

# Biogeographical modules and island roles: a comparison of Wallacea and the West Indies

Daniel W. Carstensen<sup>1\*</sup>, Bo Dalsgaard<sup>2,3</sup>, Jens-Christian Svenning<sup>4</sup>, Carsten Rahbek<sup>3</sup>, Jon Fjeldså<sup>5</sup>, William J. Sutherland<sup>2</sup> and Jens M. Olesen<sup>1</sup>

<sup>1</sup>Department of Bioscience, Aarhus University, Ny Munkegade 114, DK-8000 Aarhus, Denmark, <sup>2</sup>Conservation Science Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK, <sup>3</sup>Center for Macroecology, Evolution and Climate, Department of Biology, University of Copenhagen, Universitetsparken 15, DK- 2100 Copenhagen, Denmark, <sup>4</sup>Ecoinformatics and Biodiversity Group, Department of Bioscience, Aarhus University, Ny Munkegade 114, DK-8000 Aarhus, Denmark, <sup>5</sup>Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, DK-2100 Copenhagen, Denmark

## ABSTRACT

**Aim** In order to advance our understanding of the assembly of communities on islands and to elucidate the function of different islands in creating regional and subregional distribution patterns, we identify island biogeographical roles on the basis of the distribution of the islands' biota within the archipelago. We explore which island characteristics determine island biogeographical roles. Furthermore, we identify biogeographical subregions, termed modules.

**Location** Wallacea in Indonesia, and the West Indies in the Caribbean Sea.

**Methods** We use a network approach to detect island biogeographical roles and avian biogeographical modules. To designate the biogeographical role of an island, each island is assigned two coordinates,  $l$  and  $r$ . The position of an island in  $l$ – $r$  space characterizes its role, namely as peripheral, connector, module hub, or network hub. Island characteristics are tested as predictors of  $l$  and  $r$ .

**Results** Both Wallacea and the West Indies were found to be significantly modular and divided into four biogeographical modules. The four modules identified within Wallacea each contain all existing island roles, whereas no module in the West Indies represents all possible roles. Island area and elevation appeared to be the most important determinants of an island's  $l$  score, while measurements of isolation essentially determined the  $r$  score.

**Main conclusions** In both Wallacea and the West Indies, the geographic structuring into biogeographical modules corresponds well with our knowledge of past connections and contemporary factors. In both archipelagos, large, mountainous islands are identified as hubs and are thus responsible for faunal coherence within modules (module hubs) and across the entire archipelago (network hubs). We thus interpret these as source islands for the surrounding islands in their module (module hubs) or for the entire archipelago (network hubs). Islands positioned marginally in their module and distant from the mainland are identified as connectors or network hubs, behaving as sinks and stepping stones for dispersing species. Modularity and predictors of biogeographical roles are similar for Wallacea and the West Indies, whereas the build-up of biogeographical modules and the assortment of roles depend on the spatial constellation of islands in each archipelago.

## Keywords

Area, avifauna, birds, Caribbean, community assembly, geological history, island biogeography, isolation, network, source–sink dynamics.

\*Correspondence: Daniel W. Carstensen, Department of Bioscience, Aarhus University, Ny Munkegade 114, DK-8000 Aarhus, Denmark.  
E-mail: daniel.carstensen@gmail.com

## INTRODUCTION

Island systems play a prominent role in biogeographical analyses, with much of our understanding of biogeographical

patterns and processes originating from island biogeography (Wallace, 1881; MacArthur & Wilson, 1967; Diamond, 1975; Lack, 1976; Whittaker & Fernández-Palacios, 2007; Ricklefs & Bermingham, 2008). The effects of island characteristics – such

as area, elevation, isolation, and stage in history of an island – upon species richness are now relatively well known (MacArthur & Wilson, 1967; Ricklefs & Bermingham, 2004; Kalmar & Currie, 2006; Whittaker & Fernández-Palacios, 2007; Kreft *et al.*, 2008; Triantis *et al.*, 2008; Whittaker *et al.*, 2008). However, our understanding of the processes driving the assembly of island communities is far from complete. Islands in an archipelago influence each other through source–sink or metapopulation dynamics and by facilitating the inter-island dispersal of species. Thus, the structure of an insular community is highly influenced by regional processes (Ricklefs & Schluter, 1993). One approach to advancing our understanding of such processes is to analyse if and how individual islands, their characteristics and regional setting shape species distributions across an archipelago.

Here, we adopt a network analytical approach to identify biogeographical modules and the topological position of each island within an archipelago's island–species geographic network. In general, a network comprises nodes connected by links, and the concept may characterize many types of systems, for example social networks (Freeman, 1979), metabolic networks (Guimerà & Amaral, 2005a), plant–pollinator networks (Olesen *et al.*, 2007; Martín González *et al.*, 2010), food-webs (Dunne *et al.*, 2002) and biogeographical networks (Carstensen & Olesen, 2009). In a modular network, highly linked subgroups of nodes constitute modules, and a few nodes connect modules together to form one large coherent network. The algorithm we adopt here has previously been used, for example, in metabolic networks (Guimerà & Amaral, 2005a), in various types of ecological networks (Olesen *et al.*, 2007; Dupont & Olesen, 2009; Gómez *et al.*, 2010), and in one island biogeography study (Carstensen & Olesen, 2009).

For each archipelago, we construct a network of islands and bird species. The networks are bipartite, because they consist of two kinds of nodes, namely bird species and islands. If a bird species is present on an island there is a link between the two kinds of nodes. Islands sharing a link to a bird species will then be more similar to each other with respect to this component of their avifauna. The implicit interaction represented by the link is an assumed interchange of individuals via dispersal between islands sharing a link. As well as identifying highly linked subgroups of islands and birds, termed biogeographical modules (Carstensen & Olesen, 2009), the network methodology employed here also classifies islands according to their linkage patterns: their topological position and biogeographical role in the island–bird network. This provides information on how the individual islands contribute to biogeographical connectivity, both within each biogeographical module and across the entire archipelago. As we explain in the Discussion, this may give indications of their roles in source–sink/metapopulation dynamics, and thus in generating and maintaining the species pool of the region. This has the advantage of identifying the spatial importance of islands beyond the importance based on patterns of species richness. In addition to creating a more detailed geographic division than a traditional cluster analysis (Carstensen & Olesen, 2009), our

approach thus provides additional information in giving a more process-oriented overview.

We applied this methodology to the terrestrial breeding bird faunas in Wallacea and the West Indies, two of the largest archipelagos in the world. Both Wallacea and the West Indies are, relative to their position in the tropics, characterized by depauperate biotas with high levels of endemism (Wallace, 1869; Bond, 1948; Lack, 1976; Hedges, 1996; Myers *et al.*, 2000; Trejo-Torres & Ackerman, 2001; Vázquez-Miranda *et al.*, 2007; Ricklefs & Bermingham, 2008; Willig *et al.*, 2009). By comparing Wallacea and the West Indies, we may begin to assess generalities in island-biogeographical network structures (Kueffer & Fernández-Palacios, 2010). Specifically, we aim to (1) identify and compare biogeographical modular structures of birds and islands in Wallacea and the West Indies; (2) assess the role of historical and contemporary factors in shaping each biogeographical module; and (3) determine which island characteristics control island biogeographical roles, and whether these are similar across archipelagos. We focus on classical island characteristics, namely area, elevation and isolation.

## MATERIALS AND METHODS

Both Wallacea and the West Indies are located in tectonically complex regions and combine continental fragments and true oceanic islands (volcanic and uplifted marine sediments). The two regions are of approximately the same geographical extent. However, whereas Wallacea is positioned around the equator (11° S to 6° N), the West Indies are positioned further north (12° N to 27° N) and in a hurricane belt; these differences may affect the structure and composition of their regional biota (Presley & Willig, 2008). Biogeographically, both archipelagos function as dispersal filters between continents. Below we provide an overview of their geological histories relevant for understanding biogeographical patterns.

### Wallacea geological overview

Wallacea consists of three major island groups: the Lesser Sundas, Maluku, and the Sulawesi subregion (Monk *et al.*, 1997). The Lesser Sundas range from Lombok in the west to the Tanimbar Islands in the east and are delimited to the north by the Flores Sea. Most of these islands originate from the volcanic arc created in the subduction zone where the Indo-Australian and the Philippine plates meet. However, Sumba, Timor, and the Tanimbar Islands are continental fragments: Timor and the Tanimbar Islands are Australian whereas Sumba originates from the Sunda Shelf (Hall, 2002). For most of the fragments and volcanic islands, emergence above sea level is relatively recent, that is, < 5 Ma (Audley-Charles, 1993; Monk *et al.*, 1997; Hall, 2002). During the Last Glacial Maximum, lowered sea levels exposed shallow shelves, connecting Lombok to Sumbawa as well as interconnecting all the islands from Komodo to Lombok (Voris, 2000). These islands might even have been connected by a land bridge to Alor, which itself was connected to Timor-Roti, thus interconnect-

ing the majority of the islands in central Lesser Sundas (Monk *et al.*, 1997).

In the Maluku subregion, North and South Maluku differ in geological history. The main North Maluku islands, Morotai, Bacan, and Halmahera and its satellites, originate from volcanic activity in the Pacific and moved along the north New Guinea margin before arriving at their current position within the last *c.* 5 Myr, while the main South Maluku islands, Ambon, Seram and Buru, all are fragments from the margin of the Australian continent (Hall, 1998). These fragments, however, have remained subaerial only during the last few million years (Fortuin & de Smet, 1991; Hall, 1998, 2001). Many of the smaller islands were connected to the larger islands during the Last Glacial Maximum: Seram to its closest offshore islands, and Halmahera to Bacan and some of the smaller western islands (Voris, 2000).

The Sulawesi subregion comprises the large island of Sulawesi and its satellites, including the Talaud Islands in the north, the Sula Islands to the east and the islands in the Flores Sea south of Sulawesi. Sulawesi itself comprises at least four fragments from three geological plates, with the northern peninsula originating as a mobile volcanic chain of oceanic origin, of which the Sula Islands are also a part (Hall, 1998; Moss & Wilson, 1998). Most of these volcanic islands and fragments probably did not emerge above sea level before they reached, or were close to, their current position (Hall, 2001). During the Last Glacial Maximum, Sulawesi was joined with the islands at its south-eastern arm, except for the Tukangbesi Islands. The Banggai and Sula islands were probably not completely connected, but had the distances between them and to Sulawesi drastically reduced (Voris, 2000).

### West Indies geological overview

The West Indies consist of the Greater Antilles, Lesser Antilles, Bahamas, and the peripheral islands of the Cayman Islands, Swan Islands, San Andres and Providencia (e.g. Bond, 1948; Lack, 1976; Hedges, 1996; Ricklefs & Bermingham, 2008). The Greater Antilles are mainly large, mountainous and old islands with a complex geological origin (Iturralde-Vinent & MacPhee, 1999; Graham, 2003). Geological evidence suggests that the proto-Greater Antilles first emerged as separate fragments in the middle Eocene *c.* 49 Ma, and that each of the major Greater Antillean islands consists of several fragments, with some parts having been connected in the past (Iturralde-Vinent & MacPhee, 1999; Graham, 2003). Notably, parts of Cuba have been connected to parts of present Hispaniola and proto-Puerto Rico, but separate movements of the North American and Caribbean plates caused Cuba to detach in the early to mid-Miocene *c.* 25–20 Ma (Graham, 2003). Puerto Rico and Hispaniola separated in the Oligocene or early Miocene. Jamaica, the last of the major Greater Antillean islands, consists of two fragments, which may have been largely, or fully, submerged up until the late Miocene *c.* 12–10 Ma (Buskirk, 1985; Ricklefs & Bermingham, 2008). However, it has also been proposed that the western part of Jamaica

may have been connected to mainland America in the early Eocene, and eastern Jamaica (Blue Mountains) may have emerged as early as *c.* 35–33 Ma and was possibly connected with south-western Hispaniola (Iturralde-Vinent & MacPhee, 1999). The Virgin Islands (except St Croix), Culebra and Vieques to the east of the major Greater Antillean islands emerged in the late Eocene. They are situated on the Puerto Rican bank and were connected to Puerto Rico in the past *c.* 18 Myr (Trejo-Torres & Ackerman, 2001). Despite a potential continental origin of some parts, the current biota on the Greater Antilles was formed only minimally by vicariance, with either dispersal promoted by the Aves Ridge *c.* 35–32 Ma (Iturralde-Vinent & MacPhee, 1999) or, most likely, overwater dispersal, at least for its avifauna (Buskirk, 1985; Graham, 2003; Ricklefs & Bermingham, 2008).

Most of the Lesser Antilles, which form a classic volcanic arc, formed where the North and South American plates subduct under the Caribbean plate. The contemporary Lesser Antilles probably originated not later than 20 Ma (Ricklefs & Bermingham, 2008), and although volcanic activity continues to affect its current avifauna, this probably has a minimal effect on species communities in general (Dalsgaard *et al.*, 2007). To the east of the main volcanic arc are several younger low-lying islands consisting primarily of uplifted marine sediments, for example Antigua, Barbuda and Barbados (Ricklefs & Lovette, 1999; Ricklefs & Bermingham, 2008). Although a few islands were interconnected during the low sea level of the Last Glacial Maximum (Antigua and Barbuda; St Kitts, Nevis and St Barts; Grenada and Grenadines), most islands in the Lesser Antilles have never been interconnected (Ricklefs & Bermingham, 2004, 2008).

The Bahamas are old, low-lying sedimentary islands, being part of the North American platform (Iturralde-Vinent & MacPhee, 1999; Trejo-Torres & Ackerman, 2001). Several of the Bahamian islands were interconnected in the Pleistocene (Trejo-Torres & Ackerman, 2001; Murphy *et al.*, 2004). As with the Bahamas, the peripherally positioned Cayman Islands, Swan Islands, San Andres and Providencia to the south-west of the Greater Antilles are old, and all except Providencia are low-lying mainly sedimentary islands that have probably never been connected to the Greater Antilles (Iturralde-Vinent & MacPhee, 1999; Trejo-Torres & Ackerman, 2001).

### Data

For both Wallacea and the West Indies, we compiled a presence–absence, island–bird species matrix based on a comprehensive review of bird distributions (see Appendix S1 in Supporting Information for a list of references). We included only terrestrial breeding birds, excluding seabirds and non-breeding migratory species, as their distributions are highly affected by non-insular factors (Kalmar & Currie, 2006). We included recently extinct (since AD 1600) and recent natural colonists, but excluded human-introduced species. To make our two archipelago samples more comparable, we excluded continental land bridge islands, while oceanic islands

and continental fragments (microplates) were included in both datasets. Thus, for the Wallacea dataset, New Guinea and its continental satellites east of Lydekker's Line, and the Greater Sundas west of Wallace's Line were excluded, as were Trinidad and Tobago south of Bond's Line and all islands in the fringe of the Caribbean Sea in the West Indies dataset. The resulting matrices consisted of 564 species and 90 islands for Wallacea, and of 243 species and 62 islands for the West Indies.

**Data analysis**

If a bird species is present on an island there is a link between the island and the species. Species never connect to species, and islands never connect to islands; that is, links only connect the two kinds of nodes in the network, forming a bipartite network (Fig. 1a). We used NETCARTO software, which uses an algorithm based on simulated annealing, to assign all nodes (species and islands) to modules, that is, small groups of highly linked nodes (Guimerà & Amaral, 2005a,b). If NETCARTO is run repeatedly, the affiliation of nodes to modules has an accuracy of 90% (Guimerà & Amaral, 2005a,b); for example, in those rare cases where a node has the same number of links connecting it to those modules it is most tightly connected to, it will randomly be assigned to one of these modules. NETCARTO calculates a modularity index *M* of the matrix, 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 (for further explanation, see Guimerà & Amaral, 2005a). To test whether the network is significantly modular, we ran NETCARTO for 100 randomized networks constrained by the same linkage-level ranking as the empirical one. The linkage level of a node is the number of links it has to other nodes. If the empirical *M* value lies above the 95% confidence interval for *M* in the randomized networks, the empirical network is significantly modular.

A topological role was assigned to each node, defined by two parameters as follows (Guimerà & Amaral, 2005a; Olesen *et al.*, 2007).

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:

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

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

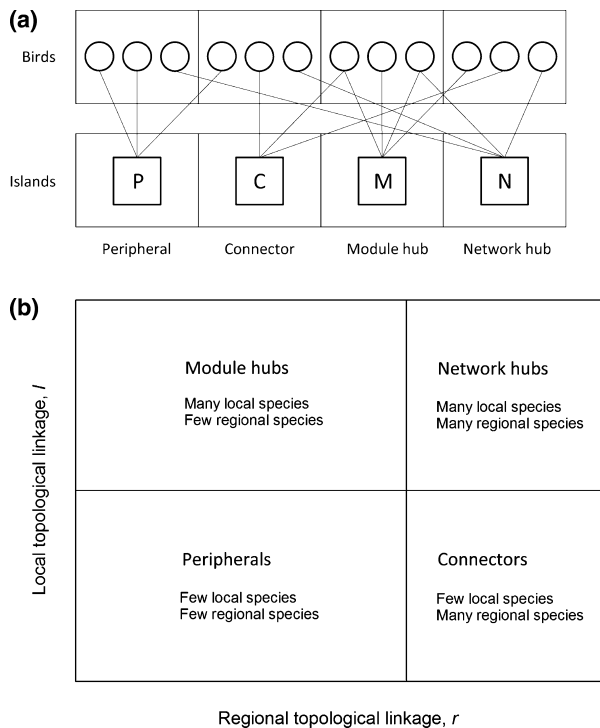
$$r_i = 1 - \sum_{t=1}^{N_M} \left( \frac{k_{it}}{k_i} \right)^2$$

where *k<sub>is</sub>* is the number of links of *i* to other nodes in its own module *s*;  $\bar{k}_s$  and *SD<sub>k<sub>s</sub></sub>* are the average and standard deviation of the within-module *k* of all nodes in *s*; *k<sub>i</sub>* is the number of links of *i*; and *k<sub>it</sub>* is the number of links from *i* to species in module *t* (including *i*'s own module). If *i* has all its links within its own module, *r* = 0; but if these are distributed evenly among modules, *r<sub>i</sub>* → 1 (*r<sub>max</sub>* for a four-module system = 0.75). The species richness of an island and the characteristics of the geographical distribution of its species thus decide the island's position in the two-dimensional *l*-*r* space.

Here we term *l* the local topological linkage and *r* the regional topological linkage in order to translate the network concepts into more context-relevant names. A schematic overview of the biogeographical meaning of an island's position in *l*-*r* space is shown in Fig. 1(b). The horizontal line represents *l* = 2.5, and the vertical line, *r* = 0.625 (for choice of threshold values, see Guimerà & Amaral, 2005a; Olesen *et al.*, 2007). Islands with *r*-values below or equal to 0.625 have at least half of their links within their own module.

An island's value of *l* thus provides information on the number of species from the local fauna (within-module) that the island shares with other islands in the module, relative to the other islands in the module. The value of *r* is a measure of how widely an island's species are shared with islands in other modules, so that an island whose fauna comprises species evenly from all modules obtains the maximum value of *r*. Following Olesen *et al.* (2007), we adopt the following terms for island roles: peripherals, connectors, module hubs and network hubs. Simple examples of each of these roles are illustrated in Fig. 1(a).

A redundancy analysis was used to test which island characteristics were important to an island's position in the *l*-*r* space. This constrained ordination technique combines a



**Figure 1** (a) Illustration of the bipartite network of islands (squares) and species (circles) in four biogeographical modules in Wallacea and the West Indies. Islands exemplify the four biogeographical roles. P, peripheral; C, connector; M, module hub; N, network hub. (b) Schematic overview of the four biogeographical roles in *l*-*r* space. See text for further explanation.

multiple regression and a principal components analysis to detect the explanatory power of the variables in one matrix for the dependent variables in another matrix. Potential explanatory parameters included were: (1) log island area (area, km<sup>2</sup>); (2) maximum elevation (elevation, m); (3) distance to nearest mainland (DNM, km); (4) inter-module isolation (IMI, km); and (5) intra-module position (IMP). Data on island area and elevation were derived from the United Nations Environment Programme island directory (UNEP, 1998), literature sources [e.g. Willig *et al.* (2009) for the West Indies], or were extracted using ARCGIS 9.2. Distance to nearest mainland was measured using GOOGLE EARTH 5.0 (Google Inc., available at <http://www.google.com/earth/index.html>) or based on Willig *et al.* (2009), as were distances used for inter-module isolation and intra-module position. The two measures of module position were calculated as: (1) the distance to the nearest island in another module (IMI); and (2) the ratio between the distance to the nearest island in its own module and the distance to the nearest island in another module (IMP). Inter-module isolation measures whether an island is positioned geographically close to another module, while intra-module position evaluates an island's relative position in its module. Distance to nearest mainland measures the isolation from the most likely mainland source. Values of *l* and *r* were standardized for the redundancy analysis. Significance of variables was assessed with permutation tests. The redundancy analysis was carried out using the *VEGAN* package for R 2.11.1. The data are available upon request from the corresponding author.

## RESULTS

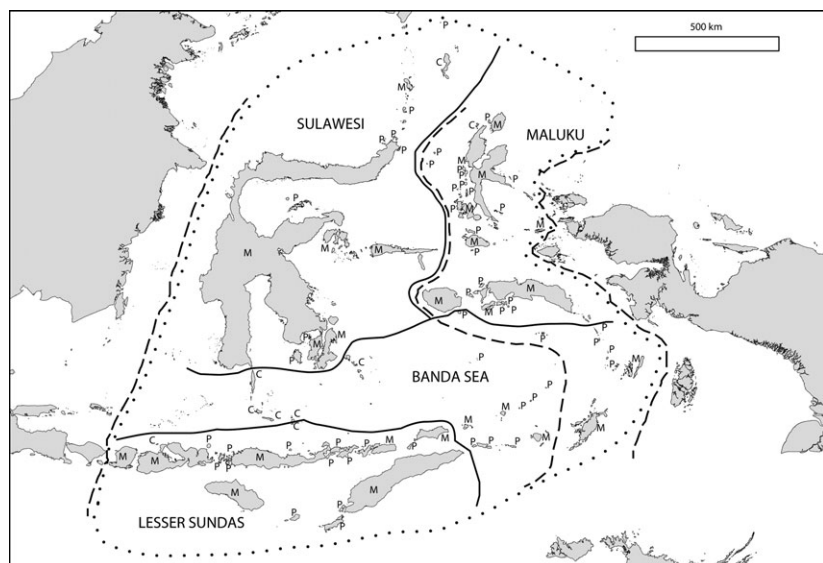
### Wallacea biogeographical modules

The Wallacea network of islands and species was significantly modular [ $M_{WA} = 0.38$ ,  $M_{WA,random} = 0.21$ ,  $P < 0.05$ ,  $M =$  modularity index,  $\in (0;1)$ ], and consisted of four bioge-

ographical modules (Fig. 2). Module names are written in small caps as follows. SULAWESI consists of the largest island in Wallacea, Sulawesi, and most surrounding islands and island groups. MALUKU includes North and South Maluku, with Halmahera as the largest island. LESSER SUNDAS comprises all the islands in the Lesser Sundas west of Timor. The small islands and archipelagos in the Banda Sea and the Flores Sea are grouped in BANDA SEA. This module had the smallest species–island ratio, caused by the many small and remote species-poor islands. In contrast, SULAWESI had the largest species–island ratio, caused by the large and species-rich island of Sulawesi (Table 1). Thus the structure of the four modules differed from each other, with a gradient from a few, large islands and many species to many, small islands and fewer species. The three islands in Wallacea with the largest local topological linkage, *l*, were Sulawesi, Flores and Halmahera, belonging to SULAWESI, LESSER SUNDAS and MALUKU, respectively. Thus these three modules were similar in structure, with one or two large species-rich islands (relative to the other islands in the module) binding the modules together. All modules contained a wide gradient of island sizes.

### West Indies biogeographical modules

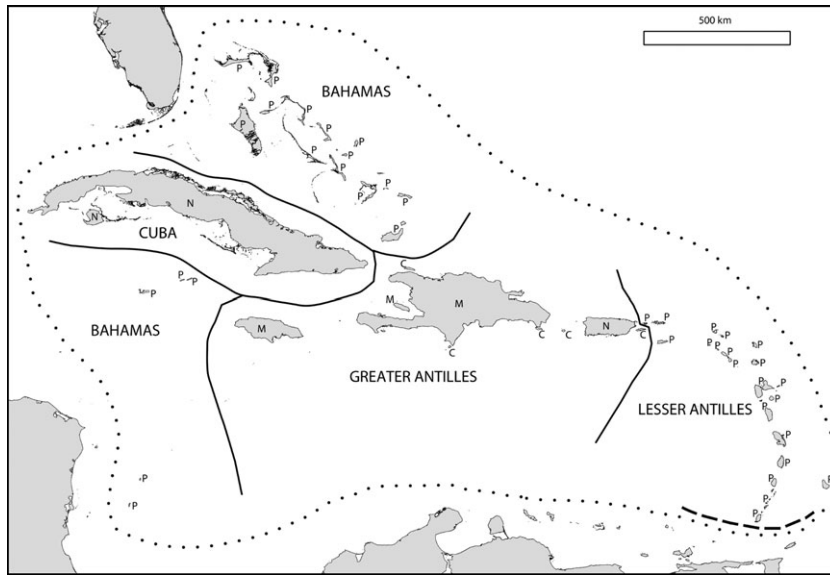
The West Indies network was also significantly modular ( $M_{WI} = 0.35$ ,  $M_{WI,random} = 0.21$ ,  $P < 0.05$ ), and again four modules were detected (Fig. 3). GREATER ANTILLES comprises all the Greater Antillean islands from Vieques westwards, except Cuba and the nearby Isle of Youth, which together form their own module CUBA. The Bahamas north-east of Cuba and the Cayman Islands, Swan Islands, San Andres and Providencia south of Cuba are joined into one module, which we named BAHAMAS, while all the Lesser Antillean and the Virgin Islands, and Culebra north-west of the Lesser Antilles form LESSER ANTILLES (Fig. 3). The difference between modules was much greater here than in Wallacea. There was a clear difference in the size distribution of islands between the modules: GREATER



**Figure 2** Wallacea, with biogeographical modules. The analysed region is delimited by the dotted line, with broken lines marking (from west) Wallace's Line, Weber's Line and Lydekker's Line. Module names are written in small caps. Island roles are indicated with letters: P, peripheral; C, connector; M, module hub. For West Indies modules, see Fig. 3.

**Table 1** Description of each biogeographical module in Wallacea and the West Indies. Module endemics is the percentage of bird species designated to a given module that are not distributed on islands outside that module. These species have a regional topological linkage (*r*) of 0. See Methods section for further explanation.

Archipelago	Module	No. of islands	No. of species	Total area (km <sup>2</sup> )	Mean no. of species per island	Module endemics (%)
Wallacea	SULAWESI	16	162	192,506	10.1	73
	MALUKU	29	162	53,564	5.6	64
	LESSER SUNDAS	22	156	82,701	7.1	64
	BANDA SEA	23	84	10,034	3.7	38
West Indies	GREATER ANTILLES	9	93	98,718	10.3	83
	LESSER ANTILLES	30	69	6836	2.3	67
	CUBA	2	42	112,945	21	71
	BAHAMAS	21	39	16,451	1.9	36



**Figure 3** West Indies, with biogeographical modules. The analysed region is delimited by the dotted line, with Bond's Line marked by the broken line to the south. Module names are written in small caps. Island roles are indicated with letters: P, peripheral; C, connector; M, module hub; N, network hub. For Wallacea modules, see Fig. 2.

ANTILLES and CUBA comprise relatively few, mostly large islands while BAHAMAS and LESSER ANTILLES are almost exclusively small islands (Table 1). This difference between Wallacea and the West Indies was also evident when comparing the *l-r* space (see below).

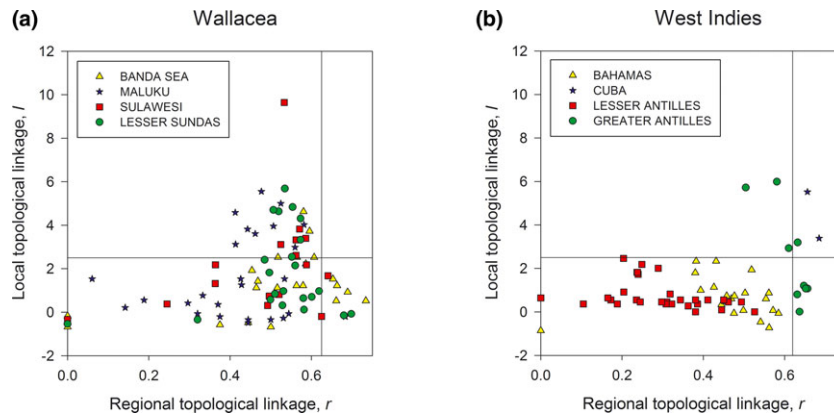
**Role–space comparison**

A higher species–island ratio in Wallacea than in the West Indies (Table 1) caused slightly higher values of *l* in Wallacea than in the West Indies (Fig. 4). The relative distributions of the islands in the *l-r* space, however, were directly comparable. There were marked differences between the two archipelagos: *l* varied as a bell-shaped function of *r* in Wallacea, while *l* varied little in the West Indies, except for some islands with very high values of both *l* and *r* (Fig. 4). Furthermore, in Wallacea there were, at most, small differences between the modules in the role of their islands in *l-r* space, all modules containing peripherals, module hubs and connectors; the archipelago contained no network hubs (Fig. 4a). In contrast, the four modules in the West Indies were strongly differentiated in *l-r*

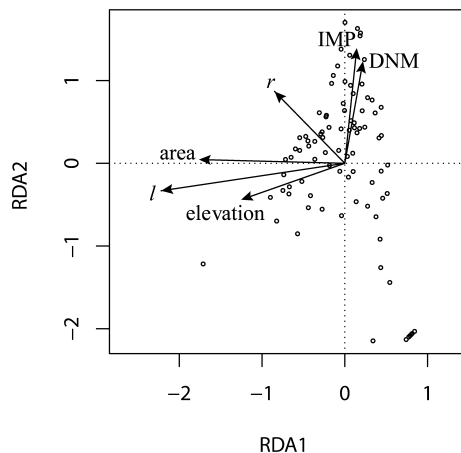
space, with LESSER ANTILLES comprising peripherals with a weak out-of-module linkage, BAHAMAS containing peripherals with a stronger out-of-module linkage, GREATER ANTILLES having connectors and module hubs and one borderline network hub, and CUBA having only strong network hubs (Fig. 4b).

**Island characteristics and roles**

For Wallacea, the redundancy analysis on island *l-r* scores (*n* = 90 islands) as a function of island characteristics explained 49% of the variation, with four island characteristics having significant effects: island area, maximum elevation, distance to nearest mainland, and intra-module position (Fig. 5). The first canonical axis (RDA1) explained 42% of the variation, reflecting an increase of *l*, and also somewhat of *r*, with increasing island area and elevation (Fig. 5). The second axis (RDA2) reflected an increase in *r* with intra-module position and distance to nearest mainland, but only explained 7% of the variation. Thus, larger and more mountainous islands tended to have larger *l* scores and also



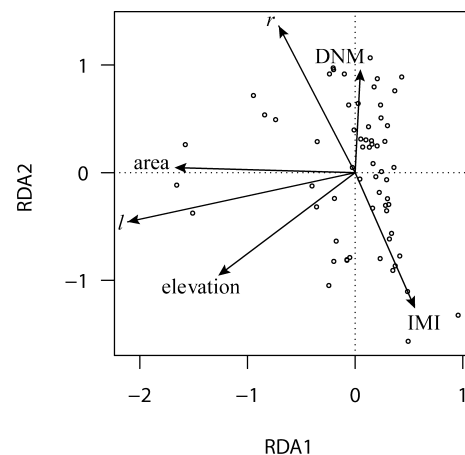
**Figure 4** Island role–space for (a) Wallacea and (b) the West Indies. Notice the strong differences in role assortment between the two regions. In Wallacea all modules contain all possible roles, while roles are highly differentiated between modules in the West Indies.



**Figure 5** Redundancy analysis ordination plot for Wallacea. All islands are plotted from weighted average scores. DNM is distance to nearest mainland, and IMP is intra-module position. 49% of the variation in island  $l$ – $r$  scores was explained by the shown island characteristics. RDA1, reflecting an increase of  $l$ , and somewhat also of  $r$ , with increasing island area and elevation, explained 42%, while RDA2, reflecting an increase in  $r$  with intra-module position and distance to nearest mainland, explained 7%.

slightly increased  $r$  scores, while islands that were far from the nearest mainland and positioned marginally and isolated in their own module had increased  $r$  scores.

For the West Indies, the redundancy analysis on island  $l$ – $r$  scores ( $n = 62$  islands) as a function of island characteristics explained 64% of the variation, again with four island characteristics having significant effects: island area, maximum elevation, distance to nearest mainland, and inter-module isolation. In this case, the first canonical axis (RDA1) explained 45% of the variation and again reflected an increase of  $l$  and  $r$  with island area and elevation, more strongly reflecting  $l$  than  $r$  (Fig. 6). The second axis (RDA2) explained 19% of the variation and reflected that  $r$  increased with distance to nearest mainland and decreased with inter-module isolation (Fig. 6).



**Figure 6** Redundancy analysis ordination plot for the West Indies. All islands are plotted from weighted average scores. DNM is distance to nearest mainland, and IMI is inter-module isolation. 64% of the variation in island  $l$ – $r$  scores was explained by the shown island characteristics. RDA1, reflecting an increase of  $l$  and  $r$  with island area and elevation, explained 45%, while RDA2, reflecting an increase in  $r$  with increased distance to nearest mainland and decreased inter-module isolation, explained 19%.

Thus, as in Wallacea, larger, more mountainous islands tend to have larger  $l$  scores and slightly increased  $r$  scores, while a position far from the nearest mainland and at the edge of its own module also increased an island's  $r$  score.

In conclusion, in both archipelagos  $l$  as well as  $r$  increased with island area and elevation, and  $r$  additionally depended on distance to nearest mainland and module position (intra-module position or inter-module isolation). A table showing area, max elevation and  $r$  and  $l$  scores for the 10 largest islands in each archipelago can be found in Appendix S2.

## DISCUSSION

The network analyses of Wallacea and the West Indies showed similar overall biogeographical structural patterns. Both are

modular systems, illustrating a non-uniform geographical distribution of their avifaunas. As discussed below, the borders of these modules, and thus the boundaries of faunal turnover correspond well with our knowledge of past connections, and contemporary factors (geographical position and island characteristics such as area and elevation), illustrating the role of dispersal barriers/routes and ecological characteristics of islands in delimiting biogeographical modules.

Despite the different distributions of islands and modules in  $l$ - $r$  space in the two archipelagos, there were strong similarities between the two archipelagos in the determinants of island network topological roles. This suggests that these island characteristics may be universally important in controlling how different islands influence the overall structure of avian distributions and the interaction between islands in terms of dispersal patterns, and source-sink dynamics. On the basis of their network topological properties we interpret non-hub islands (peripherals and connectors) potentially to be sink islands. Such islands tend to be small and less mountainous, and thus to have low speciation rates and few endemics (Mayr, 1965; Adler, 1994). Peripherals mainly receive species from source islands within their module, while connectors receive species from source islands around the entire archipelago. Connector islands may therefore be interpreted as stepping stones for dispersing species. Hub islands can then be interpreted as source islands for their modules (module hubs) or the entire archipelago (network hubs). These islands tend to be large and mountainous, thus potentially acting as speciation centres (Rosenzweig, 1995).

Modules, however, were structurally different across the two archipelagos, as were the role distributions of islands within these modules. In Wallacea, modules were 'mini archipelagos', each displaying all three existing island roles, while the modules in West Indies were much more separated in  $l$ - $r$  space, no module representing all possible roles. This highly different topological structure of the network of islands and species, with role assortment happening within modules in Wallacea but between modules in the West Indies, was unexpected from the results that similar island characteristics control island roles in both archipelagos. It is probably related to the different geographical constellation of islands and modules within each archipelago. The West Indies has peripheral modules (BAHAMAS and LESSER ANTILLES), and centre modules (CUBA and GREATER ANTILLES), organized longitudinally, almost like 'pearls on a string', while modules in Wallacea are spatially more 'clumped' together (Figs 2 & 3). Thus, the West Indies are composed of peripheral *modules* and centrally placed connector-network hub *modules* within the whole archipelago. In contrast, Wallacea comprises peripheral and centrally placed connector-hub *islands* within each module. A key explanatory factor could be the more clustered configuration of small and large islands in the West Indies compared with their more interspersed locations across Wallacea.

The assembly of local, single-island communities is influenced by metapopulation and inter-island dispersal dynamics, which are affected by the regional context in which the island is

placed (Ricklefs & Schluter, 1993). Such dynamics may be highly related to the biogeographical role of the island, and thus our results suggest that single island community composition is affected by the overall geographical constellation of islands in the archipelago. In Wallacea, a higher local persistence near the equator and the lack of hurricanes may also reduce the connectivity of islands, allowing the development of 'mini archipelagos'.

Because  $l$  is a measure of an island's links within its own module relative to the other nodes in the module, the island's number of links (its species richness) sets a limit on the maximum value of  $l$ . Species-rich islands will thus often obtain a large  $l$  because many of their species are shared with neighbouring islands. High- $l$  islands are essential for the coherence of their modules, and the species pools of these islands represent the characteristic fauna of the respective modules. Hence, as also indicated by their high proportion of endemics (Ricklefs & Bermingham, 2008), such large and mountainous high- $l$  islands could, owing to their landscape complexity, be centres for speciation (Fjeldså *et al.*, 1999) and therefore source islands to other islands in their module or to the archipelago in general. The identified module borders may thus indicate the main borderline for which islands are sinks or stepping stones for migration/colonization from such species-rich islands. Islands far from the nearest mainland generally had higher  $r$  scores in both archipelagos, possibly because a large part of the species reaching these islands are good dispersers and therefore will be widely distributed in the archipelago.

The biogeography of various taxa has been widely studied in both Wallacea (de Boer & Duffels, 1996; de Jong, 1998; Metcalfe *et al.*, 2001; Jönsson *et al.*, 2008, 2010; Carstensen & Olesen, 2009; Michaux, 2010) and the West Indies (Bond, 1948; Hedges, 1996; Trejo-Torres & Ackerman, 2001; Vázquez-Miranda *et al.*, 2007; Presley & Willig, 2008; Ricklefs & Bermingham, 2008; Willig *et al.*, 2009). For both Wallacea and the West Indies, the boundaries of our biogeographical modules conformed well to the findings in the literature (Vázquez-Miranda *et al.*, 2007; Carstensen & Olesen, 2009), as discussed in more detail below.

### Wallacea biogeographical modules

Differences in physical and climatic conditions such as precipitation and island area correspond well with the module border between LESSER SUNDAS and BANDA SEA (Monk *et al.*, 1997).

North and South Maluku have previously been found to harbour different faunas, for example regarding birds (Michaux, 1998; Carstensen & Olesen, 2009) and dispersal-limited taxa, such as cicadas (de Boer & Duffels, 1996). However, de Jong (1998) showed that North and South Maluku had similar butterfly faunas, corresponding to our findings for the complete terrestrial avifauna. This may be caused more by their common rich source, New Guinea, than by a direct species interchange between North and South Maluku. Our western and southern delimitation of MALUKU follows Weber's



Line, corresponding to the faunal balance between the Asian and Australian regions (Pelseneer, 1904).

The inclusions of the Tukangbesi Islands in *BANDA SEA* and of the Sula Islands in *SULAWESI* correspond well with inter-island connections caused by the lowered sea levels during the Last Glacial Maximum. The general pattern in Wallacea – that most islands did not emerge until *c.* 5–10 Ma (many are even younger) and emerged close to their current positions (Monk *et al.*, 1997; Hall, 2001) – indicates that long-distance dispersal must have had a strong influence upon the current distribution of birds in the region. Island origin does not seem to have a strong influence on module affinity. In *LESSER SUNDAS*, for example, Timor is of Australian origin, Sumba is of Asian origin, and the majority of the remaining islands are of volcanic origin. Similarly in *MALUKU*, the majority of the northern islands are of volcanic origin while the majority of the southern islands are continental fragments. This further indicates that dispersal, not vicariance, played a major role in shaping current species distributions.

### West Indies biogeographical modules

The long-lasting separation of Cuba from the rest of the Greater Antilles (Graham, 2003), along with its large size, mountainous landscape and high endemism, may explain why Cuba and the nearby Isle of Youth form a distinct biogeographical module (Vázquez-Miranda *et al.*, 2007). A complex geological history (Iturralde-Vinent & MacPhee, 1999), geographical proximity and all the major islands being larger and more mountainous than the surrounding low-lying islands of the Bahamas, Caymans and Virgin Islands are possible explanations for the formation of *GREATER ANTILLES*.

Despite their dispersed geographical positions, the islands forming *BAHAMAS* may have close avian similarity, because most are low-lying mainly sedimentary islands (Iturralde-Vinent & MacPhee, 1999). Hence, they may have been colonized mainly by the same widespread 'lowland' species, perhaps with a 'supertramp' life strategy (*sensu* Diamond, 1974), and therefore have few local endemics, whereas the large and mountainous Greater Antilles situated geographically in between have evolved a rich endemic avifauna (Table 1). A close affinity between the Caymans and Bahamas has also been found for orchids, suggesting that vagile animals and orchids may each show similar biogeographical patterns (Trejo-Torres & Ackerman, 2001).

The Virgin Islands have a greater affinity to the Lesser Antilles than to the Greater Antilles (Trejo-Torres & Ackerman, 2001; Willig *et al.*, 2009). This may, at first, seem surprising, as the Virgin Islands (except St Croix), Culebra and Vieques are situated on the Puerto Rican bank and were connected with the Greater Antillean island of Puerto Rico *c.* 18 Ma (Trejo-Torres & Ackerman, 2001). However, geographical proximity to the Lesser Antilles and a similar size and elevation range to many of the northern Lesser Antilles islands, in contrast to the large and mountainous Greater Antillean island of Puerto Rico, may override past geological connec-

tions. Furthermore, hurricane tracks from the Lesser Antilles towards the Virgin Islands and the Greater Antilles may further drive the mixing of the modern avifauna.

### CONCLUSIONS

We conclude that the modularity and predictors of island biogeographical roles are similar for Wallacea and the West Indies and, hence, may represent a general pattern for large archipelagos. The actual build-up of biogeographical modules, however, depends on the geographical constellation of each archipelago. On the basis of classic island characteristics, islands can be classified into biogeographical roles, signifying their importance to the local and regional avifauna. Small, flat islands will be either peripherals or connectors, while large, mountainous islands will be module hubs or network hubs. Whether islands will be connectors or not depends mainly on their spatial position within the archipelago and on the life strategies of the species inhabiting them. Our comparative analysis of bird species distributions in Wallacea and the West Indies thus provides a general description of large-scale biogeographical patterns of archipelagos and the significance of different types of islands in creating these patterns.

### 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, and Steven Presley for allowing us to use island–mainland distances for the West Indies. Financial support was provided by the Faculty of Science and Technology at Aarhus University (D.W.C.), the Danish Council for Independent Research – Natural Sciences (J.M.O. and B.D.), the Danish National Research Foundation for support to the Center for Macroecology, Evolution and Climate (C.R. and J.F.), the Weis-Fogh fund at the Department of Zoology, University of Cambridge (B.D) and Arcadia (W.J.S.). The findings of this study were presented during the Mediterranean Biogeography Symposium, International Biogeography Society (IBS) meeting, held in Crete on 7–11 January 2011.

### REFERENCES

- Adler, G.H. (1994) Diversity and endemism on tropical Indian Ocean islands. *Journal of Biogeography*, **21**, 85–95.
- Audley-Charles, M.G. (1993) Geological evidence bearing upon the Pliocene emergence of Seram, an island colonizable by land plants and animals. *The natural history of Seram* (ed. by I.D. Edwards, A.A. Macdonald and J. Proctor), pp. 13–18. Intercept Ltd, Andover.
- de Boer, A.J. & Duffels, J.P. (1996) Historical biogeography of the cicadas of Wallacea, New Guinea and the West Pacific: a geotectonic explanation. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **124**, 153–177.

- Bond, J. (1948) Origin of the bird fauna of the West Indies. *Wilson Bulletin*, **60**, 207–229.
- Buskirk, R.E. (1985) Zoogeographic patterns and tectonic history of Jamaica and Northern Caribbean. *Journal of Biogeography*, **12**, 445–461.
- Carstensen, D.W. & Olesen, J.M. (2009) Wallacea and its nectarivorous birds: nestedness and modules. *Journal of Biogeography*, **36**, 1540–1550.
- Dalsgaard, B., Hilton, G.M., Gray, G.A.L., Aymer, L., Boatswain, J., Daley, J., Fenton, C., Martin, J., Martin, L., Murrain, P., Arendt, W.J., Gibbons, D.W. & Olesen, J.M. (2007) Impacts of a volcanic eruption on the forest bird community of Montserrat, Lesser Antilles. *Ibis*, **149**, 298–312.
- Diamond, J.M. (1974) Colonization of exploded volcanic islands by birds: the supertramp strategy. *Science*, **184**, 803–806.
- Diamond, J.M. (1975) Assembly of species communities. *Ecology and evolution of communities* (ed. by M.L. Cody and J.M. Diamond), pp. 342–444. Harvard University Press, Cambridge, MA.
- Dunne, J.A., Williams, R.J. & Martinez, N.D. (2002) Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters*, **5**, 558–567.
- Dupont, Y.L. & Olesen, J.M. (2009) Ecological modules and roles of species in heathland plant–insect flower visitor networks. *Journal of Animal Ecology*, **78**, 346–353.
- Fjeldså, J., Lambin, E. & Mertens, B. (1999) Correlation between endemism and local ecoclimatic stability documented by comparing Andean bird distributions and remotely sensed land surface data. *Ecography*, **22**, 63–78.
- Fortuin, A.R. & de Smet, M.E.M. (1991) Rates and magnitudes of late Cenozoic vertical movements in the Indonesian Banda arc and the distinction of eustatic effects. *Special Publications of the International Association of Sedimentology*, **12**, 79–89.
- Freeman, L.C. (1979) Centrality in social networks conceptual clarification. *Social Networks*, **1**, 215–239.
- Gómez, J.M., Verdú, M. & Perfectti, F. (2010) Ecological interactions are evolutionarily conserved across the entire tree of life. *Nature*, **465**, 918–921.
- Graham, A. (2003) Geohistory and Cenozoic paleoenvironments of the Caribbean region. *Systematic Botany*, **28**, 378–386.
- Guimerà, R. & Amaral, L.A.N. (2005a) Functional cartography of complex metabolic networks. *Nature*, **433**, 895–900.
- Guimerà, R. & Amaral, L.A.N. (2005b) Cartography of complex networks: modules and universal roles. *Journal of Statistical Mechanics: Theory and Experiment*, P02001.
- Hall, R. (1998) The plate tectonics of Cenozoic SE Asia and the distribution of land and sea. *Biogeography and geological evolution of SE Asia* (ed. by R. Hall and J.D. Holloway), pp. 99–131. Backhuys Publishers, Leiden.
- Hall, R. (2001) Cenozoic reconstructions of SE Asia and the SW Pacific: changing patterns of land and sea. *Faunal and floral migrations and evolution in SE Asia–Australasia* (ed. by I. Metcalfe, J.M.B. Smith, M. Morwood and I. Davidson), pp. 35–56. A.A. Balkema Publishers, Lisse.
- Hall, R. (2002) Cenozoic geological and plate tectonic evolution of SE Asia and the SW Pacific: computer-based reconstructions, model and animations. *Journal of Asian Earth Sciences*, **20**, 353–431.
- Hedges, S.B. (1996) Historical biogeography of West Indian vertebrates. *Annual Review of Ecology and Systematics*, **27**, 163–196.
- Iturralde-Vinent, M.A. & MacPhee, R.D.E. (1999) Paleogeography of the Caribbean region: implications for Cenozoic biogeography. *Bulletin of the American Museum of Natural History*, **238**, 1–95.
- de Jong, R. (1998) Halmahera and Seram: different histories, but similar butterfly faunas. *Biogeography and geological evolution of SE Asia* (ed. by R. Hall and J.D. Holloway), pp. 315–325. Backhuys Publishers, Leiden.
- Jönsson, K.A., Irestedt, M., Fuchs, J., Ericson, P.G.P., Christidis, L., Bowie, R.C.K., Norman, J.A., Pasquet, E. & Fjeldså, J. (2008) Explosive avian radiations and multi-directional dispersal across Wallacea: evidence from the Campephagidae and other Crown Corvida (Aves). *Molecular Phylogenetics and Evolution*, **47**, 221–236.
- Jönsson, K.A., Bowie, R.C.K., Moyle, R.G., Christidis, L., Norman, J.A., Benz, B.W. & Fjeldså, J. (2010) Historical biogeography of an Indo-Pacific passerine bird family (Pachycephalidae): different colonization patterns in the Indonesian and Melanesian archipelagos. *Journal of Biogeography*, **37**, 245–257.
- Kalmar, A. & Currie, D.J. (2006) A global model of island biogeography. *Global Ecology and Biogeography*, **15**, 72–81.
- Kreft, H., Jetz, W., Mutke, J., Kier, G. & Barthlott, W. (2008) Global diversity of island floras from a macroecological perspective. *Ecology Letters*, **11**, 116–127.
- Kueffer, C. & Fernández-Palacios, J.M. (2010) Comparative ecological research on oceanic islands. *Perspectives in Plant Ecology, Evolution, and Systematics*, **12**, 81–82.
- Lack, D. (1976) *Island biology illustrated by the land birds of Jamaica*. Blackwell Scientific Publications, Oxford.
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ.
- Martín González, A.M., Dalsgaard, B. & Olesen, J.M. (2010) Centrality measures and the importance of generalist species in pollination networks. *Ecological Complexity*, **7**, 36–43.
- Mayr, E. (1965) Avifauna: turnover on islands. *Science*, **150**, 1587–1588.
- Metcalfe, I., Smith, J.M.B., Morwood, M. & Davidson, I. (2001) *Faunal and floral migrations and evolution in SE Asia–Australasia*. A.A. Balkema Publishers, Lisse.
- Michaux, B. (1998) Terrestrial birds of the Indo-Pacific. *Biogeography and geological evolution of SE Asia* (ed. by R. Hall and J.D. Holloway), pp. 361–391. Backhuys Publishers, Leiden.
- Michaux, B. (2010) Biogeology of Wallacea: geotectonic models, areas of endemism, and natural biogeographical units. *Biological Journal of the Linnean Society*, **101**, 193–212.
- Monk, K.A., de Fretes, Y. & Reksodiharjo-Lilley, G. (1997) *The ecology of Nusa Tenggara and Maluku*. Oxford University Press, Oxford.

- Moss, S.J. & Wilson, M.E.J. (1998) Biogeographic implications of the Tertiary palaeogeographic evolution of Sulawesi and Borneo. *Biogeography and geological evolution of SE Asia* (ed. by R. Hall and J.D. Holloway), pp. 133–165. Blackhuys Publishers, Leiden.
- Murphy, M.T., Zysik, J. & Aaron, P. (2004) Biogeography of the birds of the Bahamas with special reference to the island of San Salvador. *Journal of Field Ornithology*, **75**, 18–30.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.
- Olesen, J.M., Bascompte, J., Dupont, Y.L. & Jordano, P. (2007) The modularity of pollination networks. *Proceedings of the National Academy of Sciences USA*, **104**, 19,891–19,896.
- Pelseener, P. (1904) La ligne de Weber, limite zoologique de l'Asie et de l'Australie. *Bulletin de la Classe des Sciences Académie Royale de Belgique*, **1904**, 1001–1022.
- Presley, S.J. & Willig, W.R. (2008) Composition and structure of Caribbean bat (*Chiroptera*) assemblages: effects of inter-island distance, area, elevation and hurricane-induced disturbance. *Global Ecology and Biogeography*, **17**, 747–757.
- Ricklefs, R.E. & Bermingham, E. (2004) History and the species–area relationship in Lesser Antillean birds. *The American Naturalist*, **163**, 227–239.
- Ricklefs, R.E. & Bermingham, E. (2008) The West Indies as a laboratory of biogeography and evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **363**, 2393–2413.
- Ricklefs, R.E. & Lovette, I.J. (1999) The roles of island area *per se* and habitat diversity in the species–area relationships of four Lesser Antillean faunal groups. *Journal of Animal Ecology*, **68**, 1142–1160.
- Ricklefs, R.E. & Schluter, D. (1993) *Species diversity in ecological communities: historical and geographical perspectives*. The University of Chicago Press, Chicago.
- Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge.
- Trejo-Torres, J.C. & Ackerman, J.D. (2001) Biogeography of the Antilles based on a parsimony analysis of orchid distributions. *Journal of Biogeography*, **28**, 775–794.
- Triantis, K.A., Nogués-Bravo, D., Hortal, J., Borges, P.A.V., Adersen, H., Fernández-Palacios, J.M., Araújo, M.B. & Whittaker, R.J. (2008) Measurements of area and the (island) species–area relationship: new directions for an old pattern. *Oikos*, **117**, 1555–1559.
- UNEP (1998) *Island directory. Basic environmental and geographic information on the significant islands of the world*. United Nations Environment Programme (UNEP). Available at: <http://islands.unep.ch/isldir.htm> (accessed 28 August 2010).
- Vázquez-Miranda, H., Navarro-Sigüenza, A.G. & Morrone, J.J. (2007) Biogeographical patterns of the avifaunas of the Caribbean basin islands: a parsimony perspective. *Cladistics*, **23**, 180–200.
- Voris, H.K. (2000) Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *Journal of Biogeography*, **27**, 1153–1167.
- Wallace, A.R. (1869) *The Malay Archipelago*, 1986 edition. Oxford University Press, Oxford.
- Wallace, A.R. (1881) *Island life*. Harper, New York.
- Whittaker, R.J. & Fernández-Palacios, J.M. (2007) *Island biogeography, ecology, evolution, and conservation*, 2nd edn. Oxford University Press, Oxford.
- Whittaker, R.J., Triantis, K.A. & Ladle, R.J. (2008) A general dynamic theory of oceanic island biogeography. *Journal of Biogeography*, **35**, 977–994.
- Willig, M.R., Presley, S.J., Bloch, C.P. & Genoways, H.H. (2009) Macroecology of Caribbean bats: effects of area, elevation, latitude, and hurricane-induced disturbance. *Island bats: evolution, ecology, and conservation* (ed. by T.H. Fleming and P.A. Racey), pp. 216–264. University of Chicago Press, Chicago.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** List of references used for data compilation.

**Appendix S2** Table of the 10 largest islands in each archipelago, with their area, maximum elevation and *r* and *l* scores.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

## BIOSKETCH

**Daniel Wisbech Carstensen** is a PhD student at Aarhus University in Denmark. His main research interests are the biogeography and ecology of insular bird communities, focusing on the region of Wallacea. He has a broad interest in ecology and conservation.

Author contributions: D.W.C., B.D. and J.M.O. conceived the ideas; D.W.C., B.D. and C.R. contributed data; D.W.C., with help from J.C.S. and J.M.O., analysed the data; D.W.C. led the writing; all authors made significant comments on and improvements to the manuscript.

---

Editor: James Richardson