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thesis abstract

Ecology and biogeography of island parasitoid faunas

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Abstract. Species on islands tend to use a wider range of resources than their mainland counterparts. In this thesis I investigated whether island parasitoid communities have proportionally more idiobiont species (which tend to have a wider host range; i.e. are more generalist) than their mainland source, and which factors determine island community structure. These questions were approached using data on the distribution of Ichneumonoidea species worldwide and data from a survey conducted in the Macaronesian islands and mainland. 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 than continental areas, and the species pool for colonization is the most important determinant of island community structure. Specimens collected in the Macaronesian region were tentatively identified 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.

Keywords: community structure, DNA barcoding, host-parasitoid interactions, host range, island biogeography, island species–area relationship, Macaronesia, species pool

Islands constitute natural laboratories for the study of evolutionary and ecological processes because of their discrete and isolated nature, small size and simplified biotas. Island faunas, especially those of oceanic islands, tend to be species-poor and disharmonic, 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 (e.g. some trophic guilds can be absent from island communities). The phenomenon of ecological release, typical in many island populations, occurs when a species colonizing an island encounters a new environment in which competitors and/or predators are missing (Whittaker and Fernández-Palacios 2007). One of the consequences of this process is the expansion to empty or inviable niche space, leading to niche expansion and/or niche shifts, with species from island assemblages often using a wider range of resources than their counterparts

from the source mainland. Therefore it is not surprising that many oceanic islands have a high representation of generalist species when compared to the mainland (e.g. Olesen and Valido 2003). In addition, some evidence suggests that generalist species may simply have an *a priori* advantage during the colonization process (Piechnik et al. 2008).

Parasitoids are generally defined as insects whose larvae develop to adulthood by feeding in or on the body of an arthropod host, eventually causing its death (Quicke 1997; see more details of their biology in Santos & Quicke 2011). Parasitoids are usually divided into two different groups that reflect different life-history strategies: koinobionts, which allow the host to continue its development after oviposition of the parasitoid, and idiobionts, which do not (Askew and Shaw 1986). Many life-history traits appear to be correlated with this dichotomy (e.g. Hawkins 1994, Quicke 1997; see Table 1). Host range, i.e. the group of

Table 1. Life-history traits associated with the dichotomy idiobionts vs. koinobionts. However, there is a wide spectrum filled between idealized idiobiont and koinobiont strategies, and there are exceptions to virtually any generalization about them.

Idiobionts	Koinobionts
Ectoparasitism	Endoparasitism
Permanently paralyse their hosts	Do not paralyse their hosts (or only temporarily)
Do not allow the host to continue its development	Allow the host to continue its development
Little interaction with their hosts' immune systems	Interact with their hosts' immune systems
Attack a wider variety of hosts	Attack a more restricted number of hosts
Host generalists	Host specialists
Short larval development time	Long larval development time
Longer adult life	Short adult life
Tend to attack later host stages (except for the eggs)	Hosts are in relatively young developmental stages
Hosts live in concealed situations	Hosts are exposed
Synovigenic (produce few, large eggs that develop over the life of the adult wasp)	Pro-ovigenic (produce many small eggs, that are all fully developed the moment the wasp hatches)

potential hosts that a parasitoid species can attack successfully after exhibiting a certain pattern of searching behavior that allows it to find hosts regularly (Shaw 1994), is also related to this dichotomy, with idiobionts typically having a wider host range and koinobionts being considered more specialist (e.g. Askew and Shaw 1986, Hawkins 1994, Shaw 1994). This pattern is largely due to the fact that koinobionts interact more intimately with their hosts' immune systems, while idiobionts either do not have to deal at all with their hosts' immune system or attack hosts with reduced immunological systems, such as eggs or pupae (e.g. Shaw 1994, Quicke 1997).

Despite their ecological importance in most terrestrial systems (LaSalle and Gauld 1993), very little is known about parasitoids' diversity, distribution and biology, particularly on islands. Regarding the community assembly of island parasitoids, one could expect that island faunas are biased towards generalist species (i.e. idiobionts), since hosts on islands may be unusual or novel compared with those on the mainland. However, the few previous studies that looked into changes in host ranges at large geographical scales gave contradictory information; some showed that generalists are better in adapting to new habitats and new hosts (e.g. Cornell and Hawkins 1993), while others indicated that host range cannot be

predicted from biological or ecological traits of the parasitoids (e.g. Hawkins and Marino 1997). One study even found that the early-phase parasitoid colonists of Anak Krakatau island were dominated by taxa that are koinobionts of Lepidoptera, although no comparison with mainland communities was attempted (Maetô and Thornton 1993).

The general aim of my PhD thesis was to study the geographic patterns of generalism and specialism in island parasitoid faunas, with the main hypothesis being that island parasitoid faunas are biased towards idiobiont species when compared to the mainland faunas. This hypothesis was analysed using an interdisciplinary approach that integrated two different geographical scales: a global scale using data on the distribution of Ichneumonidae (Hymenoptera) species worldwide, and a regional scale using data collected in some islands and continental areas of the Macaronesian region.

At the *global scale*, we evaluated whether island parasitoid faunas are biased towards idiobiont species when compared with the corresponding species pool, and examined which factors, of those usually thought to control the assembly of island faunas, also have an effect on the ratio between idiobionts and koinobionts on the islands. To investigate this we used a published database on the distribution of

Braconidae and Ichneumonidae worldwide (Taxapad; Yu et al. 2005). In this database the information on parasitoid inventories is often presented for archipelagos rather than for single islands. Therefore, we first examined whether there is a consistency in the processes building up the biotas of single islands and entire archipelagos, assessing whether archipelagos follow the same species–area relationship as their constituent islands (Santos et al. 2010a). Here we found 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. 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 non-nested systems the observed archipelagic species richness should be higher than that predicted by the ISAR.

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 (Hortal et al. 2007). These data are not free from errors; it is well known that our knowledge of the geographical distribution of biodiversity is, in general, taxonomically and geographically biased (e.g. Jones et al. 2009). Therefore, prior to further analysis it is advisable to evaluate data quality,

and assess the consistency of the results among different kinds of territorial units (that can differ in size and nature). Since the database we used is a compilation of all available knowledge on the distribution of the studied families, it was expected that the quality and completeness of the data on Braconidae and Ichneumonidae faunas is also uneven. Therefore, we evaluated the biases and problems to ensure that the data used included comparable units with no major shortfalls. To achieve this, we developed a simple scoring method that did not rely on measures of sampling effort (e.g. number of survey records, individuals or traps), and that would allow assessment of which islands have comparable inventories. The protocol we proposed 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 the species–area relationship are unlikely to have been 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 (see Santos et al. 2010b).

Finally, the islands with comparable inventories were used to examine whether island faunas are biased towards idiobionts, and to evaluate the relationships between different environmental, physical and regional factors and the relative proportions of idiobionts and koinobionts in both Braconidae and Ichneumonidae. All species were classified as either idiobionts or koinobionts according to the known biology of the subfamilies they belong to. This trait is well conserved at this taxonomic level (Askew & Shaw 1986, Gauld 1988) and so this classification gives a fairly good estimate of host range (Hawkins et al. 1992). Results indicated that, for pooled data, islands have a higher proportion of idiobionts than the mainland. This does not seem to be due to the recurrent presence of certain subfamilies on is-

lands, as of the six subfamilies that are more represented on islands (i.e. that have more than 25% of their species present on islands) only two include idiobiont species. However, in pairwise comparisons most islands have a similar proportion of idiobionts to that found in the adjacent mainland species pool, and the composition of this colonization 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 (measured as the proportion between idiobiont and koinobiont species), which may be 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. Islands of the Indomalayan region are particularly dominated by idiobiont species, which might be due to the fact that these islands are home to large tropical rainforests¹, where plant architectural complexity (particularly of trees) is probably responsible for increasing idiobiont species richness (e.g. Hawkins et al. 1990, Hawkins 1994). Such results highlight the complexity of factors shaping the diversity and structure of parasitoid communities (Santos et al. 2011a).

At the *regional scale*, we studied how the diversity, parasitism rates 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, we studied the community of parasitoids attacking the tortricid moth *Acroclita subsequana* that feeds on spurges (*Euphorbia* spp., Euphorbiaceae). Traditionally, host–parasitoid interactions are ascertained through rearing, which is labour intensive, time consuming and requires experience. Moreover, this technique is very difficult to apply when studying geographical variations of host–parasitoid interactions at large scales, as it would require several field stations and the support of a large team. To overcome this problem, we investigated geographical variations in host–parasitoid interactions

using a new protocol based on host dissection and DNA barcoding (Santos et al. 2011b). Although this protocol is somewhat time consuming and requires the use of a fully equipped laboratory, it nevertheless has several advantages when compared with standard rearing methods: (i) it does not require a taxonomic specialist for identifications; (ii) a small team of researchers, or even a single person (as in the case of this thesis) is sufficient; and (iii) it 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 because available sequence databases are far from complete, and are not yet reliable enough to be used for the identification of poorly studied and hyperdiverse taxa such as parasitic Hymenoptera and Microlepidoptera. Still, depending on the goal of the particular research project, this might not be a problem because MOTUs can be used as surrogate units of diversity, enabling us to produce parasitoid food-webs and quantify host–parasitoid interactions.

Once all parasitoids found were assigned to MOTUs, we tested whether species richness and parasitism rates differ between islands and mainland, and whether island parasitoid faunas are biased towards idiobiont species (Santos et al. 2011c). Once again, species were classified as either idiobionts or koinobionts in accordance to the known biology on the subfamilies they belong to. 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 from a random model, with communities being dominated by koinobiont species; on the other hand, island parasitoid communities were dominated by idiobionts. Also, islands had higher parasitism rates by idiobionts than expected from a random model, and mainland areas showed the highest koinobi-

¹ See the global land-cover map at http://eoimages.gsfc.nasa.gov/images/news/NasaNews/ReleaseImages/LCC/Images/lcc_global_2048.jpg

ont parasitism rates. These results suggest that island parasitoid communities are biased in favour of idiobionts (that tend to be more generalist), when compared with mainland communities. The processes behind such patterns still need to be explored, but they might be related to (i) the possibility that generalist parasitoids are better dispersers; (ii) the expectation that they are less constrained by “sequential dependencies” (Holt et al. 1999), not being dependent on the presence of a particular resource; and (iii) the likelihood that island parasitoids have fewer competitors, favouring generalists.

There are obvious differences in the nature of the data 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 the available parasitoid species checklists. On the other hand, data from the regional scale originated from a particular, environmentally quite homogeneous area, and from the community of parasitoids associated with just one host system. Nevertheless, results from both scales indicate a bias towards idiobiont species on islands. At the global scale, pooled island parasitoid faunas had comparatively more idiobiont species than the entire pool of mainland areas, while at the regional scale, island hosts suffered higher attack rates by generalist parasitoids. However, in the global analyses only a small number of islands departed significantly from the structure of their colonization pool. In contrast, the structure of the island parasitoid communities studied at the regional scale differs from that of its colonization pool. A hypothesis linking together the results from both scales is that the ecological processes that determine island community structure regionally scale up and result in higher proportions of generalists at larger scales. Therefore, differences in the results from the two approaches explored here may be due to differences in scale. Following this argument, one could consider that factors acting at the biogeographical scale mask the effect of the ecological processes that lead to a general trend towards higher parasitoid generalism on islands, making the trend less apparent worldwide. Here, the structure of the species pool

would be the main determinant of the structure of island communities worldwide, but other factors would also play a role in determining island parasitoid faunas – causing some island parasitoid communities to deviate from their overall tendency to higher proportions of generalists (Santos & Quicke 2011).

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References

- Askew, R.R. & Shaw, M.R. (1986) Parasitoid communities: their size, structure and development. In: *Insect parasitoids* (ed. by J. Waage and D. Greathead), pp.225–264. Academic Press, London.
- Cornell, H.V. & Hawkins, B.A. (1993) Accumulation of native parasitoid species on introduced herbivores: a comparison of hosts as natives and hosts as invaders. *The American Naturalist*, 141, 847–865.
- Gauld, I.D. (1988) Evolutionary patterns of host utilization by ichneumonoid parasitoids (Hymenoptera: Ichneumonidae and Braconidae). *Biological Journal of the Linnean Society*, 35, 351–377.
- Hawkins, B.A. (1994) *Pattern and process in host-parasitoid interactions*. Cambridge University Press, Cambridge.
- Hawkins, B.A. & Marino, P.C. (1997) The colonization of native phytophagous insects in North America by exotic parasitoids. *Oecologia*, 112, 556–571.
- Hawkins, B.A., Askew, R.R. & Shaw MR (1990) Influences of host feeding-niche and foodplant type on generalist and specialist parasitoids. *Ecological Entomology* 15, 275–280.
- Hawkins, B.A., Shaw, M.R. & Askew, R.R. (1992) Relations among assemblage size, host specialization, and climatic variability in North-American parasitoid communities. *American Naturalist*, 139, 58–79.

- Holt, R.D., Lawton, J.H., Polis, G.A. & Martinez, N.D. (1999) Trophic rank and the species–area relationship. *Ecology*, 80, 1495–1504.
- Hortal, J., Lobo, J.M. & Jiménez-Valverde, A. (2007) Limitations of biodiversity databases: case study on seed-plant diversity in Tenerife, Canary Islands. *Conservation Biology*, 21, 853–863.
- Jones, O.R., Purvis, A., Baumgart, E. & Quicke, D.L.J. (2009) Using taxonomic revision data to estimate the geographic and taxonomic distribution of undescribed species richness in the Braconidae (Hymenoptera: Ichneumonoidea). *Insect Conservation and Diversity*, 2, 204–212.
- LaSalle, J. & Gauld, I.D. (1993) Hymenoptera and biodiversity. CAB International, Wallingford.
- Maetô, K. & Thornton, I.W.B. (1993) A preliminary appraisal of the braconid (Hymenoptera) fauna of the Krakatau Islands, Indonesia, in 1984–1986, with comments on the colonizing abilities of parasitoid modes. *Japanese Journal of Entomology*, 61, 787–801.
- Olesen, J.M. & Valido, A. (2003) Lizards as pollinators and seed dispersers: an island phenomenon. *Trends in Ecology and Evolution*, 18, 177–181.
- Piechnik, D.A., Lawler, S.P. & Martinez, N.D. (2008) Food-web assembly during a classic biogeographic study: species’ “trophic breadth” corresponds to colonization order. *Oikos*, 117, 665–674.
- Quicke DLJ (1997) Parasitic wasps. Chapman and Hall, London.
- Santos, A.M.C., Whittaker, R.J., Triantis, K.A., Borges, P.A.V., Jones, O.R., Quicke, D.L.J. & Hortal, J. (2010a) Are species–area relationships from entire archipelagos congruent with those of their constituent islands? *Global Ecology & Biogeography*, 19, 527–540.
- Santos, A.M.C., Jones, O.R., Quicke, D.L.J. & Hortal, J. (2010b) Assessing the reliability of biodiversity databases: identifying evenly inventoried island parasitoid faunas (Hymenoptera: Ichneumonoidea) worldwide. *Insect Conservation and Diversity*, 3, 72–82.
- Santos, A.M.C. & Quicke, D.L.J. (2011) Large-scale diversity patterns of parasitoid insects. *Entomological Science*, 14, 371–382.
- Santos, A.M.C., Quicke, D.L.J., Borges, P.A.V. & Hortal, J. (2011a) Species pool structure determines the degree of generalism of island parasitoid faunas. *Journal of Biogeography*, 38, 1657–1667.
- Santos, A.M.C., Besnard, G. & Quicke, D.L.J. (2011b) Applying DNA barcoding for the study of geographical variation in host–parasitoid interactions. *Molecular Ecology Resources*, 11, 46–59.
- Santos, A.M.C., Fontaine, C., Quicke, D.L.J., Borges, P.A.V. & Hortal, J. (2011c) Are island and mainland biotas different? Richness and level of generalism in parasitoids of a microlepidopteran in Macaronesia. *Oikos*, 120, 1256–1262.
- Shaw, M.R. (1994) Parasitoid host range. In: *Parasitoid Community Ecology* (ed. By B.A. & W. Sheenan), pp. 111–144. Oxford University Press, New York.
- Whittaker, R.J. & Fernández-Palacios, J.M. (2007) *Island biogeography: ecology, evolution, and conservation*. Oxford University Press, Oxford.
- Yu, D.S., van Achterberg, K.B. & Horstmann, K.I. (2005) *World Ichneumonoidea 2004: taxonomy, biology, morphology and distribution*. CD-Rom. Taxapad, Vancouver, Canada.

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