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ORIGINAL ARTICLE

Species pool structure determines the level of generalism of island parasitoid faunas

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ABSTRACT

Aim To examine whether island parasitoid faunas are biased towards generalists when compared with the mainland and their species pool, and to evaluate the effects of climate, island characteristics 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.

Location Seventy-three archipelagos distributed world-wide.

Methods We used data on the distribution and biology obtained from a digital catalogue and several literature sources. We related level of generalism, measured as the ratio between the number of idiobiont and koinobiont species, to climatic, physiographic and regional factors using generalized linear models. We compared models by means of Akaike weighting, and evaluated the spatial structure of their residuals. We used partial regressions to determine whether the final models account for all latitudinal structure in the level of generalism.

Results Islands host comparatively more idiobionts than continental areas. 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 is their source pool. This effect is stronger for ichneumonids, where generalism is higher in the Indomalayan region, arguably due to the higher diversity of endophytic hosts in its large rain forests.

Main conclusions The level of generalism of island parasitoid faunas is largely constrained by regional factors, namely by the structure of the species pool, which emphasizes the importance of including regional processes in our understanding of the functioning of ecological communities. The fact that generalist species are more predominant in islands with a large cover of rain forests pinpoints the importance of the indirect effects of ecological requirements on community structure, highlighting the complex nature of geographical gradients of diversity.

Keywords

Community structure, Ichneumonoidea, idiobionts, Indomalayan region, island biogeography, koinobionts, latitudinal gradient, parasitoids, species pool, trophic width.

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, which determine the characteristics and evolutionary history of the species present in the regional pool (e.g. Ricklefs, 1987, 2007; Rahbek & Graves, 2001; Hawkins *et al.*, 2003; Hortal *et al.*, 2008). 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

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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., Rodríguez *et al.*, 2006; Schemske *et al.*, 2009). This is especially true for invertebrates, 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, 1993). Surprisingly, several studies have suggested that the species richness of some parasitoid groups does not increase towards the tropics (Owen & Owen, 1974; Janzen, 1981; Gauld, 1986; Hawkins *et al.*, 1992; but see Noyes, 1989; Askew, 1990), contrary to the geographical gradients observed in many other taxa (e.g. Stevens, 1989; Hillebrand, 2004). However, the possibility that these findings are 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 (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 in island parasitoid communities. Island biotas are known to be species poor and disharmonic when compared with the mainland (Whittaker & Fernández-Palacios, 2007). In particular, island assemblages usually host higher numbers of generalist species than their mainland counterparts (e.g. Diamond, 1970; Olesen *et al.*, 2002; Olesen & Valido, 2003; Scott *et al.*, 2003; Ribeiro *et al.*, 2005). In many islands, especially young ones, the low species richness, together with the paucity of competitors, predators, parasitoids or pathogens, may cause the ecological space not to be fully saturated. Although competition may sometimes play an important role in the evolution of island populations (see, e.g., Losos, 1992), many times the colonizing species are subject to distinct 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). Alternatively, the predominance of generalist species on islands may also be due to an a priori advantage during the colonization process, as they are not as constrained by the presence of their resources as are specialists (e.g. Holt *et al.*, 1999; Piechnik *et al.*, 2008). Also, they tend to be less prone to extinction because their occurrence is less limited by area and they are unlikely to be affected by temporal variations in the availability of particular hosts (Holt, 2010). Specialist parasitoids colonizing islands are also likely to be affected by these processes, either being forced to use unusual or novel hosts due to a lack of preferred ones, or facing comparatively higher extinction rates due to the low densities of their particular hosts. Therefore, it can be expected that island parasitoid faunas include a comparatively high proportion of generalist species (i.e. idiobionts) when compared with their mainland counterparts.

Here we examine whether island parasitoid communities are biased towards generalist species in comparison with the mainland and their adjacent species pool. To do so, we use a database on the taxonomy and world-wide 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 (isolation, area, environmental conditions and composition of the species pool) also affect the ratio between idiobionts and koinobionts. Our results confirm that there are proportionally more generalist parasitoids on islands than on the mainland, but also show that the species pool and some environmental effects determine the patterns of island generalism world-wide.

MATERIALS AND METHODS

Data origin

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). These two families are adequate model groups for use in analyses of global patterns in parasitoid biology because they include a large number of species (over 59,000 described species and over 100,000 estimated species world-wide; Gauld, 1991; Yu *et al.*, 2005; Jones *et al.*, 2009), almost all their species are parasitic, they have a world-wide distribution, their biology is fairly well known at the subfamily level or lower and they have a balanced proportion of idiobionts and koinobionts (0.487 for the whole superfamily). Island species checklists in Taxapad are organized by archipelagos, single-island nations or other administrative units. Following the results of Santos *et al.* (2010a), 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. As the data in Taxapad may provide incomplete inventories for some areas, Santos *et al.* (2010b) set out to identify the islands with comparable inventories. Only 53 and 70 islands have comparable inventories of species of

Braconidae and Ichneumonidae, respectively, and these data were therefore used for the present analyses.

We examined several ways of identifying the territories that constitute 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 1000 km that included both islands and mainland provided the most realistic description, according to the geographical location of most islands. This definition ensured that, for most archipelagos, the source pool includes the most likely sources of immigrants, while maintaining comparability between the pools of different archipelagos. We thus defined the species pool for each island as the species found in all territories occurring within 1000 km of each island. If an island was located more than 1000 km from the mainland (e.g. Hawaii), we also included the species from the most likely source mainland area (see Table S1 in Appendix S1 in the Supporting Information).

Species from both islands and species pools were classified as either idiobionts or koinobionts, and also as ectoparasitoids or endoparasitoids (see Tables S2 & S3 in Appendix S1). This classification was based on the life-history data available from a number of literature sources, and was also reviewed by D.L.J.Q., M.R. Shaw (honorary research fellow of the National Museums of Scotland) and G.R. Broad (Natural History Museum, London). 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). For the exceptions to this rule, this classification was applied to tribe or genus level depending on data availability. Introduced species, subspecies and synonyms were excluded from all analyses.

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 the *I*/*K* ratio) and between the number of ectoparasitoid and endoparasitoid species. The values of these two ratios per island are 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 (Askew & Shaw, 1986), we used only the *I*/*K* ratio to describe the level of generalism in all subsequent analyses. The higher the value of this ratio, the higher the level of generalism of the parasitoid community.

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: (1) whether an 'island' was composed of only one island or was an archipelago (*Archipelago*); (2) 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), or continental shelf; (3) island area (*Area*); (4) highest elevation, measured from sea level (*Elev*); (5) distance (in km) to the closest larger territory (either island or mainland; *DistArea*); (6) distance (in km) to the closest mainland (*DistMainl*). *Area* was obtained as in Santos *et al.* (2010b), *Elev* 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 where the island is located (*Region*), and three continuous variables: island species richness (*RichIsl*); the level of endemism of the island faunas (*EndIsl*), a measure of how distinct the island fauna is from its species pool, measured as log(proportion of species of an island that are not present in its species pool + 1); and the level of generalism (i.e. the *I*/*K* ratio) of its species pool (*SpeciesPool*). The limits of the biogeographic realms followed the zoogeographic regions as defined by Cox (2001), except for northern Africa, where the limit of the Palaearctic was assumed to be below the Sahara Desert. Finally, we used the absolute value of latitude (*AbsLat*) to evaluate the potential existence of a latitudinal structure in the response variable.

Analyses

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 with their species pool using a Wilcoxon matched pairs test.

The effects of the environmental, physical and regional predictors on the *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; for clarity, herein we will refer to the transformed response variable as 'log *I*/*K* ratio'. Preliminary analyses using other transformations (log *I*/*K* ratio + 1, and arcsin of the proportion of generalists) gave conspicuously non-normal residuals, and were therefore discarded. All continuous predictors 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 Akaike information criterion corrected for small sample size ($\mathrm{AIC_c}$); 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 the 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 the log *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 this model. Then, these residual variables were used as predictors of log *I*/*K* ratio, using *AbsLat* and the variables from the final model separately 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 the full description and examples in Hawkins *et al.*, 2003; Hortal *et al.*, 2008). In addition, we used regressions to evaluate whether there is a latitudinal gradient in the number of idiobiont and koinobiont species.

Apart from these general analyses, we identified by means of chi-square tests which island faunas depart from the level of generalism of their respective species pools. We evaluated whether any of the abovementioned factors determines that some islands have significantly higher or lower log *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 v. 6.1 (Statsoft, 2004), except for the model comparisons with continuous variables and the correlograms, which were carried out in SAM v. 4.0 (Rangel *et al.*, 2010).

RESULTS

The level of generalism (i.e. *I*/*K* ratio) of each island braconid and ichneumonid fauna is illustrated in Fig. 1 (see also

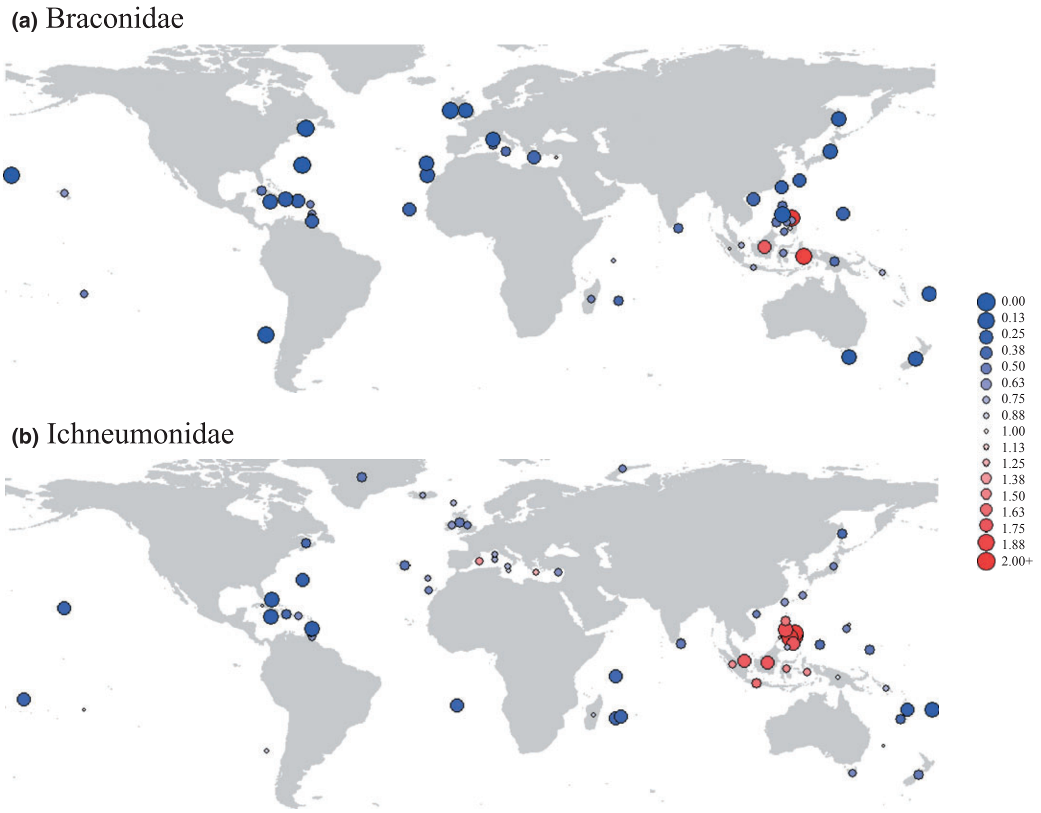


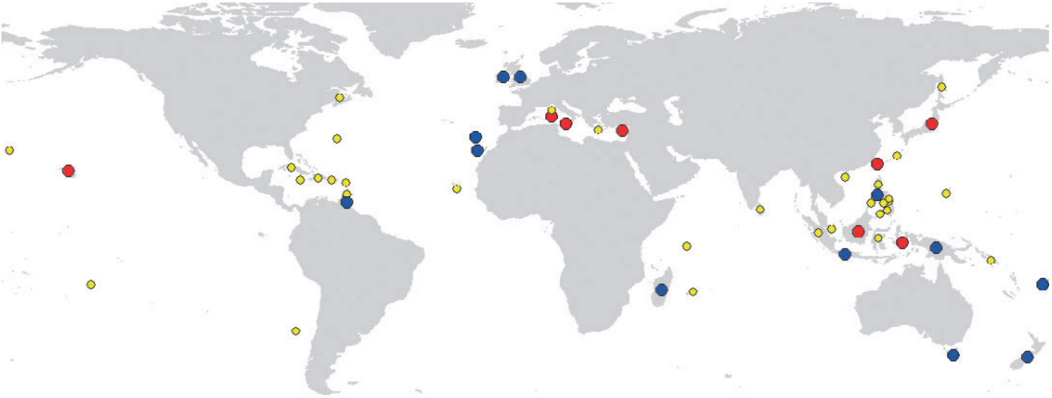
Figure 1 Level of generalism (measured as the ratio of idiobiont over koinobiont species, *I*/*K* ratio) of the island faunas of two parasitoid families: braconids and ichneumonids. The size and colour of the circles represent the level of generalism (blue, islands that have a higher proportion of specialist species; red, islands that have more generalist species). The data are from 53 (in the case of Braconidae) and 70 (in the case of Ichneumonidae) islands or archipelagos.

Table S4 in Appendix S2). When all territories are considered altogether, the proportion of generalists is greater in islands than in continental areas (Braconidae: $\chi^2 = 17.658$, 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 is not significantly greater than that of their species pools (Braconidae: Wilcoxon's $t = 511$, $Z = 1.81$, $P = 0.07$; Ichneumonidae: $t = 1050$, $Z = 1.127$, $P = 0.26$). For the braconids, eight islands show a significantly higher *I*/*K* ratio than their species pools, while in 12 islands the ratio is significantly lower than for the relevant pool (Fig. 2a, Table S4). Similarly, nine islands have a significantly higher *I*/*K* ratio than their species pool for the ichneumonids, and nine other islands display the opposite trend (Fig. 2b, Table S4).

Both temperature and precipitation have significant positive effects on the level of parasitism (i.e. log *I*/*K* ratio) for braconids, but not for ichneumonids (Table 1). Rather, ichneumonids are influenced by the distance to the closest larger territory and the geological origin of the island, with continental islands showing overall higher log *I*/*K* ratios. The log *I*/*K* ratio is influenced in both families by the absolute value of latitude, the biogeographic realm and the level of generalism of its species pool; *AbsLat* has a significant negative effect (Fig. 3), while *SpeciesPool* has a positive influence (Table 1). The level of endemism had only a significant negative effect in the case of the ichneumonids. Indomalaya is the region where islands display the highest levels of log *I*/*K* ratio for braconids, followed by the Afrotropics, Australasia, Nearctic, Neotropics and Palaearctic; for ichneumonids, Indomalaya is again the region where islands show the highest log *I*/*K* ratio, followed by Australasia, Palaearctic, Neotropics, Afrotropics and Nearctic. For braconids, the final model includes only *Temp* and *SpeciesPool* and explains 43.2% of the variance of log *I*/*K* ratio on islands, while for ichneumonids it comprises *Region* and *SpeciesPool*, which explains 53.2% of the variance (Table 1).

Partial regressions show the existence of strong covariance between the final models and latitude (*AbsLat*), indicating that these models account for the latitudinal gradient in log *I*/*K* ratio (Figs 3 & 4). The strong covariation of the predictors of log *I*/*K* ratio and latitude is more evident for the braconids, for which the

(a) Braconidae



(b) Ichneumonidae

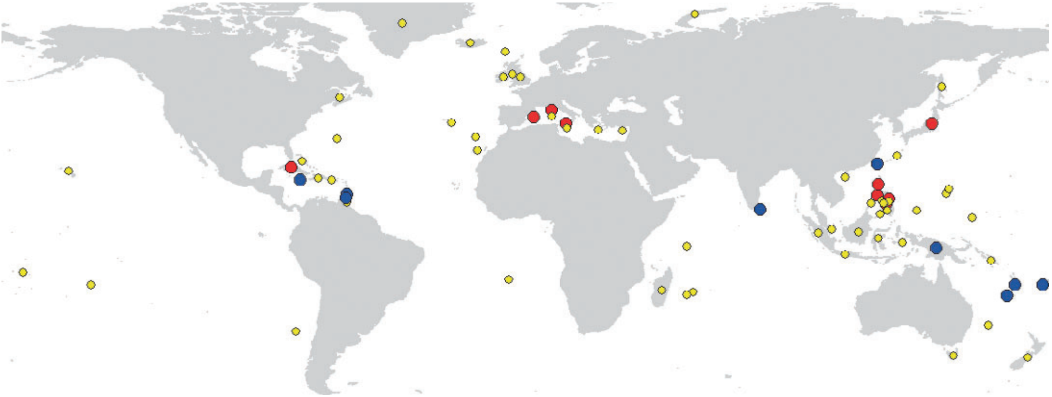


Figure 2 Departure of the level of generalism (*I*/*K* ratio) of island faunas from their correspondent species pool for both braconids and ichneumonids. Red circles represent islands with a significantly higher level of generalism than their species pool, blue circles islands with a significantly lower level of generalism than their pool and yellow circles islands that do not differ significantly from the level of generalism of their species pool. The data are from 53 (in the case of Braconidae) and 70 (in the case of Ichneumonidae) islands or archipelagos.

Table 1 Results of the regression analyses assessing the relationship between level of generalism (i.e. log *I*/*K* ratio) and several climatic, physiographic and regional factors for Braconidae and Ichneumonidae (continuous variables were standardized to mean = 0 and standard deviation = 1; see Materials and Methods). The data are from 53 (in the case of Braconidae) and 70 (in the case of Ichneumonidae) islands or archipelagos distributed world-wide.

	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 + *Temp*^{2}	50	18.876***	0.407	+ +	67	2.222	0.034	+
Prec	51	8.123**	0.120	+	68	3.108	0.030	+
Prec + *Prec*^{2}	50	4.496*	0.119	+ −	67	1.683	0.019	+ −
Archipelago	51	0.020	−0.019		68	3.016	0.028	
IslType	51	0.050	−0.019		68	8.765**	0.101	
Area	51	1.570	0.011	+	68	0.159	−0.012	+
Elev	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	−
EndIsl	51	3.408	0.044	+	68	6.652*	0.076	−
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	14.072***	0.532	

d.f., degrees of freedom; *F*, Fisher's *F*-statistic; Adj R^2, adjusted R^2; Slope, slope of the relationship between level of generalism and the explanatory variables (+ indicates a positive relationship, − a negative relationship and + − a hump-shaped relationship, i.e. a reverse U).
$^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$. Variable codes as in text.

independent effect of latitude explains 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 shows a larger independence from latitude, and the independent effect of the model explained 39.3% of the variation. The final models also remove all significant spatial autocorrelation in short distance classes for both families

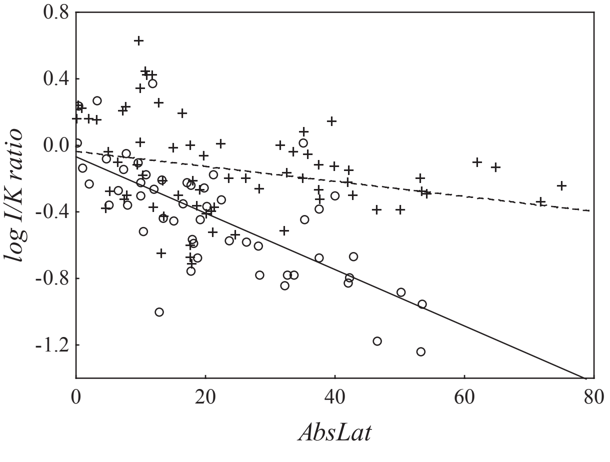


Figure 3 Relationship between the absolute value of latitude (*AbsLat*) and level of generalism (log *I*/*K* ratio) for braconids (circles; continuous line) and ichneumonids (crosses; dashed line). Level of generalism was calculated as log(idiobionts + 1/koinobionts + 1). The data are from 53 (in the case of Braconidae) and 70 (in the case of Ichneumonidae) islands or archipelagos distributed world-wide.

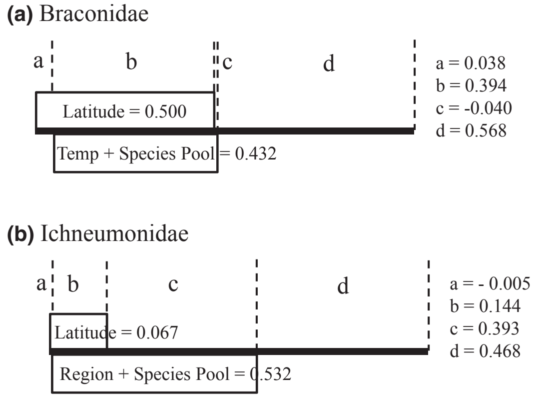


Figure 4 Results of the partial regression analyses relating the world-wide patterns of level of generalism on island parasitoids (response variable is log *I*/*K* ratio) with the independent contributions of (a) latitude (absolute value of latitude) and (c) the final model (see Table 1), as well as their shared contribution (b). The unexplained variation (d) is 1 – adjusted R^2 of a generalized linear model (GLM) including latitude and the final model. GLM results are listed in Table 1. The data are from 53 (in the case of Braconidae) and 70 (in the case of Ichneumonidae) islands or archipelagos distributed world-wide.

(Appendix S3), indicating that no spatially structured variation in island log *I*/*K* ratio remains unexplained. Interestingly, while the number of koinobiont species is positively related to *AbsLat* in both families (Braconidae: $F_{1,51} = 5.282$, $P < 0.05$, adj. $R^2 = 0.076$; Ichneumonidae: $F_{1,68} = 5.228$, $P < 0.05$, adj. $R^2 = 0.058$) the number of idiobiont species shows no significant relationship with latitude (Braconidae: $F_{1,51} = 0.698$, $P = 0.41$, adj. $R^2 = -0.006$; Ichneumonidae: $F_{1,68} = 0.975$, $P = 0.33$, adj. $R^2 < 0.000$).

Islands with parasitoid faunas with significantly higher *I*/*K* ratio than their respective species pool have higher maximum elevations in the case of braconids (*t*-value = −3.099, $P < 0.01$), and are of continental origin in the case of ichneumonids ($\chi^2 = 6.485$, 1 d.f., $P < 0.05$) (Table S5 in Appendix S2). In contrast, island faunas with a significantly lower *I*/*K* ratio than their respective species pool show higher island species richness for braconids (*t*-value = −2.653, $P < 0.05$), and higher mean precipitation for ichneumonids (*t*-value = −2.751, $P < 0.01$) (Table S6 in Appendix S2).

DISCUSSION

Our results show that, overall, island parasitoid faunas are more biased towards generalist species than mainland ones. As far as we know, there are no known transitions from koinobiosis to idiobiosis in any hymenopteran parasitoid, and they are generally considered to be unlikely (but see Sharkey, 2007; regarding transitions from ectoparasitism to endoparasitism in Chalcidoidea). Therefore, rather than being caused by repeated episodes of increasing host range, we believe that this predominance of generalists on islands is simply the consequence of their higher chances of survival after colonization, due to their lack of dependence on any particular host species. 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 & Thornton (1993) found more koinobiont (i.e. specialists) than idiobiont (i.e. generalists) species in the recently colonized Anak Krakatau island, Santos *et al.* (2011) found a higher proportion of generalists attacking the tortricid moth *Acroclita subsequana* on Macaronesian islands compared with 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, 2007). Although a connection between local and regional diversity has been largely acknowledged (e.g. Graves & Gotelli, 1983; Hortal *et al.*, 2008), 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 a higher level of generalism than their corresponding species pool are also of higher maximum elevation. 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 elevation. Therefore, it can be expected that comparatively fewer host species actually colonize high-elevation areas, favouring an imbalance towards parasitoids with wide host ranges due to the low diversity of hosts. Also, topographical relief regulates island climate, so this variable may also be capturing the departure of each island system from the general gradients in temperature and precipitation that the global climate models we used are not able to capture accurately. The final model for braconid generalism includes temperature alongside species pool, indicating the particular importance of climatic factors for this family. Interestingly, the islands with a lower level of generalism than their pool show particularly high species richness. The positive relationship between ecological specialization and species richness is well known (Hutchinson, 1959); increased specialization reduces inter-specific 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 because those with higher levels of generalism are mostly from continental islands, while those with lower levels of generalism are from islands with higher precipitation.

Perhaps one of the most interesting of our results is that the level of generalism of island parasitoid faunas appears to be largely constrained by regional factors, and not (or less importantly) by other factors known to have different effects on the richness of generalist and specialist species on islands, such as area or distance to colonization sources (see Holt, 2010). 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 of the species and lineages present in the species pool (Ricklefs, 1987, 2007), as well as on the geomorphological and environmental characteristics of the region (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.*, 2008), 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. 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 continental origin, with high elevations 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 (Bird *et al.*, 2005). These characteristics not only enhance their diversity, but also result in Indomalayan islands hosting some of the largest patches of rain forest still found on islands (Corlett & Primack, 2008). Plant architecture influences not only parasitoid species richness but also the relative diversities of idiobionts 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 rain forests when compared with other habitats. This particular effect is stronger for ichneumonids (see Fig. 1), which are those with proportionally more idiobiont species overall. In fact, the continental rain forest 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 on both 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 within rain forests. Parasitoids have been hypothesized to have inverse latitudinal richness gradients (i.e. more species in temperate regions; e.g. Askew & Shaw, 1986; Gauld, 1986; Askew, 1990; Hawkins, 1994). Although it is unclear whether this seemingly anomalous pattern is actually real or just an artefact of taxonomic and sampling biases (e.g. Jones *et al.*, 2009), it could be argued that it could be affecting to some extent the ecological structure of parasitoid communities and hence our results. However, at least in islands, this does not seem to be the case; we explicitly evaluated any effect of richness in community structure, failing to find any relationship. Rather, 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 log 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.

Our evidence adds to the wider discussion on the existence and origin of latitudinal gradients in the level of trophic specialization (see e.g. Godfray *et al.*, 1999). Both the coherence of island faunas and their mainland source pools and the results from the regressions of the number of idiobiont or koinobiont species against latitude agree with former evidence on the latitudinal gradient in the distribution of koinobionts 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, 1990). The latitudinal gradients in parasitoid richness are also known to differ according to host-feeding niche (Hawkins, 1990, 1994; Hawkins *et al.*, 1992): while richness of parasitoids feeding on exophytic hosts diminishes towards the tropics, it remains the same or actually increases towards the tropics in endophytic hosts. 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 (Hawkins, 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. the Caribbean islands), but rather only those holding large rain forests. 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 rain forests, both on islands and continental areas. As tree species richness is higher in these ecosystems than in temperate forests, they are likely to 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, 1994), ultimately resulting in a higher proportion of idiobionts in the tropics than in temperate areas.

Although our knowledge of the geographical distribution of parasitic wasps is taxonomically and geographically biased (Jones *et al.*, 2009; Baselga *et al.*, 2010; Santos *et al.*, 2010b), we believe that our results are not seriously undermined by data quality issues, as we considered only the islands with comparable inventories previously identified by Santos *et al.* (2010b). Therefore, we can conclude that although island parasitoid faunas have comparatively higher proportions 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 rain forests, 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 within tropical forests, as well as to unveil the mechanisms causing this seemly general trend. Nevertheless, the pre-eminence of the species pool as predictor of local ecological structure ratifies the view of local assemblages as an epiphenomenon determined by the ecogeographic distributions of species (as advocated by Ricklefs, 2008), stressing the importance of including regional processes in our understanding of the functioning of ecological communities.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Appendix S1 Supplementary tables: source pool and life-history trait data (Tables S1–S3).
Appendix S2 Additional statistical analyses (Tables S4–S6).
Appendix S3 Correlograms for the level of generalism (measured as log *I*/*K* ratio) and the residuals of the final model.

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BIOSKETCH

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