Research

Ecography 36: 1097–1105, 2013
doi: 10.1111/j.1600-0587.2012.00223.x

Subject Editor: Joaquin Hortal. Accepted 29 December 2012

The functional biogeography of species: biogeographical species roles of birds in Wallacea and the West Indies

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Biogeographical systems can be analyzed as networks of species and geographical units. Within such a biogeographical network, individual species may differ fundamentally in their linkage pattern, and therefore hold different topological roles. To advance our understanding of the relationship between species traits and large-scale species distribution patterns in archipelagos, we use a network approach to classify birds as one of four biogeographical species roles: peripherals, connectors, module hubs, and network hubs. These roles are based upon the position of species within the modular network of islands and species in Wallacea and the West Indies. We test whether species traits – including habitat requirements, altitudinal range-span, feeding guild, trophic level, and body length – correlate with species roles. In both archipelagos, habitat requirements, altitudinal range-span and body length show strong relations to species roles. In particular, species that occupy coastal- and open habitats, as well as habitat generalists, show higher proportions of connectors and network hubs and thus tend to span several biogeographical modules (i.e. subregions). Likewise, large body size and a wide altitudinal range-span are related to a wide distribution on many islands and across several biogeographical modules. On the other hand, species restricted to interior forest are mainly characterized as peripherals and, thus, have narrow and localized distributions within biogeographical modules rather than across the archipelago-wide network. These results suggest that the ecological amplitude of a species is highly related to its geographical distribution within and across biogeographical subregions and furthermore supports the idea that large-scale species distributions relate to distributions at the local community level. We finally discuss how our biogeographical species roles may correspond to the stages of the taxon cycle and other prominent theories of species assembly.

Several hypotheses have been proposed to explain contemporary patterns of bird distributions on islands. Some are based on extrinsic factors, such as island size, isolation and elevation, and conceive species as neutral entities (MacArthur and Wilson 1967, also cf. Hubbell 2001), while others are concerned with biotic interactions and intrinsic species traits (Wilson 1961, Ricklefs and Cox 1972, Diamond 1975, Lack 1976, Erwin 1981, Holt 2010). An integrative approach, analyzing the distributions of species using a network approach, has recently been proposed to advance our knowledge about biogeography and consequences of biotic interactions (Carstensen and Olesen 2009, Araújo et al. 2011, Carstensen et al. 2012). For instance, Carstensen et al. (2012) used network theory to identify biogeographical modules (i.e. subregions) and the structural importance, or biogeographical role, of different types of islands in the network of islands and birds in Wallacea and the West Indies.

Here, we extend the work of Carstensen et al. (2012) to classify bird species into roles according to their distributional patterns in the modular network of islands and bird species in Wallacea and the West Indies. In general, island faunas can be arranged as bipartite networks of interacting islands and species. A species and an island are linked, or interact, if the species is present on the island. Hence, the links of a species describe its geographic distribution across an archipelago, while the links of an island define its bird fauna. Consequently, species linking to the same island overlap in their distributions, while islands with links to the same species have overlapping biodiversity. Individual species and islands may differ fundamentally in their linkage pattern, and therefore hold very different

topological roles in the island-bird network. With the network analytical approach adopted here we first identify biogeographical modules, i.e. subgroups of closely linked islands and birds (Carstensen et al. 2012). Then, by quantifying the distributional pattern of each species based on their topological linkage in the modular network, we assign each species one of four biogeographical roles: peripheral, module hub, connector, or network hub (Olesen et al. 2007, Carstensen and Olesen 2009, Carstensen et al. 2012). This role assignment contains information on how individual species are connected, both within each biogeographical module and across the entire archipelago. It thus combines information on distributional range size and whether distributions are localized within modules or fragmented across modules.

How will species roles relate to species traits, such as habitat requirements and ecological amplitude? The taxon cycle theory explains species distribution patterns on the basis of phases of expansion and contraction of species-ranges (Wilson 1961). Species in different stages of the cycle show different distribution patterns, ecological amplitudes, habitat requirements and abundances. Initially, species expand their ranges and occupy mainly marginal and open lowland habitats, however, as a species progresses through the cycle its distributional range contracts and becomes increasingly fragmented to ultimately occupy only interior mountain forests of one or few islands (Ricklefs and Cox 1972, 1978, Ricklefs and Bermingham 1999, 2002, Whittaker and Fernández-Palacios 2007, Economo and Sarnat 2012). We thus expect roles to relate to habitat requirements and ecological amplitude of species, so that peripherals will associate more with interior forest habitats and less with coastal and open habitats, while the opposite pattern will be expected for connectors and hubs. Furthermore, according to the trophic island biogeography formulated by Holt (2010), species from different trophic levels and feeding guilds can be expected to colonize islands at different successional stages and of different sizes and species numbers. They can thus be expected to hold different biogeographical roles. For instance, a predator would only be able to colonize an island if its prey has already become established (Holt 2010). Species from lower trophic levels could thus be expected to establish on more islands than species from higher trophic levels and, hence, to act mainly as hubs. Finally, we expect dispersal ability to influence roles. Behavior and life history attributes associated with body size are related to dispersal distance, and a positive relationship between dispersal ability and body size is expected (Peters 1983, Paradis et al. 1998, Sutherland et al. 2000, Jenkins et al. 2007). Body size may also influence extinction/colonization dynamics, with a failure of larger species to persist on small islands (Diamond 1984). The effect of body size on our roles might thus depend on the spatial distribution of large and small islands in the two archipelagos. In general however, we expect larger bodied species to be more widespread than small bodied.

We test these expectations in a comparative framework using distributional data for the terrestrial avifaunas of Wallacea and the West Indies. Specifically, we: 1) examine whether species traits, including habitat requirements, altitudinal range-span, feeding guild, trophic level, and body length correlate with biogeographical species roles as assigned by the network analysis, 2) ask to what extent our results are similar in Wallacea and the West Indies and, thus, of general nature, and 3) discuss how our biogeographical species roles may relate to the stages of the taxon cycle and other theories of species assembly in island systems.

Methods

Distribution data and network analysis

Wallacea and the West Indies are of roughly equal land area and geographic extent, and, relative to their position in the tropics, are both characterized by depauperate local biotas with high levels of endemism (Wallace 1869, Bond 1948, Myers et al. 2000, Dalsgaard et al. 2007, Vázquez-Miranda et al. 2007, Ricklefs and Bermingham 2008). These similarities make the two archipelagos suitable for large-scale comparative analyses. Based on a comprehensive review of bird distributions (Carstensen et al. 2012), we compiled a presence/absence island-bird matrix for each archipelago. We only included terrestrial breeding birds (excluding seabirds and migratory species) in order to maintain a homogenous dataset in terms of what affects the distribution pattern of a species. Also, whenever well documented, we included recently (since 1600 AD) extinct species, but excluded human introduced species. We note that while we did attempt to include recently extinct species, data is not complete in this regard, and these effects could thus somehow affect our results (Pregill and Olson 1981, Steadman 1995). This resulted in 564 species and 90 islands for Wallacea, and 243 species and 62 islands for West Indies (Carstensen et al. 2012, Supplementary material Appendix 1).

We analyzed each network with the Netcarto (SA) algorithm of Guimerà and Amaral (2005a, b), which detects the modular structure of a network and assigns roles to nodes, i.e. species and islands, according to their linkage patterns in the network. In a modular network, highly linked subgroups of nodes constitute modules, and a few nodes connect modules together to form one large coherent network. Here, detected modules are groups of islands and species closely linked together. Thus, the module to which a species is assigned is the geographical subregion that represents the species' core area of its current distribution within the system (Carstensen and Olesen 2009, Carstensen et al. 2012). Netcarto calculates a modularity index M of each network, measuring how clearly delimited the modules of the network are. As M approaches 1 the more distinct the modules are, and as it approaches 0 the less distinct they are. To test whether the network is significantly modular, we ran Netcarto for 100 randomized networks constrained by the same degree distribution as the empirical one. If the empirical M value lies above the 95% confidence interval for M of the randomized networks, the empirical network is significantly modular. Netcarto was originally developed for unipartite networks. We do not use a modularity algorithm specifically for bipartite networks because this would create biogeographical

modules of islands and species separately (Guimerà et al. 2007), whereas we conceptually believe that biogeographical modules should consist of both islands and species. Netcarto has been used numerous times on bipartite networks, partly for the same reason, for instance, on bipartite plant-pollinator networks (Olesen et al. 2007, Dupont and Olesen 2009, 2012, Fortuna et al. 2010, Martín González et al. 2012). The role of each species in the modular network is quantified by two parameters, the standardized within-module degree, l, and the among-module connectivity, r (Guimerà and Amaral 2005b, Olesen et al. 2007). However, to take into account the bipartite nature of our network we calculated l using the average and standard deviation of within module links for only the species and not all the nodes in the module (i.e. islands and species). The two parameters are calculated as follows: 1) the standardized within-module degree, l, reflects how well a node, i, is connected within its own module relative to other nodes in its module:

$$l_i = \frac{k_{is} - \bar{k}_s}{SD_{ks}}$$

2) The among-module connectivity, r, reflects how a node in a module is positioned with respect to other modules:

$$r_i = 1 - \sum_{t=1}^{N_M} \left(\frac{k_{it}}{k_i} \right)^2$$

where k_{is} is number of links of i to other nodes in its own module s, $\bar{k}_s$ and SD_{ks} are the average and standard deviation of the within-module k of all the species in s, k_i is the number of links of i, and k_{it} is the number of links from i to nodes in module t (including i's own module). If i has all of its links within its own module, then $r = 0$; but if the links are distributed more evenly among modules, $r_i \rightarrow 1$ ($r_{\max}$ for a four-module system = 0.75, as is the case for Wallacea and the West Indies).

Here, in order to translate these network concepts into the biogeographical context, we term l the local topological linkage and r the regional topological linkage. A species' l-value provides information about the number of islands it occupies within its module, relative to other species in that module. The value of r is a measure of how widely a species is distributed across modules, i.e. across the archipelago. By plotting l as a function of r we obtain an $l - r$ space, which we term the role space (Fig. 1). This role space is then divided into quadrants delimiting four kinds of roles; the horizontal border line represents the median of l, and the vertical line, $r = 0.625$. Species with r-values ≤ 0.625 have at least half of their links within their own module (see Guimerà and Amaral 2005b and Olesen et al. 2007 for a detailed discussion of the choice of $r = 0.625$).

For species, these roles are interpreted biogeographically as peripherals, connectors, module hubs, and network hubs (Carstensen et al. 2012, based on Olesen et al. 2007). Peripherals are range-restricted species occurring on a single or a few islands; they are in the least-distributed half of the species from their own module and are scarcely distributed outside their module. Module hub species occupy more islands within their modules than peripherals. They can thus be widespread, but on islands predominantly within their own module. Connectors are present on a few, widely scattered islands, distributed over several modules. Network hub species are also distributed on islands across several modules but on more islands than connectors, i.e., they possess the properties of both module hubs and connectors. Both for connectors and network hubs less than half of their islands are from their own module, and they are thus distributed widely across the entire region. See Carstensen et al. (2012) for a similar interpretation of island roles.

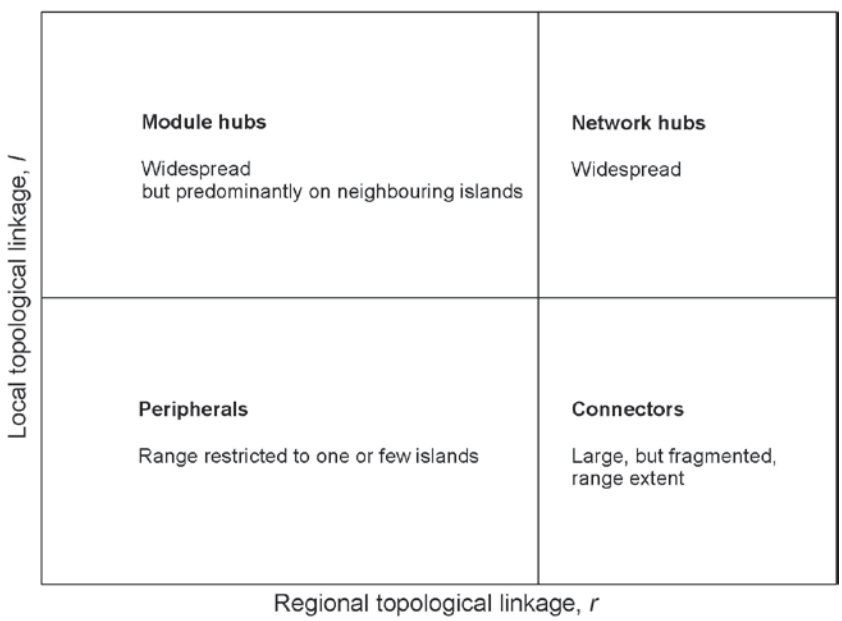

Figure 1. Schematic overview of the four biogeographical roles in $l - r$ role-space. See text for further explanation.

Species traits and biogeographical roles

To test how species traits relate to biogeographical roles, we collected species data about habitat requirements, altitudinal range-span, feeding guild membership, trophic level, and body length (Supplementary material Appendix 2). In order to assign each species to a distinct habitat requirement category, habitats were first coarsely defined as four broad habitat types: interior forest, open forest, littoral habitats, or open habitats. Interior forest included only closed forest types. Open forest included forest edges, savanna woodlands, and other types of open forest habitats. Littoral habitats included coastal forests and mangroves. Open habitats included grasslands, shrublands and other habitats with no or few trees. Each species was then assigned to one of six categories of habitat requirement: Interior: species only occupying interior forest; Open-forest: species occupying interior forest and/or open forest; Coastal: species only occupying littoral and/or open habitats; Open: species only occupying open habitats; Generalist: species occupying all four habitat types; and Other: species that did not fit into any of the previous five categories. Feeding guilds were defined and in turn arranged as three trophic levels: 1) frugivores, granivores, nectarivores, 2) insectivores and omnivores, and 3) carnivores. Because of the scarce and heterogeneous information, a finer subdivision was not possible. Body length was used as a surrogate for body mass since reliable data on body length could be found for far more species than body mass (see Supplementary material Appendix 3 for justification).

To assess how species traits relate to biogeographical roles, for each archipelago we first used an Akaike information criterion (AIC) backward-elimination multiple linear regression procedure to select the best-fit model of species traits as determinants of l and r. As trait data were not available for all species, we ran the model regarding species traits using a subset (497 species out of 564 species for Wallacea, and 179 species out of 243 species for West Indies) of the species included in the network analysis. To further examine the effect of the categorical trait variables included in the best-fit multiple regression models predicting biogeographical species roles, we used contingency tables to analyze the differences in role proportions of species among the categorical variables (habitat requirements, feeding guild, and trophic level). Fisher's exact test was used to assess whether observed counts were significantly different from expected under the null hypothesis that biogeographical species roles are independent of the tested categories. All statistical analyses were conducted in R ver. 2.13.1 (R Development Core Team).

Results

Both island-bird networks were significantly modular (Wallacea: $M = 0.38$, $M_{random} = 0.21$, $p < 0.05$; West Indies: $M = 0.35$, $M_{random} = 0.21$, $p < 0.05$), and consisted of four biogeographical modules (Fig. 2 and 3 and see also Carstensen et al. (2012)). All four biogeographical species roles were represented in both Wallacea and the West Indies

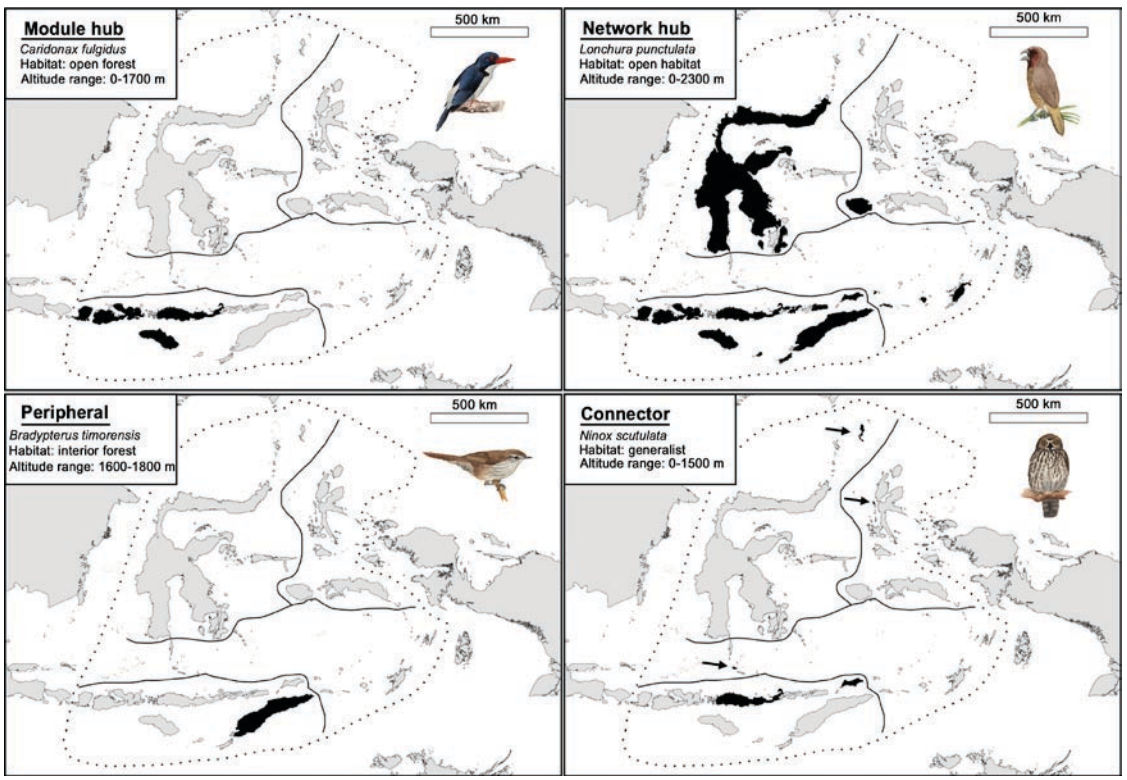

Figure 2. Examples of distribution of birds from the four biogeographical roles in Wallacea. The distribution is shown in black. *Bradypterus timorensis* is a peripheral, endemic to the island of Timor. *Caridonax fulgidus* is a module hub distributed on four islands, all within the Lesser Sundas. *Ninox scutulata* is a connector, and is distributed on five islands across all four modules while the network hub *Lonchura punctulata* is distributed on 22 islands all over Wallacea.

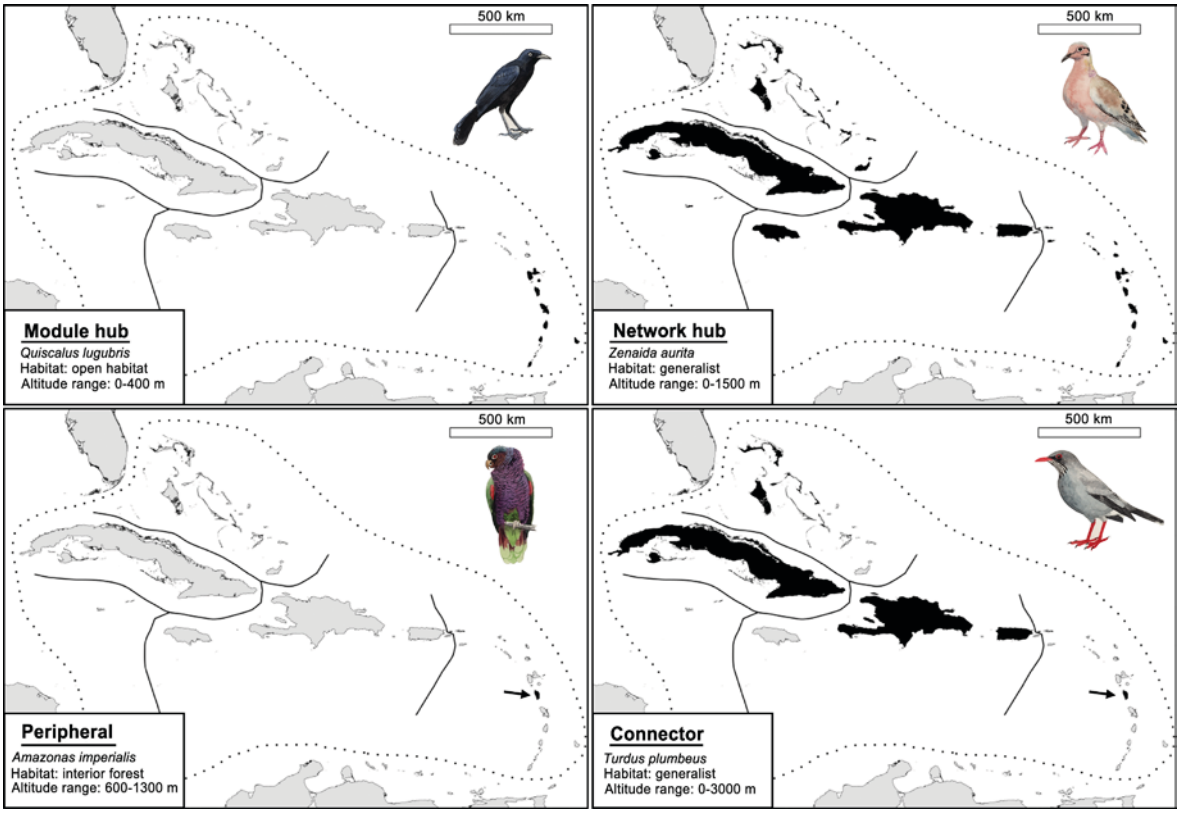

Figure 3. Examples of distribution of birds from the four biogeographical roles in the West Indies. The distribution is shown in black. *Amazonas imperialis* is a peripheral, endemic to the island of Dominica in the Lesser Antilles. *Quiscalus lugubris* is a module hub distributed on 12 islands, all within the Lesser Antilles. *Turdus plumbeus* is a connector, and is distributed on 16 islands across all four modules while the network hub *Zenaida aurita* is distributed on 58 islands all over the West Indies archipelago.

(Fig. 4). In Wallacea, 49.3% were peripherals, 41.1% module hubs, 1.2% connectors and 8.3% network hubs, while in the West Indies 50.2% were peripherals, 44.9% module hubs, 0.4% connectors and 4.5% network hubs. Module endemics, defined as species only found on islands within their own module ($r = 0$), comprised 62.8 and 68.3% of all species in Wallacea and the West Indies, respectively.

In the multiple regression analysis, for Wallacea, habitat requirements and altitudinal range-span were included in the best-fit models predicting both l and r. Additionally, body length was contained in the best model for l (Table 1).

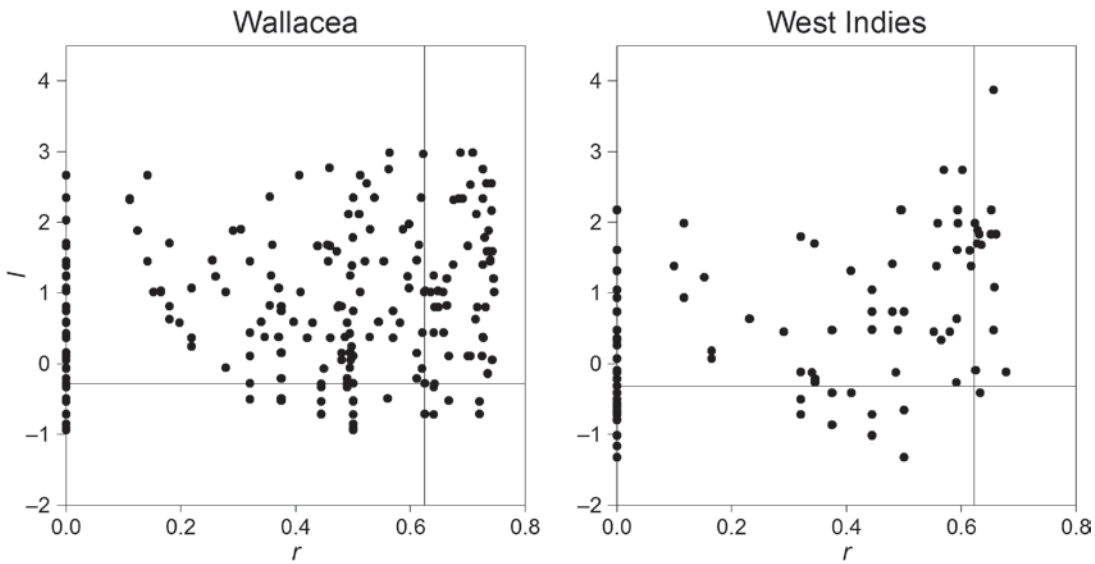

Figure 4. Species role-space for species in Wallacea and the West Indies. The horizontal and vertical lines divide species into the four different biogeographical roles.

Table 1. Full and best-fit multiple regression models for Wallacea (n = 497) and the West Indies (n = 179).

	ΔAIC		Terms in model	
	Wallacea	West Indies	Wallacea	West Indies
r				
Best-fit model	0	0	altitudinal range-span*** habitat requirements***	altitudinal range-span*** habitat requirements** body length***
Full model	8.1	4.7	altitude range-span*** habitat requirements*** body length^{NS} guild** trophic level^{NS}	altitudinal range-span*** habitat requirements** body length*** guild^{NS} trophic level^{NS}
l				
Best-fit model	0	0	altitudinal range-span* habitat requirements*** body length**	habitat requirements* body length*
Full model	1.9	7.47	altitudinal range-span* habitat requirements*** body length** guild^{+} trophic level^{NS}	altitudinal range-span^{NS} habitat requirements* body length* guild^{NS} trophic level^{NS}

***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$, $^{+}$: $0.05 < p < 0.1$, ^{NS}: $p > 0.1$.

Altitudinal range-span was positively correlated with both *l* and *r* (standardized coefficients: 0.073 and 0.224 respectively), while body length was also positively correlated with *l* (standardized coefficient: 0.141). In the West Indies, habitat requirements and body length were included in the best-fit models for both *l* and *r*. Altitudinal range-span was additionally included as a determinant for *r* (Table 1). Body length was positively correlated with both *l* and *r* (standardized coefficients: 0.198 and 0.205 respectively), while altitudinal range-span was also positively correlated with *r* (standardized coefficient: 0.245). In both archipelagos, feeding guild and trophic level were excluded from the best-fit model and not analyzed further.

In the contingency table analysis the proportion of biogeographical species roles was significantly different from what would be expected if roles were independent of habitat requirements. In Wallacea, all habitat requirement categories were significantly different, while in the West Indies, only interior forest species and generalist species had a significantly different role proportion from expected (Table 2; Fig. 5). The majority of interior forest species were peripherals in both Wallacea (72.4%) and the West Indies (77.8%) with a decreasing proportion of peripherals among open forest-, coastal- and open habitat species (Fig. 5). In both archipelagos, generalist species similarly had lower proportions of peripherals than expected. Instead, open forest-, coastal-, open habitat- and generalist species, were to a higher degree classified as connectors and/or network hubs, a pattern that was most apparent in Wallacea, but partly also in the West Indies (Fig. 5).

Table 2. Relationship between species habitat category and roles for Wallacea and the West Indies.

	Roles			
Habitat	Peripherals	Connectors	Module hubs	Network hubs
Wallacea				
Interior*				
Observed	76	2	25	2
Expected	49.67	1.87	44.02	9.43
Open forest*				
Observed	54	0	68	2
Expected	59.13	1.75	52.39	10.73
Coastal*				
Observed	2	1	3	3
Expected	4.29	0.13	3.80	0.78
Open*				
Observed	4	1	10	3
Expected	8.58	0.25	7.61	1.56
Generalist*				
Observed	27	1	32	14
Expected	35.29	1.04	31.27	6.40
West Indies				
Interior*				
Observed	21	0	6	0
Expected	14.48	0.15	11.01	1.36
Open forest				
Observed	24	0	9	1
Expected	18.23	0.19	13.87	1.71
Coastal				
Observed	1	0	1	0
Expected	1.07	0.01	0.82	0.10
Open				
Observed	3	0	5	1
Expected	4.83	0.05	3.67	0.45
Generalist*				
Observed	10	1	17	4
Expected	17.16	0.18	13.05	1.61

Stars indicate significant (i.e. $p < 0.05$) difference in role proportion from what would be expected if habitat category and species roles were independent.

Discussion

In both Wallacea and the West Indies, habitat requirements, altitudinal range-span, and body length were important determinants of biogeographical species roles. Specifically,

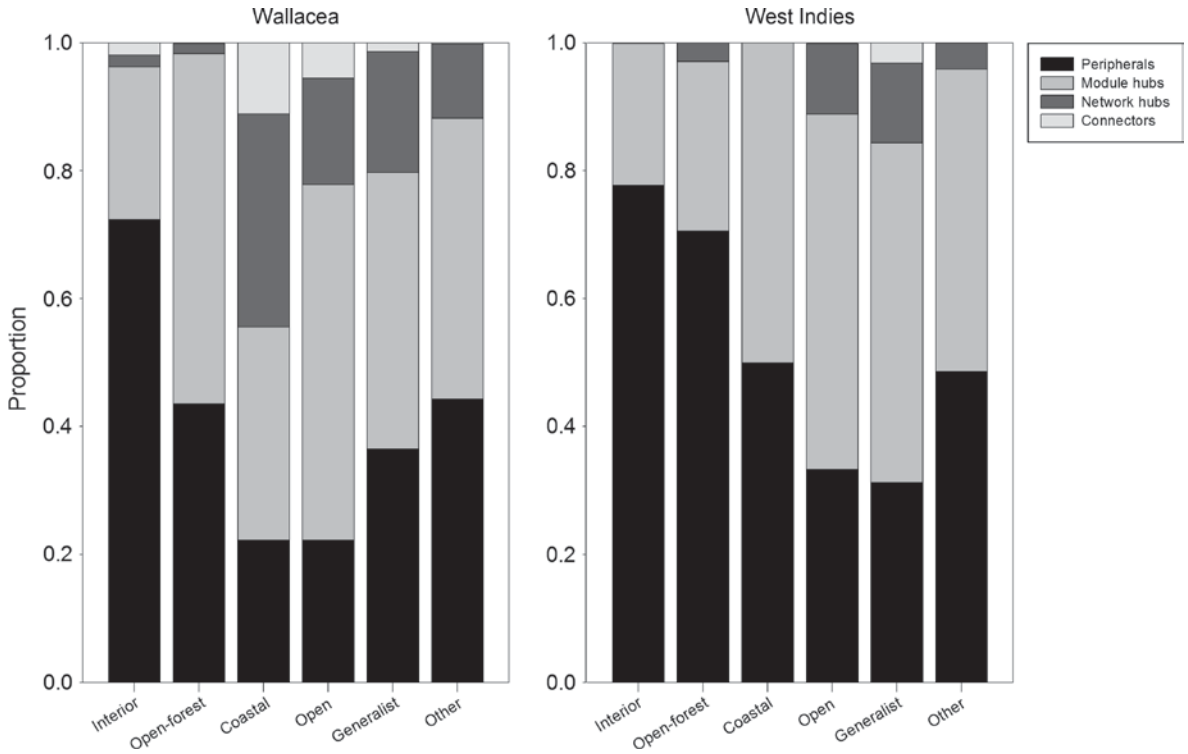

Figure 5. The role proportion of species in the six habitat categories for Wallacea and the West Indies. Stars indicate significantly (i.e. $p < 0.05$) different proportions from what would be expected if biogeographical roles were independent of habitat requirements.

interior forest species were predominantly classified as peripherals whereas coastal-, open-, and generalist species showed higher proportions of connectors and network hubs (Fig. 5). Species with a wider altitudinal range-span, i.e., larger ecological amplitude, had increased l and r values in Wallacea and increased l values in the West Indies. These species are thus more often classified as connectors and network hubs, while species with a narrow altitudinal range-span are more often classified as peripherals. Body length had a significantly positive effect on l in Wallacea and both l and r in the West Indies. Larger species, like species with large ecological amplitudes, thus tend to be more widespread rather than act as peripherals. A pattern possibly related to the higher dispersal ability of larger species.

The topological role of a species is a representation of its distributional pattern across the biogeographical network: hubs and connectors are structurally important for the coherence of the biogeographical network within modules (module hubs and network hubs) and across modules (connectors and networks hubs; Carstensen et al. 2012). Coastal-, open-, generalist species and species with a large altitudinal range-span tend to traverse modules, i.e. to be distributed across otherwise distinct biogeographical units, while interior forest species and species occurring only within a limited altitudinal range-span tend to be distributed within a single biogeographical module or subregion (Fig. 2, 3). This shows that large-scale species distribution patterns are highly related to species distributions at the local community level. The pattern was most prominent for Wallacea, but also, to some extent, evident in the West Indies.

Based on our results, we suggest that our four biogeographical roles may correspond to the four stages of the taxon cycle. According to the taxon cycle theory – as defined by Ricklefs and Cox (1972), modified from Wilson (1961) – populations of species go through phases of expansion and contraction in four stages: I) species are widespread and continuously distributed, II) species are still widespread but mostly over neighboring islands, III) species are found on fewer islands and distributions are now more fragmented, and IV) species are restricted to one or a few islands. These stages are related to habitat occupancy so that species will occupy mostly marginal habitats in stage I and gradually occupy more forested areas, ultimately being restricted to interior forests in stage IV (Wilson 1961, Ricklefs and Cox 1972, Mayr and Diamond 2001). We argue that peripherals correspond well to stage IV in the taxon cycle; they are predominantly interior forest species, occupy narrow altitudinal ranges, and are locally distributed on a single or few islands, mainly within one biogeographical module (Fig. 2, 3). Connectors and module hubs show a less clear pattern in respect to taxon cycles, and could both correspond to either stage II and III. On the other hand, network hubs correspond well to stage I species; they occupy wide altitude ranges, constituting a large proportion of coastal-, open-, and generalist species (especially in Wallacea) and being widely distributed geographically across several modules within the archipelago (Fig. 2, 3). As we are not able to explicitly test it, this relationship between our species roles and taxon cycle stages remains speculative. While the existence of taxon cycles is reasonably well documented for the West Indies (Ricklefs and Cox 1972, 1978, Ricklefs and Bermingham 1999), it is less so for Wallacea. The very existence of taxon cycles has been questioned (Pregill and Olson 1981)

and it cannot necessarily be expected that they are working in both Wallacea and the West Indies. Future studies could seek to confirm the existence of taxon cycles and the relationship with our species roles if data on time of colonization can be found for a sufficient number of species.

A local-scale study by Carstensen et al. (2011) related the geographical distribution of nectarivorous birds with their local habitat preferences on the Wallacean island of Lombok, and also proposed that they were potential examples of different stages of the taxon cycle. Similar results have been found for birds in the West Indies (Ricklefs and Cox 1978). Such both local- and archipelago-wide examples, together with this study, emphasize the relation of the spatial distribution of species at the local – and the regional scales.

Diamond (1975) categorized bird species on the basis of their distribution patterns by what he termed incidence functions. He found that species in the most widespread categories prefer the most common and ubiquitous types of habitat that exist on any island. His distributional categories were based upon how species were distributed on islands on a gradient from species-rich to species-poor, and do not include information on the geographic distributions of the inhabited islands. The categorization in the current study is thus not directly comparable with Diamond's, and the correspondence of our categories with Diamond's will depend on the spatial configuration of large and small islands within a given archipelago. However, our results support similar conclusions; that habitat requirements partly determine the distribution of bird species in island archipelagoes.

In conclusion, the strong relationship of biogeographical species roles to habitat requirements and altitudinal range-span and not to feeding guild and trophic level indicates that ecological amplitude is a better determinant of the geographical distribution patterns of bird species and their biogeographical roles than their feeding and functional ecology. This is in line with what would be expected from earlier assembly theory (Ricklefs and Cox 1972, Diamond 1975). As our method provide an objective way of classifying species into distributional categories it can prove valuable in facilitating future testing of underlying causes of species distribution patterns within and across biogeographical units, both in regional studies such as this one, and at the global scale.

Acknowledgements – We are grateful to R. Guimerà and co-workers for allowing us to use their software. We thank Louis A. Hansen and Christoffer Grubb for data compilation, Jean-Philippe Lessard for assistance on supplemental analyses, and Joaquín Hortal for constructive comments on our paper. Financial support was provided by the Faculty of Science and Technology at Aarhus Univ. (DWC), Fundacão de Amparo à Pesquisa do Estado de São Paulo (FAPESP) (DWC), the Danish Council for Independent Research | Natural Sciences (JMO and BD), the Danish National Research Foundation for support to the Center for Macroecology, Evolution and Climate (CR and JF), the Carlsberg Foundation (BD), the Weis-Fogh fund at the Dept of Zoology, Univ. of Cambridge (BD), and Arcadia (WJS).

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Supplementary material (Appendix ECOG-00223 at <www.oikosoffice.lu.se/appendix>). Appendix 1–3.