Journal of Biogeography

WILEY

Journal of Biogeography

RESEARCH ARTICLE OPEN ACCESS

Species Traits and Island Biogeography: Wing Metrics Linked to Avian Dispersal Ability Predict Species Occurrence on Remote Islands Worldwide

Ana Maria Bastidas-Urrutia[1] | Matthias F. Biber[1,2] | Katrin Böhning-Gaese[3,4] | Susanne A. Fritz[5,6,7] | Holger Kreft[8,9,10] | Joseph A. Tobias[11] | Patrick Weigelt[8,9,10] | Christian Hof[1,12]

[1]Terrestrial Ecology Research Group, Department for Life Science Systems, School of Life Sciences, Technical University of Munich, Freising, Germany | [2]Terrestrial Zoology, Senckenberg Research Institute and Nature Museum, Frankfurt am Main, Germany | [3]Helmholtz Centre for Environmental Research UFZ, Leipzig, Germany | [4]Institute for Ecology, Evolution & Diversity, Goethe University Frankfurt, Frankfurt am Main, Germany | [5]Senckenberg Biodiversity and Climate Research Centre (SBiK-F), Frankfurt am Main, Germany | [6]Institute für Geowissenschaften, Goethe University Frankfurt, Frankfurt am Main, Germany | [7]German Centre for integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig & Friedrich Schiller University Jena, Germany | [8]Biodiversity, Macroecology and Biogeography, Faculty for Forest Sciences and Forest Ecology, University of Göttingen, Göttingen, Germany | [9]Centre of Biodiversity and Sustainable Land Use (CBL), University of Göttingen, Göttingen, Germany | [10]Campus-Institute Data Science, Göttingen, Germany | [11]Department of Life Sciences, Imperial College London, Ascot, UK | [12]Chair of Global Change Ecology, Biocenter, University of Würzburg, Würzburg, Germany

Correspondence: Ana Maria Bastidas-Urrutia (anamaria.bastidas-urrutia@tum.de)

Received: 12 March 2022 | **Revised:** 10 October 2024 | **Accepted:** 13 October 2024

Funding: This work was supported by Deutsche Forschungsgemeinschaft.

Keywords: birds | colonisation | community assembly | dispersal | ecomorphology | functional traits | hand-wing index | island biogeography | isolation | Kipp's distance

ABSTRACT

Aim: We assessed the influence of island isolation on the composition of insular bird assemblages with a particular focus on species traits associated with dispersal. To do so, we tested whether ecomorphological metrics of dispersal ability, namely hand-wing index and Kipp's distance, increase with increasing island isolation.

Location: Global.

Taxon: Birds.

Methods: We integrated global datasets of island characteristics with distribution and ecomorphological trait information of birds; our final dataset comprised information for 2034 native, resident and terrestrial species inhabiting 2399 islands. Species restricted to islands were removed to avoid potentially confounding effects of speciation, such as the evolution of flightlessness or poor flight on islands. Using the generalised additive models, we tested for the relationship between hand-wing index or Kipp's distance and island isolation, accounting for the effects of island area and spatial autocorrelation. We performed the analyses separately for (i) continental and oceanic islands and (ii) for all terrestrial birds and for passerine birds only.

Results: Hand-wing index and Kipp's distance were positively related to island isolation on oceanic islands, that is bird communities on more isolated oceanic islands were composed of species with wings that had a higher aspect ratio and were more elongated. However, this relationship did not hold for continental islands. We found these patterns to be consistent for all terrestrial birds as well as for passerine birds only.

Main Conclusion: Our study provides strong evidence that island isolation influences the trait composition of island bird assemblages at a global scale. Our results highlight the variation of dispersal-related ecomorphological traits among bird assemblages

https://doi.org/10.1111/jbi.15038

on islands, suggesting that these traits play an important role in mediating the influence of island isolation on community assembly processes on islands.

1 | Introduction

The decrease of species richness on islands with decreasing area and increasing isolation from the nearest mainland is one of the best-known and most frequently investigated patterns in island biogeography. Many previous studies have shown patterns of species richness consistent with this expected relationship (Diamond 1974; Kadmon and Pulliam 1993; Kohn and Walsh 1994; Kreft et al. 2008; Lomolino 1982; MacArthur and Wilson 1963; Matthews et al. 2019; Ricklefs and Lovette 1999; Valente et al. 2020; Weigelt and Kreft 2013), whereas only a few have shown exceptions (Westman 1983; Williamson 1988). While the pattern itself has received much attention, the underlying processes have been less frequently investigated. The classic equilibrium theory of island biogeography (ETIB) assumes that processes such as immigration are only related to the characteristics of the island—with a decrease of immigration rate as isolation increases. Thus, the predictions of the theory are essentially neutral in the sense that they ignore species' identity or functional characteristics (Gravel et al. 2011; Lomolino 2000) and the role of insular geological dynamics for shaping the patterns of species diversity and ecological assemblages (Whittaker et al. 2017).

In recent years, the potential influence of species' traits on diversity patterns in general, but especially on community assembly processes on islands has gained much attention. In a seminal paper, Gravel et al. (2011) suggested that the classic ETIB is limited since it does not consider different trophic guilds or interactions among species and does not predict species identity in local communities. Lomolino (2000) and Jacquet et al. (2017) remarked that the classic ETIB assumes functional equivalence, giving all species the same probability of colonising islands, the isolation-immigration relationship could also be approached from a trait-based perspective (Schrader et al. 2021; Schrader, Wright, Kreft, et al. 2024; Schrader, Wright, Kreft, et al. 2023).

The probability of a species dispersing to an island is not only influenced by the distance from the nearest land area where the respective species occurs, but also by the species' dispersal ability (Lasky et al. 2017; Si et al. 2017; Weigelt et al. 2015) and the geological origin of the islands (Whittaker et al. 2017). As dispersal, we here define the ability of organisms to disperse long distances away from their source of origin (Jonsson et al. 2016; Nathan 2001). Stronger dispersers should be able to cross large distances more easily and are thus more likely to colonise more isolated islands than species with weaker dispersal abilities. Dispersal is a key factor shaping the rate and extent of geographical range expansion and it influences levels of gene flow among populations (Matthysen 2013; Ronce 2007). In a study on Australian archipelagos, for instance, Weeks and Claramunt (2014) showed that dispersal has inhibited diversification, probably because stronger dispersal abilities helped to reduce the effectiveness of isolation effects in limiting gene flow and thus decreasing speciation rates.

The question of how dispersal limitation and isolation have shaped island communities has been studied for decades. Research has focused on how island isolation reduces island species diversity (Lomolino 1982; MacArthur and Wilson 1967) or transforms island species composition compared to the mainland (Kadmon and Pulliam 1993). Other research explains how species (in this case, birds) increase their chances of colonisation over long distances by prioritising dispersal at the expenses of competitive ability, as seen in supertramp species that excel at colonising newly available habitats (Diamond 1974), despite being negatively affected by their isolation (Valente et al. 2020). In a more trait-based approach to dispersal, Cody and Overton (1996) describe how island plant populations over time show a reduction in relative dispersal potential compared to their mainland counterparts. Additionally, research on the passive dispersal of species found how non-standard vectors, such as wind, ocean currents, storms and bird migration, influence the assembly of communities of angiosperms (Baldwin and Wagner 2010; Heleno and Vargas 2015; Renner 2004; Vargas et al. 2014), arthropods and crustaceans (Gillespie et al. 2012), in different archipelagos throughout the planet. When focusing on active dispersal, researchers found that dispersal traits constitute a fundamental part of community assembly. For example, using a trait-based approach, Jacquet et al. (2017) developed an extension of the theory of island biogeography by creating a theoretical framework that explains the scaling of body size with island area and isolation. In turn, Donati et al. (2019) described how dispersal-related traits, as well as historical reef dynamics, can shape tropical fish communities.

Previous studies have revealed a positive relationship between wing trait measures and the ability of birds to fly large distances (Bell 2018; Claramunt 2021; Dawideit et al. 2009; Weeks and Claramunt 2014). Specifically, it has been shown that birds with larger values of the hand-wing index or Kipp's distance, which measure the aspect-ratio of the wing and the elongation of the wing tip, respectively, travel over greater distances (Claramunt and Wright 2017; Dawideit et al. 2009; Lasky et al. 2017; Sheard et al. 2020; Weeks et al. 2022).

In this study, we assess whether birds' dispersal ability, indicated by the respective ecomorphological traits, increases the likelihood of occurrence on remote islands. To address this question, we combine information from global datasets of bird geographic distributions with data on dispersal-related ecomorphological traits and island characteristics to investigate the relationship between dispersal traits of island bird communities and island isolation at the global scale. We expect that dispersal ability increases with increasing island isolation. Since island area and geological history are also thought to play a role, we also control for island area and investigate patterns separately for continental and oceanic islands.

2 | Materials and Methods

2.1 | Data

2.1.1 | Island Data

Island data were obtained from a shapefile of 85,138 islands globally, which includes comprehensive information on island characteristics (Weigelt, Jetz, and Kreft 2013). We considered isolation, area and connection with the mainland during the last glacial maximum as variables representing island characteristics for this study. As an isolation measure, we calculated the shortest distance between the islands' shore and the shore of the nearest landmass larger than 100,000 km^2 using the 'sf' (Pebesma 2018) and 'rgeos' (Bivand and Rundel 2021) packages in R (R Core Team 2021) (Figure S1). The connection with the mainland during the last glacial maximum allowed us to broadly categorise islands into "continental" or "oceanic": continental islands were here defined as those connected to the mainland during the last glacial maximum (18,000 y BP) and oceanic islands as those that were not connected (Weigelt, Jetz, and Kreft 2013). For the analyses, we considered islands with an isolation larger than 1 km (assuming that this distance reflects a dispersal barrier for birds) and smaller than 2045 km (because for isolation values greater than that just two islands remained, with almost 4000 km, creating a statistical gap) and an area larger than 1 km^2 (assuming this as the minimum area needed for the establishment of bird communities). This step reduced the number of islands considered to a total of 13,920 islands (9615 continental and 4305 oceanic) for the analyses.

2.1.2 | Bird Data

2.1.2.1 | Distribution Data. Bird distributions were obtained from two different data sets:

1. BirdLife International and Handbook of the Birds of the World (2018) (referred to as "BirdLife" hereafter). This dataset consists of expert range maps (polygons of geographical distributions) of all bird species globally (11,125). Every species has information related to its presence (e.g., extant, probably extant, possibly extant, possibly extinct, extinct), origin (e.g., native, reintroduced, introduced, vagrant, origin uncertain, assisted colonisation) and seasonality (e.g., resident, breeding season, non-breeding season, passage, seasonal occurrence, uncertain).

2. eBird (2020). This database consists of occurrence points where birds were observed, documenting the distribution, abundance, habitat use and trends of birds through species lists collected by birders. These observations were collected on a global scale and experts review unusual records. For our focal islands, we obtained a total of 54,731,644 records with more than 947,862,800 species observations.

To compile a birds-on-islands dataset, we separately intersected the expert range maps (BirdLife) and the occurrence points (eBird) of each bird species with the island polygons. Doing so resulted in two occurrence matrices with information on the presence and absence of each bird species on each island. For the BirdLife data, we kept all attributes that describe the status of the species, resulting in a total of 7289 island bird species on 17,771 islands. For the eBird data, we kept the records of bird species observed and we found a total of 7318 species on 4030 islands. The database is very comprehensive in many locations but does not provide systematic global coverage, so it is known to underestimate species' presence in some regions of the world (Hurlbert and White 2005; Meyer et al. 2015).

Distribution maps created by BirdLife estimate distributional ranges by extrapolating data according to the habitat of the respective species. Thus, BirdLife maps do not necessarily provide information on the actual presence of the species but on their potential distribution; that is BirdLife's expert range maps are extent-of-occurrence estimates known to overestimate species' presence (Eyres, Böhning-Gaese, and Fritz 2017; Hurlbert and White 2005; La Sorte and Hawkins 2007; Meyer et al. 2016). To increase the likelihood that our bird dataset only contains actual species presences with the correct presence, origin and seasonality, that is to reduce the number of false presences and increase the accuracy of the distributions, we only kept species records from the BirdLife range maps which were also confirmed by species presence records from eBird and vice versa. We are well aware that this is a conservative approach which reduces the sample size of our dataset significantly and records might be excluded even though good historical information may be available for the respective species occurrence. Nevertheless, we assume our intersection approach does increase the reliability of the data used so that it becomes suitable for our analyses.

To match the two occurrence matrices in this way, we intersected them using the species names and the island identity, allowing us to validate the presence of birds on islands. As a result, we obtained a common dataset of 5123 species on 3713 islands.

Finally, we focused on terrestrial, extant, native and resident birds. To do so, we filtered the matching dataset by five aspects: (1) We excluded all bird species which have likely evolved on islands (1248 species), as for these species it is more likely that wing shapes have undergone evolutionary changes which may blur the focus on the ecological processes of dispersal and island colonisation. To do so, we pragmatically assumed that species being present exclusively on islands have a high probability of having evolved there in situ. Vice versa, we assumed that species occurring both on islands and the mainland can more firmly be expected to have colonised islands from a mainland, which represents the set of species of interest, that is those species for which we can infer potential effects of isolation. Following these assumptions, we excluded all species that only occur on islands and kept those species recorded on islands and mainland regions. (2) We excluded all aquatic birds (783 species, including marine and freshwater species), that is all species that can rest on water and for which the distance between terrestrial areas is thus no effective dispersal barrier. (3) We excluded extinct species (191 species), since we did not have information on their ecomorphological traits. The extinct category was derived from the BirdLife data. (4) We excluded all introduced birds (189 species defined by BirdLife as occurring outside of their historical distribution range through either direct or indirect human activity) because they typically did not reach the respective island by covering long distances via active flight but because of human assistance. (5) We excluded all migratory birds (1279 species), that is species that either only breed or winter on the respective island, as for them isolation does not act as a physical barrier, since they can cover long flight distances and their relationship with the islands is seasonal. To exclude the migratory birds, we used the BirdLife International and Handbook of the Birds of the World (2018) classification for seasonality and eliminated all species listed as “breeding season”, “non-breeding season”, “passage, seasonal occurrence”, and “uncertain”, from our dataset.

Our final dataset consisted of 2034 bird species (20.4% of all birds and 39.7% of all island bird's species) on 2399 islands (17.5% of all islands globally) (Figure S2). We also created a subset containing just passerine bird species (order Passeriformes), thereby increasing the comparability of ecomorphological traits and life histories. This passerine subset contained a total of 1165 species on 2187 islands.

2.1.2.2 | Trait Data. As surrogates for dispersal ability, we used information on ecomorphological traits based on museum specimen measurements (Tobias et al. 2022). We used the wing measurements hand-wing index and Kipp's distance for each bird species (Figure 1). The hand-wing index is an estimate of the wing-aspect ratio and therefore provides a correlate of flight efficiency linked to long-distance dispersal. Hand-wing index is considered to be a good surrogate for dispersal ability in birds as well as a strong predictor of natal dispersal distance (Claramunt and Wright 2017; Weeks et al. 2022) and geographic range size (Baldwin et al. 2010; Berthold 1996; Sheard et al. 2020). Kipp's distance measures the tip length of a bird's wing, with larger Kipp's distances indicating a larger elongation of the wing tip, which have been shown to correlate well with birds' dispersal ability (Baldwin et al. 2010; Dawideit et al. 2009). Note that the hand-wing index and Kipp's distance are related traits (Figure 1) and indeed highly correlated (Claramunt and Wright 2017; Weeks et al. 2022). Before integrating information from species distribution and trait databases, we standardised species names in line with those used in the global bird phylogeny (Jetz et al. 2012).

As the island-specific average trait value for the response variable, we first identified the lowest quartile of species for each dispersal trait, that is the smallest 25% hand-wing indices (or Kipp's distances) of all bird species, on each island. Then we calculated the average value across the species in the lower-quartile, to generate a value for each island. To do so, we excluded all islands with fewer than four bird species. We used this lower-quartile approach since we assume that the birds with the smallest dispersal trait values represent the species with the weakest dispersal abilities, thus potentially reflecting a threshold that captures the lower dispersal ability required to reach an island at a certain distance from the next mainland source. In addition, averaging across the lower-quartile provides a value that is less influenced by extreme values in single species than taking a minimum value would be (for a sensitivity analysis using alternative average measures of the hand-wing index, see Table S1 and Figure S3). Thus, we finally worked with 876 species on 1744 islands; specifically, 680 species on 1160 continental islands and 371 species on 584 oceanic islands for all birds; and for Passeriformes with a total of 492 species on 1442 islands; specifically, 418 species on 1008 continental islands and 171 species on 434 oceanic islands (see Figure 2 for an overview).

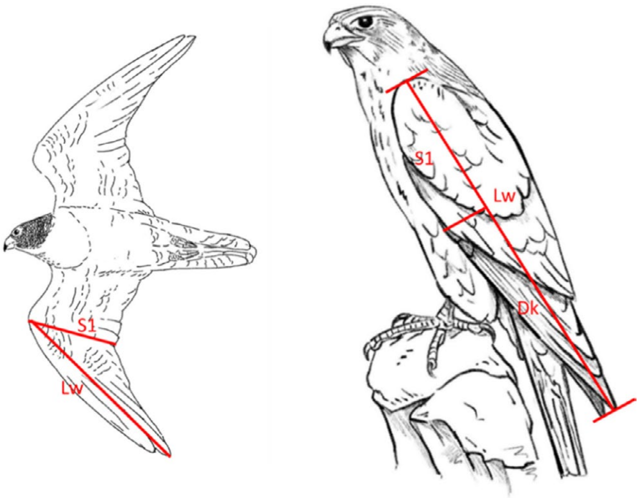

FIGURE 1 | Measurements of dispersal traits on birds. Diagram showing linear measurements: Wing chord (Lw) is the distance from the carpal joint to the tip of the longest primary feather; secondary length (S1) is the distance from carpal joint to the tip of the first secondary feather; Kipp's distance (Dk) is the difference between wing chord and secondary length (Lw—S1); the hand-wing index is calculated as the ratio of Kipp's distance multiplied by 100 and divided by wing chord (100*Dk/Lw). (Own drawing with wing measurements after Sheard et al. (2020)).

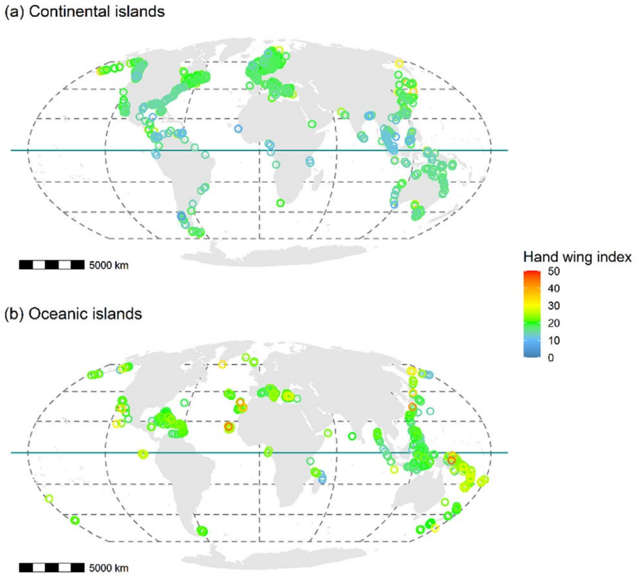

FIGURE 2 | Geographical variation of island isolation as well as the average of the lower-quartile values of hand-wing index for bird assemblages on continental (a) and oceanic (b) islands.

2.2 | Statistical Analyses

To test whether bird communities on more isolated islands possess greater dispersal abilities indicated by their dispersal traits, we used generalised additive models (GAMs). GAMs use a smooth function that provides a flexible approach to identify the effects of independent variables on the dependent variables. They are easy to interpret because they have the same structure as generalised linear models (GLMs) and are more flexible because a strictly linear relationship between the variables is not expected (Hastie and Tibshirani 1986; Wood 2017). With this approach, it is possible to recognise hidden patterns that are omitted in parametric methods. We used the average of the lower-quartile of the dispersal trait value of the bird community as the response variable and island isolation, island area, latitude and longitude as the predictor variables. Latitude and longitude were used in the model as smoothed terms, with a bivariate smooth basis to correct for spatial autocorrelation. Spatial autocorrelation was confirmed to be present using a Moran's I analysis (Moran's $I=0.0060$; ***$p<0.001$), calculated with the "ape" package (Paradis and Schliep 2004).

All GAMs were run in R, using the bam() function from the "mgcv" package (Wood 2011) with a REML smoothing parameter for estimation. The REML method integrates the unpenalized and parametric effects out of the marginal likelihood optimised for the smoothing parameters, that is it leads to the best results in simulations as they tend to avoid occasional severe under-smoothing (Wood 2011). All analyses were performed separately for all terrestrial native resident birds as well as for Passeriformes (as an evolutionarily and ecologically more homogeneous group) and separately for each of the continental and oceanic island datasets.

3 | Results

After controlling for the effects of area and spatial autocorrelation, we found that the hand-wing index increased with island isolation for oceanic islands (Table 1a,b and Figure 3a,b, see also Figure 2 for a geographical depiction of the pattern), but not for continental islands, that is species occurring on more isolated

TABLE 1 | Summary of the effects of island isolation and area as well as spatial autocorrelation on the average of the lower-quartile values of the hand-wing index for all terrestrial native resident birds (first row) and Passeriformes (second row), analysed separately for continental (a, c) and oceanic (b, d) islands. Results are obtained from a generalised additive model (GAM) with a Gaussian family and an identity link function.

All terrestrial native resident birds						
	(a) Continental islands ($n=1160$)			(b) Oceanic islands ($n=584$)		
Parametric coefficients:						
	Estimate	Std. Error	t	Estimate	Std. Error	t
Intercept	18.7	0.083	224.7***	19.8	0.14	146.2***
Smooth terms:						
	edf	p		edf	p	
s(Isolation)	0.000041	0.56		0.70	0.0079**	
s(Area)	1.6	0.0017**		0.48	0.25	
s(Lon, Lat)	54.9	<0.001***		65.0	<0.001***	
		adj. $R^2=0.30$			adj. $R^2=0.46$	
Passeriformes only						
	(c) Continental islands ($n=1008$)			(d) Oceanic islands ($n=434$)		
Parametric coefficients:						
	Estimate	Std. Error	t	Estimate	Std. Error	t
Intercept	17.2	0.058	294.8***	17.2	0.077	223.4***
Smooth terms:						
	edf	p		edf	p	
s(Isolation)	0.000047	0.43		0.26	0.036*	
s(Area)	1.39	0.015*		1.06	0.13	
s(Lon, Lat)	68.01	<0.001***		57.56	<0.001***	
		adj. $R^2=0.57$			adj. $R^2=0.62$	

Abbreviation: edf = effective degrees of freedom.
*$p<0.05$.
**$p<0.01$.
***$p<0.001$.

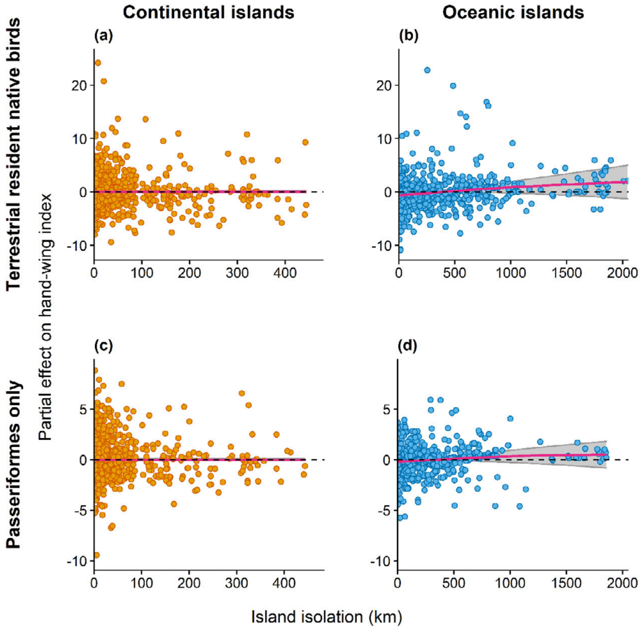

FIGURE 3 | Generalised additive model (GAM) plots showing the partial effects of island isolation on the mean of the lower-quartile values of the hand-wing index for all terrestrial native resident bird species (a, b), and exclusively the species of Passeriformes (c, d), and analysed separately for continental (a, c) and oceanic (b, c) islands. The y-axis represents the partial effect function of isolation on hand-wing index, taking into account the effects of island area and spatial autocorrelation (see Table 1). Light grey shadows indicate 95% confidence bounds. (note that the scale of the *y*-axis differs between the two panel rows and the scale of the x-axis differs between the two panel columns).

oceanic islands showed wing shape consistent with stronger dispersal abilities. For oceanic islands, the effect of isolation on the hand-wing index increased gradually with increasing isolation (Figure 3b). The value of the effective degrees of freedom (edf = 0.70, Table 1b) corroborates that the relationship between the hand-wing index and isolation is close to linear.

The most isolated oceanic islands in our dataset were those of the Fiji archipelago (Figure S1), with an isolation of more than 2000 km, followed by the islands of the New Hebrides archipelago with an isolation of more than 1800 km (Figure S1). However, these islands were not the ones with the largest value for the raw (individual) and lower-quartile average hand-wing index values. Instead, the highest value for the raw and lower-quartile average hand-wing index on oceanic islands was found Benukanare Island (Bismarck Archipelago—Papua New Guinea; Figure 2b), where the isolation value was 254 km, followed by Ilheu Raso island (Cape Verde) with an isolation of 782 km (Figure 2b).

The results were consistent when repeating the analyses only for the subset of Passeriformes (Table 1c,d and Figure 3c,d), even though they showed a weaker effect of isolation on the hand-wing index than for the dataset containing all terrestrial native resident birds (see Table S2 and Figure S4 for the pattern of non-Passeriformes). Results were also largely consistent when using alternative calculations of the average measure of the bird communities' dispersal ability (Table S1 and Figure S3).

When including all terrestrial birds and species that only occurred on islands, we found no relationship between dispersal ability (hand-wing index) and island isolation for continental and oceanic islands, respectively (Table S3 and Figure S5).

When using an alternative ecomorphological trait (Kipp's distance), we found largely consistent results, however with several deviances. The relationship between Kipp's distance and isolation was significant for continental and oceanic islands only when we accounted for body mass in the model (which is important as Kipp's distance scales allometrically with body mass; Table S4c,d and Figure S6c,d). When body mass was excluded from the model, we only found a significant relationship for continental islands (Table S4a,b and Figure S6a,b).

3.1 | Discussion

3.1.1 | Main Findings

In this study, we found evidence for the effect of island isolation on birds' dispersal abilities, as reflected by ecomorphological traits. As expected, the hand-wing index increased on average with the isolation of oceanic islands from the nearest mainland, which suggests that bird species on more isolated islands have stronger dispersal abilities. This finding implies a dispersal filter acting on birds with low dispersal ability on isolated islands, highlighting the importance of dispersal traits for island colonisation. It also suggests that species should not be treated as equal when analysing colonisation processes and biogeographical distributions.

3.1.2 | Hand-Wing Index Versus Isolation

The positive relationship between island isolation and the hand-wing index (as a dispersal trait) was consistent for the analyses of terrestrial native resident birds and the dataset of Passeriformes on oceanic islands. This relation supports the suggestion that the hand-wing index is important in the birds' ability to achieve long flight distances and consequently long distance dispersal (Baldwin et al. 2010; Dawideit et al. 2009; Lockwood, Swaddle, and Rayner 1998). Wings with bigger aspect ratio and more elongated tips are more aerodynamic, as longer and narrower wings reduce drag at higher speed, enhance gliding and soaring ability, reduce the energetic flight costs and allow birds to achieve longer distances with less energy (Baldwin et al. 2010; Bowlin 2007; Bowlin and Wikelski 2008; Lockwood, Swaddle, and Rayner 1998). This may contribute to the observation that birds with bigger aspect ratios and longer wing tips occur more frequently on more isolated islands.

Although the relationship between dispersal ability and island isolation was positive for oceanic islands, it was not significant for continental islands. According to the definition we used here, continental islands were only separated from the mainland for a maximum of 18,000 years (the time of the last glacial maximum). Therefore, the bird communities on those islands are likely a mixture of species that (1) already occurred there before the separation from the mainland, (2) species that went extinct on the island after the last glacial maximum and that have re-immigrated and (3) species that just immigrated for the first time. Our results imply that dispersal traits cannot explain the assembly of bird communities on continental islands.

The ability to disperse over long distances plays a crucial role in the arrival of species to islands, as highlighted by our results. Species must reach the islands before they can interact and establish themselves and dispersal limitations often influence this process (Ord et al. 2017; Vanoverbeke, Urban, and De Meester 2016). However, the subsequent colonisation process requires more than just reaching the island; it also relies on the habitat structure and the variety of species already present on the island, which impact the availability of niche space and, consequently, the success of colonisation (Chase 2007).

In our particular case, we assume that birds would survive under two conditions: (1) that they have the chance to return to the mainland source (reverse colonisation) (Bellemain and Ricklefs 2008), evidencing that there is no entire dependence on the island itself, which would probably be the case for migratory species, that is birds just breeding or wintering on the island; or (2) that they find a food resource on the island (Whittaker and Fernandez-Palacios 2007) (i.e., if the island has vegetation) or in the surroundings or on nearby islands (in the case the island lacks vegetation). The first condition was discarded from our study since we only considered species with resident status on the islands, which implies an establishment of populations and a direct, year-round interaction between the species and the habitat and biophysical conditions of the islands.

While the equilibrium theory of island biogeography (MacArthur and Wilson 1963) already states that the effect of island isolation mainly acts via dispersal, the universality of this theory relies on the assumption of species' neutrality, that is the absence of species-specific differences. In fact, MacArthur and Wilson themselves stressed that this assumption is unrealistic (MacArthur and Wilson 1967). Our findings offer further evidence for the functional non-equivalence of birds. Specifically, the traits related to dispersal in birds influence their ability to reach islands, the possibility of colonisation and the composition of bird communities on the islands. These findings support the conclusions of Jacquet et al. (2017) and the allometric theory of island biogeography, which suggests that functional traits scale with island isolation. Furthermore, our study contributes to a broad range of similar results at various spatial and taxonomic scales (Baldwin et al. 2010; Bowlin and Wikelski 2008; Claramunt 2021; Dawideit et al. 2009; Gillespie et al. 2012).

3.1.3 | Hand-Wing Index in Passeriformes

Separating the analysis into Passeriformes is particularly interesting because they represent the most diverse and widespread order of birds (Jetz et al. 2012), with a wide range of ecological roles and behaviours (Kennedy et al. 2020). This diversity allows us to explore how isolation affects a broad array of species with different dispersal abilities, foraging strategies and habitat requirements, providing a more detailed understanding of the effects of isolation. Additionally, Passeriformes are known for their varying degrees of flight specialisation (Claramunt et al. 2012), making them an ideal group to test whether isolation drives specific adaptations, such as higher hand-wing index values, across species that may otherwise occupy similar habitats. The similarity of the results for all terrestrial native resident birds and terrestrial Passeriformes reinforces the assumption that isolation on oceanic islands has a positive effect on hand-wing.

Initially, we expected that Passeriformes, due to their varying degrees of flight specialisation, would exhibit a more robust pattern than the entire bird dataset. Contrary to our expectations, our findings revealed that passerines displayed a weaker pattern than all terrestrial native resident birds.

There are several potential reasons for this unexpected outcome: (1) high dispersal ability: Passeriformes have strong flight capabilities, enabling large travel distances, which reduce the geographical barriers imposed by isolation, allowing them to more easily colonise distant islands (Claramunt et al. 2012; Warren et al. 2015; Weeks and Claramunt 2014); (2) behavioural flexibility: although Passeriformes depend on island habitats, they exploit a wide range of ecological niches, allowing them to overcome challenges associated with isolated environments (Sol, Timmermans, and Lefebvre 2002); (3) diverse diets: many Passeriformes have varied diets and are not strictly dependent on specific food sources, enabling them to thrive in different environments and exploit niches in different ways (Wilman et al. 2014); Passeriformes are less likely to go extinct upon the arrival of humans to their islands, due to their relatively small body sizes and generalist habits. This allows them to escape predators and to adapt more readily to new conditions, colonising new habitats (Boyer 2008; Owens and Bennett 2000).

A clear example of this is Taveuni Island in the Fiji Archipelago (Figure S1b). It is the most isolated island in our dataset; however, it harbours a highly diverse bird community, including species with a very small hand-wing index, with Passeriformes among them. These results are in line with what Haila, Jarvinen, and Kuusela (1983) described for the Philippines: they found that for some islands, colonisation is regulated by autecological requirements, that is these birds colonise islands depending on the available habitat and their flexibility in habitat use and Taveuni island does exhibit a heterogeneous topography and high habitat diversity. Within our results, we observed some cases which illustrate the relevance of factors other than dispersal limitation for shaping island bird communities.

3.1.4 | Caveats

Our study shows a consistent positive relationship between the hand-wing index and island isolation. However, in ecology and biogeography, especially in global-scale analyses, no single factor drives a pattern. Instead, multiple variables are at play, making it challenging to understand the interplay between isolation, area and the trophic characteristics that structure island communities (Gravel et al. 2011; Holt et al. 1999).

Among others, two additional factors influence the trait spaces of island birds and the variation of dispersal traits: species interactions (Clegg and Owens 2002; Grant and Abbott 1980) and evolutionary processes (Emerson and Patiño 2018; Grant et al. 1976). With regard to species interactions, while we have excluded from our analyses all species that only occur on islands (because they are not informative in terms of dispersal as we have approached it in our study), all other species already present on the island interact directly with those species immigrating into the island community. The species that are already present influence the establishment of new species because they potentially compete for resources such as food and habitat. Considering species richness on each island and its impact on colonisation success is essential, as it may be an indicator for niche availability and competition potential (MacArthur and Wilson 1967). If all niches are already occupied, species with traits suited for long distances may not be able to establish themselves on an island (Tilman 2004). However, we chose not to include species richness in our analyses due to significant correlation between some of the smooth terms in our model. Specifically, there is strong multicollinearity between area and species richness, with a value close to 1 (0.99). This suggests that including species richness as a predictor variable could affect the stability of our model estimates and lead to overfitting and potentially misleading interpretations of the results.

Evolutionary processes are crucial for understanding the relationship between isolation and dispersal traits on islands. While our study highlights the influence of isolation on the hand-wing index, this relationship is also shaped by evolutionary changes that occur over time. Anagenesis, or the gradual evolution of species without branching, is particularly significant in insular environments, where isolation can drive changes in species morphology and behaviour (Losos and Ricklefs 2009; Whittaker et al. 2017). Studies of island bird species have demonstrated that selection pressures on islands, such as limited space and resources, lead to distinct evolutionary outcomes, including changes in flight and dispersal traits. For instance, Clegg et al. (2008) showed how long-term phenotypic changes, including wing morphology, are shaped by island-specific selection pressures and vary across different timescales, while Kennedy et al. (2016) revealed that wing traits are linked to dispersal capacities and species distributions, particularly in Corvides. These examples emphasise how traits, especially those linked to flight, are shaped by isolation and local environmental factors.

Moreover, evolutionary shifts such as flightlessness or morphological adaptations to limited dispersal can occur rapidly, as evidenced by Kirchman (2009), who found parallel speciation of flightless birds on islands, emphasising the role of genetic factors. This highlights how isolation can push species towards lower dispersal capacities over time. Similarly, Weeks and Claramunt (2014) demonstrated that limited dispersal significantly affects avian diversification in archipelagos, while Wright and Steadman (2012) showed how island isolation influences specific adaptive traits in avian species on Neotropical continental islands. Together, these studies suggest that evolutionary processes are critical in determining island trait spaces and can obscure or complicate the relationship between isolation and dispersal-related traits. While all of these studies illustrate the interplay between dispersal, morphological adaptations and selection pressures in shaping island bird evolution, global-scale studies on this complex interplay are scarce. Our global analysis aligns with this body of work, as the positive relationship between isolation and the hand-wing index in our global analysis disappeared when we included species that only occur on islands. (Table S3 and Figure S5). This suggests that evolutionary changes, such as reduced dispersal ability, can influence the overall trait space and blur the relationship between isolation and dispersal traits (Hosner et al. 2017; Wright, Steadman, and Witt 2016).

In particular, global-scale data on intraspecific trait variation are scarce even in birds (Tobias et al. 2022) and datasets comparing islands with mainland populations are lacking for the taxonomic scale of our analysis (Renner and Van Hoesel 2017). We stress again that the trait values for our study represent an overall, species-level average, without differentiation between continental and island populations. Future studies should compare wing measurements from islands and continents within species, as well as species that only occur on islands to their closest relative still surviving on the mainland. These methods were used by Benítez-López et al. (2021) to assess the influence of island isolation on avian wing length and other morphological traits related to body size. Extending these methods to the hand-wing index and Kipp's distance would provide clearer and more precise information on colonisation dynamics and adaptation in relation to dispersal and biogeographical context. This information would not only further clarify the influence of dispersal traits on immigration processes, but would also allow us to understand how these traits are transformed on islands due to island characteristics. While such an analysis is beyond the specific scope of our study, it is a logical next step for further investigations. Despite this, our sensitivity analyses (Table S1 and Figure S3) showed that despite some deviances in different subsets, the overall trend is robust. This implies that isolation has a consistent effect on the dispersal traits of bird species, irrespective of the assemblage assessed.

Finally, it is worth mentioning the long history of extreme anthropogenic impacts on insular species assemblages. Human disturbance, invasive species and habitat transformations have affected natural species interactions on islands (Si et al. 2017), leading to significant extinction and a considerable loss of functional diversity on the islands (Boyer and Jetz 2014), with major impacts on the observed patterns of dispersal traits, for example hand-wing index in birds (Matthews et al. 2022). Species with lower dispersal capacity are more likely to become extinct in the face of anthropogenic intervention (Matthews et al. 2022; see also Boyer 2008; Duncan, Boyer, and Blackburn 2013; Steadman 1995). Also, area and isolation influence extinction processes, with smaller and more remote islands exhibiting higher extinction rates (Matthews et al. 2022; see also Boyer 2010; Duncan, Boyer, and Blackburn 2013). Thus, neglecting the effect of extinct species may represent a possible bias in our interpretation, as the communities of remote islands would probably include more extinct species with weaker dispersal abilities. Although a shortage of data on both the distribution of extinct species across islands and their morphological traits meant that we could not address this issue in our study, we encourage future studies exploring the influence of extinctions on current patterns of island trait spaces and diversity (Fritz et al. 2013; Matthews et al. 2022).

4 | Conclusion

Although different factors affect the assembly processes of island bird communities, our findings suggest that the interplay of island isolation and dispersal ability plays an important role in better understanding the process of colonisation as well as species distributions in general. Furthermore, our results highlight the opportunities for trait-based approaches to test the predictions and assumptions of the theory of island biogeography. Ecomorphological traits related to crucial ecological processes may help us understand how island communities are assembled and such trait-based perspectives of functional ecology are an excellent way to promote the integration of ecological and evolutionary research that is needed to advance the field of island biogeography.

Author Contributions

Ana Maria Bastidas-Urrutia, Christian Hof and Katrin Böhning-Gaese conceived the ideas; Holger Kreft, Patrick Weigelt and Joseph A. Tobias contributed data; Ana Maria Bastidas-Urrutia performed the analyses, with support by Matthias F. Biber and Christian Hof; Ana Maria Bastidas-Urrutia wrote the paper, with significant input of Christian Hof and all other co-authors.

Acknowledgements

This work was supported by the German Research Foundation (DFG) via the research unit DynaCom (FOR 2716; grants HO3952/3-1 & HO3952/3-2). We are grateful to BirdLife International for providing the dataset on global bird species distributions and to the Cornell Lab of Ornithology for providing the eBird Basic dataset in bird species occurrences. We thank also all colleagues from DynaCom and the Terrestrial Ecology Research Group at TUM for their constant and inspiring feedback. Special thanks to Benjamin Leroy for his continuous statistical support, advice and to Matt Biddick for his insights in island biogeography. We also thank two anonymous reviewers for their constructive comments on previous versions of the manuscript. No fieldwork permissions were required.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data is openly available. Island information is available from https://doi.org/10.1073/pnas.1306309110; birds range maps are available from http://datazone.birdlife.org/species/requestdis; bird occurrence information is available from https://ebird.org/data/download and information about dispersal traits on birds is available from https://doi.org/10.6084/m9.figshare.16586228.v3.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.