies in the Macaronesian region (including Porto Santo). Indeed, each island population is genetically distinct from both each other and the mainland populations. Sea barriers may have limited gene flow between islands and mainland, promoting an allopatric divergence of *A. subsequana* populations. Determining whether this divergence is associated with behavioral, ecological and/or morphological differences between populations

still remains to be investigated and should bring additional insights on the speciation processes of this taxon.

Despite the challenges discussed above, our results indicate that DNA barcoding can be useful for solving ecological and/or biogeographical questions related to host-parasitoid interactions. Our method enables the definition of MOTUs without the need for rearing or morphology-based identification, allowing non-taxonomists to study both hosts and parasitoids. Since it provides a surrogate method for identifying units of diversity, it enables to produce parasitoid foodwebs and to quantify interactions. Although it is still difficult to assign species names to each MOTU, this may not be a problem for ecologists and biogeographers, depending on the particular purpose of the study being carried out. With time, the combined efforts of taxonomy and DNA barcoding will generate more and more sequences with a correct species name, and the application of protocols such as the one described here will even be more useful.

Chapter 6: Are island and mainland biotas different? Richness and level of generalism in parasitoids of a microlepidopteran in Macaronesia[5]

6.1. Abstract

Island communities are exposed to several evolutionary and ecological processes that lead to changes in their diversity and structure compared to mainland biotas. These phenomena have been observed for various taxa but not for parasitoids, a key group in terms of community diversity and functioning. Here we use the parasitoid communities associated with the moth *Acroclita subsequana* (Lepidoptera: Tortricidae) in the Macaronesian region, to test whether species richness differs between islands and mainland, and whether island parasitoid faunas are biased towards generalist species. Host larvae were collected in several islands and adjacent mainland, carefully searched for ectoparasitoid larvae and dissected to recover any endoparasitoids. Parasitoids were classified as idiobionts, which usually have a wide host range (i.e. generalists), or koinobionts that are considered specialists. Mainland species richness was lower than expected by chance, with most of the species being koinobionts. On the other hand, island communities showed a greater proportion of idiobiont species. Overall parasitism rates were similar between islands and mainland, but islands had higher rates of parasitism by idiobionts than expected by chance, and mainland areas showed the highest koinobiont parasitism rates. These results suggest that island parasitoid communities are dominated by generalists, in comparison to mainland communities. Several hypotheses may explain this pattern: (i) generalist parasitoids might have better dispersal abilities; (ii) they may be less constrained by "sequential dependencies"; and (iii) island parasitoids probably have fewer competitors and/or predators, thus favouring the establishment of generalists. New studies including multiple hosts, other habitats and/or more islands are necessary to identify which of these processes shape island parasitoid communities.

[5]This chapter is the basis of: Santos, A.M.C., Fontaine, C., Quicke, D.L.J., Borges, P.A.V. & Hortal, J., which is a manuscript that has been submitted for publication.

6.2. Introduction

Island faunas tend to be species–poor and disharmonic in relation to the mainland, and this is especially the case for oceanic islands (Williamson, 1981; Whittaker & Fernández-Palacios, 2007). Typically, islands have fewer species than an area of similar size on the mainland, which often results in some functional groups (i.e. trophic or ecological guilds) being missing or underrepresented in their communities. In addition to these differences in the species pool, the feeding interactions among species often vary as well. Following a founding event, several evolutionary and ecological processes take place (see Losos & Ricklefs, 2009), including ecological release, density compensation, niche expansion and niche shifts. These processes are promoted by factors such as the existence of empty or invasible niche space, low interspecific competition, and lack of entire groups of predators, parasitoids or pathogens, which usually contribute to increase the number of species using a broader range of resources (Whittaker & Fernández-Palacios, 2007). In other words, oceanic islands tend to host more generalist species than their source mainlands, both because generalists may have an *a priori* advantage during the colonization process (e.g. Piechnik *et al.*, 2008), and because some species are able to increase their niche width after reaching a new territory (e.g. Schlotfeldt & Kleindorfer, 2006). This tendency for island populations to have wide ecological niches seems to be a general pattern, and has been observed at least in birds (e.g. Diamond, 1970; Olesen & Valido, 2003a, 2004; Scott *et al.*, 2003; Schlotfeldt & Kleindorfer, 2006), lizards (e.g. Olesen *et al*., 2002*;* Olesen & Valido, 2003b; 2004) and several insect groups (e.g. Kitahara & Fujii, 1997; Olesen *et al*., 2002*;* Ribeiro *et al.*, 2005a).

Parasitoids are insects whose larvae develop by feeding on (ectoparasitoids) or within (endoparasitoids) an arthropod host, eventually killing it (Eggleton & Belshaw, 1992; Godfray, 1994; Quicke, 1997; but see Eggleton & Gaston, 1990). Although they are best known from the parasitic Hymenoptera, which account for approximately three-quarters of the total number of known species, other orders such as Diptera, Coleoptera, Lepidoptera and Neuroptera also include parasitoid species (Eggleton & Belshaw, 1992; Godfray, 1994). Parasitoids can be divided into two groups, depending on their life history strategies: koinobionts, which allow the host to continue its development after oviposition, and idiobionts, that do not (Askew & Shaw, 1986). Many life history traits, including host ranges

and mode of parasitism, appear to be correlated with this dichotomy (Sheehan & Hawkins, 1991; Hawkins, 1994; Quicke, 1997; Mayhew & Blackburn, 1999).

The host range of a particular parasitoid species is the group of potential hosts that it can usually attack successfully, after exhibiting a pattern of searching behaviour that allows it to find them regularly (Shaw, 1994). Koinobionts usually have a narrower host range than idiobionts (Askew & Shaw, 1986; Sato, 1990; Sheehan & Hawkins, 1991; Hawkins, 1994; Althoff, 2003; but see Mills, 1992) because they have a more prolonged interaction with their hosts' immune system; therefore, the adaptations needed to overcome this problem are believed to restrict the number of hosts that koinobionts can attack successfully. On the other hand, when attacking larval hosts, idiobionts paralyse their hosts on the moment of oviposition, and their interaction with the host immune system is minimal, allowing them to be physiologically able to develop on a wider range of hosts (Askew & Shaw, 1986; Hawkins, 1994). Consequently, idiobionts are expected to be able to shift on to novel hosts more readily than koinobionts can (Cornell & Hawkins, 1993; Shaw, 1994). In the absence of detailed rearing records, the koinobiont/idiobiont dichotomy represents a practical criterion for distinguishing between parasitoids that tend to be specialists (koinobionts) and parasitoids that are potentially more generalists (idiobionts) in terms of the host range attacked (Hawkins *et al*., 1990).

Realized host range may change over both evolutionary and biological time. Parasitoids can exhibit plasticity in the range of hosts they attack, and thus are able to respond to inconstant and uneven environments (e.g. Cornell & Hawkins, 1993; Godfray *et al.*, 1995; Hawkins & Marino, 1997; Tanaka *et al.*, 2007). Since hosts on islands may be unusual or novel compared to those on the mainland, parasitoids arriving on islands may be forced to attempt to utilize less preferred or novel hosts. Therefore island faunas would be expected to be biased towards generalist species (i.e. idiobionts), at least in the initial stages of their colonization. Although there are some studies on the dispersal, colonization and establishment of parasitoids in new areas, most focus on the landscape level (e.g. Kruess & Tscharntke, 1994; 2000; Nouhuys & Hanski, 2002; Cronin, 2004; Esh *et al.*, 2005; Elzinga *et al.*, 2007). Few studies analyse parasitoids' host ranges (and host shifts) on a wider geographic scale, and those that do usually rely on literature records (e.g. Cornell & Hawkins, 1993; Hawkins, 1994; Hawkins & Marino, 1997; but see Stone *et al*., 1995). The

diversity patterns of parasitoids remain particularly poorly known for oceanic islands, for which the only published works are mostly limited to checklists (e.g. Gauld & Carter, 1983; Belokobylskij & Maetô, 2008; Bennet, 2008), and are usually biased towards introduced species and agricultural habitats (e.g. Funasaki *et al.*, 1988; Peck *et al.*, 1998; Santos *et al.*, 2005; Lozan *et al.*, 2008; but see Maetô & Thornton, 1993; Schoener *et al.*, 1995; Hodkinson *et al.*, 2004).

Here we study how the diversity and attack strategy of parasitoid communities associated with the moth *Acroclita subsequana* (Lepidoptera: Tortricidae) feeding on spurges (*Euphorbia* spp., Euphorbiaceae) vary between the islands and adjacent mainland of the Macaronesian region. This study system provides an opportunity to investigate how parasitoid communities change geographically, because it consists of populations of a single host scattered throughout a region for which biogeographical patterns are well known (e.g. Triantis *et al.*, 2010). We specifically test whether for a given host: (i) parasitoid species richness differs between island and mainland territories; (ii) the island parasitoid communities are biased towards generalist species (i.e., islands have a higher number of idiobiont species); and (iii) whether these changes in composition and diversity of the parasitoid communities translate into variation in the parasitism rates.

6.3. Methods

This study was conducted in different islands and adjacent mainland areas from the Macaronesian region (NE Atlantic). Larvae of the moth *Acroclita subsequana* (Herrich-Schäffer, 1851) (Lepidoptera: Tortricidae) found feeding on *Euphorbia* spp. (Euphorbiaceae) spurges were collected from 55 study sites located in the islands of Madeira, La Gomera, La Palma and Tenerife, as well as in Morocco (western and northern regions) and mainland Portugal (Fig. 6.1; Table 6.1). A detailed description of the sampling protocol and identification methods is presented in Chapter 5. Briefly, concealed tortricid larvae were collected by hand, preserved in ethanol and stored below 5º C until they were dissected in order to find ectoparasitoid and/or endoparasitoid larvae. Both hosts and parasitoids were sequenced for a c. 650 base pairs 5′ fragment of the mitochondrial cytochrome oxidase I

gene (COI), and assigned to molecular operational taxonomic units (MOTUs). Parasitoids were grouped into 12 MOTUs belonging to the Hymenoptera (Bethylidae, Braconidae, Ichneumonidae and Chalcidoidea) and Diptera (Cecidomyidae and Tachinidae) (see Table 5.2 in Chapter 5). These MOTUs were assumed to correspond to different parasitoid species, that were easily classified as idio- or koinobionts according to the known biology of the families and subfamilies they belong to. Specimens that were not sequenced or were only identified to superfamily level (e.g. Chalcidoidea), were classified according to the attack strategy observed during the dissection process: ectoparasitoids were classified as idiobionts and endoparasitoids were assumed to be koinobionts (following Hawkins, 1994 and Mayhew & Blackburn, 1999). Hosts comprised six MOTUs, each one found in one of the sampled areas, except for Northern Morocco and Portugal mainland that share the same host MOTU (Table 6.1). Although these host MOTUs can potentially correspond to different cryptic species within the currently valid species *A. subsequana* (Chapter 5), for the purpose of this study they can be considered the same (or very similar) type of resource.

Parasitoid species richness was estimated using five non-parametric estimators: Abundance-based Coverage Estimator (ACE), Chao's abundance-based estimator (Chao1), 1st order Jackknife (Jack1), 2nd order Jackknife (Jack2) and Michaelis-Menten (MM) (see Colwell & Coddington, 1994; Gotelli & Colwell, 2001; Hortal *et al*., 2006; for more details on these estimators and their performance). All these calculations were done in ESTIMATES 8.2.0 software (Colwell, 2009), randomising the order of the samples 1,000 times.

We used a bootstrap procedure to evaluate whether observed species richness and parasitism rates (i.e. number of parasitoid individuals per number of hosts collected) differed from what could be expected by chance. For a given locality where N caterpillars were collected, the expected null distribution was created by resampling the total dataset with replacement to create 5,000 samples of the same size. Parasitoid richness and parasitism rates of both idio- and koinobionts were calculated for each of these samples to obtain the distributions of random expectations. Observed values were then compared to these distributions, and were considered significantly different from the null expectation when falling outside the 90% confidence interval. These analyses were performed using a script written in R (R Development Core Team, 2005).

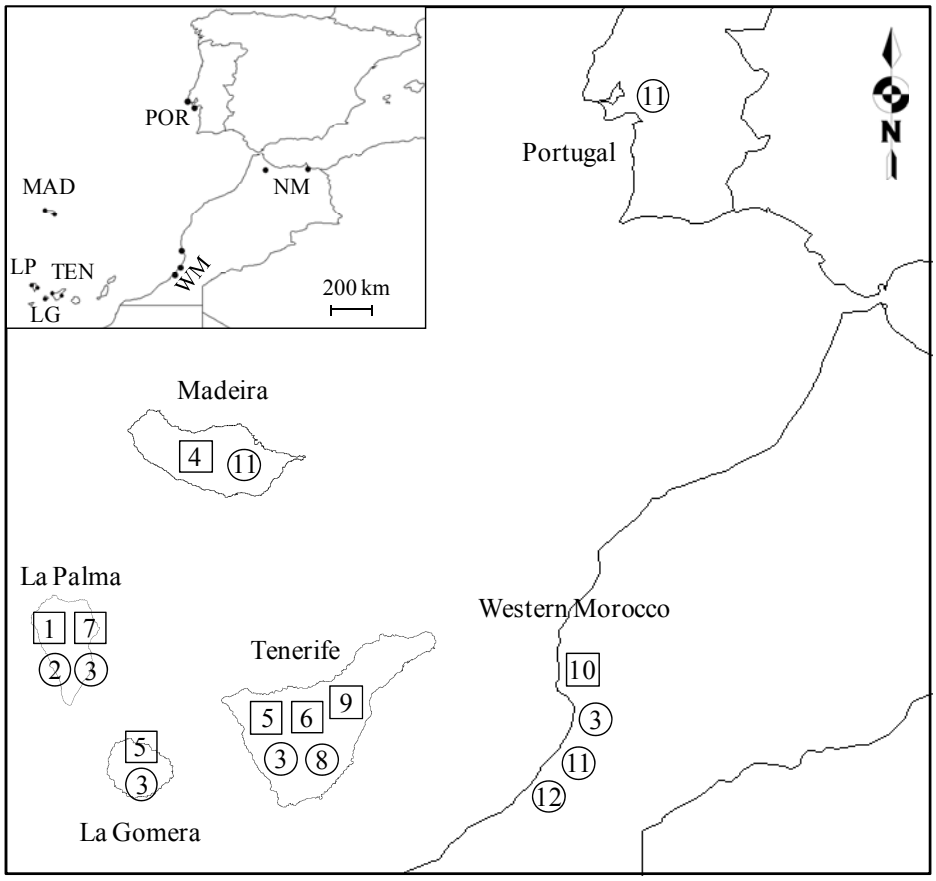


Figure 6.1. Geographical distribution of the parasitoid species found in the studied islands and mainland areas of Macaronesia. Squares represent idiobionts and circles are koinobionts. Numbers correspond to the code given to each parasitoid MOTU (see Chapter 5 for more information). The scale of the islands and the distance between them and the mainland are modified for the ease of visualization. The map in the inset is correctly scaled, and shows the actual position of each island and the location of the different sampling areas (represented by the black dots). MAD – Madeira Island; LG – La Gomera; LP – La Palma; TEN – Tenerife; WM – Western Morocco; NM – Northern Morocco; POR – Portugal.

6.4. Results

A total of 1,415 *A. subsequana* larvae were collected and dissected (see Table 6.1). Seventy-nine parasitoids were found attacking these larvae, 65 of which were successfully sequenced and assigned to 12 MOTUs (see Table 5.2 in Chapter 5). In total, 34 parasitoid larvae were classified as idiobionts, and 45 were considered to be koinobionts (Table 6.1).

Table 6.1. Abundance and species richness of hosts and parasitoids collected on each study area.

Area	Number of Sites	Host identifier	Number of Hosts	Idiobiont species	Koinobiont species	Number Idiobionts	Number Koinobionts
Islands							
Madeira	5	hMOTU13	57	1	1	6	2
La Gomera	8	hMOTU14	180	1	1	6	6
La Palma	7	hMOTU15	187	2	2	6	5
Tenerife	9	hMOTU16	240	3	2	10	3
Mainland							
W Morocco	16	hMOTU17	472	1	3	6	20
N Morocco	4	hMOTU18	92	0	0	0	0
Portugal	6	hMOTU18	187	0	1	0	9

Number of sites indicates the number of sites sampled per study area; Host identifier is the code given to each host molecular operational taxonomic unit (MOTU) collected from the study areas (see more details in Chapter 5). Number of Hosts is the total number of *Acroclita subsequana* larvae collected. Idiobiont species and Koinobiont species correspond to the number of idio- and koinobiont MOTUs, respectively, and Number Idiobionts and Number Koinobionts are the number of host larvae that were attacked by idio- or koinobionts, respectively.

Mainland species richness was significantly lower than expected by chance (see Table 6.2; Appendix A4.1). Islands as a whole had more than twice as many species than observed in all mainland areas. When the study sites were compared, Tenerife was the richest, followed by La Palma and Western Morocco. Portugal had the lowest richness and Northern Morocco was the only region where no parasitoids were found (see Fig. 6.1; Table 6.1). Due to this, the latest area will not be mentioned any further in this work. Estimated species richness values differed from the observed ones (Table 6.3), with the Chao1 estimates being the most similar to the observed data, while Jack2 usually showed higher values. Tenerife was estimated to be the study area with the most parasitoid species, while Portugal was the one with the least (Fig. 6.2; Table 6.3).

Table 6.2. Comparison between observed and randomised parasitoid species richness and parasitism rate of each study area.

	Madeira	La Gomera	La Palma	Tenerife	Western Morocco	Portugal
Total parasitoid species richness	+	–*	–	–	– **	– **
Idiobiont species richness	+	–	–	–	– ***	– *
Koinobiont species richness	+	–	+	+	+	–
Total parasitism rate	+ ***	+	+	–	+	–
Idiobiont parasitism rate	+ ***	+	+	+*	–	– **
Koinobiont parasitism rate	+	+	–	– *	+	+

Cases where observed results are lower than the median of the null expectation are represented by (–). Cases where observed results are higher than the median of the random distribution are represented by (+). Cases outside the 90% confidence interval (i.e., significantly different from the overall pool) are represented by * $p < 0.1$; ** $p < 0.05$; *** $p < 0.01$. Randomization results are presented in Appendices A4.1 to A4.6.

Table 6.3. Observed (S*obs*) and estimated parasitoid species richness in each study area.

	Uniques	Duplicates	*Sobs*	ICE	Chao2 ± SD	Jack1 ± SD	Jack2 ± SD	MM
Madeira	1	0	2	3.11	2 ± 0.35	2.98 ± 0.98	3.95 ± 0	2.57
La Gomera	1	0	2	3.11	2 ± 0.35	2.99 ± 0.99	3.98 ± 0	3.96
La Palma	1	2	4	4.5	4 ± 0.17	4.99 ± 0.99	4.02 ± 0	7.43
Tenerife	2	1	5	6.65	5.5 ± 1.29	6.99 ± 1.41	7.99 ± 0	8.51
W Morocco	1	0	4	4.41	4 ± 0.43	5 ± 1	5.99	4.69
Portugal	0	0	1	1	1 ± 0.01	1	1 ± 0	1.17
All Islands	3	2	10	11.7	11 ± 1.82	13 ± 1.73	14 ± 0	14.44
All Mainland	1	0	4	4.59	4 ± 0.43	5 ± 1	6	4.39
All sites	3	2	12	13.65	13 ± 1.82	15 ± 1.73	16 ± 0	14.45

Uniques and Duplicates are the number of parasitoid species that occur in only one or two samples (i.e. host larvae), respectively. ICE, Chao2, Jack1, Jack2 and MM correspond to the different species richness estimators used (Abundance-based Coverage Estimator, Chao's abundance-based estimator, Jackknife 1, Jackknife 2 and Michaelis-Menten, respectively; see Colwell, 2009 and Methods for further information). When relevant, the standard deviations of the estimations (SD) are shown next to the estimated values. All Islands corresponds to all islands as a whole; All Mainland to all mainland areas; and All sites corresponds to all study areas. Northern Morocco not shown due to the lack of recorded parasitoids.

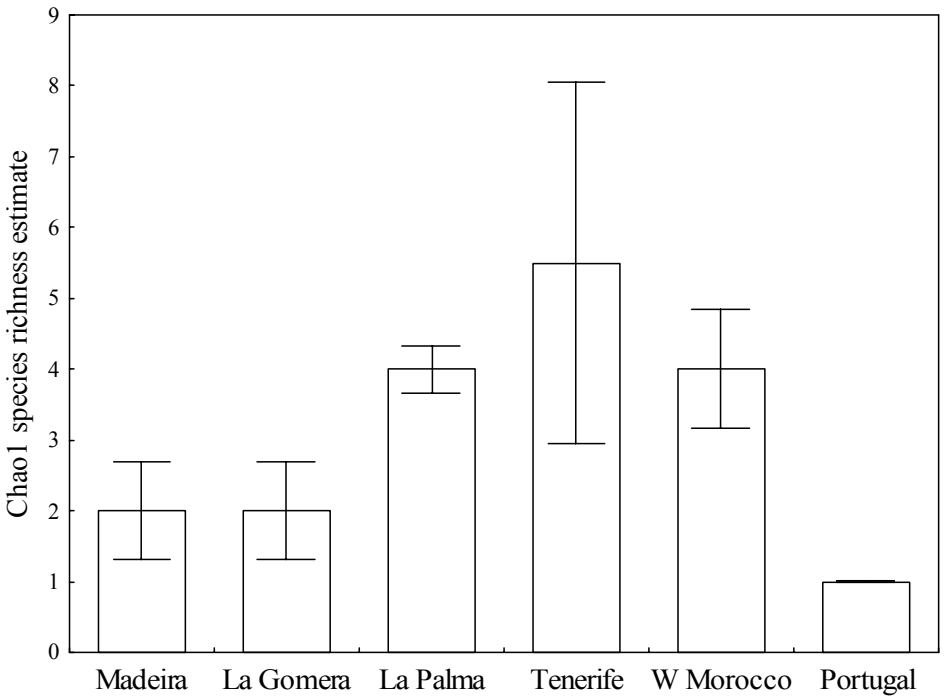


Figure 6.2. Parasitoid species richness in each study area, as estimated by Chao 1 (see also Table 6.3). Bars correspond to the 95% confidence intervals

A greater proportion of idiobiont species was found in Tenerife, while Western Morocco had the highest number of koinobiont species (see Fig. 6.1); no idiobionts were found in Portugal. Two koinobiont species were found on both island and mainland areas, while there were no shared idiobionts between these two types of study areas. Although more idiobiont species were detected on islands (only one species was found on the mainland) (Fig. 6.1), there was no significant difference between the number of idio- and koinobiont species found on island and mainland study areas ($\chi^2 = 1.4$; 1 d.f.; $p = 0.237$). Nevertheless, while observed idiobiont richness from Western Morocco and Portugal was significantly lower than the correspondet null expectation of bootstrapped values (Table 6.2; Appendix A4.2), there were no significant differences between koinobiont richness and the corresponding null expectation (Table 6.2; Appendix A4.3).

The overall parasitism rate across study areas was 5.6%. Although the proportion of host larvae attacked was slightly higher on the islands than on mainland, the difference was not significant ($\chi^2 = 2.584$; 1 d.f.; $p = 0.108$). The highest parasitism rate (14.0%) was found

on Madeira, this value being significantly higher than the null expectation (Table 6.2; Appendix A4.4). On the contrary, Portugal showed the lowest parasitism rate (4.8%).

The ratio of number of larvae parasitized by idiobionts to those parasitized by koinobionts differed significantly between islands and mainland (Table 6.4). The highest parasitism rate by idiobionts was found in Madeira (10.5%), and the lowest (apart from Portugal) was registered in Western Morocco (1.3%; Table 6.1). Conversely, the attack rate by koinobionts was highest in Portugal (4.8%) and lowest in Tenerife (1.3%). Observed idiobiont parasitism rates from Madeira and Tenerife were significantly higher than the correspondent null expectation, while in Portugal observed idiobiont parasitism rate was significantly lower than the null expectation (Table 6.2; Appendix A4.5). Finally, koinobiont parasitism rates observed in Tenerife were significantly lower than those given by the null expectation (Table 6.2; Appendix 4.6).

Table 6.4. Pairwise comparisons of the number of host larvae parasitized by idio- and koinobionts between study areas (H_0 = no differences in the proportions of larvae parasitized on each study area).

	Madeira	**La Gomera**	**La Palma**	**Tenerife**	**W Morocco**
La Gomera	1.25				
La Palma	0.833	0.048			
Tenerife	0.01	1.963	1.343		
W Morocco	7.222**	2.754[a]	3.493[b]	10.386**	
Portugal	10.432**	6.3*	7.013**	12.692***	2.507

Values correspond to the results of χ^2 analyses. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; [a] $p = 0.097$; [b] $p = 0.062$.

6.5. Discussion

Islands commonly have fewer species than apparently comparable mainland areas (Diamond, 1969; MacArthur *et al.*, 1972; Rosenzweig, 1995; Whittaker & Fernández-Palacios, 2007). Apart from isolation (MacArthur & Wilson, 1967), another reason for this pattern might be that the ability of many species to colonize and survive on islands is constrained by the lack of suitable host/food resources (Holt *et al.*, 1999). Contrary to this expectation, the island and mainland areas studied showed comparable richness values; La Palma had a similar number of parasitoid species as Western Morocco, while Tenerife was even richer.

We also found that the strength of the host-parasitoid interaction, measured as parasitism rate, was slightly, though not significantly, higher on islands. The highest parasitism rate was registered for Madeira Island, which was also one of the studied areas with the lowest species richness. Rodriguez & Hawkins (2000) and Connahs *et al.* (2009) similarly found higher rates of parasitism associated with lower parasitoid diversity for Great Britain and for Costa Rica, Ecuador and Panama, respectively (but see Tylianakis *et al.*, 2006).

Although the overall parasitism rates were similar on islands and mainland, their community structure differed. Our results showed that island parasitoid communities are biased in favour of idiobiont species, which are considered to be generalists, whereas mainland communities are dominated by koinobionts, which are considered to be more specialised (see section 6.2). The lack of species specialised on attacking *A. subsequana* on the islands could be compensated for by the higher number of presumed generalists that are potentially able to feed on a higher number of hosts. This suggests that if our survey encompassed a larger number of host species, the total parasitoid species richness would certainly be smaller on islands, since numerous host species would be parasitized by a reduced group of generalist parasitoid species.

Although the trend for island populations to be more generalist (in terms of either habitat or feeding niche) than their mainland counterparts has already been suggested for many taxa (e.g. Diamond, 1970; Olesen & Valido, 2003b; 2004; Schlotfeldt & Kleindorfer, 2006; Whittaker & Fernández-Palacios, 2007), as far as we know this is the first time that this pattern has been observed for parasitoids. Several hypotheses may be formulated to explain the tendency for parasitoid faunas to be composed by more generalist species on

islands. First, idiobionts (which are often more generalist) may simply be better dispersers than koinobionts. However, although it is known that parasitoids can disperse on the scale of kilometres (e.g. Antolin & Strong, 1987; references in Godfray, 1994; Jones *et al.*, 1996), and that dispersal ability varies between species (e.g. Nouhuys & Hanski, 2002; Elzinga *et al.*, 2007), very little is known about the eventual existence of a relationship between dispersal ability and the potential host range of the parasitoids. A second alternative hypothesis would be that generalist parasitoids colonize islands before specialists because they are less constrained by "sequential dependencies" than specialists (Holt *et al*., 1999), being more likely to be able to consume any early-arriving hosts (see Piechnik *et al.*, 2008). However, the level of generalism on island and mainland parasitoid communities has never been compared before (but see Chapter 4); the few available evidences are contradictory, indicating either that island parasitoid faunas are biased towards koinobionts (Maetô & Thornton, 1993), that no ecological or biological factors correlate with the probability of colonizing new hosts (Godfray *et al*., 1995; Hawkins & Marino, 1997), or that generalists can more readily include new hosts on their host range (Cornell & Hawkins, 1993). Here it is important to take into account that these studies were carried out in very recent communities that are probably not in equilibrium. Given that the time required for the evolution and full acquisition of parasitoids by some hosts may fall between 100 and 10,000 years (Cornell & Hawkins, 1993), it is difficult to extend these interpretations to our study system. Finally, a third hypothesis for explaining the preponderance of generalist parasitoids on the Macaronesian islands would be ecological release, a phenomenon that is typical in many island populations (e.g. Diamond, 1970; Olesen *et al.*, 2002; Scott *et al.*, 2003; see Whittaker & Fernández-Palacios, 2007). When a species colonizes an island it often encounters a new environment in which competitors and predators are absent, being therefore able to exploit a wider niche space, which in turn leads to niche expansion and/or niche shifts (e.g. Cox & Ricklefs, 1977).

Unfortunately, our data do not allow a formal test of any of these hypotheses. First, we focused on the parasitoid community of a single host species, and therefore we have no information on the complete host range of each parasitoid species. Second, we studied only larval parasitoids, which might be different from parasitoids attacking hosts on their pupal state. Finally, although the species accumulation curves indicate that the sampling effort was

appropriate to provide a reliable inventory of the diversity of each study area (Chapter 5), the total number of parasitoid individuals collected on each area is still small. Nevertheless, we showed that for a particular host species, island parasitoid communities are at least as species rich as those found on the mainland, but that the species composition changed markedly from communities dominated by specialists in the mainland to communities dominated by generalists on islands. These patterns are probably the outcome of several interacting processes, some of which we discussed above. Further work is yet necessary to unveil the causes of the higher numbers of idiobionts associated with *A. subsequana* on the Macaronesian islands in relation to the mainland. Expanding this type of approach to multiple hosts, or other habitats and islands, will provide further insights into the ecology of parasitoids communities, and ultimately to the understanding of the processes shaping species interactions in a biogeographical context.

Chapter 7: General Discussion

The results obtained in this thesis have already been discussed extensively in the preceding chapters. Hence, in this final discussion I will give a short overview of the main results obtained at each scale, discussing briefly what they show about island parasitoid faunas, as well as on the general hypothesis evaluated here. Then, I present guidelines for future work on this subject, based on the lessons learned from the results of this study, and on the questions raised by my research. Finally, I present the general conclusions that can be drawn from this thesis.

The main aim of this thesis was to study the ecology and biogeography of island parasitoid faunas, particularly the geographic patterns of the level of generalism on islands. More specifically, I wanted to test the hypothesis that island parasitoid faunas are biased towards generalist species. Initially, I intended to investigate this at three different scales: global, regional and local. However, the work at the local scale using experimental islands rendered very little data, so I had to discard that part of the study. Therefore, I approached the hypothesis above from two different scales, global and regional.

7.1. Global Scale

Most studies on large-scale diversity gradients are based on biodiversity databases that compile information on the distribution of species gathered from an often heterogeneous range of different inventories and methodologies (Soberón *et al.*, 1996, 2000; Hortal *et al.*, 2007). This data is not free from errors; it is well known that our knowledge of the geographical distribution of biodiversity is, in general, taxonomically and geographically biased (Brown & Lomolino, 1998; Lomolino, 2004; Whittaker *et al.*, 2005). In addition, biodiversity databases usually include information on heterogeneous territorial units that differ in size and nature (e.g. islands and archipelagos, or countries, such as in Taxapad; Yu *et al.*, 2005). In spite of this, many studies on diversity gradients use the information coming from such databases directly, without any previous analysis of data quality, and no

assessment on the consistency of the results among different kinds of territorial units. However, both kinds of problems can seriously compromise the description of species distributions provided by these databases, or the comparability of the biotas from different territorial units.

In this thesis, such biases and problems were evaluated to assure that the data used included comparable units with no major shortfalls. In Chapter 2, it was shown that archipelagos do often follow the same island species–area relationship (ISAR) of their constituent islands, and that the archipelagic point (corresponding to the total area and richness of the island group) is congruent with its ISAR. Among other things, such consistency implies that both islands and archipelagos can be used as distinct units themselves in large-scale biogeographical and macroecological studies. Departure of the archipelagic point from its ISAR occurred mainly in the archipelagos of oceanic origin, where the slopes of the ISAR are low, observed species richness is higher than expected by the ISAR and/or distance to the mainland is small. The archipelagic residual (calculated as the residual of the prediction provided by the ISAR using the total area of the archipelago, standardized by total richness) indicated that the ISAR underpredicts archipelagic richness in the least isolated archipelagos. Also, the magnitude of the departure from the ISAR was related to nestedness; the more nested the biota of the archipelago, the lower the archipelagic residual. Departures from the ISAR are thus expected in systems that are either highly nested or not nested at all; in highly–nested systems, the predicted number of species for the total area of the archipelago will be higher than the observed species richness, while in highly non–nested systems the observed archipelagic species richness should be higher than that predicted by the ISAR.

In Chapter 3, a simple scoring method was developed to assess which islands have comparable inventories. Several methods have already been developed to identify and account for different types of bias and limitations of biodiversity data, but most of them rely on measures of sampling effort (e.g. number of survey records, individuals or traps) that are not always available. The protocol presented in this chapter is based in three criteria: (i) completeness at high taxonomic levels, which accounts for the effort made in describing and inventorying species from different high-level taxa and indicates any potential bias towards particular taxa; (ii) congruence with well-established ecological relationships, which assumes

that obvious outliers in well-established ecological relationships, such as the species–area relationship, are unlikely to have been completely (or, at least, adequately) inventoried; and (iii) publication effort received, which determines whether a significant amount of inventory effort was devoted to the territorial unit, using the number of pages in the works compiled in the database as a proxy for sampling effort. In total, from the 118 islands included in the database, 53 and 70 were considered sufficiently well inventoried for Braconidae and Ichneumonidae, respectively.

Finally, in Chapter 4, the islands with comparable inventories were used to examine whether island faunas of Braconidae and Ichneumonidae are biased towards generalists, and to evaluate the effects of different environmental, physical and regional factors on the relative proportions of idiobionts (i.e., generalists) and koinobiont (i.e. specialists) of each of these two families. Results showed that, in general, islands have a higher proportion of generalists than the mainland. However, most islands have a similar proportion of generalists to that found in their species pool. In fact, the composition of the pool seems to be a key factor determining the structure of island parasitoid communities. There is also a latitudinal gradient in the level of generalism of island faunas, which in fact is the outcome of some environmental factors and island characteristics, such as temperature, altitude and island species richness in the case of the braconids, or region, island type and precipitation in the case of the ichneumonids. Island biotas seem to be especially biased towards generalists in the Indomalayan region. This might be related to the particular characteristics of the islands from this region, which are located at low latitudes, have a mixed geological origin, warm and humid climates and high altitudes. Perhaps more importantly, they are home to large tropical rainforests that probably include a large proportion of endophytic herbivores within their insect biotas, which are in turn known to be mainly attacked by idiobiont species. Such results highlight the complexity of factors shaping the diversity and structure of parasitoid communities.

7.2. Regional Scale

The study of parasitoid diversity, distribution and biology is challenged by their typically small size, high number of species, the complexities of their life cycles, and the difficulties in their taxonomy. Host-parasitoid interactions are still poorly understood, mostly because of the problems associated with rearing techniques, which are labour intensive, time consuming, and require experience. Also, records are prone to misidentifications of the host and/or parasitoid, and wrong associations of a parasitoid with the host due to contamination of the rearing system (Noyes, 1994; Shaw, 1997). Moreover, these techniques are very difficult to apply when studying geographical variations of host-parasitoid interactions at large scales, as it would be necessary to have several field stations spread out along all sampling areas, and the support of a large team of members collecting insects and constantly monitoring and recording parasitoids emergence. In fact, most of the existing studies on host-parasitoid interactions come from more or less delimited areas (e.g. Smith *et al.*, 2006, 2007, 2008; Elzinga *et al.*, 2007; Janzen *et al.*, 2009). An alternative to study geographical variations of host-parasitoid interactions has been to use reviews of the available literature on studies of parasitoids reared from individual hosts (e.g. Hawkins, 1994). However, such an approach can be of limited value, since most of the information comes from incompatible sources that have no standard design, and is generally biased towards agricultural habitats, making it difficult to relate to other systems (Askew & Shaw, 1986). These studies could also be done using species distribution models (e.g. Warren *et al.*, 2010), but in this case the interactions between host and parasitoids are only presumed and are not based on real data.

In this research, geographical variations in host-parasitoid interactions were investigated using a new protocol based on host dissection and DNA barcoding (Chapter 5). Although this protocol is somewhat time consuming and requires the use of a fully equipped laboratory, it nevertheless presents several advantages when compared to the "typical" rearing methods: (i) it is appropriate for use by non-taxonomists; (ii) it can be used by a small team of researchers, or even a single person, such as in the case of this thesis; and (iii) can be used for studies spread across several different regions. This protocol allows each sequence (i.e. specimen) to be assigned to a Molecular Taxonomic Operational Unit (MOTU) that is usually defined as a cluster of sequences with pairwise distances below a certain threshold.

However, it might not always be possible to correctly identify each MOTU to the species level, as available sequence databases are far from complete, and are not yet reliable to be used for the identification of poorly studied and hyperdiverse taxa such as parasitic Hymenoptera and microlepidoptera. Still, and depending on the goal of the particular research project, this might not be a problem as MOTUs can be used as surrogate units of diversity, enabling us to produce parasitoid food-webs and to quantify host-parasitoid interactions. Another potential downfall of this protocol is the fact that small parasitoid larvae and eggs might be overlooked during the dissection process, and therefore parasitism rates might be underestimated (Symondson & Hemingway, 1997). Nevertheless, this problem is minimized if the same protocol is applied in the different areas being compared. Also, the overall parasitism rate found in this study (5.6%) does not differ much from those obtained from long-term rearing projects (e.g. Smith *et al*., 2007, 2008).

Once all parasitoids found were assigned to MOTUs, the parasitoid communities associated with the moth *Acroclita subsequana* in the Macaronesian region were studied in order to test whether species richness and parasitism rates differ between islands and mainland, and whether island parasitoid faunas are biased towards generalist species (Chapter 6). The results showed that overall parasitoid species richness and parasitism rate were similar on islands and mainland. However, mainland species richness was lower than expected by chance, with most of the species being koinobionts, while island parasitoid communities were dominated by idiobionts. Also, islands had higher parasitism rates by idiobionts than expected by chance, and mainland areas showed the highest koinobiont parasitism rates. These results suggest that island parasitoid communities are biased in favour of generalists, when compared to mainland communities. The processes behind such patterns still need to be explored, but they might be related to the fact that (i) generalist parasitoids might be better dispersers; (ii) they may be less constrained by "sequential dependencies", not being dependent on the presence of a particular resource; and (iii) island parasitoids probably have fewer competitors, which favours the establishment of generalists.

7.3. Are island parasitoid faunas biased towards generalist species?

There are obvious differences between the two scales studied in this thesis. Data from the global scale came from a great variety of habitats and hosts, and refer to complete parasitoid biotas. On the other hand, data from the regional scale originated from a particular area, relatively environmentally homogeneous, and from the community of parasitoids associated with just one host system. In spite of such differences, results from both scales indicate a bias towards generalist species on islands. At the global scale, overall island parasitoid faunas had comparatively more generalist species than the whole of the mainland areas together, while at the regional scale, island hosts suffered higher attack rates by generalist parasitoids. In spite of this apparent coincidence, in the global analyses only a small number of islands departed significantly from the structure of their species pool. This seems to be the general trend worldwide, and appears to be influenced by different factors only secondarily (see above). In contrast, the structure of the island parasitoid communities studied at the regional scale differs from that of its species pool.

A seemingly plausible hypothesis tying together the results from both scales analysed is that the ecological processes that determine island community structure regionally scale up and result in the observed higher proportion of generalists worldwide. This hypothesis necessarily implies that the differences in the results from the two approaches explored in this thesis are due to differences in the scale. Following this argument, the effect of the ecological processes leading to a general trend towards higher parasitoid generalism on islands would be obscured by other factors acting at the biogeographical scale, making such trend less apparent at the global extent. Here, the composition of the species pool would be the major determinant of the structure of island communities worldwide (following the hypothesis raised by Ricklefs, 2008), but other factors such as the latitudinal gradients in temperature, precipitation, the biogeographical region to which the island belongs to, the particular characteristics of the island (e.g. altitude or island type), as well as parasitoid species richness, will also play a role in determining island parasitoid faunas. All these effects would sum up, deviating island parasitoid communities from their tendency to higher level of generalism.

7.4. Future work

The findings from this thesis leave some unanswered questions that can be the subject of future study. First of all, it would be interesting to determine whether what I found at the regional scale, and regarding only one host system, is a pattern common to other parasitoid communities, and therefore whether ecological processes affecting the assembly of island communities are responsible for the higher proportion of generalists found on islands than on the mainland at the global scale. To achieve this, future works should follow two types of approaches. On the one hand, focus on one particular host system and cover a wider geographical extent; this could be done using other species from the genus *Acroclita* or even from other genera of Tortricidae, and studying *Euphorbia* sp. spurges from other parts of the world (e.g. Hawaii). On the other hand, new studies could include other hosts and their parasitoids from the same region, such as my example in Macaronesia, in order to have a wider coverage of the parasitoid communities.

Also, the ability of the species pool to account for latitudinal variations in the level of generalism identified at the global scale analysis implies that parasitoid generalism is geographically structured in both island and continental areas. Therefore, it would be important to study the geographical structure of such patterns in continental areas worldwide, also analysing whether these are correlated with any particular habitat type, as we argue in Chapter 4. It would also be interesting to evaluate how these patterns relate to species richness, in order to help resolve the debate on the reasons behind the apparently inverse latitudinal gradients of parasitoid diversity (see Chapter 1).

One side question for the objectives of this research, but of potentially important implications for island biogeography, comes from the results of Chapter 2. Further studies should be developed in order to understand the complexities of the influence of different factors, such as dispersal ability, island age and habitat diversity, on the degree of departure of the archipelagic point from the ISAR. It would also be important to determine the exact nature of the relationship between such departure and nestedness, either by extending the same type of analysis carried out in this thesis to a wider range of islands and taxa, or by using theoretical formulations of the relationship between species richness, assemblage similarity and island area through null model analysis. Moreover, it would be worth investigating whether the pattern of departure of archipelagic data points from their

constituent ISARs holds for other types of insular system, such as habitat islands in fragmented landscapes (see a related approach in Yaacobi *et al.*, 2007).

Regarding the protocol used in Chapter 5, its usefulness in ecological studies may depend on the completeness of available sequence databases. Future effort should be allocated into sequencing more parasitoid and microlepidoptera species. Development of other methods for MOTUs delimitation could be helpful, as the ones commonly used (e.g. the use of threshold values to separate intra- and interspecific genetic distances) have been criticized because of their arbitrary nature, and because of the overlap between intra- and interspecific variability that commonly occurs in some taxa. My sequencing results indicate that *Acroclita subsequana* may actually be a complex of at least seven species or subspecies in the Macaronesian region (including Porto Santo). To ascertain the taxonomic status of these lineages and characterize the ongoing process of diversification it is necessary to study their morphology, behavior and ecology in more detail, eventually extending such analyses to the rest of its distributional range. It would not be surprising to find that many other populations of this species (e.g. the ones that occur in the United Kingdom) are in fact different subspecies, and that some of them may even be distinct species.

7.5. Conclusions

The main conclusions of this thesis are:

- Archipelagos usually follow the same island species–area relationship (ISAR) as their constituent islands.
- Departures of the archipelago from the ISAR of its constituent islands are related with richness-ordered nestedness.
- Many islands host comparable parasitoid inventories worldwide, this number being currently higher for the Ichneumonidae than for the Braconidae.
- Island parasitoid faunas have a comparatively higher proportion of generalist species than continental areas worldwide.
- The composition of the species pool is an important determinant of the structure of island parasitoid communities.

- Combining host dissections and DNA barcoding provides a practical and fairly easy approach for the study of the geographical variation in host-parasitoid interactions.
- The community of parasitoids attacking *Euphorbia*-feeding *Acroclita subsequana* larvae in the Macaronesian islands is biased towards generalists when compared to the mainland, both in terms of species number and attack rate.
- There is a general trend towards higher proportions of generalist parasitoids on islands than on continental areas; however, this tendency is obscured by a number of factors acting at the biogeographical scale.

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Appendix A1.1. Islands and variables used in this work, regarding the Braconidae.

Island	Region	Area	S	Subf	WSubf	Pub	Pages	C - HT	C - SAR	C - P	Score
Bioko	Afrotropic	2007	7	4	4	10	1752	N	Y	N	1
Cape Verde Islands	Afrotropic	4076	71	13	8	16	2371	Y	Y	N	2
Comoros	Afrotropic	2170	8	6	3	9	1281	N	Y	N	1
Madagascar	Afrotropic	587713.3	489	24	9	102	9867	Y	Y	N	2
Mauritius	Afrotropic	1865	18	8	7	29	3322	Y	Y	Y	3
Réunion	Afrotropic	2535.2	16	7	5	17	1907	N	Y	N	1
Rodrigues Island	Afrotropic	107.8	2	1	1	2	310	N	N	Y	1
Saint Helena	Afrotropic	122	1	1	1	1	5	N	-	N	0
Seychelles	Afrotropic	444	9	4	4	11	742	N	Y	Y	2
Socotra	Afrotropic	3606.7	4	3	3	9	1285	N	N	N	0
American Samoa	Australasia	197	8	4	4	3	46	N	Y	N	1
Caroline Islands	Australasia	1195	6	3	3	1	12	N	Y	N	1
Christmas Island	Australasia	135	1	1	1	1	25	N	-	N	0
Chuuk Islands	Australasia	113.9	2	2	2	1	12	N	N	N	0
Cook Islands	Australasia	241	1	1	1	1	19	N	-	N	0
East Lesser Sunda Islands	Australasia	36687.6	7	4	4	9	713	N	N	N	0
Fiji	Australasia	18272	52	11	10	35	1868	Y	Y	N	2
Guam	Australasia	541	13	6	5	8	1121	N	Y	Y	2
Mariana Islands	Australasia	471	2	1	1	1	12	N	N	N	0
Marquesas Islands	Australasia	1081.2	1	1	1	2	72	N	-	N	0
Midway Islands	Australasia	6.2	3	3	2	2	45	N	Y	Y	2
New Caledonia	Australasia	19103	22	10	5	21	1420	N	Y	N	1

Appendix A1.1 (continued)

Island	Region	Area	S	Subf	WSubf	Pub	Pages	C - HT	C - SAR	C - P	Score
New Guinea	Australasia	785753	387	24	10	148	25039	Y	Y	N	2
New Zealand	Australasia	267077.3	72	15	9	117	2170	Y	Y	N	2
Norfolk Island	Australasia	36	1	1	0	1	239	N	-	N	0
North Moluccas	Australasia	31652	31	7	5	22	1426	N	Y	N	1
Palau	Australasia	494	1	1	1	1	12	N	-	N	0
Society Islands	Australasia	1628	9	7	7	6	650	Y	Y	N	2
Solomon Islands	Australasia	31001	32	10	7	19	2114	Y	Y	N	2
South Moluccas	Australasia	46478	35	8	6	22	1646	Y	Y	N	2
Sulawesi	Australasia	197680	107	19	8	56	3699	Y	Y	N	2
Tasmania	Australasia	67900	68	15	8	38	3188	Y	Y	N	2
Timor	Australasia	28564.9	4	3	3	6	1420	N	N	N	0
Tonga	Australasia	699	8	5	4	10	150	N	Y	N	1
Vanuatu	Australasia	12190	18	6	5	10	1360	N	Y	N	1
West Lesser Sunda Islands	Australasia	19492.8	14	8	5	12	1071	N	Y	N	1
Western Samoa	Australasia	2935	19	5	5	11	550	N	Y	N	1
Andaman Islands	IndoMalaya	5240.2	1	1	1	1	1	N	-	N	0
Bohol	IndoMalaya	3864	3	2	2	2	539	N	N	N	0
Bonin Islands	IndoMalaya	104	1	1	0	1	2	N	-	N	0
Borneo	IndoMalaya	743244	374	25	8	141	10560	Y	Y	N	2
Cebu	IndoMalaya	4421	2	1	1	1	26	N	N	N	0
Chagos Archipelago	IndoMalaya	60	1	1	1	3	757	N	-	N	0
Java	IndoMalaya	131188	219	19	8	120	7766	Y	Y	N	2
Leyte	IndoMalaya	7213	13	5	5	8	920	Y	Y	N	2
Luzon	IndoMalaya	116519.8	285	17	8	94	5424	Y	Y	N	2

Appendix A1.1 (continued)

Island	Region	Area	S	Subf	WSubf	Pub	Pages	C - HT	C - SAR	C - P	Score
Masbate	IndoMalaya	4047.7	3	2	2	3	348	N	N	N	0
Mindanao	IndoMalaya	99078	159	15	8	52	3133	Y	Y	N	2
Mindoro	IndoMalaya	9735	42	8	6	13	1724	Y	Y	N	2
Negros	IndoMalaya	13670	38	9	6	18	2738	Y	Y	N	2
Nicobar Islands	IndoMalaya	1617.1	1	1	1	1	2	N	-	N	0
Palawan	IndoMalaya	14896.3	28	9	8	13	1342	Y	Y	N	2
Panay	IndoMalaya	12300	5	3	2	7	763	N	N	N	0
Philippines - other islands	IndoMalaya	5469.4	18	7	7	8	1483	Y	Y	N	2
Samar	IndoMalaya	13429	8	4	4	5	730	Y	Y	N	2
Singapore	IndoMalaya	536.4	83	12	7	35	2336	Y	Y	Y	3
Sri Lanka	IndoMalaya	67654.5	145	17	8	99	6305	Y	Y	N	2
Sumatra	IndoMalaya	483533.2	209	14	8	70	5073	Y	Y	N	2
Greenland	Nearctic	2175600	16	6	4	14	1546	N	N	N	0
Hawaii	Nearctic	16687.6	38	13	9	192	4763	Y	Y	N	2
Prince Edward Island	Nearctic	5620	14	9	8	10	498	Y	Y	N	2
Antigua	Neotropic	282	6	4	4	6	1065	N	Y	Y	2
Bahamas	Neotropic	13934	5	3	3	5	266	N	N	N	0
Barbados	Neotropic	431	5	2	2	8	408	N	Y	N	1
Bermuda	Neotropic	53	14	7	6	10	1325	Y	Y	Y	3
Cayman Islands	Neotropic	259	2	1	1	2	63	N	N	N	0
Cuba	Neotropic	1111463	89	14	8	64	5935	Y	Y	N	2
Dominica	Neotropic	790	6	3	2	7	100	N	Y	N	1
Falkland Islands	Neotropic	12175	1	1	1	1	7	N	-	N	0
Fernando de Noronha	Neotropic	18.4	3	3	3	1	8	N	Y	N	1

Appendix A1.1 (continued)

Island	Region	Area	S	Subf	WSubf	Pub	Pages	C - HT	C - SAR	C - P	Score
Galápagos	Neotropic	7845	1	1	1	1	22	N	-	N	0
Grenada	Neotropic	311	63	14	8	26	3169	Y	Y	Y	3
Guadeloupe	Neotropic	1510	6	5	4	9	400	N	Y	N	1
Hispaniola	Neotropic	73147	23	11	7	23	2003	Y	Y	N	2
Jamaica	Neotropic	11526	12	6	5	13	1692	Y	Y	N	2
Juan Fernández Islands	Neotropic	148.5	5	3	3	3	1065	N	Y	Y	2
Martinique	Neotropic	1106	4	4	4	5	557	N	N	N	0
Monserrat	Neotropic	104	1	1	1	1	16	N	-	N	0
Netherlands Antilles	Neotropic	1020	1	1	1	1	41	N	-	N	0
Puerto Rico	Neotropic	8960	47	12	8	42	3517	Y	Y	N	2
Saint Kitts and Nevis	Neotropic	261	3	2	2	4	1091	N	N	Y	1
Saint Lucia	Neotropic	604	3	2	2	3	204	N	N	N	0
Saint Vincent	Neotropic	345	82	17	8	30	3565	Y	Y	Y	3
Trinidad and Tobago	Neotropic	5128	81	15	8	68	3983	Y	Y	N	2
Virgin Islands	Neotropic	346	7	5	4	8	315	N	Y	N	1
Azores	Palaearctic	2328	9	6	5	13	317	N	Y	N	1
Balearic Islands	Palaearctic	5015	16	8	5	6	1485	N	Y	N	1
Canary Islands	Palaearctic	7301.3	138	17	11	46	3129	Y	Y	N	2
Corsica	Palaearctic	8722	63	11	10	30	3117	Y	Y	N	2
Crete	Palaearctic	8260	85	16	11	21	1716	Y	Y	N	2
Cyprus	Palaearctic	9251	118	14	9	54	4680	Y	Y	N	2
Faroe Islands	Palaearctic	1399	37	7	7	4	310	N	Y	N	1
Hainan Island	Palaearctic	33209.8	70	14	10	38	3443	Y	Y	N	2
Iceland	Palaearctic	101826	48	6	6	21	1918	N	Y	N	1

Appendix A1.1 (continued)

Island	Region	Area	S	Subf	WSubf	Pub	Pages	C - HT	C - SAR	C - P	Score
Ireland	Palaearctic	85114	569	26	11	194	9325	Y	Y	N	2
Japan	Palaearctic	375799	611	32	11	377	14514	Y	Y	N	2
Madeira	Palaearctic	796	75	14	10	19	1749	Y	Y	Y	3
Novaya Zemlya	Palaearctic	80324.7	3	3	2	6	592	N	N	N	0
Okinawa	Palaearctic	1201	56	11	10	33	907	Y	Y	N	2
Sakhalin	Palaearctic	74056	505	27	11	100	4713	Y	Y	N	2
Sardinia	Palaearctic	23833	82	17	11	26	2431	Y	Y	N	2
Sicily	Palaearctic	25460	134	18	11	59	6097	Y	Y	N	2
Svalbard	Palaearctic	62380	2	1	0	3	82	N	N	N	0
Taiwan	Palaearctic	34506.6	486	29	11	201	13254	Y	Y	N	2
United Kingdom	Palaearctic	229850	1171	30	11	730	20756	Y	Y	N	2

Area is measured in km^2. S is the number of species. Subf is the number of subfamilies. WSubf is the number of widspread subfamilies. Pub is the number of publications. Pages is the number of published pages. C - HT is the completness at higher taxonomic levels criterion, C - SAR is the species–area relationship criterion and C - P is the publication effort criterion; Y denotes that the island passes the criterion, and N that it does not. Score is the score level for inventory completeness. See Chapter 3 for more details.

Appendix A1.2. Islands and variables used in this work, regarding the Ichneumonidae.

Island	Region	Area	S	Subf	WSubf	Pub	Pages	C - HT	C - SAR	C - P	Score
Ascension Island	Afrotropic	97	1	1	1	1	52	N	-	N	0
Comoros	Afrotropic	2170	3	2	2	3	91	N	N	N	0
Madagascar	Afrotropic	587713.3	552	19	7	46	5513	Y	Y	N	2
Maldives	Afrotropic	298	1	1	1	2	544	N	-	N	0
Mauritius	Afrotropic	1865	16	5	5	12	973	Y	Y	N	2
Réunion	Afrotropic	2535.2	17	7	7	5	717	Y	Y	N	2
Rodrigues Island	Afrotropic	107.8	2	2	2	1	7	N	N	N	0
Saint Helena	Afrotropic	122	4	4	3	7	829	N	Y	Y	2
Seychelles	Afrotropic	444	15	7	5	3	445	Y	Y	N	2
Socotra	Afrotropic	3606.7	2	1	0	2	18	N	N	N	0
American Samoa	Australasia	197	2	2	2	1	12	N	N	N	0
Caroline Islands	Australasia	1195	2	1	1	1	611	N	N	N	0
Christmas Island	Australasia	135	1	1	1	3	731	N	-	N	0
Chuuk Islands	Australasia	113.9	12	5	4	5	701	Y	Y	Y	3
Cook Islands	Australasia	241	1	1	1	1	13	N	-	N	0
East Lesser Sunda Islands	Australasia	36687.6	10	3	3	6	1590	N	Y	N	1
Fiji	Australasia	18272	24	7	6	16	1919	Y	Y	N	2
Guam	Australasia	541	11	6	5	6	743	Y	Y	N	2
Kiribati Islands	Australasia	810	1	1	1	1	53	N	-	N	0
Lord Howe Island	Australasia	14.5	2	2	1	2	410	N	Y	Y	2
Mariana Islands	Australasia	471	8	6	5	4	684	Y	Y	N	2
Marshall Islands	Australasia	181	2	2	1	1	53	N	N	N	0
Midway Islands	Australasia	6.2	1	1	1	1	8	N	-	N	0
New Caledonia	Australasia	19103	45	9	7	17	3048	Y	Y	N	2

Appendix A1.2 (continued)

Island	Region	Area	S	Subf	WSubf	Pub	Pages	C - HT	C - SAR	C - P	Score
New Guinea	Australasia	785753	428	16	7	92	10011	Y	Y	N	2
New Zealand	Australasia	267077.3	80	16	7	75	3725	Y	Y	N	2
Norfolk Island	Australasia	36	2	1	1	2	723	N	N	Y	1
North Moluccas	Australasia	31652	55	6	3	16	3121	N	Y	N	1
Palau	Australasia	530	13	7	5	4	221	Y	Y	N	2
Society Islands	Australasia	1628	15	6	5	12	2006	Y	Y	N	2
Solomon Islands	Australasia	31001	68	8	4	18	3915	Y	Y	N	2
South Moluccas	Australasia	46478	62	10	5	23	2783	Y	Y	N	2
Sulawesi	Australasia	197680	245	14	6	41	3387	Y	Y	N	2
Tasmania	Australasia	67900	90	14	7	37	2732	Y	Y	N	2
Timor	Australasia	28564.9	6	3	3	5	1354	N	N	N	0
Tonga	Australasia	699	2	2	2	3	40	N	N	N	0
Vanuatu	Australasia	12190	35	9	6	12	2795	Y	Y	N	2
West Lesser Sunda Islands	Australasia	19492.8	5	3	3	5	1212	N	N	N	0
Western Samoa	Australasia	2935	14	9	7	6	748	Y	Y	N	2
Bohol	IndoMalaya	3864	30	5	4	6	1445	Y	Y	N	2
Bonin Islands	IndoMalaya	104	6	3	1	3	195	N	Y	N	1
Borneo	IndoMalaya	743244	282	13	6	109	16461	Y	Y	N	2
Cebu	IndoMalaya	4421	6	2	2	4	1015	N	Y	N	1
Chagos Archipelago	IndoMalaya	60	2	2	2	2	629	N	N	Y	1
Java	IndoMalaya	131188	369	15	6	88	9496	Y	Y	N	2
Leyte	IndoMalaya	7213	17	5	4	7	1585	Y	Y	N	2
Luzon	IndoMalaya	116519.8	311	16	6	70	7076	Y	Y	N	2
Masbate	IndoMalaya	4047.7	3	2	2	2	685	N	N	N	0

Appendix A1.2 (continued)

Island	Region	Area	S	Subf	WSubf	Pub	Pages	C - HT	C - SAR	C - P	Score
Mindanao	IndoMalaya	99078	189	12	6	28	3969	Y	Y	N	2
Mindoro	IndoMalaya	9735	144	12	6	28	5973	Y	Y	N	2
Negros	IndoMalaya	13670	125	12	6	30	4962	Y	Y	N	2
Nicobar Islands	IndoMalaya	1617.1	4	4	2	2	537	N	N	N	0
Palawan	IndoMalaya	14896.3	48	9	6	13	2378	Y	Y	N	2
Panay	IndoMalaya	12300	20	7	5	9	2102	Y	Y	N	2
Philippines - other islands	IndoMalaya	5469.4	25	9	5	16	2905	Y	Y	N	2
Samar	IndoMalaya	13429	65	8	5	12	2435	Y	Y	N	2
Singapore	IndoMalaya	536.4	68	10	6	26	5721	Y	Y	Y	3
Sri Lanka	IndoMalaya	67654.5	190	15	6	53	6367	Y	Y	N	2
Sumatra	IndoMalaya	483533.2	177	13	6	52	6809	Y	Y	N	2
Greenland	Nearctic	2175600	91	13	8	36	4184	Y	Y	N	2
Hawaii	Nearctic	16687.6	59	10	7	77	5451	Y	Y	N	2
Prince Edward Island	Nearctic	5620	165	16	8	40	8198	Y	Y	N	2
Saint Pierre and Miquelon	Nearctic	241	1	1	1	1	17	N	-	N	0
Anguilla	Neotropic	90.7	1	1	1	1	309	N	-	N	0
Antigua	Neotropic	282	2	2	2	2	372	Y	N	N	1
Bahamas	Neotropic	13934	8	2	2	2	318	Y	Y	N	2
Barbados	Neotropic	430	1	1	1	2	489	N	-	N	0
Bermuda	Neotropic	53	13	6	3	7	1212	Y	Y	Y	3
Cuba	Neotropic	1111463	122	13	5	35	3923	Y	Y	N	2
Dominica	Neotropic	790	2	1	1	1	309	N	N	N	0
Easter Island	Neotropic	173	1	1	1	1	2	N	-	N	0
Falkland Islands	Neotropic	12175	2	2	1	4	567	N	N	N	0

Appendix A1.2 (continued)

Island	Region	Area	S	Subf	WSubf	Pub	Pages	C - HT	C - SAR	C - P	Score
Galápagos	Neotropic	7845	6	1	1	1	11	N	N	N	0
Grenada	Neotropic	311	24	11	4	7	918	Y	Y	Y	3
Guadeloupe	Neotropic	1510	2	2	2	3	480	Y	N	N	1
Hispaniola	Neotropic	73147	29	6	4	14	2502	Y	Y	N	2
Jamaica	Neotropic	11526	29	6	5	13	1770	Y	Y	N	2
Juan Fernández Islands	Neotropic	148.5	7	5	3	2	21	Y	Y	N	2
Martinique	Neotropic	1106	1	1	1	1	309	N	-	N	0
Montserrat	Neotropic	101	1	1	1	1	309	N	-	N	0
Netherlands Antilles	Neotropic	1020	1	1	1	1	309	N	-	N	0
Puerto Rico	Neotropic	8960	32	9	5	18	4212	Y	Y	N	2
Saint Kitts and Nevis	Neotropic	261	2	1	1	1	309	N	N	N	0
Saint Lucia	Neotropic	604	3	1	1	1	309	N	N	N	0
Saint Vincent	Neotropic	345	19	10	4	3	669	Y	Y	N	2
Trinidad and Tobago	Neotropic	5128	28	8	5	13	2475	Y	Y	N	2
Virgin Islands	Neotropic	346	4	2	1	3	403	N	Y	N	1
Azores	Palaearctic	2434.5	27	9	7	11	667	Y	Y	N	2
Balearic Islands	Palaearctic	5015	49	7	6	36	3408	Y	Y	N	2
Canary Islands	Palaearctic	7301.3	150	14	10	45	869	Y	Y	N	2
Channel Islands	Palaearctic	194.2	3	3	3	3	292	N	Y	N	1
Corsica	Palaearctic	8722	488	22	10	60	3017	Y	Y	N	2
Crete	Palaearctic	8260	15	6	5	8	670	Y	Y	N	2
Cyprus	Palaearctic	9251	51	14	9	29	2752	Y	Y	N	2
Faroe Islands	Palaearctic	1399	45	9	7	6	114	Y	Y	N	2
Hainan Island	Palaearctic	33209.8	58	13	8	28	3531	Y	Y	N	2

Appendix A1.2 (continued)

Island	Region	Area	S	Subf	WSubf	Pub	Pages	C - HT	C - SAR	C - P	Score
Iceland	Palaearctic	101826	100	15	10	29	2879	Y	Y	N	2
Ireland	Palaearctic	85114	528	22	10	70	2406	Y	Y	N	2
Isle of Man	Palaearctic	575	59	12	9	7	39	Y	Y	N	2
Japan	Palaearctic	375799	1350	29	10	402	18262	Y	Y	N	2
Madeira	Palaearctic	796	95	13	9	20	1109	Y	Y	N	2
Malta	Palaearctic	316	26	9	8	6	163	Y	Y	N	2
Novaya Zemlya	Palaearctic	80324.7	38	8	5	14	2224	Y	Y	N	2
Okinawa	Palaearctic	1201	217	19	10	57	3298	Y	Y	N	2
Sakhalin	Palaearctic	74056	604	26	10	122	5467	Y	Y	N	2
Sardinia	Palaearctic	23833	133	16	10	46	3081	Y	Y	N	2
Sicily	Palaearctic	25460	205	17	10	53	7123	Y	Y	N	2
Svalbard	Palaearctic	62380	17	5	3	10	453	N	Y	N	1
Taiwan	Palaearctic	34506.6	715	23	10	200	11945	Y	Y	N	2
United Kingdom	Palaearctic	229850	2397	33	10	649	22538	Y	Y	N	2

Area is measured in km^2. S is the number of species. Subf is the number of subfamilies. WSubf is the number of widspread subfamilies. Pub is the number of publications. Pages is the number of published pages. C - HT is the completness at higher taxonomic levels criterion, C - SAR is the species–area relationship criterion and C - P is the publication effort criterion; Y denotes that the island passes the criterion, and N that it does not. Score is the score level for inventory completness. See Chapter 3 for more details.

Appendix A2.1. Territories whose faunas constitute the species pool of each island or archipelago analyzed (see Chapter 4), following the geographical divisions in Yu *et al.* (2005). *Indicates mainland territories that were located more than 1,000 km from the island or archipelago.

Antigua: Barbados, Dominica, Grenada, Guadeloupe, Guyana, Hispaniola, Martinique, Netherlands Antilles, Puerto Rico, St. Kitt and Nevis, St. Lucia, St. Vincent, Trinidad & Tobago, Venezuela.

Azores: Madeira, Portugal*.

Bahamas: Cuba, Hispaniola, Jamaica, Puerto Rico, USA - Alabama, USA - Florida, USA - Georgia, USA - North Carolina, USA - South Carolina.

Balearic Isl.: Algeria, Andorra, Austria, Corsica, Croatia, France, Germany, Italy, Liechtenstein, Monaco, Morocco, Portugal, Sardinia, Sicily, Slovenia, Spain, Switzerland, Tunisia.

Bermuda: USA - North Carolina*.

Bohol: Borneo, Cebu, Leyte, Luzon, Masbate, Mindanao, Mindoro, Negros, North Moluccas, Palawan, Panay, Philippines - others, Samar, Sulawesi, Vietnam*.

Borneo: Bohol, Cambodia, Cebu, East Lesser Sunda Isl., Java, Leyte, Luzon, Malaysia - Peninsula, Masbate, Mindanao, Mindoro, Negros, North Moluccas, Palawan, Panay, Philippines - others, Samar, Singapore, South Moluccas, Sulawesi, Sumatra, Thailand, Timor, Vietnam, West Lesser Sunda Isl.

Canary Isl.: Algeria, Madeira, Mali, Mauritania, Morocco, Portugal, Western Sahara.

Cape Verde: Gambia, Guine - Bissau, Guinea, Mauritania, Senegal, Western Sahara.

Chuuk Isl.: Australia–Queensland*.

Corsica: Albania, Algeria, Andorra, Austria, Balearic Isl., Belgium, Bosnia - Hercegovina, Croatia, Czech Republic, Former Czechoslovakia, France, Germany, Greece, Hungary, Italy, Libya, Liechtenstein, Luxembourg, Malta, Monaco, Netherlands, Romania, Sardinia, Serbia and Montenegro, Sicily, Slovakia, Slovenia, Spain, Switzerland, Tunisia.

Crete: Albania, Bosnia - Hercegovina, Bulgaria, Cyprus, Egypt, Greece, Israel, Italy, Jordan, Lebanon, Libya, Malta, Romania, Serbia and Montenegro, Sicily, Syria, Turkey.

Cuba: Bahamas, Belize, Colombia, El Salvador, Guatemala, Hispaniola, Honduras, Jamaica, Mexico, Nicaragua, Puerto Rico, USA - Alabama, USA - Florida, USA - Georgia, USA - Louisiana, USA - Mississippi, USA - South Carolina, Venezuela, Virgin Isl.

Cyprus: Bulgaria, Crete, Egypt, Greece, Iraq, Israel, Jordan, Lebanon, Libya, Saudi Arabia, Syria, Turkey.

Faroe Isl.: Denmark, Iceland, Ireland, Isle of Man, Norway, United Kingdom.

Fiji: Australia – Queensland*, Tonga, Vanuatu, Western Samoa.

Greenland: Canada - New Foundland & Labrador, Canada - Nunavut, Canada - Quebec, Iceland, Svalbard.

Grenada: Anguilla, Antigua, Barbados, Barbuda, Brazil, Colombia, Dominica, Guadeloupe, Guyana, Martinique, Monserrat, Netherlands Antilles, Puerto Rico, St. Croix, St. Kitt and Nevis, St. Lucia, St. Vincent, Surinam, Trinidad & Tobago, Venezuela, Virgin Isl.

Guam: Australia – Queensland*, Mariana Isl.

Hainan: Cambodia, China - Fujian, China - Guangdong, China - Guangxi, China - Guizhou, China - Hong Kong, China - Hubei, China - Hunan, China - Jiangxi, China - Sichuan, China - Yunnan, Laos, Myanmar, Thailand, Vietnam.

Hawaii: USA – California*.

Hispaniola: Anguilla, Antigua, Bahamas, Barbuda, Colombia, Cuba, Dominica, Florida, Guadeloupe, Jamaica, Martinique, Montserrat, Netherlands Antilles, Puerto Rico, St. Croix, St. Kitt and Nevis, St. Lucia, St. Vincent, Venezuela, Virgin Isl.

Iceland: Faroe Isl., Greenland, Norway, United Kingdom.

Ireland: Belgium, Denmark, Faroe Isl., France, Germany, Isle of Man, Luxembourg, Netherlands, Norway, Spain, United Kingdom.

Isle of Man: Belgium, Denmark, Faroe Isl., France, Germany, Ireland, Luxembourg, Netherlands, Norway, United Kingdom.

Jamaica: Bahamas, Colombia, Cuba, Hispaniola, Honduras, Mexico, Netherlands Antilles, Nicaragua, Panama, Puerto Rico, USA - Florida, Venezuela.

Japan: China - Heilongjang, China - Jiangsu, China - Jilin, China - Liaoning, China - Shandong, China - Shangai, China - Zhejiang, Korea, Okinawa, Russia - Amur Oblast, Russia - Khabarovsk Krai, Russia - Primorye Krai, Russia - Yevreyskaya Oblast, Sakhalin.

Java: Borneo, Christmas Isl., East Lesser Sunda Isl, Malaysia - Peninsula, Singapore, Sulawesi, Sumatra, Timor, West Lesser Sunda Isl.

Juan Fernandez Isl.: Argentina, Chile.

Leyte: Bohol, Borneo, Cebu, Luzon, Masbate, Mindanao, Mindoro, Negros, North Moluccas, Palawan, Panay, Philippines - others, Samar, Sulawesi, Vietnam*.

Lord Howe Island: Australia - New South Wales, Australia - Queensland.

Luzon: Bohol, Borneo, Cebu, China - Fujian, China - Guangdong, China - Hong Kong, China - Jiangxi, China - Macau, China - Zhejiang, Leyte, Masbate, Mindanao, Mindoro, Negros, Palawan, Panay, Philippines - others, Samar, Taiwan.

Madagascar: Comoros, Malawi, Mauritius, Mozambique, Reunion, Tanzania.

Madeira: Algeria, Azores, Canary Isl., Mauritania, Morocco, Portugal, Western Sahara.

Malta: Albania, Algeria, Balearic Isl., Bosnia - Hercegovina, Corsica, Crete, Croatia, Greece, Italy, Libya, Sardinia, Serbia and Montenegro, Sicily, Tunisia.

Mariana Isl.: Australia – Queensland*, Guam.

Mauritius: Reunion, Madagascar, Mozambique*, Rodrigues Isl.

Midway Isl.: Kiribati, USA – California*.

Mindanao: Bohol, Borneo, Cebu, Leyte, Luzon, Masbate, Mindoro, Negros, New Guinea, North Moluccas, Palau, Palawan, Panay, Philippines - others, Samar, South Moluccas, Sulawesi, Vietnam*.

Mindoro: Bohol, Borneo, Cebu, Leyte, Luzon, Masbate, Mindanao, Negros, Palawan, Panay, Philippines - others, Samar, Taiwan, Vietnam*.

Negros: Bohol, Borneo, Cebu, Leyte, Luzon, Masbate, Mindanao, Mindoro, North Moluccas, Palawan, Panay, Philippines - others, Samar, Sulawesi, Vietnam*.

New Caledonia: Australia – Queensland*, Norfolk, Vanuatu.

New Guinea: Australia - Northern Territories, Australia - Queensland, East Lesser Sunda Isl., Mindanao, North Moluccas, Palau, Solomon Isl., South Moluccas, Sulawesi, Timor.

New Zealand: Australia - New South Wales*, Norfolk.

Novaya Zemlya: Finland, Norway, Russia - Arkangelsk Oblast, Russia - Karel'skaya Respublika, Russia - Komi Respublika, Russia - Krasnoyarsk Krai, Russia - Murmansk Oblast, Russia - Tyumen Oblast, Russia - Zemlya Frantsa Iosifa, Svalbard.

Okinawa: China - Anhui, China - Fujian, China - Guangdong, China - Jiangsu, China - Jiangxi, China - Shangai, China - Zhejiang, Japan, Korea, Luzon, Taiwan.

Palau: Australia - Northern Territories*, Mindanao, New Guinea, North Moluccas.

Palawan: Bohol, Borneo, Cebu, Leyte, Luzon, Masbate, Mindanao, Mindoro, Negros, Panay, Philippines - others, Samar, Sulawesi, Vietnam.

Panay: Bohol, Borneo, Cebu, Leyte, Luzon, Masbate, Mindanao, Mindoro, Negros, Palawan, Philippines - others, Samar, Sulawesi, Vietnam*.

Philippines - others: Bohol, Borneo, Cebu, Leyte, Luzon, Masbate, Mindanao, Mindoro, Negros, North Moluccas, Palawan, Panay, Samar, Sulawesi, Vietnam*.

Prince Edward Isl.: Canada - New Brunswick, Canada - New Foundland & Labrador, Canada - Nova Scotia, Canada - Ontario, Canada - Quebec, USA - Connecticut, USA - Maine, USA - Massachusetts, USA - New Hampshire, USA - New York, USA - Rhode Island, USA – Vermont.

Puerto Rico: Anguilla, Antigua, Bahamas, Barbados, Colombia, Cuba, Dominica, Grenada, Guadeloupe, Hispaniola, Jamaica, Martinique, Montserrat, Netherlands Antilles, St. Croix, St. Kitt and Nevis, St. Lucia, St. Vincent, Trinidad & Tobago, Venezuela, Virgin Isl.

Réunion: Mauritius, Madagascar, Mozambique*, Rodrigues Isl.

Sakhalin: China - Heilongjang, China - Jilin, Japan, Russia - Amur Oblast, Russia - Kamchatka Oblast, Russia - Khabarovsk Krai, Russia - Magadanskaya Oblast, Russia - Primorye Krai, Russia - Yakutskaya Respublika, Russia - Yevreyskaya Oblast.

Samar: Bohol, Borneo, Cebu, China – Guangdong*, Leyte, Luzon, Masbate, Mindanao, Mindoro, Negros, Palawan, Panay, Philippines – others.

Sardinia: Albania, Algeria, Andorra, Austria, Balearic Isl., Belgium, Bosnia - Hercegovina, Corsica, Croatia, Czech Republic, Former Czechoslovakia, France, Germany, Greece, Hungary, Italy, Libya, Liechtenstein, Luxembourg, Malta, Monaco, Serbia and Montenegro, Sicily, Slovakia, Slovenia, Spain, Switzerland, Tunisia.

Seychelles: Kenya, Madagascar, Somalia*.

Sicily: Albania, Argelia, Austria, Balearic Isl., Bosnia - Hercegovina, Bulgaria, Corsica, Crete, Croatia, Czech Republic, Former Czechoslovakia, France, Germany, Greece, Hungary, Italy, Libya, Liechtenstein, Luxembourg, Malta, Monaco, Romania, Sardinia, Serbia and Montenegro, Slovakia, Slovenia, Spain, Switzerland, Tunisia, Turkey.

Singapore: Borneo, Cambodja, Java, Malaysia - Peninsula, Sumatra, Thailand, Vietnam.

Society Isl.: Australia - New South Wales*, Australia – Queensland*, Cook Isl.

Solomon Isl.: Australia – Queensland*, New Caledonia, New Guinea, Vanuatu.

South Moluccas: Australia - Northern Territories, Borneo, East Lesser Sunda Isl., Mindanao, New Guinea, North Moluccas, Sulawesi, Timor, West Lesser Sundas Isl.

Sri Lanka: India, Maldives.

Sulawesi: Australia - Western Australia*, Bohol, Borneo, Cebu, East Lesser Sunda Isl., Java, Leyte, Mindanao, Negros, New Guinea, North Moluccas, Palawan, Philippines - others, South Moluccas, Timor, West Lesser Sunda Isl.

Sumatra: Andaman Isl., Borneo, Cambodia, Christmas Isl., Java, Malaysia - Peninsula, Myanmar, Nicobar Isl., Singapore, Thailand, Vietnam.

St. Helena: Angola*, Namibia*.

St. Vincent: Anguilla, Antigua, Barbados, Barbuda, Brazil, Dominica, Grenada, Guadeloupe, Guyana, Hispaniola, Martinique, Montserrate, Netherlands Antilles, Puerto Rico, St. Croix, St. Kitt and Nevis, St. Lucia, Surinam, Trinidad & Tobago, Venezuela, Virgin Isl.

Taiwan: China - Anhui, China - Fujian, China - Guangdong, China - Guangxi, China - Hong Kong, China - Hubei, China - Hunan, China - Jiangsu, China - Jiangxi, China - Shangai, China - Zhejiang, Luzon, Mindoro, Okinawa.

Tasmania: Australia - New South Wales, Australia - South Australia, Australia - Victoria.

Trinidad & Tobago: Anguilla, Antigua, Barbados, Barbuda, Brazil, Colombia, Dominica, French Guyana, Grenada, Guadeloupe, Guyana, Martinique, Montserrate, Netherlands Antilles, Puerto Rico, St. Croix, St. Kitt and Nevis, St. Lucia, St. Vincent, Surinam, Venezuela, Virgin Isl.

United Kingdom: Austria, Belgium, Czech Republic, Former Czeckoslavakia, Denmark, Faroe Isl., France, Germany, Iceland, Ireland, Isle of Man, Italy, Liechtenstein, Netherlands, Norway, Poland, Portugal, Spain, Sweden, Switzerland.

Vanuatu: Australia – Queensland*, Fiji, New Caledonia, Solomon Isl.

Western Samoa: Australia – Queensland*, Fiji, Tonga.

Appendix A2.2. Life history traits of the Braconidae.

Subfamily	Idiobiont	Koinobiont	Ectoparasitoid	Endoparasitoid	Hosts attacked
Acampsohelconinae	N	Y	N	Y	COL
Agathidinae	N	Y	N	Y	LEP
Alysiinae	N	Y	N	Y	DIP
Amicrocentrinae	N*	Y*	N	Y	LEP
Aphidiinae	N	Y	N	Y	HOM
Apozyginae	N/A	N/A	N/A	N/A	N/A
Betylobraconinae	N/A	N/A	N/A	N/A	N/A
Blacinae	N	Y	N	Y	COL+MEC
Brachistinae	N	Y	N	Y	COL
Braconinae					
Aspidobraconina	Y	N	N	Y	LEP
All other taxa	Y	N	Y	N	COL+DIP+HYM+LEP
Cardiochilinae	N	Y	N	Y	LEP
Cenocoeliinae	N	Y	N	Y	COL
Charmontinae	N	Y	N	Y	LEP
Cheloninae	N	Y	N	Y	LEP
Diospilinae	N	Y	N	Y	COL
Dirrhopinae	N	Y	N	Y	LEP
Doryctinae					
Sericobracon sp.	N	Y	N	Y	EMB
Ypsistocerini	N/A	N/A	N/A	N/A	N/A
All other taxa	Y	N	Y	N	COL+HYM+LEP
Ecnomiinae	N/A	N/A	Y	N	N/A
Euphorinae					
Meteorini	N	Y	N	Y	COL+ LEP
Neoneurini	Y	N	N	Y	HYM
All other taxa	N	Y	N	Y	COL+HET+HYM+NEU+ORT+PSO
Exothecinae	Y	N	Y	N	COL+DIP+HYM+LEP
Gnamptodontinae	N	Y	N*	Y*	LEP
Helconinae	N	Y	N	Y	COL
Histeromerinae	Y	N	Y	N	COL
Homolobinae	N	Y	N	Y	LEP

Appendix A2. 2 (continued)

Subfamily	Idiobiont	Koinobiont	Ectoparasitoid	Endoparasitoid	Hosts attacked
Hormiinae	Y	N	Y	N	COL+ LEP
Hydrangeocolinae	N/A	N/A	Y*	N*	DIP
Ichneutinae	N	Y	N	Y	HYM+ LEP
Khoikhoiinae	N/A	N/A	N*	Y*	N/A
Lysiterminae					
Katytermus sp.	N/A	N/A	N	Y	ORT
All other taxa	Y	N	Y	N	LEP
Macrocentrinae	N	Y	N	Y	LEP
Masoninae	N/A	N/A	N/A	N/A	N/A
Maxfischeriinae	N*	Y*	Y*	N*	N/A
Mendesellinae	N/A	N/A	N/A	N/A	N/A
Mesostoinae					
Mesostoa sp.	N	N	N	N	PLANTS
All other taxa	Y	N	N/A	N/A	N/A
Meteorideinae	N	Y	N	Y	LEP
Microgastrinae	N	Y	N	Y	LEP
Microtypinae	N	Y	N	Y	LEP
Miracinae	N	Y	N	Y	LEP
Opiinae	N	Y	N	Y	DIP
Orgilinae	N	Y	N	Y	LEP
Pambolinae	Y	N	Y	N	COL+ LEP
Rhysipolinae	N	Y	Y	N	LEP
Rhyssalinae	Y	N	Y	N	COL+ LEP
Rogadinae	N	Y	N	Y	LEP
Sigalphinae					
Pselphaninae group[1]	N/A	N/A	N/A	N/A	N/A
All other taxa	N	Y	N	Y	LEP
Trachypetinae	N/A	N/A	N*	Y*	N/A
Xiphozelinae	N*	Y*	N	Y	LEP

Y denotes that the taxon exhibits a certain trait, while N indicates that it does not have such trait, and N/A that there is no information available. COL – Coleoptera; DIP – Diptera; EMB – Embioptera; HET – Heteroptera; HOM – Homoptera; HYM – Hymenoptera; LEP – Lepidoptera; MEC – Mecoptera; NEU – Neuroptera; ORT – Orthoptera; PSO – Psocoptera. [1]Synonymized by Quicke *et al.* (2008); *Biology presumed from other traits.

Appendix 2.2 (continued)

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Appendix A2.3. Life history traits of the Ichneumonidae.

Subfamily	Idiobiont	Koinobiont	Ectoparasitoid	Endoparasitoid	Hosts attacked
Acaenitinae	N	Y	N	Y	COL
Adelognathinae	N	Y	Y	N	HYM
Agriotypinae	Y	N	Y	N	TRI
Anomaloninae					
Anomalonini	N	Y	N	Y	COL+LEP
Gravenhorstiini	N	Y	N	Y	LEP
All other taxa	N	Y	N	Y	COL+LEP
Banchinae	N	Y	N	Y	LEP
Brachyscleromatinae[1]	N	Y	N	Y	COL
Brachycyrtinae	Y	N	Y	N	NEU
Campopleginae[2]					
Diadegma sp.	N	Y	N	Y	LEP+TRI[△]
Three Genera[a]	N	Y	N	Y	HYM
Four Genera[b]	N	Y	N	Y	COL
Nemeritis sp.	N	Y	N	Y	LEP+RAP
All other taxa	N	Y	N	Y	LEP
Claseinae[3]	Y	N	Y*	N*	COL
Collyriinae	N	Y	N	Y	HYM
Cremastinae	N	Y	N	Y	COL+LEP
Cryptinae					
Cryptini	Y	N	Y	N	ARA+COL+HYM+LEP
Hemigasterini	Y	N	Y	N	COL+HYM+LEP
Phygadeuontini	90%[†]	10%[†]	85%[†]	15%[†]	ARA+COL+DIP+HEM+HYM+LEP+NEU
Ctenopelmatinae					
Perilissini	N	Y	N	Y	HYM+LEP
All other taxa	N	Y	N	Y	HYM
Cylloceriinae[1]	N	Y	N	Y	DIP
Diacritinae	N/A	N/A	N/A	N/A	N/A
Diplazontinae	N	Y	N	Y	DIP
Eucerotinae	N	Y	N	Y	HYM+LEP
Ichneumoninae	50%[†]	50%[†]	N	Y	LEP

Appendix A2.3 (continued)

Subfamily	Idiobiont	Koinobiont	Ectoparasitoid	Endoparasitoid	Hosts attacked
Labeninae					
Groteini	Y	N	Y	N	HYM
Labenini	Y	N	Y	N	COL
Poecilocryptini	Y	N	Y	N	PLANTS
Xenothyrini	N/A	N/A	N/A	N/A	N/A
Lycorininae	N	Y	Y*	N*	LEP
Mesochorinae	N	Y	N	Y	COL+DIP+HEM+HYM+LEP+PSO
Metopiinae	N	Y	N	Y	LEP
Microleptinae	N	Y	N	Y	DIP
Nesomochorinae[2]	N	Y	N	Y	COL
Ophioninae					
Hellwigia sp., *Skiapus* sp.[4]	N	Y	N	Y	N/A
All other taxa	N	Y	N	Y	COL$^{\triangle}$+LEP
Orthocentrinae[1]	N	Y	N	Y	DIP
Orthopelmatinae	N	Y	N	Y	HYM
Oxytorinae	N*	Y*	N*	Y*	N/A
Paxylommatinae	N/A	N/A	N/A	N/A	HYM
Pedunculinae	Y	N	Y	N	ARA
Pimplinae					
Delomeristini	Y	N	Y	N	COL+HYM+LEP
Ephialtini	95%†	5%†	Y	N	ARA+COL+DIP+HYM+LEP
Pimplini	Y	N	20%†	80%†	HYM+LEP
Poemeniinae					
Poemeniini	Y	N	Y	N	COL+HYM
Pseudorhyssini	Y	N	Y	N	HYM
Rodrigamini	Y*	N*	Y*	N*	N/A
Rhyssinae	Y	N	Y	N	COL+HYM
Stilbopinae	N	Y	N	Y	LEP
Tatogastrinae	N/A	N/A	N/A	N/A	N/A
Tersilochinae					
Neorhacodinae group[1]	N*	Y*	N	Y	HYM
Phrudinae group[1]	N	Y	N	Y	COL
All other taxa	N	Y	N	Y	COL+HYM

Appendix A2.3 (continued)

Subfamily	Idiobiont	Koinobiont	Ectoparasitoid	Endoparasitoid	Hosts attacked
Tryphoninae					
Tryphonini & Exenterini	N	Y	Y	N	HYM
Phytodietini	N	Y	Y	N	LEP
Oedemopsini	N	Y	Y	N	LEP
Eclytini	N	Y	Y	N	HYM
Sphinctini	N	Y	Y	N	LEP
Idiogrammatini	N	Y	Y	N	HYM
Xoridinae	Y	N	Y	N	COL+HYM

Y denotes that the taxon exhibits a certain trait, while N indicates that it does not have such trait, and N/A that there is no information available. ARA – Araneae; COL – Coleoptera; DIP – Diptera; HEM – Hemiptera; HYM – Hymenoptera; LEP – Lepidoptera; NEU – Neuroptera; PSO – Psocoptera; RAP – Rhapidioptera; TRI - Trichoptera. [1]Following classification on Quicke *et al.* (2009); [2]Following classification on Quicke *et al.* (2005; 2009); [3]Following classification on Laurenne *et al.* (2006); [4]Following classification on Quicke *et al.* (2005); [†]Gavin Broad and Mark Shaw (pers. comm.); [a]*Dolophron* sp., *Lathrostizus* sp., *Olesicampe* sp.*;* [b] *Bathyplectes* sp., *Lathroplex sp*., *Lemophagus* sp., *Rhimphoctona* sp.; *Biology presumed from other traits; [△]only one species of this host taxon is attacked.

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Appendix A2.4. Characteristics of the islands used in Chapter 4.

Island	Arch	IslType	Region	Area	Alt	DistArea	DistMainl	Temp	Prec	Long	Lat
Antigua	N	Oceanic	Neotropics	282	402	60	700	26.4	1250	-61.789	17.086
Azores	Y	Oceanic	Palaearctic	2328	2351	830	1350	18	1484	-25.498	37.805
Bahamas	Y	Continental	Neotropics	13934	63	100	100	26.1	1501	-76.703	24.600
Balearic Isl.	Y	Continental	Palaearctic	5015	1445	90	90	17.5	805	2.912	39.614
Bermuda	Y	Oceanic	Neotropics	53	79	1000	1000	21.5	1511	-64.755	32.309
Bohol	N	Continental	IndoMalaya	3864	865	20	1600	27.5	2205	124.167	9.833
Borneo	N	Continental	IndoMalaya	743244	4095	100	500	27.6	4274	114.423	0.389
Canary Isl.	Y	Oceanic	Palaearctic	7301.3	3718	90	90	20.5	564	-16.521	28.292
Cape Verde	Y	Oceanic	Afrotropics	4076	2829	550	550	25.2	540	-23.615	15.112
Chuuk Isl.	Y	Oceanic	Australasia	113.9	439	1450	2200	27.5	3788	153.700	5.300
Corsica	N	Continental	Palaearctic	8722	2710	10	85	15.9	1005	9.050	42.188
Crete	N	Continental	Palaearctic	8260	2456	100	100	19.1	1041	24.916	35.308
Cuba	N	Continental	Neotropics	1111463	1974	200	200	26.4	2010	-80.500	22.380
Cyprus	N	Continental	Palaearctic	9251	1951	70	70	19.4	988	33.436	35.133
Faroe Isl.	Y	Oceanic	Palaearctic	1399	882	320	320	6.9	1568	-6.990	62.127
Fiji	Y	Oceanic	Australasia	18272	1241	1150	2650	25.9	3147	177.973	-17.791
Greenland	Y	Continental	Nearctic	2175600	3700	800	800	1.5	2233	-42.177	71.802
Grenada	N	Oceanic	Neotropics	311	840	130	150	27.4	2231	-61.699	12.113
Guam	N	Oceanic	Australasia	541	393	1250	2700	27.3	2429	144.781	13.458
Hainan	N	Continental	Palaearctic	33209.8	1892	20	20	25.9	1958	109.828	19.159
Hawaii	Y	Oceanic	Nearctic	16688	4169	4000	4000	23.3	1273	-156.948	21.226
Hispaniola	N	Continental	Neotropics	73147	3087	90	580	28	1878	-71.227	18.877
Iceland	N	Oceanic	Palaearctic	101826	1479	200	860	5.5	2039	-19.021	64.964
Ireland	N	Continental	Palaearctic	85114	1032	20	20	10.6	1592	-7.603	53.294
Isle of Man	N	Continental	Palaearctic	575	621	30	30	8.8	1218	-4.555	54.238
Jamaica	N	Continental	Neotropics	11526	2256	160	650	26.7	2945	-77.323	18.032
Japan	Y	Mixed	Palaearctic	375799	3776	180	180	19.2	3437	139.838	37.488
Java	N	Continental	IndoMalaya	131188	3676	25	850	27.8	4327	109.901	-7.327
Juan Fernández	Y	Oceanic	Neotropics	148.5	1649	610	610	15.7	1043	-78.878	-33.638
Leyte	N	Mixed	IndoMalaya	7213	1349	2	1500	27.1	3460	124.896	10.785
Lord Howe Isl.	N	Oceanic	Australasia	14.5	875	580	580	19.1	1582	159.085	-31.555
Luzon	Y	Mixed	IndoMalaya	116520	2934	350	650	27.3	3963	121.327	16.510
Madagascar	N	Continental	Afrotropics	587713.3	2876	400	400	26.8	3289	46.950	-19.771
Madeira	Y	Oceanic	Palaearctic	796	1861	420	650	18.8	836	-16.969	32.750
Malta	Y	Continental	Palaearctic	316	253	90	250	18.8	540	14.384	35.939
Mariana Isl.	Y	Oceanic	Australasia	471	965	160	2900	26.9	2025	145.700	15.150
Mauritius	Y	Oceanic	Afrotropics	1865	828	150	1900	24	1993	57.551	-20.279
Midway Isl.	Y	Oceanic	Australasia	6.2	13	700	5400	22.5	1088	-177.375	28.210
Mindanao	Y	Oceanic	IndoMalaya	99078	2954	330	1500	27.2	3281	124.248	7.691
Mindoro	N	Mixed	IndoMalaya	9735	2585	20	1200	27.5	3134	121.100	12.900

Appendix A2.4 (continued)

Island	Arch	IslType	Region	Area	Alt	DistArea	DistMainl	Temp	Prec	Long	Lat
Negros	N	Mixed	IndoMalaya	13670	2464	20	1450	27.8	2804	123.000	10.000
New Caledonia	Y	Oceanic	Australasia	19103	1618	1300	1300	23.7	2298	165.500	-21.400
New Guinea	N	Continental	Australasia	785753	4884	150	150	27.3	6485	141.360	-5.200
New Zealand	Y	Oceanic	Australasia	267077.3	3764	1700	1700	16.4	5325	172.470	-42.790
Novaya Zemlya	Y	Continental	Palaearctic	80324.7	1312	50	50	-4.4	450	58.194	75.071
Okinawa	Y	Mixed	Palaearctic	1201	498	200	350	24	2411	127.800	26.350
Palau	Y	Oceanic	Australasia	530	242	830	2000	27.5	3659	134.564	7.531
Palawan	Y	Mixed	IndoMalaya	14896.3	2085	130	1050	27.1	2933	118.750	10.000
Panay	N	Mixed	IndoMalaya	12300	2049	150	1400	27.3	4412	122.600	11.100
Philippines others	Y	Mixed	IndoMalaya	5469.4	2057	50	1500	27	2276	122.000	6.500
Prince Edward I.	N	Continental	Nearctic	5620	134	15	15	6	1147	-63.757	46.503
Puerto Rico	Y	Continental	Neotropics	8960	1338	120	700	26.7	2621	-66.466	18.235
Reunion	N	Oceanic	Afrotropics	2535.2	3069	700	1700	23.8	1963	55.536	-21.115
Sakhalin	N	Continental	Palaearctic	74056	1609	10	10	4.7	1046	143.187	50.153
Samar	N	Mixed	IndoMalaya	13429	850	20	1450	27.3	4064	125.012	11.802
Sardinia	N	Continental	Palaearctic	23833	1834	180	180	17.6	978	9.000	40.000
Seychelles	Y	Continental	Afrotropics	444	905	1050	1300	26.6	2281	55.487	-4.684
Sicily	N	Continental	Palaearctic	25460	3320	3	3	18	826	14.038	37.474
Singapore	N	Continental	IndoMalaya	536.4	166	2	2	26.7	2966	105.230	1.083
Society Isl.	Y	Oceanic	Australasia	1628	2241	1900	5500	26.8	2635	-149.376	-17.690
Solomon Isl.	Y	Oceanic	Australasia	31001	2447	50	1450	27.1	4014	160.127	-9.557
South Moluccas	Y	Mixed	Australasia	46478	3027	140	350	27	4022	129.500	-3.260
Sri Lanka	N	Continental	IndoMalaya	67654.5	2524	30	30	28.1	4095	80.790	7.874
St. Helena	N	Oceanic	Afrotropics	122	819	1900	1900	20.6	657	-5.720	-15.950
St. Vincent	N	Oceanic	Neotropics	345	1234	50	280	26.8	2709	-61.200	13.250
Sulawesi	Y	Oceanic	Australasia	197680	3455	115	1100	27	3894	121.405	-1.974
Sumatra	Y	Continental	IndoMalaya	483533.2	3804	60	60	27.4	4155	100.637	-0.144
Taiwan	N	Continental	Palaearctic	34506.6	3997	150	150	24.9	4589	121.036	23.738
Tasmania	N	Continental	Australasia	67900	1617	210	210	13.3	3108	147.000	-42.000
Trin. & Tobago	Y	Continental	Neotropics	5128	940	15	15	26.4	2838	-61.427	10.386
United Kingdom	Y	Continental	Palaearctic	229850	1333	35	35	10.6	2160	-1.749	53.377
Vanuatu	Y	Oceanic	Australasia	12190	1879	360	1800	26.3	4413	168.300	-17.750
Western Samoa	Y	Oceanic	Australasia	2935	1858	830	3800	26.8	5690	-172.482	-13.617

Arch indicates if the unit used is an individual island (N) or an archipelago (Y). IslType indicates the geological origin of the island. Region corresponds to the biogeographic realm. Area is measured in Km^2. Alt is the altitude, measured in meters above sea level. DistArea is the distance (in km) to the closest larger territory. DistMainl is the distance (in km) to the closest mainland. Temp is the average temperature, and Prec the annual precipitation. Long is longitude and Lat latitude. See Chapter 4 for more details.

Appendix A2.5. Level of generalism and pairwise comparisons between islands and species pool (chi-square test) for braconids and ichneumonids.

	Braconidae							Ichneumonidae						
		Island	Pool	Idi/Koin	Island	Pool	Ect/End		Island	Pool	Idi/Koin	Island	Pool	Ect/End
Island	Rich	Idi/Koin	Idi/Koin	χ^2	Ect/End	Ect/End	χ^2	Rich	Idi/Koin	Idi/Koin	χ^2	Ect/End	Ect/End	χ^2
Antigua	6	0.500	0.533	0.005	0.500	0.533	0.005	-	-	-	-	-	-	-
Azores	-	-	-	-	-	-	-	27	0.444	0.644	0.726	0.357	0.355	0.000
Bahamas	-	-	-	-	-	-	-	7	0.167	0.463	0.974	0.167	0.475	1.026
Balearic Isl.	-	-	-	-	-	-	-	49	1.402	0.529	**12.095*** **	0.556	0.425	0.807
Bermuda	14	0.077	0.313	2.093	0.077	0.333	2.317	13	0.238	0.467	0.941	0.204	0.583	2.187
Bohol	-	-	-	-	-	-	-	30	4.825	1.629	**5.410***	0.685	0.755	0.066
Borneo	386	1.718	0.714	**55.997*** **	1.718	0.733	**52.773*** **	282	1.719	1.588	0.340	0.972	0.781	2.761
Canary Isl.	138	0.160	0.371	**9.209****	0.160	0.364	**8.765****	150	0.541	0.670	1.218	0.391	0.448	0.430
Cape Verde	71	0.340	0.604	3.247	0.365	0.604	2.530	-	-	-	-	-	-	-
Chuuk Isl.	-	-	-	-	-	-	-	12	0.463	1.018	1.611	0.348	0.696	1.097
Corsica	63	0.145	0.176	0.254	0.145	0.177	0.269	488	0.706	0.519	**10.243****	0.554	0.419	**7.970****
Crete	85	0.349	0.254	1.581	0.349	0.254	1.581	15	1.239	0.501	3.228	0.485	0.405	0.106
Cuba	89	0.459	0.321	2.306	0.459	0.326	2.093	122	1.012	0.590	**8.524****	0.740	0.469	**5.914***
Cyprus	118	1.034	0.283	**48.572*** **	1.034	0.283	**48.572*** **	51	0.614	0.485	0.651	0.678	0.450	2.024
Faroe Isl.	-	-	-	-	-	-	-	45	0.772	0.503	2.013	0.560	0.441	0.585
Fiji	52	0.156	0.391	**4.973***	0.156	0.365	**4.235***	24	0.171	0.852	**8.853****	0.176	0.649	**5.586***
Greenland	-	-	-	-	-	-	-	91	0.446	0.486	0.137	0.295	0.409	1.640
Grenada	63	0.537	0.680	0.768	0.537	0.701	0.974	24	0.387	1.138	**6.020***	0.459	0.742	1.190
Guam	13	0.300	0.440	0.330	0.300	0.409	0.214	11	0.549	1.024	0.965	0.287	0.698	1.553
Hainan	70	0.346	0.216	2.823	0.373	0.226	3.292	58	0.522	0.758	1.749	0.376	0.359	0.024
Hawaii	38	0.652	0.220	**10.183****	0.652	0.223	**9.892****	59	0.284	0.508	3.389	0.142	0.602	**15.276*** **
Hispaniola	23	0.167	0.372	1.715	0.167	0.381	1.816	29	0.401	0.645	1.312	0.312	0.416	0.419
Iceland	-	-	-	-	-	-	-	100	0.723	0.502	3.132	0.458	0.438	0.040
Ireland	569	0.056	0.164	**32.811*** **	0.058	0.164	**31.441*** **	528	0.628	0.524	3.708	0.500	0.426	2.662
Isle of Man	-	-	-	-	-	-	-	59	0.490	0.519	0.043	0.540	0.428	0.728

Appendix A2.5 (continued)

	Braconidae							Ichneumonidae						
		Island	Pool	Idi/Koin	Island	Pool	Ect/End		Island	Pool	Idi/Koin	Island	Pool	Ect/End
Island	Rich	Idi/Koin	Idi/Koin	χ^2	Ect/End	Ect/End	χ^2	Rich	Idi/Koin	Idi/Koin	χ^2	Ect/End	Ect/End	χ^2
Jamaica	12	0.200	0.361	0.594	0.200	0.376	0.683	29	0.160	0.761	**10.082****	0.090	0.530	**8.793****
Japan	611	0.210	0.114	**23.884*****	0.215	0.122	**20.805*****	1350	0.540	0.391	**17.796*****	0.415	0.548	**13.109*****
Java	219	0.711	1.112	**8.543****	0.698	1.117	**9.442****	369	1.601	1.564	0.032	0.822	0.623	**4.561***
Juan Fernández Isl.	5	0.000	0.495	2.463	0.000	0.546	2.713	7	0.892	1.154	0.115	1.121	0.898	0.085
Leyte	13	0.625	0.830	0.246	0.625	0.854	0.300	17	3.250	1.632	1.488	0.308	0.757	2.612
Lord Howe Island	-	-	-	-	-	-	-	2	1.000	0.932	0.002	0.111	0.679	0.766
Luzon	285	0.447	0.412	0.339	0.439	0.413	0.200	311	1.558	0.953	**14.956*****	0.741	0.657	0.904
Madagascar	489	0.552	1.220	**35.714*****	0.547	1.220	**36.488*****	552	0.858	0.795	0.353	0.543	0.199	**43.553*****
Madeira	75	0.154	0.313	**3.915***	0.154	0.313	**3.915***	95	0.668	0.636	0.047	0.472	0.419	0.248
Malta	-	-	-	-	-	-	-	26	0.864	0.617	0.729	0.444	0.460	0.006
Mariana Isl.	-	-	-	-	-	-	-	8	0.951	0.999	0.005	0.441	0.684	0.321
Mauritius	18	0.385	0.664	1.071	0.385	0.659	1.041	16	0.333	0.847	2.740	0.111	0.540	**4.339***
Midway Isl.	3	0.000	0.220	0.658	0.000	0.223	0.668	-	-	-	-	-	-	-
Mindanao	159	0.893	0.719	1.671	0.893	0.724	1.564	189	1.719	1.378	1.893	0.697	0.696	0.000
Mindoro	42	0.077	0.890	**25.941*****	0.077	0.915	**26.795*****	144	1.791	1.040	**9.036****	0.635	0.726	0.559
Negros	38	0.583	0.839	1.142	0.583	0.864	1.336	125	2.222	1.647	2.144	0.881	0.745	0.772
New Caledonia	-	-	-	-	-	-	-	45	0.404	0.870	**4.903***	0.236	0.652	**6.865****
New Guinea	387	0.434	0.632	**7.462****	0.405	0.613	**9.010****	428	0.915	1.275	**7.544****	0.536	0.560	0.121
New Zealand	72	0.200	0.474	**6.258***	0.200	0.478	**6.399***	80	0.493	0.798	2.712	0.203	0.649	**11.913*****
Novaya Zemlya	-	-	-	-	-	-	-	38	0.551	0.483	0.149	0.490	0.447	0.069
Okinawa	56	0.244	0.212	0.176	0.244	0.216	0.135	217	0.623	0.652	0.093	0.598	0.528	0.684
Palau	-	-	-	-	-	-	-	13	0.413	1.142	2.968	0.461	0.619	0.241
Palawan	28	0.474	0.847	2.072	0.474	0.873	2.296	48	1.038	1.619	2.273	0.395	0.745	**3.865***
Panay	-	-	-	-	-	-	-	20	2.922	1.609	1.367	0.887	0.745	0.148
Philippines - others	18	0.500	0.838	1.074	0.500	0.863	1.202	25	0.767	1.649	3.665	0.529	0.759	0.725
Prince Edward Isl.	14	0.000	0.178	2.488	0.077	0.184	0.743	165	0.401	0.440	0.264	0.392	0.403	0.022
Puerto Rico	47	0.237	0.493	3.788	0.237	0.493	3.788	32	0.584	0.961	1.742	0.359	0.587	1.433
Reunion	-	-	-	-	-	-	-	17	0.349	0.861	2.768	0.164	0.541	3.224

Appendix A2.5 (continued)

	Braconidae							Ichenumonidae						
Island	Rich	Island Idi/Koin	Pool Idi/Koin	Idi/Koin χ^2	Island Ect/End	Pool Ect/End	Ect/End χ^2	Rich	Island Idi/Koin	Pool Idi/Koin	Idi/Koin χ^2	Island Ect/End	Pool Ect/End	Ect/End χ^2
Sakhalin	505	0.130	0.121	0.189	0.140	0.130	0.247	604	0.402	0.407	0.017	0.622	0.518	3.806
Samar	8	3.000	0.835	2.775	3.000	0.835	2.775	65	2.736	1.467	**4.757***	0.757	0.820	0.095
Sardinia	82	0.491	0.177	**19.432*****	0.491	0.178	**19.209*****	133	0.734	0.522	3.717	0.528	0.420	1.534
Seychelles	9	0.800	0.563	0.273	0.800	0.559	0.283	15	0.357	0.773	1.788	0.190	0.477	1.793
Sicily	134	0.411	0.188	**16.362*****	0.411	0.190	**16.009*****	205	0.757	0.518	**7.020****	0.379	0.421	0.452
Singapore	83	0.729	1.015	2.074	0.729	1.040	2.389	68	1.704	1.574	0.091	0.533	0.822	2.691
Society Isl.	9	0.500	0.457	0.016	0.500	0.437	0.036	15	1.000	0.923	0.023	0.154	0.690	**4.508***
Solomon Isl.	32	0.778	0.456	2.170	0.778	0.431	2.672	68	0.755	0.901	0.474	0.313	0.602	**5.047***
South Moluccas	35	1.917	0.788	**6.408***	1.917	0.770	**6.777****	62	1.417	1.343	0.041	0.505	0.640	0.738
Sri Lanka	145	0.436	0.297	3.775	0.408	0.288	2.981	190	0.494	0.875	**12.502*****	0.331	0.655	**15.413*****
St. Helena	-	-	-	-	-	-	-	4	0.333	0.647	0.335	0.429	0.119	1.468
St. Vincent	82	0.608	0.700	0.381	0.608	0.723	0.541	19	0.173	1.142	**11.123*****	0.166	0.764	**6.444***
Sulawesi	107	0.576	0.823	2.874	0.606	0.802	1.824	245	1.454	1.363	0.203	0.322	0.814	**35.521*****
Sumatra	209	1.039	0.914	0.707	1.039	0.938	0.448	177	1.435	1.231	0.879	0.668	0.551	1.359
Taiwan	486	0.266	0.181	**8.018****	0.266	0.181	**8.058****	715	0.631	0.870	**10.412****	0.494	0.564	1.637
Tasmania	68	0.133	0.429	**9.311****	0.117	0.430	**10.683****	90	0.587	0.771	1.038	0.519	0.692	1.112
Trinidad & Tobago	81	0.270	0.729	**13.662*****	0.270	0.751	**14.476*****	28	0.633	1.153	2.396	0.560	0.748	0.533
United Kingdom	1171	0.110	0.166	**13.403*****	0.111	0.167	**13.478*****	2397	0.527	0.506	0.631	0.446	0.416	1.779
Vanuatu	-	-	-	-	-	-	-	35	0.224	0.903	**10.884*****	0.326	0.600	2.283
Western Samoa	-	-	-	-	-	-	-	14	0.315	0.939	3.194	0.279	0.669	1.867

Rich is the species richness of each island. Idio/Koin is the ratio between the number of idibiont and koinobiont species (i.e. level of generalism) of the parasitoid faunas of both island and its species pool (Pool). Ect/End is the ratio between the number of ecto- and endoparasitoid species. χ^2 is the result of the chi-square test for both types of ratio, that compares the ratios of islands and their species pool; significant values are in bold (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

Appendix A2.6. Comparision between the characteristics of islands with significantly higher level of generalism than their species pool, and those where the level of generalism does not depart from the observed in the pool.

	a) Braconidae				**b) Ichneumonidae**			
	Means not higher	**Means higher**	**df**	**t-value**	**Means not higher**	**Means higher**	**df**	**t-value**
Temp	23.391	22.125	51	0.554	21.715	22.956	68	-0.458
Prec	2588.489	2548.375	51	0.078	2574.951	2383.222	68	0.394
Area	102052.734	159407.450	51	-0.650	108668.162	185556.311	68	-0.667
Alt	1910.733	3271.125	51	-3.099**	1889.066	2273.222	68	-0.899
DistArea	305.978	602.875	51	-1.164	445.557	99.222	68	1.513
DistMainl	944.711	679.125	51	0.564	997.820	606.444	68	1.023
AbsLat	20.551	24.838	51	-0.762	24.088	25.577	68	-0.231
RichIsl	127.667	236.250	51	-1.335	147.984	307.111	68	-1.296
SpeciesPool	0.535	0.333	51	1.898	0.909	0.848	68	0.444
	Isl not higher	**Isl higher**	**df**	**χ^2**	**Isl not higher**	**Isl higher**	**df**	**χ^2**
Archipelago			1	0.354			1	1.354
Single isl.	23	5			28	6		
Archipelago	22	3			33	9		
IslType			2	1.935			2	9.627**
Oceanic	17	1			27	0		
Mixed	8	2			7	4		
Continental	20	5			27	5		
Region			5	9.793			5	7.014
Afrotropics	4	0			5	0		
Australasia	9	1			16	0		
Indomalaya	12	1			11	4		
Nearctic	1	1			3	0		
Neotropics	10	0			9	1		
Palaearctic	9	5			17	4		

"Means not higher" correspond to the mean value of the predictor on the islands where the level of generalism is not higher than that of the species pool. "Means higher" correspond to the mean value of the predictor on the islands where the level of generalism is significantly higher than that of the species pool. "df" is the degrees of freedom, and "t-value" is the result of the t-test. "Isl not higher" corresponds to the number of islands where the level of generalism is not higher than that of the species pool. "Isl higher" corresponds to the number of islands where the level of generalism is significantly higher than that of the species pool. χ^2 is the result of the chi-square tests. ** $p < 0.01$.

Appendix A2.7. Comparison between the characteristics of islands with significantly lower level of generalism than their species pool, and those where the level of generalism does not depart from the observed in the pool.

	a) Braconidae				**b) Ichneumonidae**			
	Means not lower	**Means lower**	**df**	**t-value**	**Means not lower**	**Means lower**	**df**	**t-value**
Temp	23.846	20.992	51	1.487	21.215	26.344	68	-1.944
Prec	2440.585	3067.083	51	-1.447	2387.033	3656.889	68	-2.751**
Area	89556.212	182985.659	51	-1.252	120477.108	105517.900	68	0.129
Alt	2015.244	2460.583	51	-1.101	1888.836	2274.778	68	-0.904
DistArea	350.171	352.917	51	-0.012	403.148	386.667	68	0.071
DistMainl	975.000	664.167	51	0.774	969.918	795.556	68	0.453
AbsLat	19.455	27.157	51	-1.633	25.614	15.239	68	1.639
RichIsl	104.195	280.250	51	-2.653*	168.557	167.667	68	0.007
SpeciesPool	0.484	0.574	51	-0.960	0.892	0.965	68	-0.534
	Isl not lower	**Is lower**	**df**	**χ^2**	**Isl not lower**	**Is lower**	**df**	**χ^2**
Archipelago			1	0.050			1	1.354
Single isl.	22	6			28	6		
Archipelago	19	6			33	3		
IslType			2	1.355			2	2.399
Oceanic	14	4			22	4		
Mixed	9	1			11	0		
Continental	18	7			28	5		
Region			5	3.903			5	7.650
Afrotropics	3	1			5	0		
Australasia	6	4			12	4		
Indomalaya	11	2			14	1		
Nearctic	2	0			3	0		
Neotropics	9	1			7	3		
Palaearctic	10	4			20	1		

"Means not lower" correspond to the mean value of the predictor on the islands where the level of generalism is not lower than that of the species pool. "Means lower" correspond to the mean value of the predictor on the islands where the level of generalism is significantly lower than that of the species pool. "df" is the degrees of freedom, and "t-value" is the result of the t-test. "Isl not lower" corresponds to the number of islands where the level of generalism is not lower than that of the species pool. "Isl lower" corresponds to the number of islands where the level of generalism is significantly lower than that of the species pool. χ^2 is the result of the chi-square tests. * $p < 0.05$; ** $p < 0.01$.

Appendix A3.1. Study sites codes, their geographical location and the number of larvae collected.

Code	Area	Locality	Toponym	UTM	X	Y	Alt	Tort	Par
MAD13	Madeira	Ribeira da Janela	Ribeira Funda	28	299051	3636214	21	2	0
MAD14	Madeira	Ribeira da Janela	Ribeira Funda	28	298441	3637177	21	50	7
MAD15	Madeira	Arco da Calheta	Arco da Calheta	28	299343	3620805	352	5	1
MAD16	Madeira	Paúl do Mar	Ribeira das Galinhas	28	291039	3627372	93	0	0
MAD17	Madeira	Porto Novo	Porto Novo	28	330150	3615327	35	0	0
LG5	La Gomera	S. Sebastián de La Gomera	Monumento al Sagrado Corazón de Jesus	28	291552	3108369	240	6	0
LG9	La Gomera	Imada	Roque de Imada	28	279376	3108717	1081	1	0
LG10	La Gomera	Antocojo	Antocojo	28	280843	3104210	555	22	2
LG16	La Gomera	Valle Hermoso	La Quilla	28	276930	3118531	291	28	6
LG17	La Gomera	Valle Hermoso	Valle Abajo	28	278343	3120864	69	10	0
LG18	La Gomera	Valle Hermoso	Tunel de la Culata	28	278921	3119600	313	16	0
LG19	La Gomera	Agulo	Tunel de Agulo	28	284163	3120470	275	62	2
LG21	La Gomera	Las Toscas	Las Toscas	28	282916	3107690	728	35	2
LP5	La Palma	Las Lomadas	Road to Playa de Nogales	28	232726	3184123	113	59	4
LP6	La Palma	Los Cancajos	Close to La Caleta de la Ballena	28	230329	3171499	48	38	3
LP9	La Palma	San Simon	Road to Playa La Martina	28	229058	3165439	281	44	4
LP14	La Palma	Morro de San Jacinto	Barranco de Las Angustias	28	215675	3176634	220	31	2
LP16	La Palma	Bermudez	San Juan	28	229820	3187450	208	6	0
LP17	La Palma	Santo Domingo de Garafia	Los Hondos	28	211080	3192227	223	9	0
LP18	La Palma	Tigueronte	Barranco de Santa Clara	28	227232	3162906	487	0	0
TEN3	Tenerife	Igueste de San Andrés	Lomito del Llano	28	285692	3155536	89	5	1
TEN6	Tenerife	Los Silos	Pina (Tavalera)	28	321295	3138222	218	75	4
TEN9	Tenerife	Buenavista del Norte	La Cuesta	28	319276	3138078	343	53	2
TEN12	Tenerife	Güimar	Malpaís (Poligono Industrial)	28	362260	3130077	489	12	0
TEN14	Tenerife	El Tablero	Tabaiba Alta	28	369188	3144110	432	2	1
TEN15	Tenerife	Güimar	Malpaís (Poligono Industrial)	28	365555	3133870	59	8	2
TEN16	Tenerife	Pajara	Ladera de Güimar	28	362315	3130100	480	25	1
TEN19	Tenerife	Teno Bajo	Buenavista del Norte	28	313140	3138018	103	14	1
TEN21	Tenerife	Los Carrizales	Los Carrizales	28	317101	3134050	436	46	1

Appendix A3.1 (continued)

Code	Area	Locality	Toponym	UTM	X	Y	Alt	Tort	Par
MOR1	Western Morocco	Tamri	Tamri (Km 107-108)	29	421604	3403948	88	58	0
MOR4	Western Morocco	Tamri	Cape Rhir	29	416083	3394115	68	14	2
MOR5	Western Morocco	Tamri	Cape Rhir	29	415316	3392545	26	14	1
MOR6	Western Morocco	Agadir	Tarhazoute	29	429093	3380389	55	0	0
MOR9	Western Morocco	Tamri	Pointe Imessouane	29	422341	3412970	91	20	2
MOR18	Western Morocco	Tamri	Cape Rhir	29	415272	3390451	34	8	4
MOR19	Western Morocco	Tamri	Tamri	29	419888	3396491	20	56	1
MOR21	Western Morocco	Tiznit	Boun Soun	29	426223	3289943	186	21	1
MOR22	Western Morocco	Tiznit	Boun Soun	29	426178	3290826	171	12	0
MOR23	Western Morocco	Tiznit	Tadouarte	29	423976	3298656	124	99	3
MOR24	Western Morocco	Tiznit	Aglou	29	417057	3294138	43	26	0
MOR25	Western Morocco	Tiznit	Sidi-bou-Ifedaïl	29	409825	3286338	105	81	5
MOR26	Western Morocco	Sidi Ifni	El Msaidira	29	393126	3259692	93	43	7
MOR27	Western Morocco	Sidi Ifni	Sidi Ifni	29	389641	3251893	169	17	0
MOR28	Western Morocco	Tiznit	Road to Sidi Ifni	29	417473	3282817	292	1	0
MOR29	Western Morocco	Tiznit	Road to Sidi Ifni	29	414578	3278621	289	2	0
MOR7	Northern Morocco	Chefchaouen	P. N. Talassemtane	30	302328	3883965	1127	37	0
MOR10	Northern Morocco	Bab-Taza	Road to Fifi	30	293458	3886222	402	18	0
MOR11	Northern Morocco	Bab-Taza	Road to Fifi	30	298924	3876230	1254	14	0
MOR20	Northern Morocco	Nador	Nador	30	500948	3888620	118	23	0
PNA1	Portugal	Arrábida	Pinheirinhos (Cova da Mijona)	29	487425	4253669	90	42	0
PNA4	Portugal	Arrábida	Vale da Rasca	29	504924	4261984	87	36	0
PNA6	Portugal	Arrábida	Alambe	29	497139	4259976	122	53	0
PNA8	Portugal	Arrábida	Sesimbra	29	492464	4254510	85	25	0
PNSC3	Portugal	Cascais	Biscaia	29	458792	4290048	147	27	9
PNSC4	Portugal	Cascais	Cabo da Roca	29	456820	4292611	138	4	0

UTM - UTM zone; X – Longitude; Y – Latitude; Alt – Altitude in meters above sea level; Tort – Number of tortricid larvae collected; Par – Number of parasitized tortricid larvae.

Appendix A3.2. List of the specimens collected and sequenced during this study.

Host identifier	H. acces. no.	Par	Par. identifier	Par. acces. no.	Type	Area	Site	Year
MAD045	FN665431	N	-	-	-	MAD	MAD14	2006
MAD052	FN665432	N	-	-	-	MAD	MAD14	2006
MAD056	FN665433	N	-	-	-	MAD	MAD14	2006
MAD057	FN665434	Y	PAR230	FN662372	Ect	MAD	MAD14	2006
MAD058	FN665435	N	-	-	-	MAD	MAD14	2006
MAD096	FN665436	Y	PAR263	-	End	MAD	MAD15	2007
MAD097	FN665437	N	-	-	-	MAD	MAD15	2007
MAD100	FN665438	Y	PAR264	FN662373	Ect	MAD	MAD14	2007
MAD101	FN665439	Y	PAR265	FN662374	Ect	MAD	MAD14	2007
MAD102	FN665440	Y	PAR266	FN662375	Ect	MAD	MAD14	2007
MAD103	FN665441	N	-	-	-	MAD	MAD14	2007
MAD110	FN665442	N	-	-	-	MAD	MAD14	2007
MAD121	FN665443	N	-	-	-	MAD	MAD14	2007
MAD125	FN665444	N	-	-	-	MAD	MAD14	2007
MAD130	FN665445	Y	PAR267	FN662376	Ect	MAD	MAD14	2007
MAD142	FN665446	Y	PAR333	FN662368	End	MAD	MAD14	2006
MAD143	FN665447	Y	PAR334	FN662377	Ect	MAD	MAD14	2006
LG088	FN665448	N	-	-	-	LG	LG19	2006
LG089	FN665449	N	-	-	-	LG	LG19	2006
LG090	FN665450	N	-	-	-	LG	LG19	2006
LG094	FN665451	Y	PAR038	-	Ect	LG	LG19	2006
LG098	FN665452	N	-	-	-	LG	LG19	2006
LG099	FN665453	N	-	-	-	LG	LG19	2006
LG180	FN665454	Y	PAR187	-	End	LG	LG16	2006
LG181	FN665455	Y	PAR020	-	Ect	LG	LG16	2006
LG182	FN665456	N	-	-	-	LG	LG16	2006
LG192	FN665457	N	-	-	-	LG	LG16	2006
LG194	FN665458	Y	PAR025	-	Ect	LG	LG16	2006
LG197	FN665459	N	-	-	-	LG	LG16	2006
LG203	FN665460	Y	PAR097	-	End	LG	LG16	2006
LG205	FN665461	Y	PAR098	-	Ect	LG	LG16	2006
LG206	FN665462	Y	PAR099	-	Ect	LG	LG16	2006
LG518	FN665463	N	-	-	-	LG	LG18	2006
LG526	FN665464	N	-	-	-	LG	LG18	2006
LG662	FN665465	N	-	-	-	LG	LG5	2006
LG721	FN665466	N	-	-	-	LG	LG9	2007
LG726	FN665467	N	-	-	-	LG	LG10	2007
LG741	FN665468	Y	PAR268	FN662401	End	LG	LG10	2007

Appendix A3.2 (continued)

Host identifier	H. acces. no.	Par	Par. identifier	Par. acces. no.	Type	Area	Site	Year
LG742	FN665469	N	-	-	-	LG	LG10	2007
LG746	FN665470	Y	PAR336	FN662402	End	LG	LG10	2007
LG748	FN665471	N	-	-	-	LG	LG19	2007
LG756	FN665472	N	-	-	-	LG	LG19	2007
LG761	FN665473	Y	PAR270	FN662400	Ect	LG	LG19	2007
LG770	FN665474	N	-	-	-	LG	LG19	2007
LG777	FN665475	N	-	-	-	LG	LG19	2007
LG793	FN665476	Y	PAR271	-	End	LG	LG21	2007
LG800	FN665477	N	-	-	-	LG	LG21	2007
LG810	FN665478	N	-	-	-	LG	LG21	2007
LG815	FN665479	N	-	-	-	LG	LG21	2007
LG817	FN665480	N	-	-	-	LG	LG21	2007
LG825	FN665481	Y	PAR273	FN662412	End	LG	LG21	2007
LG828	FN665482	N	-	-	-	LG	LG17	2007
LP001	FN665483	Y	PAR163	FN662389	End	LP	LP5	2006
LP002	FN665484	Y	PAR164	-	Ect	LP	LP5	2006
LP007	FN665485	Y	PAR165	FN662413	End	LP	LP5	2006
LP010	FN665486	N	-	-	-	LP	LP5	2006
LP170	FN665487	Y	PAR126	FN662391	End	LP	LP9	2006
LP208	FN665488	N	-	-	-	LP	LP9	2006
LP212	FN665489	Y	PAR127	-	End	LP	LP6	2006
LP237	FN665490	N	-	-	-	LP	LP5	2006
LP240	FN665491	N	-	-	-	LP	LP5	2006
LP436	FN665492	N	-	-	-	LP	LP14	2006
LP474	FN665493	Y	PAR190	FN662392	Ect	LP	LP9	2006
LP522	FN665494	N	-	-	-	LP	LP9	2006
LP529	FN665495	Y	PAR203	FN662393	Ect	LP	LP9	2006
LP540	FN665496	N	-	-	-	LP	LP9	2006
LP543	FN665497	N	-	-	-	LP	LP16	2006
LP548	FN665498	N	-	-	-	LP	LP5	2006
LP610	FN665499	N	-	-	-	LP	LP14	2007
LP625	FN665500	N	-	-	-	LP	LP5	2007
LP630	FN665501	N	-	-	-	LP	LP5	2007
LP635	FN665502	N	-	-	-	LP	LP5	2007
LP650	FN665503	Y	PAR274	FN662414	End	LP	LP17	2007
LP655	FN665504	N	-	-	-	LP	LP5	2007
LP664	FN665505	Y	PAR275	FN662395	Ect	LP	LP6	2007
LP667	FN665506	Y	PAR276	FN662396	Ect	LP	LP6	2007

Appendix A3.2 (continued)

Host identifier	H. acces. no.	Par	Par. identifier	Par. acces. no.	Type	Area	Site	Year
LP675	FN665507	Y	PAR277	FN662394	Pupae	LP	LP9	2007
LP680	FN665508	N	-	-	-	LP	LP9	2007
LP682	FN665509	N	-	-	-	LP	LP9	2007
LP688	FN665510	N	-	-	-	LP	LP9	2007
LP705	FN665511	N	-	-	-	LP	LP6	2007
LP711	FN665512	N	-	-	-	LP	LP6	2007
LP720	FN665513	N	-	-	-	LP	LP17	2007
LP721	FN665514	N	-	-	-	LP	LP17	2007
LP722	FN665515	N	-	-	-	LP	LP17	2007
LP732	FN665516	N	-	-	-	LP	LP14	2007
TEN104	FN665517	N	-	-	-	TEN	TEN14	2006
TEN105	FN665518	Y	PAR243	FN662397	Ect	TEN	TEN14	2006
TEN106	FN665519	Y	PAR332	FN662411	End	TEN	TEN3	2006
TEN110	FN665520	N	-	-	-	TEN	TEN3	2006
TEN145	FN665521	N	-	-	-	TEN	TEN16	2006
TEN152	FN665522	N	-	-	-	TEN	TEN16	2006
TEN153	FN665523	Y	PAR245	FN662378	Ect	TEN	TEN16	2006
TEN160	FN665524	N	-	-	-	TEN	TEN16	2006
TEN165	FN665525	N	-	-	-	TEN	TEN21	2006
TEN175	FN665526	N	-	-	-	TEN	TEN21	2006
TEN182	FN665527	Y	PAR246	FN662379	Ect	TEN	TEN21	2006
TEN189	FN665528	N	-	-	-	TEN	TEN21	2006
TEN190	FN665529	N	-	-	-	TEN	TEN21	2006
TEN236	FN665530	Y	PAR252	FN662380	Ect	TEN	TEN6	2006
TEN240	FN665531	N	-	-	-	TEN	TEN6	2006
TEN243	FN665532	Y	PAR253	FN662398	Ect	TEN	TEN6	2006
TEN253	FN665533	Y	PAR254	FN662399	Ect	TEN	TEN6	2006
TEN256	FN665534	N	-	-	-	TEN	TEN6	2006
TEN260	FN665535	N	-	-	-	TEN	TEN6	2006
TEN272	FN665536	N	-	-	-	TEN	TEN9	2006
TEN280	FN665537	N	-	-	-	TEN	TEN9	2006
TEN284	FN665538	N	-	-	-	TEN	TEN9	2006
TEN290	FN665539	Y	PAR258	FN662381	Ect	TEN	TEN9	2006
TEN305	FN665540	N	-	-	-	TEN	TEN6	2007
TEN310	FN665541	N	-	-	-	TEN	TEN12	2007
TEN320	FN665542	N	-	-	-	TEN	TEN9	2007
TEN334	FN665543	N	-	-	-	TEN	TEN12	2007
TEN340	FN665544	N	-	-	-	TEN	TEN6	2007

Appendix A3.2 (continued)

Host identifier	H. acces. no.	Par	Par. identifier	Par. acces. no.	Type	Area	Site	Year
TEN351	FN665545	N	-	-	-	TEN	TEN21	2007
TEN354	FN665546	N	-	-	-	TEN	TEN9	2007
TEN355	FN665547	N	-	-	-	TEN	TEN9	2007
TEN362	FN665548	N	-	-	-	TEN	TEN15	2007
TEN366	FN665549	Y	PAR279	-	Ect	TEN	TEN15	2007
TEN367	FN665550	Y	PAR280	FN662382	Ect	TEN	TEN15	2007
TEN370	FN665551	N	-	-	-	TEN	TEN9	2007
TEN372	FN665552	Y	PAR281	FN662369	End	TEN	TEN9	2007
TEN380	FN665553	N	-	-	-	TEN	TEN6	2007
TEN396	FN665554	Y	PAR282	FN662370	End	TEN	TEN6	2007
TEN400	FN665555	N	-	-	-	TEN	TEN19	2007
TEN405	FN665556	Y	PAR284	FN662390	Ect	TEN	TEN19	2007
TEN408	FN665557	N	-	-	-	TEN	TEN19	2007
MOR001	FN665558	N	-	-	-	WM	MOR25	2007
MOR009	FN665559	Y	PAR285	FN662403	End	WM	MOR25	2007
MOR010	FN665560	N	-	-	-	WM	MOR25	2007
MOR029	FN665561	N	-	-	-	WM	MOR25	2007
MOR030	FN665562	N	-	-	-	WM	MOR25	2007
MOR040	FN665563	N	-	-	-	WM	MOR25	2007
MOR045	FN665564	N	-	-	-	WM	MOR25	2007
MOR046	FN665565	Y	PAR286	FN662404	End	WM	MOR25	2007
MOR050	FN665566	N	-	-	-	WM	MOR25	2007
MOR060	FN665567	N	-	-	-	WM	MOR25	2007
MOR070	FN665568	N	-	-	-	WM	MOR26	2007
MOR071	FN665569	Y	PAR287	FN662415	End	WM	MOR26	2007
MOR074	FN665570	Y	PAR288	FN662405	End	WM	MOR26	2007
MOR076	FN665571	Y	PAR289	FN662406	End	WM	MOR26	2007
MOR080	FN665572	N	-	-	-	WM	MOR26	2007
MOR084	FN665573	Y	PAR290	FN662416	End	WM	MOR26	2007
MOR090	FN665574	N	-	-	-	WM	MOR26	2007
MOR093	FN665575	Y	PAR291	FN662407	End	WM	MOR26	2007
MOR098	FN665576	N	-	-	-	WM	MOR26	2007
MOR100	FN665577	Y	PAR292	FN662408	End	WM	MOR26	2007
MOR103	FN665578	Y	PAR293	-	End	WM	MOR26	2007
MOR107	FN665579	N	-	-	-	WM	MOR23	2007
MOR110	FN665580	N	-	-	-	WM	MOR23	2007
MOR115	FN665581	Y	PAR295	-	End	WM	MOR23	2007

Appendix A3.2 (continued)

Host identifier	H. acces. no.	Par	Par. identifier	Par. acces. no.	Type	Area	Site	Year
MOR120	FN665582	N	-	-	-	WM	MOR23	2007
MOR140	FN665583	N	-	-	-	WM	MOR23	2007
MOR145	FN665584	N	-	-	-	WM	MOR23	2007
MOR150	FN665585	N	-	-	-	WM	MOR23	2007
MOR160	FN665586	N	-	-	-	WM	MOR23	2007
MOR180	FN665587	N	-	-	-	WM	MOR23	2007
MOR193	FN665588	Y	PAR296	FN662383	Ect	WM	MOR23	2007
MOR195	FN665589	Y	PAR297	FN662409	End	WM	MOR21	2007
MOR200	FN665590	N	-	-	-	WM	MOR21	2007
MOR210	FN665591	N	-	-	-	WM	MOR21	2007
MOR235	FN665592	Y	PAR298	FN662384	Ect	WM	MOR23	2007
MOR249	FN665593	N	-	-	-	WM	MOR5	2007
MOR250	FN665594	Y	PAR299	FN662358	End	WM	MOR5	2007
MOR311	FN665595	Y	PAR300	FN662386	Ect	WM	MOR25	2007
MOR321	FN665596	Y	PAR301	FN662410	End	WM	MOR25	2007
MOR325	FN665597	N	-	-	-	WM	MOR19	2007
MOR330	FN665598	N	-	-	-	WM	MOR19	2007
MOR360	FN665599	N	-	-	-	WM	MOR19	2007
MOR370	FN665600	N	-	-	-	WM	MOR19	2007
MOR390	FN665601	N	-	-	-	WM	MOR19	2007
MOR397	FN665602	Y	PAR302	FN662371	End	WM	MOR19	2007
MOR409	FN665603	Y	PAR303	FN662387	Pupae	WM	MOR25	2007
MOR413	FN665604	N	-	-	-	WM	MOR18	2007
MOR415	FN665605	Y	PAR305	FN662357	End	WM	MOR18	2007
MOR417	FN665606	Y	PAR306	FN662359	End	WM	MOR18	2007
MOR418	FN665607	Y	PAR307	FN662360	End	WM	MOR18	2007
MOR419	-	Y	PAR304	FN662388	Ect	WM	MOR18	2007
MOR432	FN665608	N	-	-	-	WM	MOR9	2007
MOR440	FN665609	Y	PAR308	FN662361	End	WM	MOR9	2007
MOR445	FN665610	Y	PAR309	FN662385	Ect	WM	MOR9	2007
MOR469	FN665611	Y	PAR310	FN662362	End	WM	MOR4	2007
MOR470	FN665612	N	-	-	-	WM	MOR4	2007
MOR476	FN665613	Y	PAR311	FN662363	End	WM	MOR4	2007
MOR477	FN665614	N	-	-	-	NM	MOR7	2008
MOR500	FN665615	N	-	-	-	NM	MOR7	2008
MOR526	FN665616	N	-	-	-	NM	MOR11	2008
MOR530	FN665617	N	-	-	-	NM	MOR11	2008
MOR534	FN665618	N	-	-	-	NM	MOR11	2008

Appendix A3.2 (continued)

Host identifier	H. acces. no.	Par	Par. identifier	Par. acces. no.	Type	Area	Site	Year
MOR535	FN665619	N	-	-	-	NM	MOR11	2008
MOR540	FN665620	N	-	-	-	NM	MOR20	2008
MOR560	FN665621	N	-	-	-	NM	MOR20	2008
MOR570	FN665622	N	-	-	-	NM	MOR10	2008
PNA001	FN665623	N	-	-	-	POR	PNA1	2008
PNA010	FN665624	N	-	-	-	POR	PNA1	2008
PNA020	FN665625	N	-	-	-	POR	PNA1	2008
PNA030	FN665626	N	-	-	-	POR	PNA1	2008
PNA040	FN665627	N	-	-	-	POR	PNA1	2008
PNA052	FN665628	N	-	-	-	POR	PNA4	2008
PNA060	FN665629	N	-	-	-	POR	PNA4	2008
PNA082	FN665630	N	-	-	-	POR	PNA4	2008
PNA095	FN665631	N	-	-	-	POR	PNA8	2008
PNA100	FN665632	N	-	-	-	POR	PNA8	2008
PNA115	FN665633	N	-	-	-	POR	PNA6	2008
PNA130	FN665634	N	-	-	-	POR	PNA6	2008
PNA150	FN665635	N	-	-	-	POR	PNA6	2008
PNSC001	FN665636	N	-	-	-	POR	PNSC4	2008
PNSC004	FN665637	N	-	-	-	POR	PNSC4	2008
PNSC005	FN665638	Y	PAR312	FN662352	End	POR	PNSC3	2008
PNSC010	FN665639	N	-	-	-	POR	PNSC3	2008
PNSC015	FN665640	Y	PAR313	FN662364	End	POR	PNSC3	2008
PNSC017	FN665641	Y	PAR314	FN662355	End	POR	PNSC3	2008
PNSC018	FN665642	Y	PAR315	FN662353	End	POR	PNSC3	2008
PNSC021	FN665643	Y	PAR316	FN662365	End	POR	PNSC3	2008
PNSC022	FN665644	Y	PAR317	FN662366	End	POR	PNSC3	2008
PNSC023	FN665645	Y	PAR318	FN662354	End	POR	PNSC3	2008
PNSC025	FN665646	N	-	-	-	POR	PNSC3	2008
PNSC029	FN665647	Y	PAR319	FN662367	End	POR	PNSC3	2008
PNSC030	FN665648	Y	PAR320	FN662356	End	POR	PNSC3	2008

Host identifier is the identification code of each tortricid larva; H. acces. no. is the GenBank accession number of each tortricid larva; Par indicates if a tortricid larva was (Y) or was not (N) parasitized; Par. identifier is the identification code of the parasitoid larvae found to parasitize the tortricid larvae; Par. acces. no. is the GenBank accession number of each parasitoid larva; Type corresponds to the attack strategy of the parasitoids (Ect – ectoparasitoid; End – endoparasitoid); Area is the region from where the specimens were collected (MAD – Madeira, LG – La Gomera, LP – La Palma, TEN – Tenerife, WM – Western Morocco, NM – Northern Morocco, POR – Portugal; see Fig. 5.1); Site is the location from where the specimens were collected (see details in Appendix A3.1); Year corresponds to the year when the specimens were collected.

Appendix A3.3. Details of the sequences used for computing the neighbor-joining and the maximum likelihood trees, that correspond to parasitoids or hosts collected outside our study sites.

Identifier	Accession number	Locality	References
BRAC Agathidinae *Disophrys* sp.	FN662417	-	This study
BRAC Agathidinae *Earinus* sp.	FN662418	Finland	This study
BRAC Agathidinae *Sesioctonus* sp.	FN662419	Costa Rica	This study
BRAC Braconinae *Bracon* sp.	FN662420	Papua New Guinea	This study
BRAC Braconinae *Coeloides sordidator*	AY935355	Switzerland	(1)
BRAC Cardiochilinae	FN662421	Papua New Guinea	This study
BRAC Charmontinae *Charmon* sp.	FN662422	UK	This study
BRAC Cheloninae *Chelonus* sp.	FN662423	Finland	This study
BRAC Cheloninae *Phanerotoma tritoma*	FN662424	-	This study
BRAC Doryctinae *Doryctes heydenii*	DQ498945	Palaearctic	(2)
BRAC Euphorinae *Centistes* sp.	FN662425	Madagascar	This study
BRAC Euphorinae *Meteorus* sp.	FN662426	Madagascar	This study
BRAC Exothecinae *Colastes* sp.	AY935350	UK: Berkshire	(1)
BRAC Exothecinae *Ondigus* sp.	DQ498970	French Guyana	(2)
BRAC Gnamptodontinae *Gnamptodon* sp. 1	FN662427	Madagascar	This study
BRAC Gnamptodontinae *Gnamptodon* sp. 2	FN662428	Madagascar	This study
BRAC Homolobinae *Homolobus* sp. 1	FN662429	Madagascar	This study
BRAC Homolobinae *Homolobus* sp. 2	FN662430	Madagascar	This study
BRAC Hormiinae *Hormius* sp. 1	FN662431	Papua New Guinea	This study
BRAC Hormiinae *Hormius* sp. 2	FN662432	Papua New Guinea	This study
BRAC Ichneutinae *Ichneutes* sp.	FN662433	Finland	This study
BRAC Ichneutinae *Proterops* sp.	FN662434	Finland	This study
BRAC Lysiterminae *Pentatermus* sp.	FN662435	Madagascar	This study
BRAC Lysiterminae *Tetratermus* sp.	AY935382	Uganda: Kibale	(1)
BRAC Macrocentrinae	FN662437	La Palma	This study
BRAC Macrocentrinae *Macrocentrus cingulum*	FJ617018	Asia	(3)
BRAC Macrocentrinae *Macrocentrus* sp.	FN662436	Madagascar	This study
BRAC Mendesellinae *Epsilogaster* sp.	DQ538845	-	(4)
BRAC Microgastrinae *Apanteles* sp.	EU396633	Costa Rica: Guacanaste	(5)
BRAC Microgastrinae *Cotesia* sp.	EU397666	Costa Rica: Guacanaste	(5)
BRAC Microgastrinae *Dolichogenidea* sp.	EU398010	Costa Rica: Guacanaste	(5)
BRAC Microgastrinae *Glyptapanteles* sp.	EU398103	Costa Rica: Guacanaste	(5)
BRAC Miracinae *Mirax* sp. 1	FN662438	Costa Rica	This study

Appendix A3.3 (continued)

Identifier	Accession number	Locality	References
BRAC Miracinae *Mirax* sp. 2	FN662439	Costa Rica	This study
BRAC Orgilinae *Orgilus* sp.	FJ413828	Canada: Manitoba	(6)
BRAC Orgilinae *Stantonia scutellaris*	FN662440	Papua New Guinea	This study
BRAC Pambolinae *Notiopambolus* sp.	FN662441	Australia	This study
BRAC Pambolinae *Pambolus* sp.	FN662442	Nigeria	This study
BRAC Rhysipolinae *Rhysipolis temporalis*	AY935376	Russia: Primorskii Krai	(1)
BRAC Rhyssalinae *Oncophanes* sp.	AY935407	UK: Berkshire	(1)
BRAC Rhyssalinae *Rhyssalus clavator*	AY935409	Poland: Kazimierz	(1)
BRAC Rogadinae *Aleiodes bicolor*	FN662443	UK	This study
BRAC Rogadinae *Spinaria* sp.	FN662444	Thailand	This study
ICH Anomaloninae *Barylypa* sp.	FN662445	Madagascar	This study
ICH Banchinae *Diradops tamaska*	FN662446	Costa Rica	This study
ICH Banchinae *Lissonota coracina*	FJ414444	Canada: Manitoba	(6)
ICH Banchinae *Meniscomorpha* sp.	FN662447	Costa Rica	This study
ICH Campopleginae *Charops* sp.	FN662448	Costa Rica	This study
ICH Campopleginae *Diadegma* sp.	FJ413969	Canada: Manitoba	(6)
ICH Campopleginae *Dusona* sp.	FN662449	Madagascar	This study
ICH Cremastinae *Creagrura nigripes*	FN662450	Costa Rica	This study
ICH Cremastinae *Eiphosoma* sp.	FN662451	Costa Rica	This study
ICH Cryptinae *Atractodes* sp.	FJ413678	Canada: Manitoba	(6)
ICH Cryptinae *Encrateola* sp.	FN662452	UK: Berkshire	This study
ICH Cryptinae *Mastrus* sp.	FJ414362	Canada: Manitoba	(6)
ICH Ctenopelmatinae *Mesoleius affinis*	FN662453	Finland	This study
ICH Ctenopelmatinae *Scopesis* sp.	FN662454	Finland	This study
ICH Ctenopelmatinae *Sympherta* sp.	FN662455	Hungary	This study
ICH Ichneumoninae *Diacantharius* sp.	FN662458	Costa Rica	This study
ICH Ichneumoninae *Joppa* sp.	FN662459	Costa Rica	This study
ICH Ichneumoninae *Tricholabus* sp.	FN662460	Costa Rica	This study
ICH Lycorininae *Lycorina* sp. 1	FN662461	Costa Rica	This study
ICH Lycorininae *Lycorina* sp. 2	FN662462	Bolivia	This study
ICH Mesochorinae *Mesochorus* sp.	FN662463	Costa Rica	This study
ICH Mesochorinae *Plectochorus* sp.	FN662464	Russia	This study
ICH Metopiinae *Chorinaeus* sp.	FN662465	Finland	This study
ICH Metopiinae *Leurus caeruliventris*	FN662466	Costa Rica	This study
ICH Ophioninae *Enicospilus bozai*	FN662467	Costa Rica	This study
ICH Ophioninae *Ophion obscuratus*	FN662468	UK	This study

Appendix A3.3 (continued)

Identifier	Accession number	Locality	References
ICH Paxylommatinae *Hybrizon* sp. 1	FN662456	UK: Berkshire	This study
ICH Paxylommatinae *Hybrizon* sp. 2	FN662457	Russia	This study
ICH Pimplinae *Pimpla* sp.	FN662469	USA: Akaska	This study
ICH Pimplinae *Scambus planatus*	FN662470	UK	This study
ICH Stilbopinae *Panteles* sp.	FN662471	UK: Chobham	This study
ICH Tryphoninae *Ctenochira genalis*	FN662472	Finland	This study
ICH Tryphoninae *Netelia* sp.	FN662473	Myanmar	This study
BET Bethylidae *Rhabdepyris* sp.	AJ514364	Mongolia	(7)
CHAL Aphelinidae *Encarsia formosa*	FM210160	-	(8)
CHAL Aphelinidae *Eretmocerus mundus*	FM210168	-	(8)
CHAL Chalcididae *Brachymeria lasus*	AY317221	-	(9)
CHAL Encyrtidae *Leptomastidea abnormis*	FM210175	-	(8)
CHAL Encyrtidae *Metaphycus flavus*	FM210164	-	(8)
CHAL Eulophidae *Diglyphus isaea*	FM210157	-	(8)
CHAL Eulophidae *Tamarixia radiata*	FJ152421	USA: Texas	(10)
CHAL Pteromalidae *Dibrachys* sp.	FJ438100	-	(11)
CHAL Pteromalidae *Nasonia giraulti*	EU746516	-	(12)
DIP Bombyliidae *Anthrax* sp.	AY165731	-	(13)
DIP Bombyliidae *Bombylius validus*	AY165655	-	(13)
DIP Cecidomyiidae *Dasineura folliculi*	EU375702	-	(14)
DIP Cecidomyiidae *Rhopalomyia foliorum*	AB299107	Japan: Okinawa	(15)
DIP Tachinidae *Belvosia* sp.	DQ348819	Costa Rica: Guanacaste	(16)
DIP Tachinidae *Germaria ruficeps*	FJ656175	-	(17)
DIP Tachinidae *Tachina nigrohirta*	FJ656180	-	(17)
DIP Tachinidae *Winthemia* sp.	EF182583	Costa Rica: Guanacaste	(18)
A. subsequana Fuerteventura1	FN665425	Fuerteventura: S. Betancuria	This study
A. subsequana Fuerteventura2	FN665424	Fuerteventura: S. Betancuria	This study
A. subsequana Madeira1	FN665428	Madeira Island: Ponta de São Lourenço	This study
A. subsequana Madeira2	FN665429	Madeira Island: Porto Moniz	This study
A. subsequana Porto Santo1	FN665426	Porto Santo	This study
A. subsequana Porto Santo2	FN665427	Porto Santo	This study
A. subsequana Spain	FN665423	Spain: Valencia	This study
A. subsequana Tenerife	FN665430	Tenerife: Los Cristianos	This study
Choristoneura rosaceana	FJ412308	Canada: British Columbia	(19)
Cydia pomonella	FJ217762	USA: Oregon	(20)
Epinotia tsugana	FJ412476	Canada: British Columbia	(19)
Homona trachyptera	EF070847	Papua New Guinea: Madang	(21)

Appendix A3.3 (continued)

Identifier	Accession number	Locality	References
Olethreutes sp.	FJ412847	Canada: British Columbia	(19)
Pammene albuginana	GQ149501	-	(19)
Rhopobota naevana	FJ412946	Canada: British Columbia	(19)
Spilonota ocellana	FJ412964	Canada: British Columbia	(19)
Thaumatographa youngiella	FJ412992	Canada: British Columbia	(19)
Zeiraphera improbana	FJ413032	Canada: British Columbia	(19)

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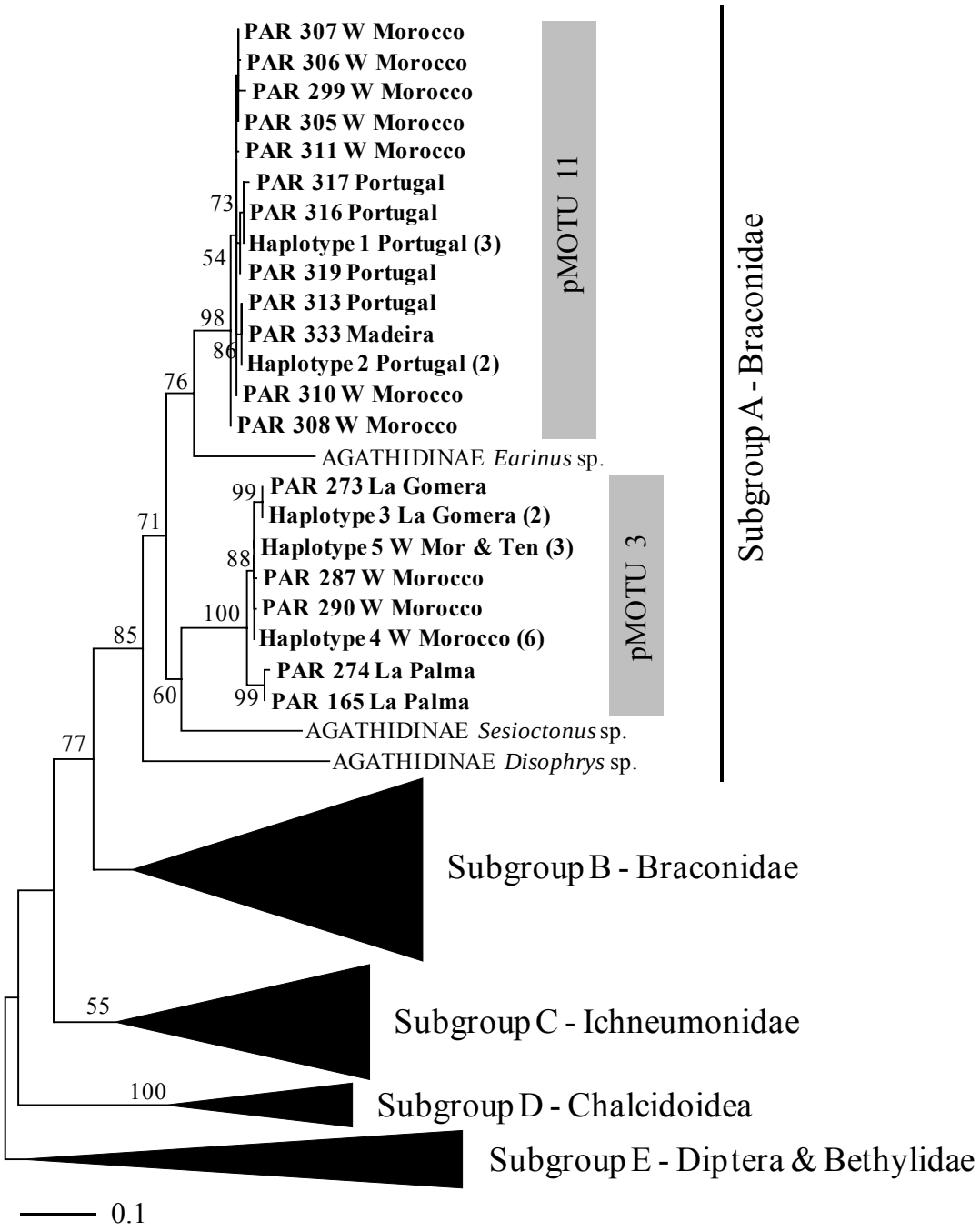
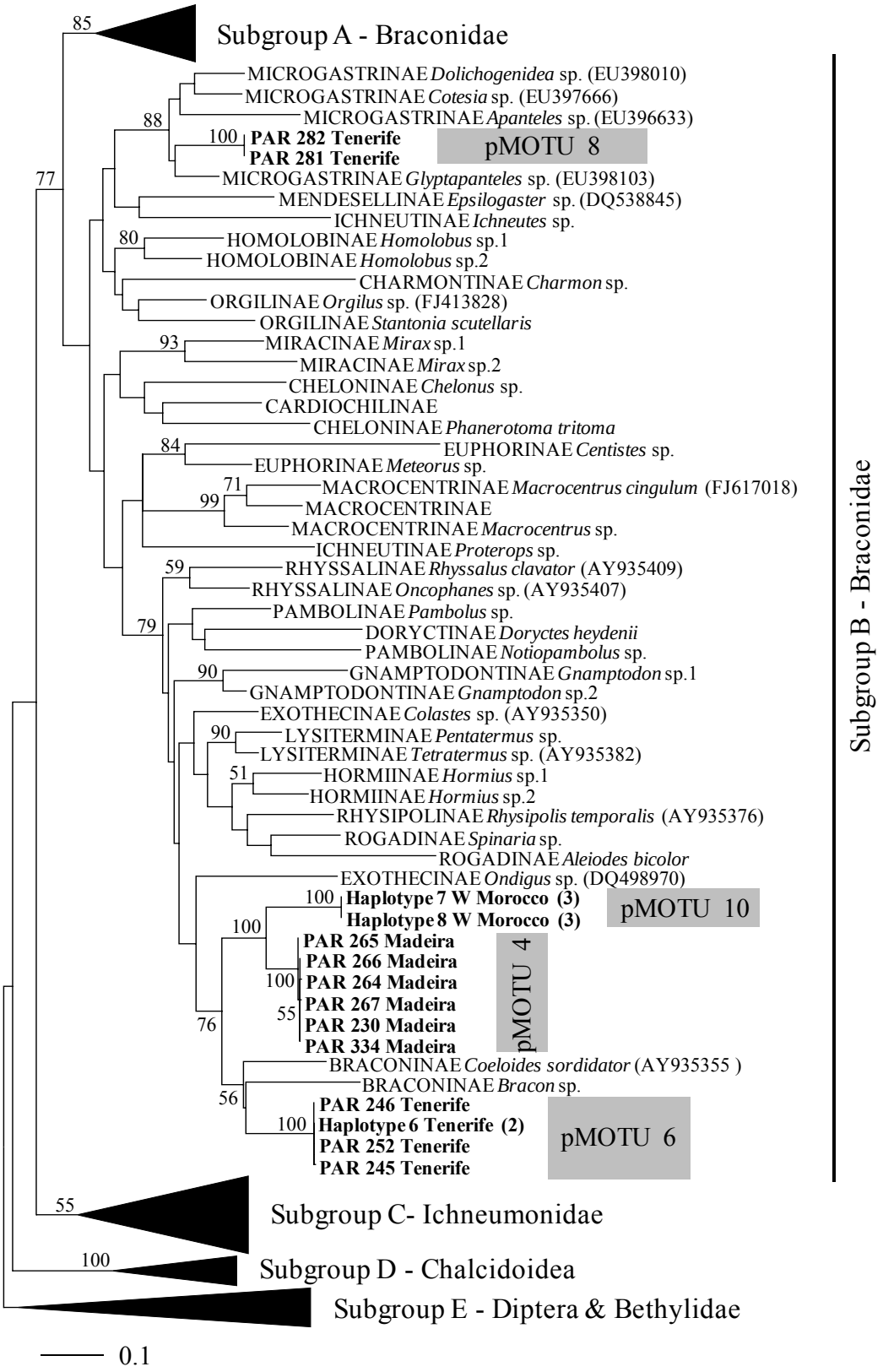
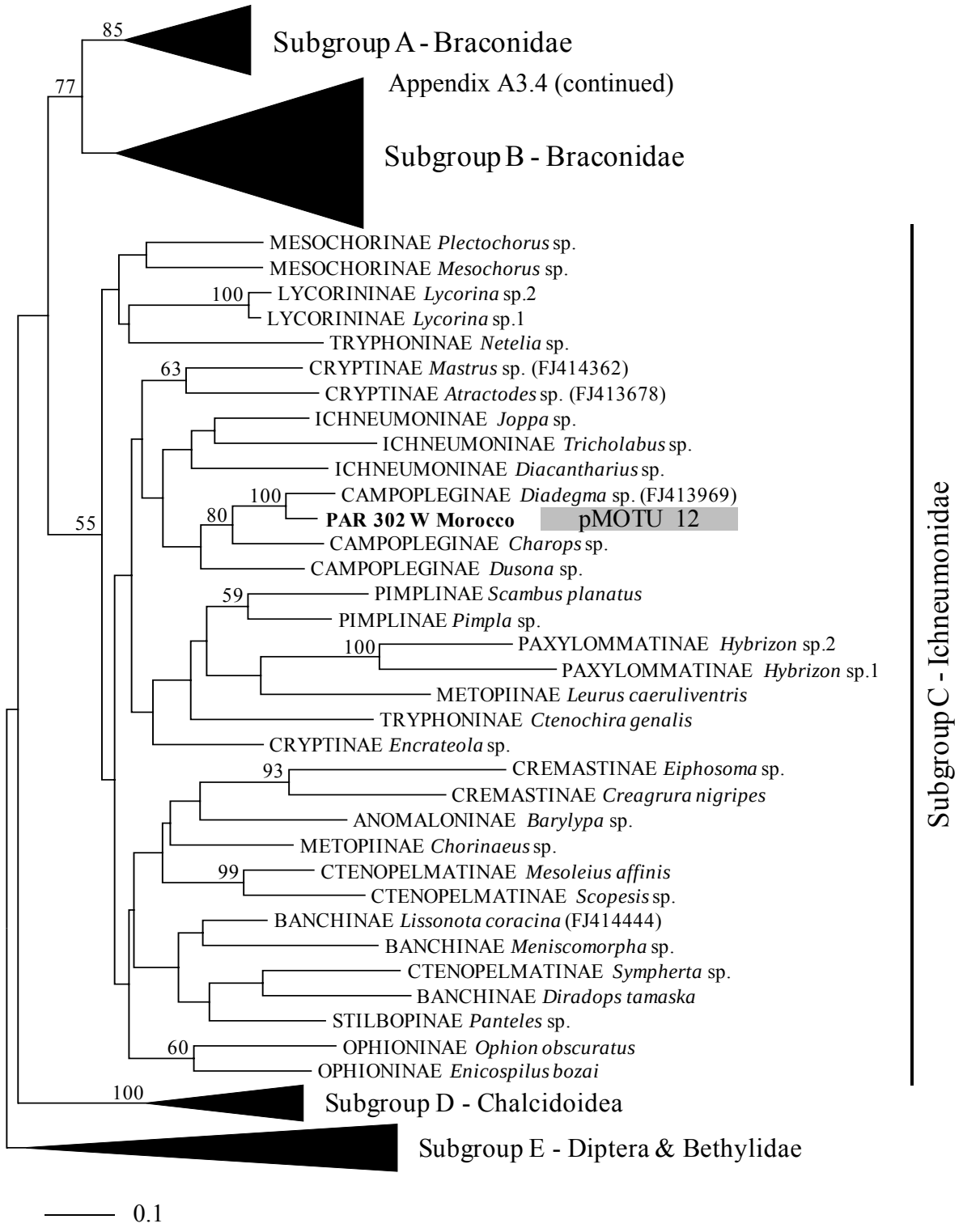
Appendix A3.4. Maximum likelihood tree of the parasitoid barcode COI sequences (based on 157 specimens) under the GTR+I+Γ substitution model showing the existence of 12 MOTUs (in grey). Some branches are collapsed into subgroups for ease of visualization. Sequences obtained from specimens collected in this study are represented in bold. Accession numbers of sequences obtained from GenBank are also represented. Numbers next to branches represent the bootstrap values obtained after 100 replications and values lower than 50% are not represented. Scale bar indicates 10% sequence divergence.



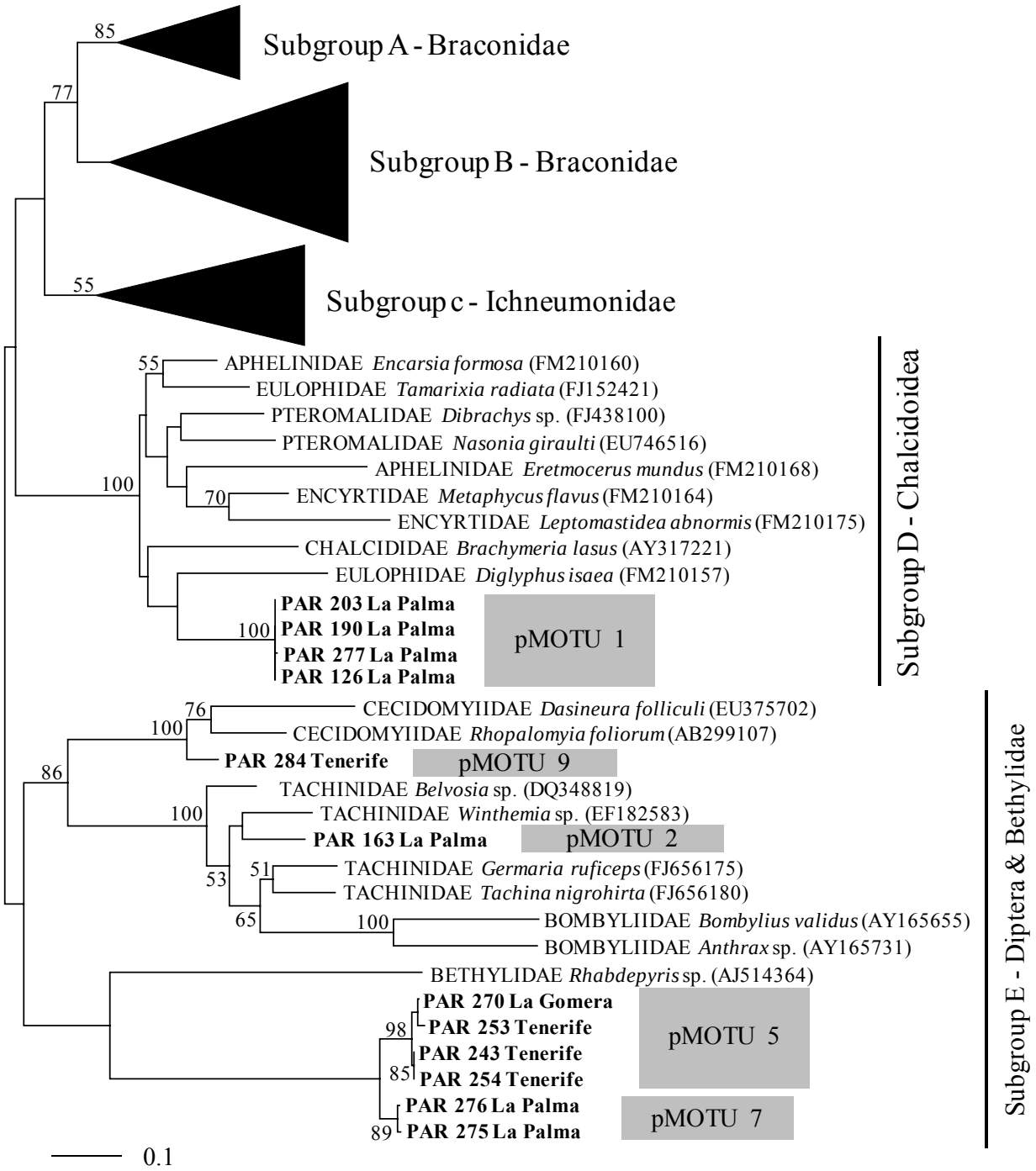
Appendix A3.4 (continued)



Appendix A3.4 (continued)



Appendix A3.4 (continued)



Appendix A3.5. Tentative identification (ID) of the tortricid specimens using genetic distances, tree- and similarity- based methods.

Code	Area	Haplotype	MOTU	BOLD		GenBank		NJ ID	ML ID	Final ID
				ID	%	ID	%			
MAD045	MAD	1	13	*Olethreutes lacunanum*	92	*Homona* sp. near *salaconia*	90	*A. subs.*C	*A. subs.*C	*A. subs.*C
MAD052	MAD	2	13	*Olethreutes lacunanum*	92	*Homona* sp. near *salaconia*	90	*A. subs.*C	*A. subs.*C	*A. subs.*C
MAD056	MAD	-	13	*Olethreutes lacunanum*	92	*Homona* sp. near *salaconia*	90	*A. subs.*C	*A. subs.*C	*A. subs.*C
MAD057	MAD	2	13	*Olethreutes malana*	92	*Homona* sp. near *salaconia*	90	*A. subs.*C	*A. subs.*C	*A. subs.*C
MAD058	MAD	-	13	*Olethreutes malana*	92	*Homona* sp. near *salaconia*	90	*A. subs.*C	*A. subs.*C	*A. subs.*C
MAD096	MAD	-	13	*Olethreutes lacunanum*	92	*Homona* sp. near *salaconia*	90	*A. subs.*C	*A. subs.*C	*A. subs.*C
MAD097	MAD	-	13	*Olethreutes malana*	92	*Homona* sp. near *salaconia*	90	*A. subs.*C	*A. subs.*C	*A. subs.*C
MAD100	MAD	-	13	*Olethreutes malana*	92	*Olethreutes* sp.	91	*A. subs.*C	*A. subs.*C	*A. subs.*C
MAD101	MAD	-	13	*Olethreutes sericoranum*	92	*Homona* sp. near *salaconia*	90	*A. subs.*C	*A. subs.*C	*A. subs.*C
MAD102	MAD	1	13	*Olethreutes malana*	92	*Homona* sp. near *salaconia*	90	*A. subs.*C	*A. subs.*C	*A. subs.*C
MAD103	MAD	-	13	*Olethreutes malana*	92	*Homona* sp. near *salaconia*	90	*A. subs.*C	*A. subs.*C	*A. subs.*C
MAD110	MAD	-	13	*Olethreutes sericoranum*	92	*Homona* sp. near *salaconia*	89	*A. subs.*C	*A. subs.*C	*A. subs.*C
MAD121	MAD	-	13	*Olethreutes malana*	92	*Homona* sp. near *salaconia*	90	*A. subs.*C	*A. subs.*C	*A. subs.*C
MAD125	MAD	2	13	*Olethreutes lacunanum*	92	*Homona* sp. near *salaconia*	90	*A. subs.*C	*A. subs.*C	*A. subs.*C
MAD130	MAD	3	13	*Olethreutes sericoranum*	92	*Homona* sp. near *salaconia*	90	*A. subs.*C	*A. subs.*C	*A. subs.*C
MAD142	MAD	3	13	*Olethreutes sericoranum*	92	*Homona* sp. near *salaconia*	90	*A. subs.*C	*A. subs.*C	*A. subs.*C
MAD143	MAD	1	13	*Olethreutes lacunanum*	92	*Homona* sp. near *salaconia*	90	*A. subs.*C	*A. subs.*C	*A. subs.*C
LG088	LG	-	14	*Argyrotaenia lautana*	92	*Homona* sp. near *salaconia*	90	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG089	LG	4	14	*Pammene rhediella*	92	*Homona* sp. near *salaconia*	90	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG090	LG	4	14	*Pammene rhediella*	92	*Homona* sp. near *salaconia*	90	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG094	LG	4	14	*Pammene rhediella*	92	*Homona* sp. near *salaconia*	90	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG098	LG	4	14	*Olethreutes lacunanum*	92	*Homona* sp. near *salaconia*	90	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG099	LG	5	14	*Pammene rhediella*	92	*Homona* sp. near *salaconia*	91	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG180	LG	5	14	*Pammene rhediella*	92	*Homona* sp. near *salaconia*	91	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG181	LG	4	14	*Olethreutes lacunanum*	92	*Homona* sp. near *salaconia*	90	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG182	LG	4	14	*Pammene rhediella*	92	*Homona* sp. near *salaconia*	90	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG192	LG	4	14	*Pammene rhediella*	92	*Homona* sp. near *salaconia*	90	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG194	LG	4	14	*Pammene rhediella*	92	*Homona* sp. near *salaconia*	90	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG197	LG	4	14	*Olethreutes lacunanum*	92	*Homona* sp. near *salaconia*	90	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG203	LG	-	14	*Argyrotaenia lautana*	92	*Homona* sp. near *salaconia*	91	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG205	LG	-	14	*Pammene rhediella*	92	*Homona* sp. near *salaconia*	90	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG206	LG	4	14	*Pammene rhediella*	92	*Homona* sp. near *salaconia*	90	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG518	LG	5	14	*Olethreutes lacunanum*	92	*Homona* sp. near *salaconia*	91	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG526	LG	-	14	*Pammene rhediella*	92	*Homona* sp. near *salaconia*	90	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG662	LG	5	14	*Pammene rhediella*	92	*Homona* sp. near *salaconia*	91	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG721	LG	4	14	*Olethreutes lacunanum*	92	*Homona* sp. near *salaconia*	90	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG726	LG	4	14	*Pammene rhediella*	92	*Homona* sp. near *salaconia*	90	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG741	LG	4	14	*Pammene rhediella*	92	*Homona* sp. near *salaconia*	90	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG742	LG	-	14	*Pammene rhediella*	92	*Homona* sp. near *salaconia*	90	*A. subs.* F	*A. subs.* F	*A. subs.* F

Appendix A3.5 (continued)

Code	Area	Haplotype	MOTU	BOLD		GenBank		NJ ID	ML ID	Final ID
				ID	%	ID	%			
LG746	LG	4	14	*Pammene rhediella*	92	*Homona* sp. near *salaconia*	90	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG748	LG	4	14	*Pammene rhediella*	92	*Homona* sp. near *salaconia*	90	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG756	LG	4	14	*Olethreutes lacunanum*	92	*Homona* sp. near *salaconia*	90	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG761	LG	4	14	*Pammene rhediella*	92	*Homona* sp. near *salaconia*	90	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG770	LG	5	14	*Pammene rhediella*	92	*Homona* sp. near *salaconia*	91	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG777	LG	5	14	*Olethreutes lacunanum*	92	*Homona* sp. near *salaconia*	91	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG793	LG	5	14	*Pammene rhediella*	92	*Homona* sp. near *salaconia*	91	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG800	LG	4	14	*Pammene rhediella*	92	*Homona* sp. near *salaconia*	90	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG810	LG	4	14	*Olethreutes lacunanum*	92	*Homona* sp. near *salaconia*	90	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG815	LG	4	14	*Pammene rhediella*	92	*Homona* sp. near *salaconia*	90	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG817	LG	4	14	*Olethreutes lacunanum*	92	*Homona* sp. near *salaconia*	90	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG825	LG	-	14	*Pammene rhediella*	92	*Homona* sp. near *salaconia*	91	*A. subs.* F	*A. subs.* F	*A. subs.* F
LG828	LG	4	14	*Pammene rhediella*	92	*Homona* sp. near *salaconia*	90	*A. subs.* F	*A. subs.* F	*A. subs.* F
LP001	LP	-	15	*Olethreutes sericoranum*	93	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP002	LP	6	15	*Olethreutes viburnanum*	93	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP007	LP	7	15	*Olethreutes sericoranum*	94	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP010	LP	7	15	*Olethreutes sericoranum*	94	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP170	LP	7	15	*Olethreutes lacunanum*	93	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP208	LP	6	15	*Olethreutes sericoranum*	94	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP212	LP	-	15	*Olethreutes sericoranum*	93	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP237	LP	6	15	*Olethreutes sericoranum*	93	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP240	LP	-	15	*Olethreutes sericoranum*	93	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP436	LP	-	15	*Olethreutes sericoranum*	93	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP474	LP	6	15	*Olethreutes sericoranum*	94	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP522	LP	-	15	*Olethreutes sericoranum*	94	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP529	LP	6	15	*Olethreutes sericoranum*	94	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP540	LP	7	15	*Olethreutes sericoranum*	94	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP543	LP	-	15	*Olethreutes sericoranum*	93	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP548	LP	-	15	*Olethreutes viburnanum*	93	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP610	LP	-	15	*Olethreutes sericoranum*	94	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP625	LP	7	15	*Olethreutes viburnanum*	93	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP630	LP	-	15	*Olethreutes sericoranum*	94	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP635	LP	7	15	*Olethreutes sericoranum*	94	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP650	LP	-	15	*Olethreutes sericoranum*	94	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP655	LP	6	15	*Olethreutes sericoranum*	93	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP664	LP	6	15	*Olethreutes sericoranum*	94	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP667	LP	6	15	*Olethreutes viburnanum*	93	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP675	LP	6	15	*Olethreutes viburnanum*	93	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP680	LP	6	15	*Olethreutes sericoranum*	93	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP682	LP	6	15	*Olethreutes viburnanum*	93	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP688	LP	6	15	*Olethreutes sericoranum*	93	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP705	LP	7	15	*Olethreutes sericoranum*	94	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP711	LP	7	15	*Olethreutes sericoranum*	94	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP720	LP	6	15	*Olethreutes viburnanum*	93	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP721	LP	-	15	*Olethreutes viburnanum*	93	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP722	LP	6	15	*Olethreutes sericoranum*	93	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D
LP732	LP	-	15	*Olethreutes sericoranum*	94	*Zeiraphera diniana*	91	*A. subs.* D	*A. subs.* D	*A. subs.* D

Appendix A3.5 (continued)

Code	Area	Haplotype	MOTU	BOLD		GenBank		NJ ID	ML ID	Final ID
				ID	%	ID	%			
TEN104	TEN	-	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN105	TEN	-	16	*Gypsonoma parryana*	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN106	TEN	8	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN110	TEN	8	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN145	TEN	-	16	*Gypsonoma salicicolana*	93	*Homona* sp. near *salaconia*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN152	TEN	9	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN153	TEN	9	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN160	TEN	10	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN165	TEN	9	16	*Gypsonoma salicicolana*	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN175	TEN	9	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN182	TEN	10	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN189	TEN	9	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN190	TEN	-	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN236	TEN	9	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN240	TEN	10	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN243	TEN	10	16	*Olethreutes sericoranum*	92	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN253	TEN	10	16	*Olethreutes sericoranum*	92	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN256	TEN	9	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN260	TEN	10	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN272	TEN	-	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN280	TEN	9	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN284	TEN	-	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN290	TEN	-	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN305	TEN	9	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN310	TEN	9	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN320	TEN	-	16	*Olethreutes sericoranum*	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN334	TEN	9	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN340	TEN	10	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN351	TEN	10	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN354	TEN	10	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN355	TEN	9	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN362	TEN	-	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN366	TEN	10	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN367	TEN	-	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN370	TEN	9	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN372	TEN	9	16	*Olethreutes sericoranum*	92	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN380	TEN	9	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN396	TEN	9	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN400	TEN	10	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN405	TEN	9	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
TEN408	TEN	10	16	*Gypsonoma* sp.	93	*Homona mermerodes*	91	*A. subs.* E	*A. subs.* E	*A. subs.* E
MOR001	WM	11	17	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR009	WM	-	17	*Olethreutes sericoranum*	92	*Homona mermerodes*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR010	WM	11	17	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR029	WM	-	17	*Olethreutes malana*	93	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR030	WM	12	17	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR040	WM	11	17	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A

Appendix A3.5 (continued)

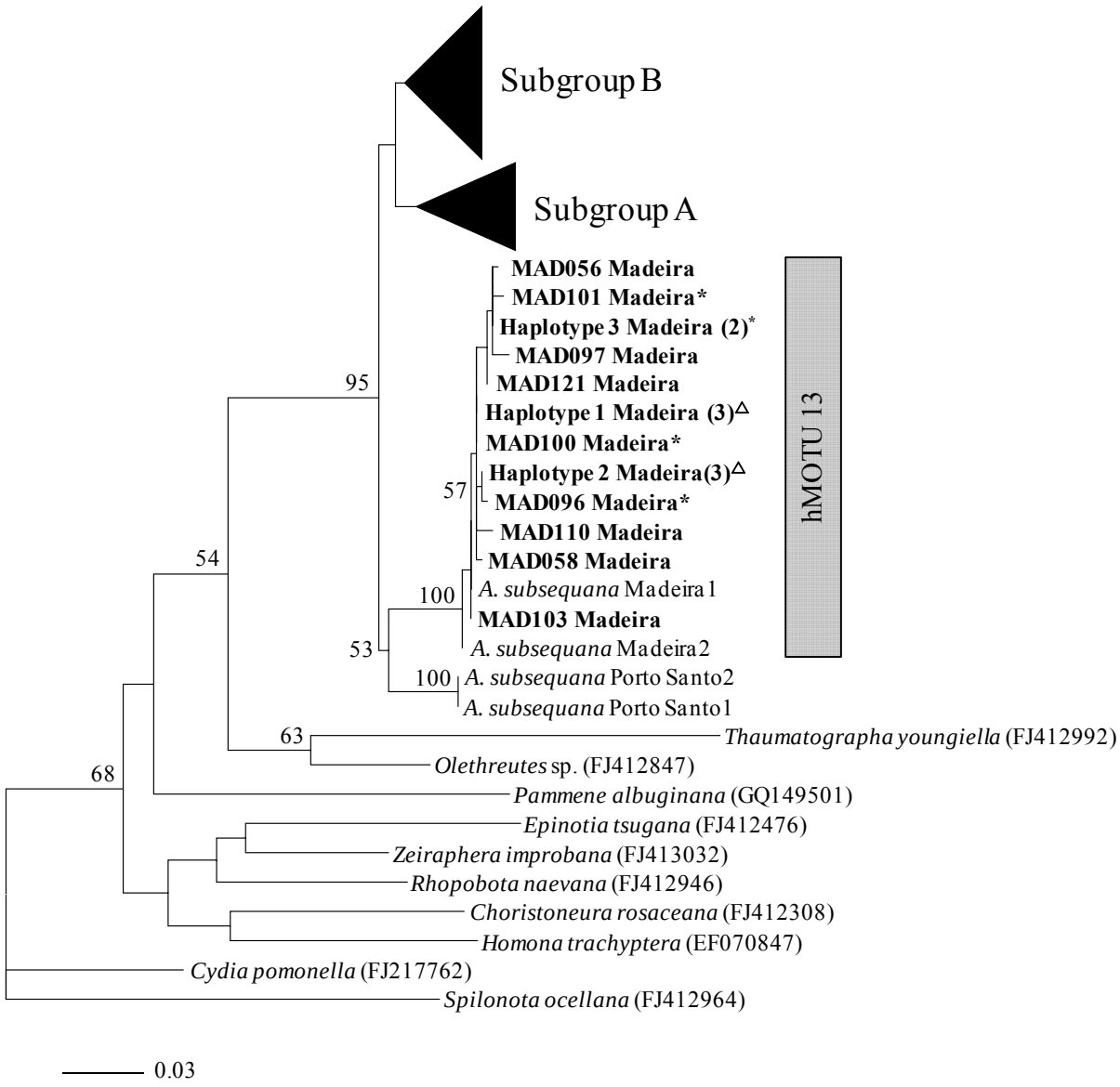
Code	Area	Haplotype	MOTU	BOLD		GenBank		NJ ID	ML ID	Final ID
				ID	%	ID	%			
MOR045	WM	11	17	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR046	WM	11	17	*Olethreutes malana*	92	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR050	WM	11	17	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR060	WM	11	17	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR070	WM	11	17	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR071	WM	13	17	*Olethreutes malana*	93	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR074	WM	11	17	*Olethreutes malana*	92	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR076	WM	11	17	*Olethreutes malana*	92	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR080	WM	13	17	*Olethreutes malana*	93	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR084	WM	11	17	*Olethreutes malana*	92	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR090	WM	-	17	*Olethreutes sericoranum*	92	*Homona* sp. near *salaconia*	90	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR093	WM	11	17	*Olethreutes malana*	92	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR098	WM	11	17	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR100	WM	-	17	*Olethreutes malana*	93	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR103	WM	-	17	*Olethreutes malana*	93	*Homona mermerodes*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR107	WM	14	17	*Olethreutes malana*	93	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR110	WM	11	17	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR115	WM	11	17	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR120	WM	-	17	*Olethreutes sericoranum*	92	*Homona* sp. near *salaconia*	90	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR140	WM	-	17	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR145	WM	11	17	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR150	WM	-	17	*Olethreutes malana*	92	*Homona* sp. near *salaconia*	90	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR160	WM	13	17	*Olethreutes malana*	93	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR180	WM	12	17	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR193	WM	-	17	*Olethreutes sericoranum*	92	*Homona mermerodes*	90	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR195	WM	11	17	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR200	WM	11	17	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR210	WM	11	17	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR235	WM	11	17	*Olethreutes malana*	92	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR249	WM	15	17	*Olethreutes sericoranum*	92	*Homona* sp. near *salaconia*	90	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR250	WM	13	17	*Olethreutes malana*	93	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR311	WM	-	17	*Olethreutes sericoranum*	92	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR321	WM	-	17	*Strepsicrates semicanella*	92	*Homona* sp. near *salaconia*	90	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR325	WM	14	17	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR330	WM	16	17	*Olethreutes malana*	93	*Homona* sp. near *salaconia*	90	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR360	WM	15	17	*Olethreutes sericoranum*	92	*Homona* sp. near *salaconia*	90	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR370	WM	16	17	*Olethreutes malana*	93	*Homona* sp. near *salaconia*	90	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR390	WM	11	17	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR397	WM	-	17	*Olethreutes malana*	92	*Homona* sp. near *salaconia*	90	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR409	WM	11	17	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR413	WM	13	17	*Olethreutes malana*	93	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR415	WM	15	17	*Olethreutes sericoranum*	92	*Homona* sp. near *salaconia*	90	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR417	WM	13	17	*Olethreutes malana*	93	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR418	WM	13	17	*Olethreutes malana*	93	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR432	WM	11	17	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR440	WM	-	17	*Olethreutes sericoranum*	92	*Homona* sp. near *salaconia*	90	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR445	WM	15	17	*Olethreutes sericoranum*	92	*Homona* sp. near *salaconia*	90	*A. subs.* A	*A. subs.* A	*A. subs.* A

Appendix A3.5 (continued)

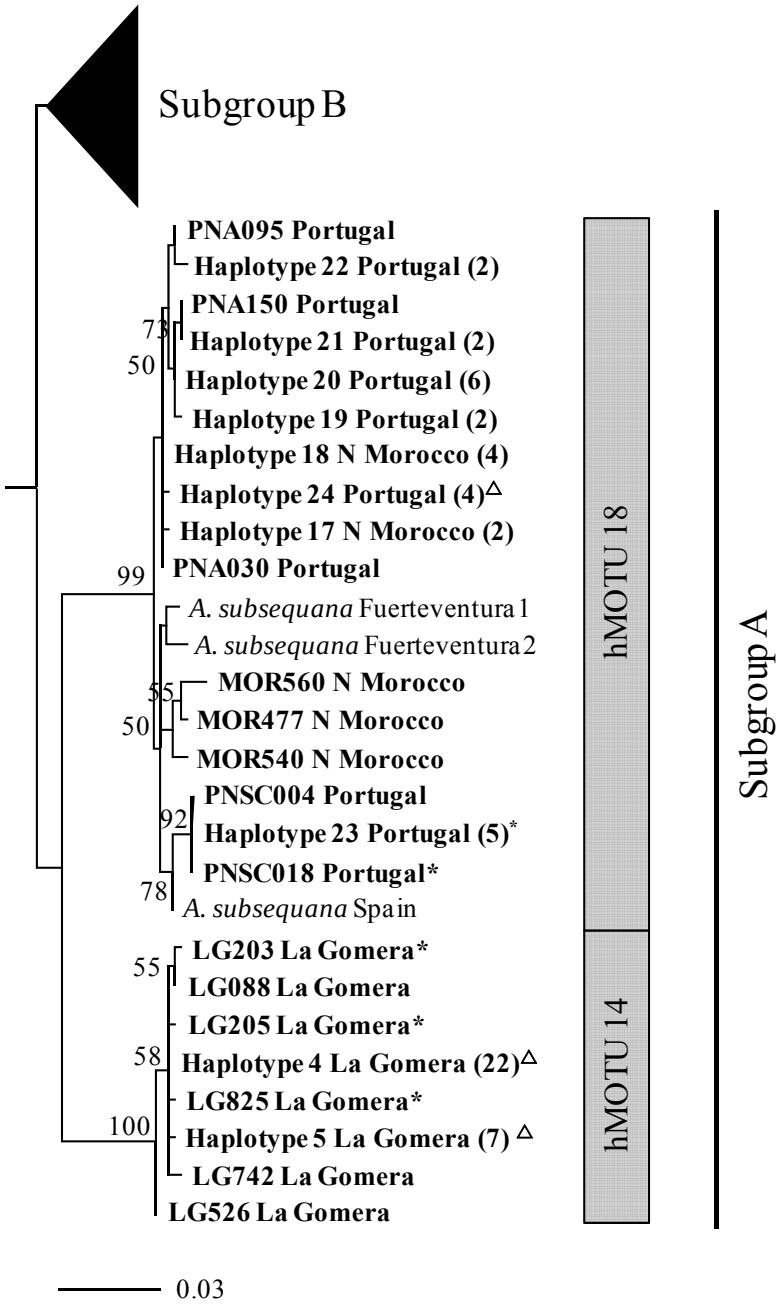
Code	Area	Haplotype	MOTU	BOLD		GenBank		NJ ID	ML ID	Final ID
				ID	%	ID	%			
MOR469	WM	11	17	*Olethreutes malana*	92	*Homona* sp. near *salaconia*	91	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR470	WM	15	17	*Olethreutes sericoranum*	92	*Homona* sp. near *salaconia*	90	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR476	WM	15	17	*Olethreutes sericoranum*	92	*Homona* sp. near *salaconia*	90	*A. subs.* A	*A. subs.* A	*A. subs.* A
MOR477	NM	-	18	*Olethreutes malana*	92	*Homona mermerodes*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
MOR500	NM	17	18	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
MOR526	NM	18	18	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
MOR530	NM	18	18	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
MOR534	NM	18	18	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
MOR535	NM	18	18	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
MOR540	NM	-	18	*Olethreutes malana*	92	*Homona mermerodes*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
MOR560	NM	-	18	*Apotomis albeolana*	92	*Homona mermerodes*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
MOR570	NM	17	18	*Olethreutes baccatanum*	93	*Homona* sp. near *salaconia*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
PNA001	POR	19	18	*Olethreutes sericoranum*	92	*Zeiraphera diniana*	91	*A. subs.* B	*A. subs.* B	*A. subs.* B
PNA010	POR	20	18	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
PNA020	POR	20	18	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
PNA030	POR	-	18	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
PNA040	POR	20	18	*Olethreutes malana*	92	*Homona* sp. near *salaconia*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
PNA052	POR	20	18	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
PNA060	POR	20	18	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
PNA082	POR	20	18	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
PNA095	POR	-	18	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
PNA100	POR	19	18	*Olethreutes malana*	92	*Zeiraphera diniana*	91	*A. subs.* B	*A. subs.* B	*A. subs.* B
PNA115	POR	21	18	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
PNA130	POR	21	18	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
PNA150	POR	-	18	*Olethreutes sericoranum*	93	*Zeiraphera diniana*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
PNSC001	POR	22	18	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
PNSC004	POR	-	18	*Olethreutes baccatanum*	92	*Zeiraphera diniana*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
PNSC005	POR	23	18	*Megalota crassana*	92	*Zeiraphera diniana*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
PNSC010	POR	24	18	*Olethreutes sericoranum*	92	*Homona* sp. near *salaconia*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
PNSC015	POR	23	18	*Megalota crassana*	92	*Zeiraphera diniana*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
PNSC017	POR	23	18	*Olethreutes baccatanum*	92	*Zeiraphera diniana*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
PNSC018	POR	-	18	*Olethreutes devotana*	92	*Zeiraphera diniana*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
PNSC021	POR	24	18	*Olethreutes malana*	92	*Homona* sp. near *salaconia*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
PNSC022	POR	24	18	*Olethreutes malana*	92	*Homona* sp. near *salaconia*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
PNSC023	POR	23	18	*Olethreutes baccatanum*	92	*Zeiraphera diniana*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
PNSC025	POR	22	18	*Olethreutes sericoranum*	93	*Homona* sp. near *salaconia*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
PNSC029	POR	24	18	*Olethreutes sericoranum*	92	*Homona* sp. near *salaconia*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B
PNSC030	POR	23	18	*Olethreutes baccatanum*	92	*Zeiraphera diniana*	90	*A. subs.* B	*A. subs.* B	*A. subs.* B

Area is the region where the specimens were collected (MAD – Madeira, LG – La Gomera, LP – La Palma, TEN – Tenerife, WM – Western Morocco, NM – Northern Morocco, POR – Portugal); see Fig. 5.1 for more details. MOTU is the molecular taxonomic unit, as defined by the percentage of sequence divergence given by the K2P model, and by the tree-based methods. % is the percentage of maximum sequence identity given by BOLD and BLAST. NJ ID and ML ID are the identifications given by the neighbor-joining tree and the maximum likelihood tree, respectively. A final identification (Final ID) is given incorporating results from the different approaches.

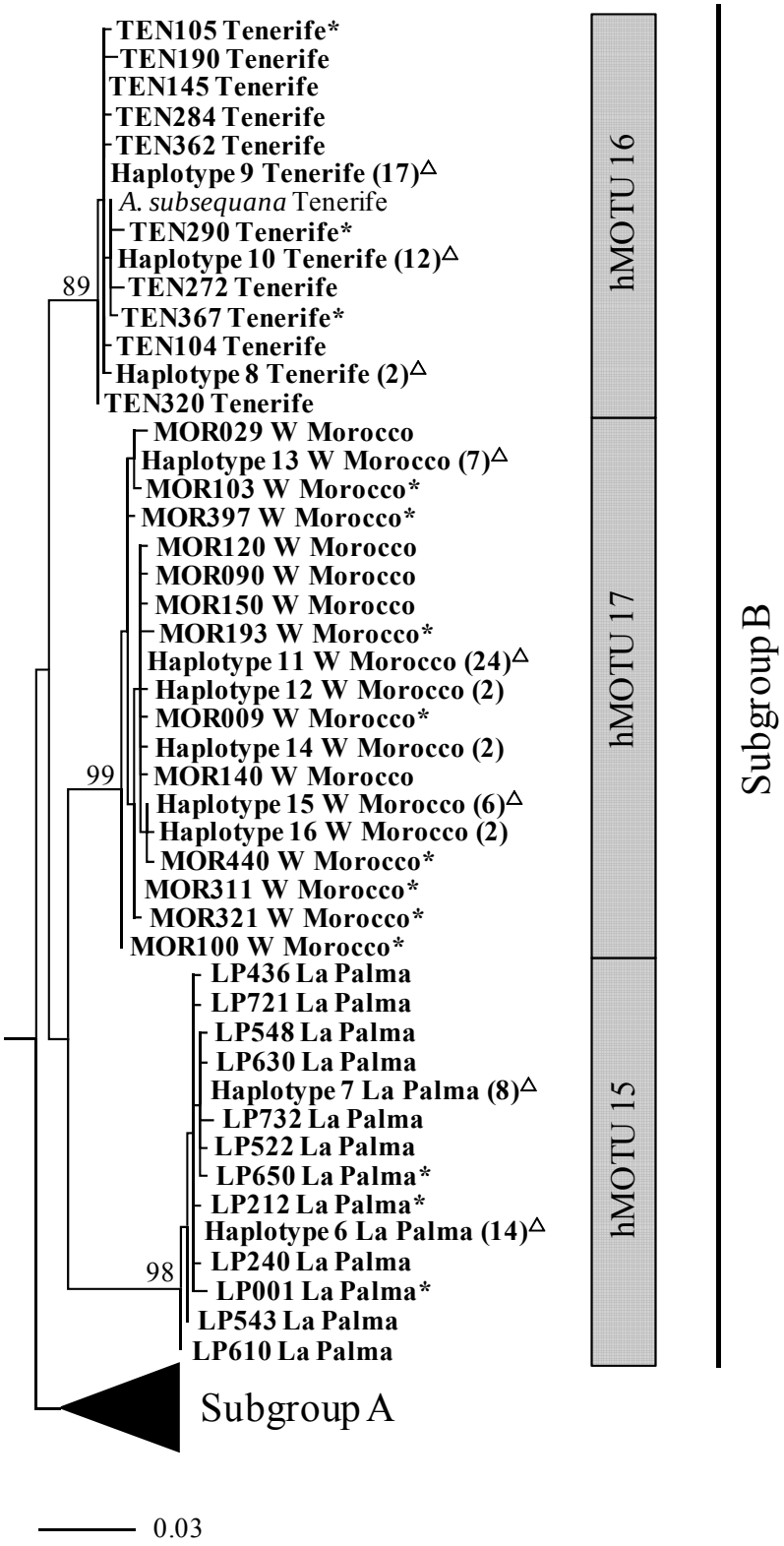
Appendix A3.6. Maximum likelihood tree of the tortricid barcode COI sequences (based on 236 specimens) under the GTR+I+Γ substitution model, showing the existence of six MOTUs from our study area (in grey). *indicates specimens that were parasitized; △indicates haplotypes with both parasitized and non-parasitized specimens. Some branches are collapsed into subgroups for ease of visualization. Sequences obtained from specimens collected in this study are represented in bold. Accession numbers of sequences obtained from GenBank are also represented. Numbers next to branches represent the bootstrap values obtained after 100 replications and values lower than 50 are not represented. Scale bar indicates 3% sequence divergence.



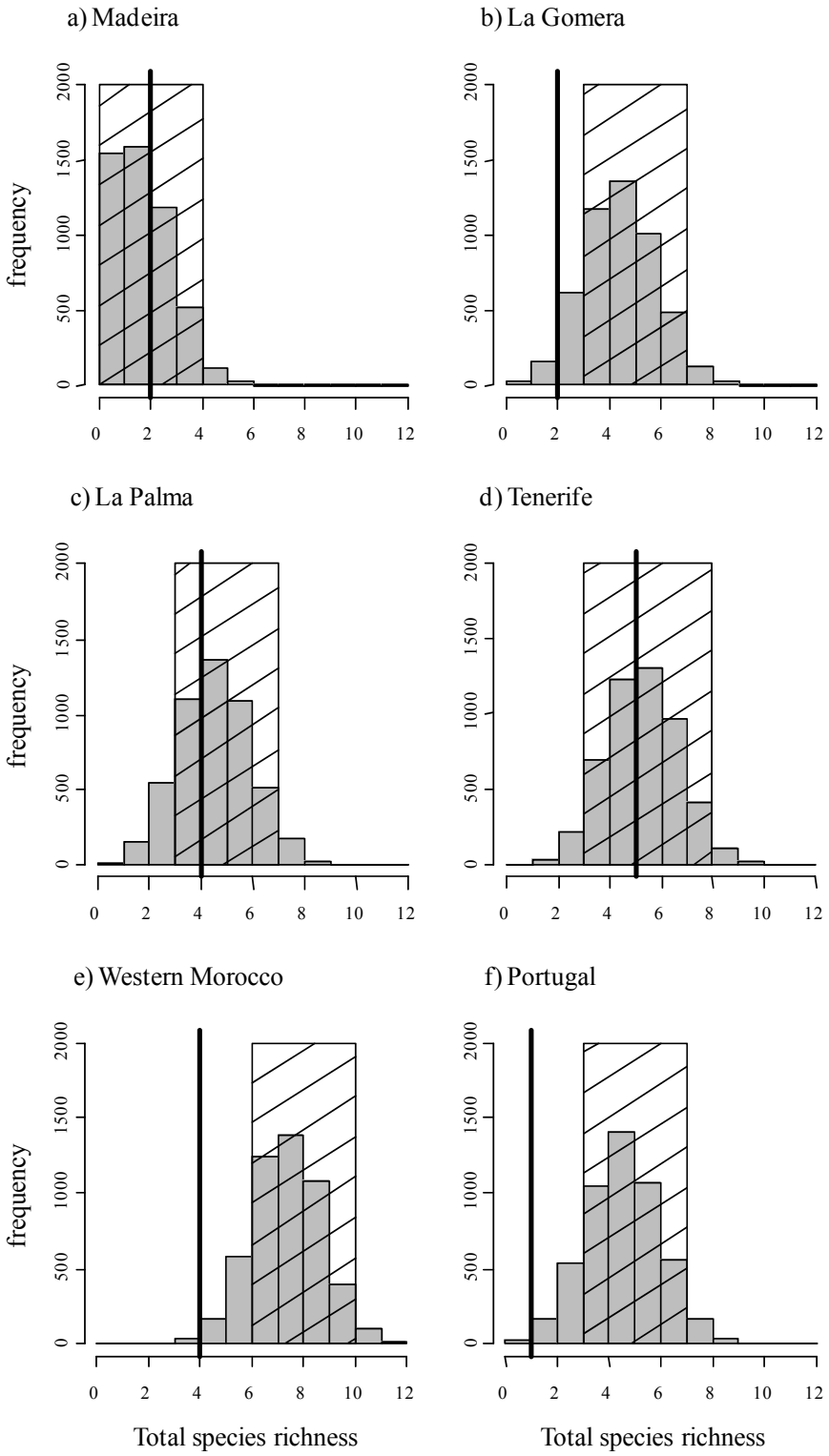
Appendix A3.6 (continued)



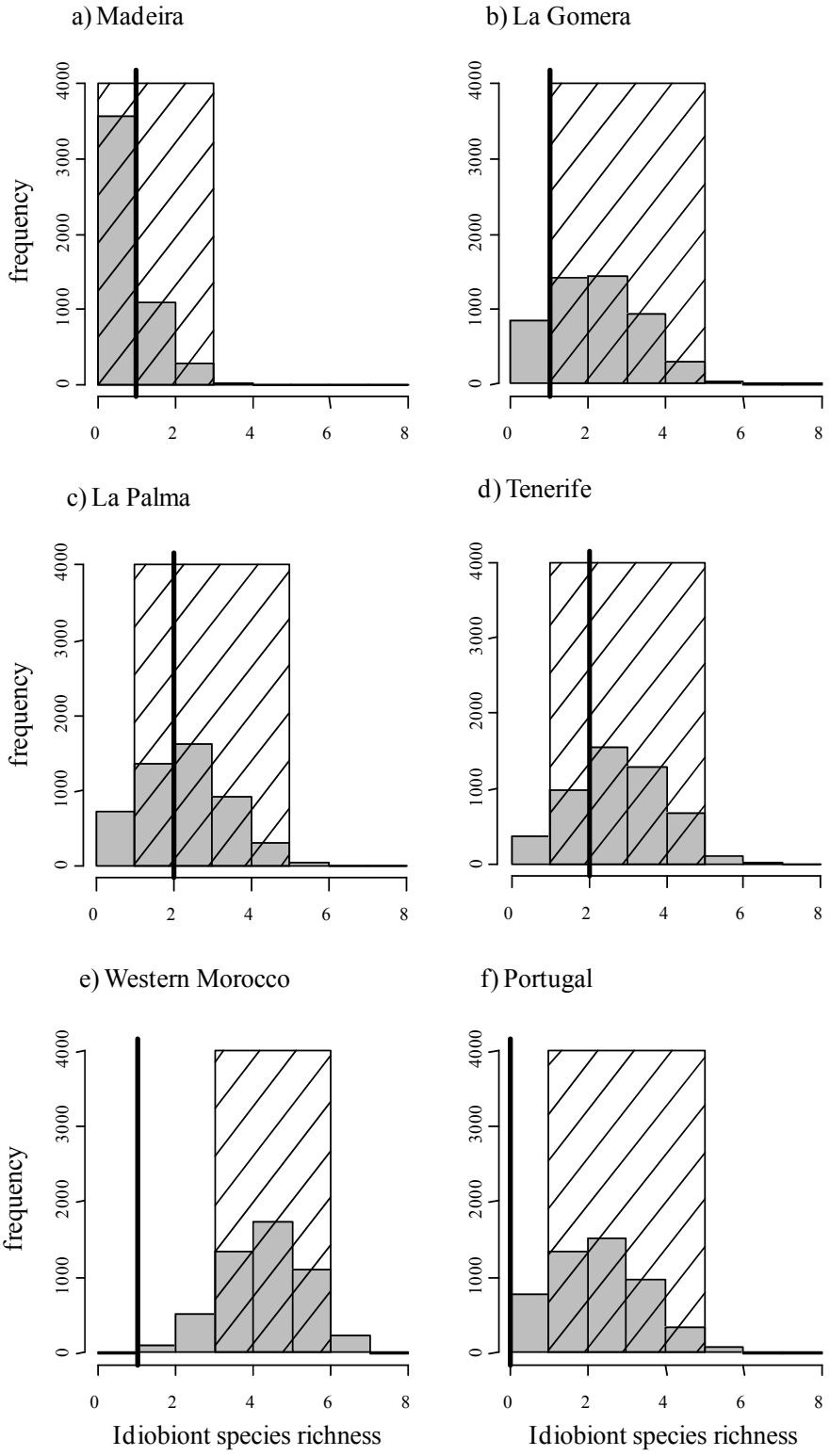
Appendix A3.6 (continued)



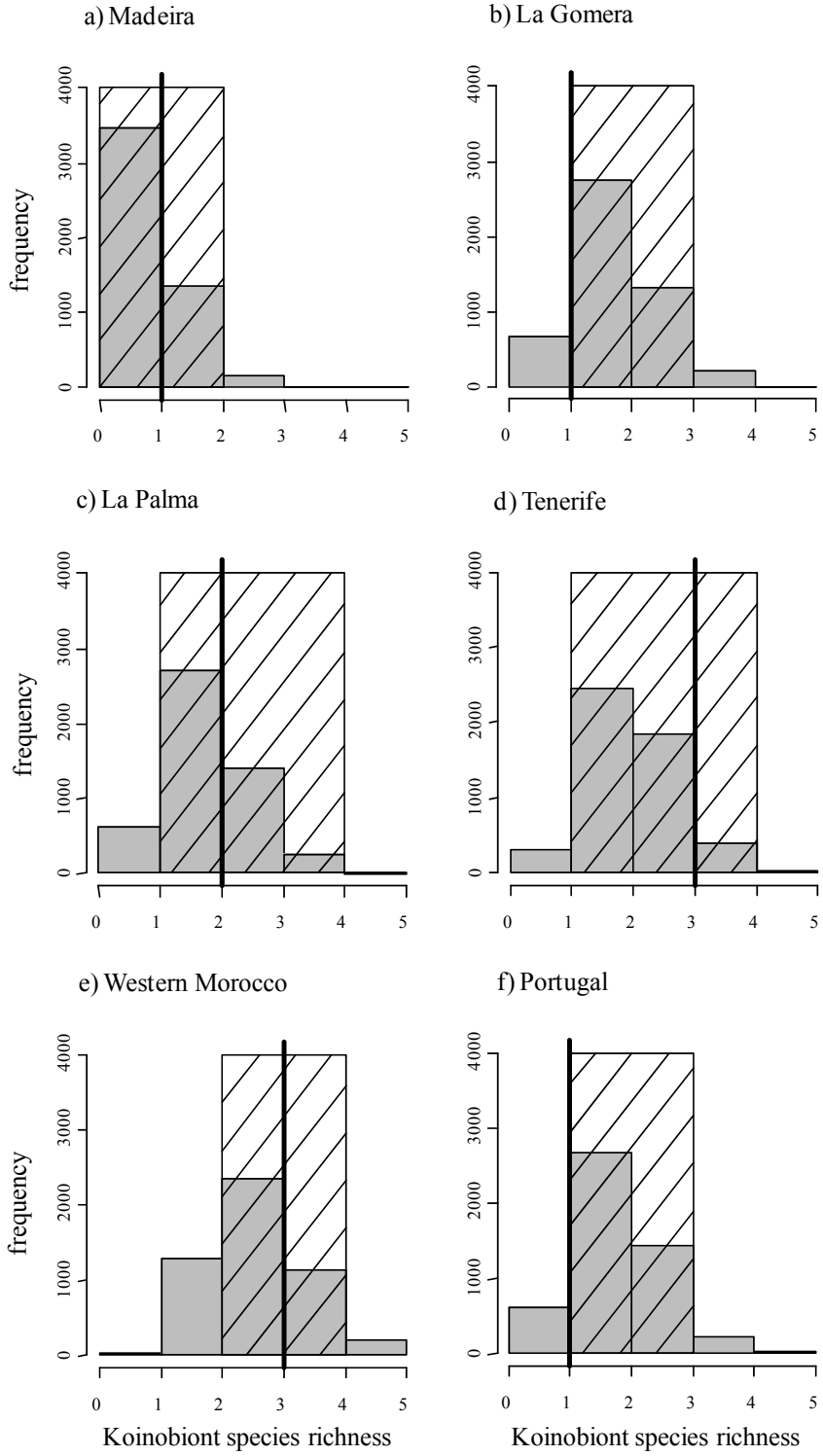
Appendix A4.1. Frequency distributions of the boostrapped values of total parasitoid species richness for each study area (Northern Morocco not shown). The continuous line represents the observed values, and the shaded area corresponds to the 90% confidence interval.



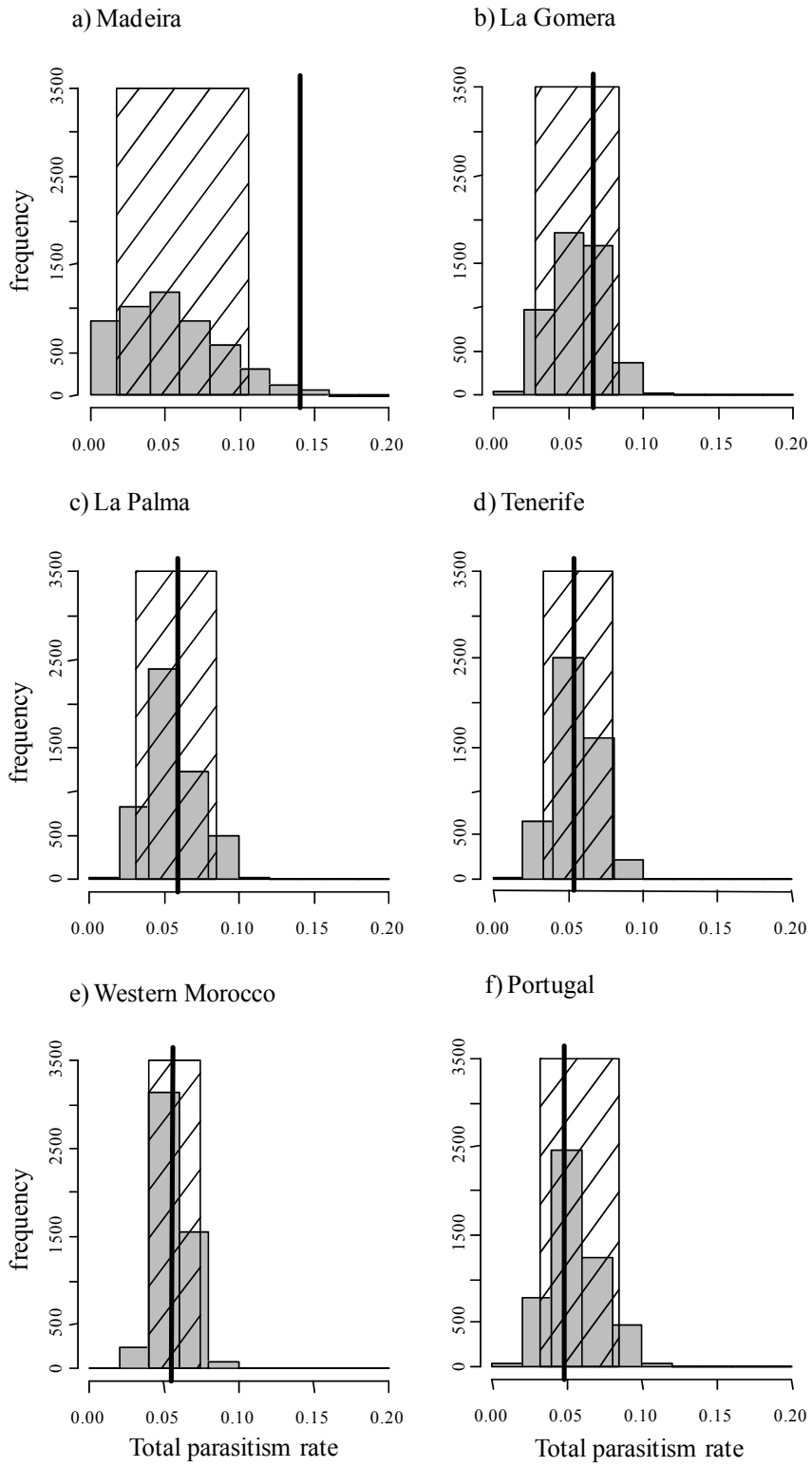
Appendix A4.2. Frequency distributions of the boostrapped values of idiobiont species richness for each study area (Northern Morocco not shown). The continuous line represents the observed values, and the shaded area corresponds to the 90% confidence interval.



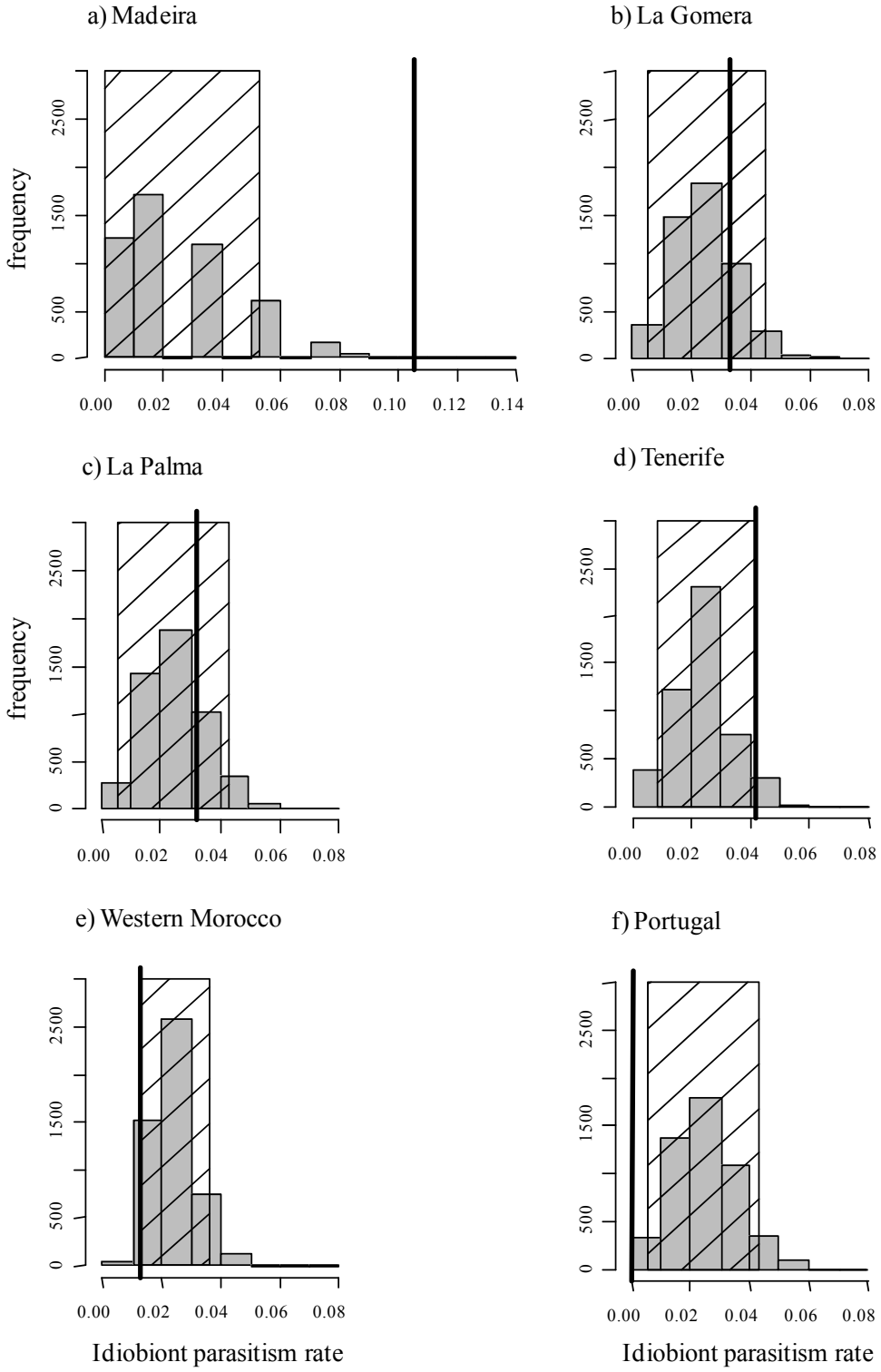
Appendix A4.3. Frequency distributions of the boostrapped values of koinobiont species richness for each study area (Northern Morocco not shown). The continuous line represents the observed values, and the shaded area corresponds to the 90% confidence interval.



Appendix A4.4. Frequency distributions of the boostrapped values of total parasitism rate for each study area (Northern Morocco not shown). The continuous line represents the observed values, and the shaded area corresponds to the 90% confidence interval.



Appendix A4.5. Frequency distributions of the boostrapped values of idiobiont parasitism rate for each study area (Northern Morocco not shown). The continuous line represents the observed values, and the shaded area corresponds to the 90% confidence interval.



Appendix A4.6. Frequency distributions of the boostrapped values of koinobiont parasitism rate for each study area (Northern Morocco not shown). The continuous line represents the observed values, and the shaded area corresponds to the 90% confidence interval.