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SPECIAL FEATURE

Approaches for general rules of biodiversity patterns in space and time

The influence of ecological traits and environmental factors on the co-occurrence patterns of birds on islands worldwide

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Abstract

To understand the mechanisms shaping global species diversity patterns, we focused on species assembly of bird communities on islands, which are ideal for detecting ecological and historical processes. We tested the hypotheses that species traits and island environments interactively shape the phylogenetic structure of island bird assemblages through a variety of ecological processes: habitat filtering, in-situ speciation, extinction, dispersal limitation and competitive exclusion. We assessed the effects of species ecological traits and environment factors on the phylogenetic fields, which defined as phylogenetic distance between individual bird species and co-occurred species within each island, using phylogenetic generalized linear mixed models. Climate and isolation were the most important factors driving the co-occurrence patterns of island bird species: the species' phylogenetic fields were significantly clustered on tropical and/or isolated islands. We also found that the phylogenetic fields strongly correlated with the ecological traits especially for the diet and habitat preferences: the phylogenetic fields tended to over-disperse for granivores and species inhabiting in wetlands or coasts, while frugivores showed clustered phylogenetic fields. Moreover, mobility and body size had substantial effects on species assemblages: long-distance dispersers had clustered phylogenetic fields and small-bodied species showed overdispersed phylogenetic fields.

KEYWORDS

avian ecology, community assembly, functional traits, island biogeography, phylogenetic fields

1 | INTRODUCTION

Reconciling ecological and evolutionary processes that shape the global species diversity patterns is one of the most challenging questions in community ecology and macroecology (Brown, 2014; Wiens & Donoghue, 2004). In this context, the investigations of the phylogenetic relationship among co-occurring species within a site have provided insights of site-specific assembly history (Cardillo, Gittleman, & Purvis, 2008; Cavender-Bares, Kozak, Fine, & Kembel, 2009). For example, Cardillo et al. (2008) suggested that the assemblages on insular mammals are likely to be shaped predominantly by colonization and endemic speciation with some weak effect of extinction. On the other hand, many macroevolutionary studies have revealed the effects of species traits on

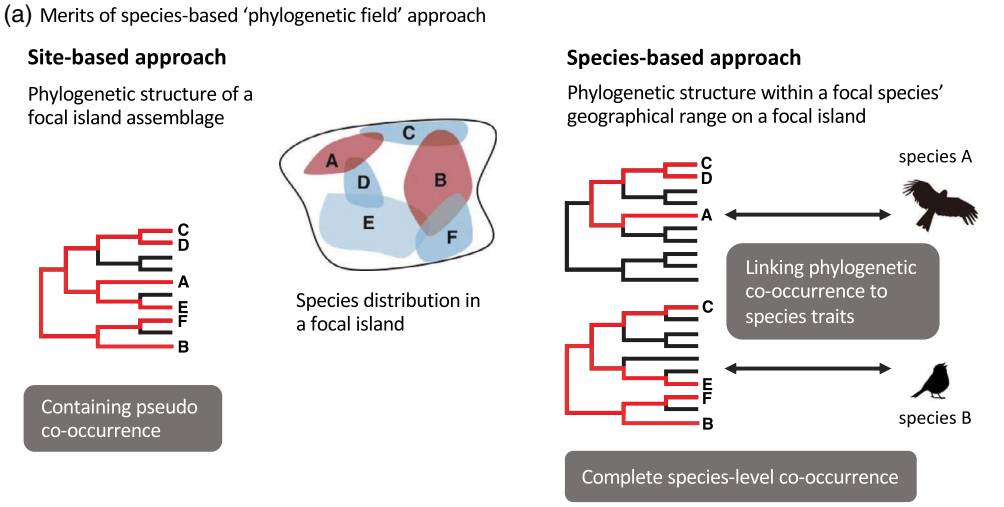
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diversification dynamics using the branching patterns of phylogenetic trees without spatial information. Burin, Kissling, Guimarães, Sekercioglu, and Quental (2016) compared the differences in diversification rate among bird foraging guilds, and showed the lower speciation rate in omnivore guilds compared with the other more specialized ones. However, how site-specific and species-specific characteristics jointly influence species assembly and their relative contributions remain unclear. Therefore, combining these site-based and species-based approaches is a promising way to better understand the mechanisms underpinning global patterns of species diversity and co-occurrence (Barnagaud et al., 2014; Villalobos, Rangel, & Diniz-Filho, 2013).

Species-based "phylogenetic fields," which is recently proposed by Villalobos et al. (2013), allows us to investigate the impacts of species' ecological attributes on species co-occurrence patterns directly. Species-based phylogenetic fields are defined as the phylogenetic structure of species co-occurrence within a focal species' geographical range (Villalobos et al., 2013), which can be measured by ordinary phylogenetic metrics, such as net relatedness index. Phylogenetic fields can directly be linked with ecologically relevant traits of individual species: Barnagaud et al. (2014) revealed the role of key traits, such as body size and migratory behavior, in shaping geographical patterns of species co-occurrence in birds worldwide; Villalobos et al. (2017) showed geographical patterns of phylogenetic and body size structure within focal species' ranges. Furthermore, Miller, Wagner, Harmon, and Ricklefs (2017) combined the species-based phylogenetic fields with functional traits of birds to addresses how environmental factors and/or ecological attributes jointly play a predominant role in species co-occurrence in terms of geographical context. Another merit of a species-based approach is that allows the examination of real co-occurrence among species in a spatial context. Under the site-based approach, there is the high possibility of containing pseudo co-occurrence, because the occurrences of the species were measured at the unit of the "site" which has several spatial extents (Figure 1a; example of island assemblages). In the species-based approach of phylogenetic fields, the co-occurrence could be examined for the "unit cells" which are equal in their sizes even between islands differing in their sizes.

Island assemblages are ideal for analyzing the role of ecological traits and environmental factors on species co-occurrence. As discrete systems, islands allow the detection of historical processes such as dispersal and in-situ speciation that shape the diversity of ecological assemblages (Cardillo et al., 2008; Warren et al., 2015). Island-specific geographic characteristics, for example, area and isolation, are measurable and the critical drivers of island biodiversity (MacArthur & Wilson, 1967; Weigelt, Jetz, & Kreft, 2013). For example, Weigelt et al. (2015) showed that species filtering associated with dispersability, environmental constraints and in-situ speciation leave strong signals in the phylogenetic structure of island floras. Especially in bird species, global distributions (BirdLife International & NatureServe, 2015), phylogenetic relationships (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012) and ecological traits (Del Hoyo, Elliott, & Sargatal, 2013; Del Hoyo, Elliott, Sargatal, Christie, & de Juana, 2018) of almost all species are available, which allow us to investigate the effects of traits on the species coexistence within islands worldwide. Using species-level data on dispersal and migration, which is often difficult to obtain in other taxonomic groups, the role of dispersal limitation can be also examined by hypothesizing that some very mobile bird species can colonize remote islands while species with relatively low dispersal ability are less likely to colonize new islands. Although Kalmar and Currie (2006) analyzed the relationship between taxonomic diversity and island characteristics worldwide, phylogeny or ecological traits of insular bird species have never been linked to island biogeography at the global scale yet.

In this study, we tested the hypotheses that both species traits and island environments shape the phylogenetic structure of island bird assemblages through ecological and historical processes; habitat filtering, in-situ speciation, extinction, dispersal limitation and competitive exclusion (Figure 1b). We examined the four ecological characteristics/traits of birds: habitat, diet, mobility and body size, with examining the phylogenetic constraints, that is, phylogenetic signals, of these traits. The difference in habitat preference among species should affect phylogenetic fields through the process of habitat filtering. Gianuca, Dias, Debastiani, and Duarte (2014) showed that strong niche filtering in harsh environment lead to the clustered phylogenetic fields. If in-situ speciation events affect the phylogenetic structure of island bird assemblages, the species of specialized diet guilds should show the clustered phylogenetic fields, although the effects of inter-specific competition should be taken into account. Mobility (migration and dispersal) is the fundamental factor strongly affecting the island assemblage as shown by the classical model of island biogeography (MacArthur & Wilson, 1967). The dispersal propensity should relate with more clustered phylogenetic fields on more isolated islands because of the dispersability being phylogenetically conserved (Emerson & Gillespie, 2008) and also promoting the diversification by increasing the probability of colonization followed by in-situ speciation events (Rolland, Jiguet, Jønsson, Condamine, & Morlon, 2014). These effects of dispersal propensity should reflect on the island environments; immigration rates should decline with the



(b) Predictions of how ecological traits of birds and island characteristics influence the phylogenetic structure (overdispersion, clustering) of species co-occurrences ('phylogenetic fields')

	Clustered ⟷ Overdispersed			Potential processes	Hypothesis	References
Traits	harsh	Habitat		Habitat filtering	i	Gianuca, Dias, Debastiani, and Duarte (2014)
	specialized guilds	Diet	omnivores	Diversification in specialists	ii	Burin et al. (2016)
	yes	Migration	no	Diversification in migrants	iii	Rolland et al. (2014)
	yes	Dispersal	no	Dispersal limitation	iv	Emerson and Gillespie (2008)
	small ←	Body size	→ large	Diversification in smaller-bodied species Intense competitive exclusion of larger-bodied species	v	Bokma (2004); Olson et al. (2009)
Environments	large ←	Area	→ small	*In-situ* speciation in larger and/or warmer islands	vi	Losos and Schluter (2000); Emerson and Gillespie (2008); Cabral et al. (2014)
	broad ←	Elevation range	→ narrow			
	warm, wet ←	Climate	→ cold, dry			
	stable ←	Climate stability	→ unstable			
	more isolated ←	Isolation	→ less isolated	Dispersal limitation *In-situ* speciation in isolated islands	iv, vi	

FIGURE 1 Testing framework of species-based "phylogenetic field" and site(assemblage)-based approaches for predicting the influence of ecological traits and island characteristics on phylogenetic assembly on islands. While (a) the site(assemblage)-based approach prone to contain commission error (pseudo co-occurrence), e.g., species inhabit a same island but their ranges do not overlay as coexistence, (b) species-based approach is able to capture complete co-occurrence by focusing on a species' geographical range instead of a site. Moreover, species-specific phylogenetic fields (clustering or overdispersion against whole co-occurring species) easily be linked to species and/or island properties. Using species-based phylogenetic field approach that focuses on species-specific geographic range, we can hypothesize that phylogenetic assembly of island birds are shaped through ecological and historical processes related to habitat filtering, in-situ speciation, extinction, dispersal limitation and competitive exclusion that are mediated by species traits and island characteristics

isolation of the island. On the remote islands, predominant effects of in-situ speciation following rare immigration events lead to clustered phylogenetic structure of the assemblages (Cabral, Weigelt, Kissling, & Kreft, 2014). The habitat heterogeneity should also promote the in-situ speciation which lead the clustered phylogenetic fields of the species inhabited the islands. However, competitive exclusion among phylogenetically close species counteracts the phylogenetic structure of the assemblages if the traits are phylogenetically conserved. The body size is frequently linked with the competitive ability of the birds on islands (Clegg et al., 2002; Grant, 1968). Barnagaud et al. (2014) showed that species body mass is negatively correlated with phylogenetic clustering because of intense competitive exclusion of larger-bodied species for the global bird assemblage on the continents.

We firstly calculated the phylogenetic fields for individual bird species using phylogenetic relationship among co-occurring species within their geographical range in each island. We tested nonrandomness patterns of phylogenetic fields (clustering and overdispersion) and then assessed their relationships with ecological traits and environmental variables. Specifically, we tested the following five predictions derived from prior researches (Figure 1b). (a) Dietary specialists have more clustered phylogenetic fields; (b) the dispersal propensity could be linked with more clustered phylogenetic fields on more isolated islands; (c) species body masses negatively correlate with phylogenetic clustering. (d) species inhabiting on islands with harsh environmental conditions exhibits clustered phylogenetic fields; (e) phylogenetic clustering is predominant in species living on larger islands with substantial habitat heterogeneity (via island area and elevational range) and/or under warmer climatic conditions. Based on these predictions, we assessed the importance of ecological and historical processes in shaping species assembly on islands, and finally discussed that how species traits and island characteristics concertedly have patterned the phylogenetic fields of bird species co-occurring on the islands worldwide.

2 | METHODS

2.1 | Distributional data

Using global breeding range maps for all bird species (BirdLife International & NatureServe, 2015), we identified 5,174 terrestrial and freshwater bird species, which inhabit 1,407 islands larger than 100 km^2, excluding Greenland, which is mostly (80%), covered with ice. Island polygons were taken from the Global Administrative Areas (GADM) database (https://gadm.org/data.html). We obtained co-occurring species within a focal species' geographic range per island by evaluating geographical co-occurrence among species at 11 km grid cell level (equivalent to 0.1° near the equator). This means the number of grid cells for each island ranges from 4 (100 km^2) to 6,960 (786,000 km^2 for New Guinea). This size was minimum for the practical calculation times on the NIG supercomputer system at the ROIS National Institute of Genetics (Mishima, Japan). For the analysis of species pools, we assigned each of 9,001 all terrestrial and freshwater extant birds to the 19 zoogeographic regions (Holt et al., 2013). These geographical data compilations were performed using ESRI ArcGIS 10.3 software (http://www.esri.com/software/arcgis).

2.2 | Phylogeny and traits of birds

We used the phylogeny of extant birds (Jetz et al., 2012) and all computations and statistical analyses were repeated using 100 trees randomly chosen from 10,000 possible tree topologies based on the Ericson backbone.

For the analysis, habitat preference, dietary guilds and mobility of each species were determined from a global bird ecology database that covers all the bird species of the world (see Horns, Adler, & Şekercioğlu, 2018) and is regularly updated with Del Hoyo et al. (2018) and other publications. Dietary guilds were classified into seven categories: herbivores, granivores, frugivores, nectarivores, invertebrate eaters, carnivores (including scavenger) and omnivores. Habitat types were classified into forest (forest and woodland), grassland (grassland, plains, savanna and shrub), wetland/coastal (riparian, wetland and coastal) and rocky/desert (rocky and desert). In the present analysis, "major" dietary guild and habitat type for each species determined in the database were utilized. Mobility is summarized into four binary variables related to dispersal and migration behavior: latitudinal migration (yearly, regular, long-distance movement), altitudinal migration (regular movements from high to low altitudes or vice versa based on seasons), post-natal long-distance dispersal (usually once in a lifetime, after leaving nest) and irregular dispersal (nomadic, erratic, irruptive and other irregular movements based on irregular weather patterns, including floods, droughts, etc.). Body size of each species was obtained from Dunning (2008) and Olson et al. (2009) and log-transformed.

2.3 | Environmental variables

We extracted island environmental variables from a dataset of the world's islands (Weigelt et al., 2013): island

area (Area; log km^2), surrounding landmass proportion (SLMP; log proportion) as a measure of isolation, elevational range (Elev; log m), latitude (Lat; °), annual mean temperature (Temp; °C), temperature seasonality (varT; annual range, °C), climate change velocity in temperature (CCVT; log m/year) since the Last Glacial Maximum (LGM) of 21,000y BP, annual precipitation (Prec; mm) and precipitation seasonality (varP; coefficient of variation of monthly means).

2.4 | Phylogenetic fields

We calculated phylogenetic fields (Villalobos et al., 2013) for individual species inhabiting islands: species-based phylogenetic fields indicate phylogenetic assembly pattern of co-occurring species within each species' geographical range on individual islands. In this study, co-occurring species at the island was defined as the species sharing at least one grid cell in the focal island, which could represent the differences in habitat requirement, etc., among species even within an island. Thus, each species occurred on the focal island (species-island set) could show different species-specific values of phylogenetic fields. Phylogenetic fields were measured by "focal" net relatedness index (NRI_F) (Barnagaud et al., 2014) which is a modified version of the NRI (Webb, Ackerly, McPeek, & Donoghue, 2002). While NRI quantifies phylogenetic relatedness of all pairs of species in a focal site, NRI_F focuses on the phylogenetic distance between a species and co-occurring species within geographical range for the focal species (Barnagaud et al., 2014). For a given tree t from 100 replicated phylogenies, NRI_F of individual species i was calculated by the following equation:

$$NRI_{F,i,t} = -1 \times \frac{\text{obs.MPD}_{F,i,t} - \text{mean}\left(\text{rand.MPD}_{F,i,t}\right)}{\text{standard deviation}\left(\text{rand.MPD}_{F,i,t}\right)}$$

Here, obs.MPD_F is the observed mean pairwise phylogenetic distance (in million years) between species i and the all co-occurring species, whereas rand.MPD_F is suit of random expectations of MPD_F. We generated 100 values of rand.MPD_F by a proportional resampling of co-occurring species according to the relative range size of species in a zoogeographic region (sensu Holt et al., 2013) where the focal island is located. In this null model, the number of co-occurring species for focal species in each island was fixed. Positive values of NRI_F indicate phylogenetic clustering whereas negative values indicate overdispersion (Barnagaud et al., 2014). Computation of NRI_F was performed using Python 2.6.6.

2.5 | Statistical analyses

Since habitat/dispersal filtering would cause phylogenetic clustering when the habitat/dispersal related traits are phylogenetically conserved, we checked the strength of phylogenetic signals for each trait. We used Pagel's λ (Pagel, 1999) for continuous data (body size) and the D statistic (Fritz & Purvis, 2010) for categorical data (habitat, diet and mobility). A λ of 0 indicates focal trait is randomly distributed on a phylogeny (i.e., there is no phylogenetic signal), whereas a λ of 1 indicates an expectation of the Brownian motion model (Freckleton, Harvey, & Pagel, 2002). A D statistic of 1 indicates random distribution of focal trait on a phylogeny, while a D of 0 indicates clumped distribution of the trait on the phylogeny as the Brownian motion model (Fritz & Purvis, 2010).

Then we assessed the effects of ecological traits and environments on the phylogenetic fields using phylogenetic generalized linear mixed models (PGLMMs) for 5,161 species on 1,407 islands. In total, 94,542 species × island sets of phylogenetic fields were evaluated in the following analyses. In the PGLMM model, we set NRI_F as the response variables, and the suit of ecological traits: habitat types (categorical); mobility (categorical); body size (continuous) and environmental variables as the fixed explanatory variables. We used the phylogenetic matrix, island, and zoogeographic region as the random effects. To avoid a potential impact of multicollinearity, we summarized nine environmental variables (Area, SLMP, Elev, Lat, Temp, varT, CCVT, Prec and varP) into two principal component axes (PC 1 and PC 2). The PC1 explained 44.9% of the total variance and was correlated strongly with SLMP, Lat, Temp, varT, CCVT and Prec, while the PC2 explained 21.7% of the total variance and correlated strongly with Area, Elev and varP (Figure S1). We scaled continuous predictor variables to improve interpretation of regression coefficients (Schielzeth, 2010). To evaluate the relative importance of each explanatory variable in the PGLMM model, we tested all combination of the explanatory variables and calculated the sum of weight of the deviance-of- information, which is equivalent to Akaike weight, from models accounting for that variable (Burnham & Anderson, 2002). We estimated the model parameters using Markov chain Monte Carlo (MCMC) method where MCMC sampling was repeated for 11,000 iterations with a thinning interval of 10 iterations. We discarded the first 1,000 iterations as burn-in. We sampled a total of 1,000 iterations and checked autocorrelation levels among the MCMC samples; whether it was lower than 0.1 (Hadfield, 2017). We also examined model convergence by running three independent MCMC chains and observing Gelman–Rubin diagnostics; whether the scale reduction factor was lower than 1.1 (Gelman & Rubin, 1992). For random effects, an inverse Wishart prior with

$V = 1$ and $nu = 0.002$ were specified (Gelman & Hill, 2007). Our results were robust to 1,000-fold increases to nu.

The λ and D statistics were calculated with R 3.3.2 (R Core Team, 2016), caper (Orme et al., 2013) and phytools (Revell, 2012) packages. PGLMMs and model ranking were performed with MCMCglmm (Hadfield, 2010) and MuMIn (Barton, 2010) packages.

3 | RESULTS

3.1 | Pattern of phylogenetic fields

Island birds showed a wide range of phylogenetic fields in terms of NRI_F ranged from −7.97 ± 0.06 (mean ± *SD*) to 15.38 ± 5.89, with a mean value of 0.13 ± 0.03 across the 100 replicated phylogenetic trees (Figure 2). Of these, 29,134 (31%) species-island sets exhibited a statistically significant phylogenetic clustering within their geographic range, while 27,358 (29%) species-island sets showed overdispersion evaluated by the consistent positive or negative values for 100 replicated phylogenetic trees. The most clustered phylogenetic fields were observed in pigeons (genus *Columba* and *Streptopelia*) found on small northern (e.g., Faroe Islands). Tropical species such as barbets (genus *Megalaima*) and woodpeckers (genus *Dinopium* and *Dendrocopos*) of Bali, honeyeaters (genus *Myzomela* and *Meliphaga*) of New Guinea and honeycreepers of Hawaii (genus *Hemignathus*, *Himatione*, *Vestiaria*, etc.) also exhibited substantial phylogenetic clustering (see Table S1 for NRI_F of all species-island pairs).

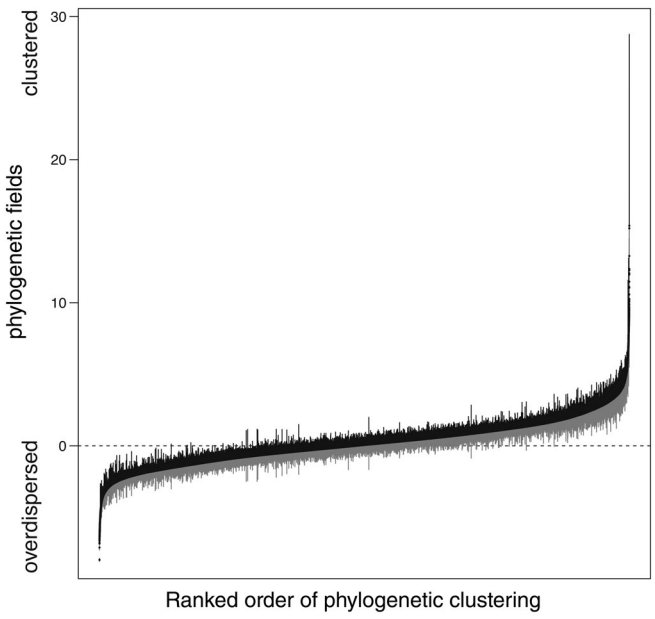


FIGURE 2 Pattern of the phylogenetic fields of 5,161 insular bird species across 1,407 islands. Species-island pairs are ranked by increasing order of phylogenetic clustering. Phylogenetic fields across species geographic range show species-specific values that range from negative (overdispersion), in which species co-occur with distantly related species, to positive (clustering) in which species co-occur with closely related species, compared to a null expectation of phylogenetically random assemblages. For each species-island pair, phylogenetic fields are represented by their mean (solid line) and 5–95% quantiles (dark and light gray shades) across 100 replicated phylogenetic trees

3.2 | Phylogenetic signal in each ecological trait

Body size and diet guilds showed strong phylogenetic signals: the estimated values of λ for body size differed significantly from 0, and D values of diet guilds (except omnivores) significantly deviated from 1 but not from 0 (Table 1). Habitat preference and mobility had

TABLE 1 Phylogenetic signals of species ecological traits. Mean values for 100 phylogenetic trees were shown

Trait	Test statics	*p* (random)	*p* (Brownian)
Body size	λ = 0.97	<.001	
Habitat			
Forest	$D = 0.34$	<.001	<.001
Grassland	$D = 0.51$	<.001	<.001
Wetland/coastal	$D = 0.24$	<.001	.01
Rocky/desert	$D = 0.51$	<.001	<.001
Diet			
Invertebrate eaters	$D = -0.10$	<.001	.91
Herbivores	$D = 0.25$	<.001	.06
Granivores	$D = -0.09$	<.001	.79
Frugivores	$D = -0.05$	<.001	.72
Nectarivores	$D = -0.40$	<.001	1.00
Carnivores	$D = -0.30$	<.001	.99
Omnivores	$D = 0.45$	<.001	<.001
Latitudinal migration	$D = 0.45$	<.001	<.001
Altitudinal migration	$D = 0.76$	<.001	<.001
Post-natal long-distance dispersal	$D = 0.69$	<.001	<.001
Irregular dispersal	$D = 0.70$	<.001	<.001

Note: Phylogenetic signal and its level of statistical significance were evaluated as the test statistics (Pagel's λ and D statics for continuous and categorical data, respectively) and *p*-values, respectively. λ = 0 or $D = 1$ if there were no phylogenetic signals. *p*-values indicate whether the statics is significantly deviated from random or Brownian expectation.

relatively weak phylogenetic signals: *D* values of these traits deviated from both 0 and 1.

3.3 | Relationship with ecological traits and environments

Both ecological and environmental factors had strong effects on phylogenetic fields for individual species (Table 2). PC1, which was positively correlated with Temp and Prec and negatively correlated with SLMP, Lat, varT and CCVT, was a predominant variable and positively correlated with phylogenetic clustering. Moreover, habitat preference and diet guilds had substantial effects. Birds of wetland and/or coastal habitats and granivores showed phylogenetic overdispersion, while frugivorous birds showed phylogenetic clustering. Body mass was positively correlated with phylogenetic clustering. Post-natal long-distance dispersers also showed phylogenetic clustering.

TABLE 2 Drivers of species' phylogenetic fields. The relative importance of environmental factors and ecological traits are evaluated by phylogenetic generalized linear mixed models

Variables	Importance	Coefficients in average
Bird species attributes		
Habitat	0.79	
Forest		(reference)
Grassland		−0.03 (−0.09/0.03)
Wetland or coastal		**−0.20 (−0.29/−0.11)**
Rocky or desert		0.03 (−0.15/0.20)
Diet	0.89	
Invertebrate eaters		(reference)
Herbivores		−0.01 (−0.21/0.20)
Granivores		**−0.17 (−0.31/−0.02)**
Frugivores		**0.18 (0.05/0.31)**
Nectarivores		−0.11 (−0.35/0.13)
Carnivores		0.10 (−0.07/0.27)
Omnivores		0.01 (−0.09/0.11)
Latitudinal migration	0.58	0.02 (−0.01/0.06)
Altitudinal migration	0.57	−0.04 (−0.09/0.01)
Post-natal long-distance dispersal	0.32	**0.05 (0.02/0.08)**
Irregular dispersal	0.48	0.004 (−0.03/0.04)
Body size	0.48	**0.05 (0.0004/0.09)**
Island attributes		
PC1: Isolation (+), temperature (+), precipitation (+), climate change (−)	0.99	**0.12 (0.06/0.17)**
PC2: Area (+), elevation range (+)	0.3	0.01 (−0.01/0.02)

Note: We report sum of weight of models accounting for the variable, which represent the relative likelihood of models, as importance of each variable. For categorical traits, coefficients are expressed as the difference of phylogenetic fields relative to a reference level fixed to 0. Confidence limits for coefficient estimates at 95% CI set are given in brackets. Averaged coefficients with consistently positive or negative slopes indicated by confidence limits are shown in boldface. Plus and minus signs in brackets show whether the environments variable is positively or negatively correlated with PC axes. All values are represented as their mean across 100 replicated phylogenetic trees.

4 | DISCUSSION

Species ecological traits and island environments well explained the species co-occurrence patterns of island bird assemblage at the global scale, which showed parallels with a previous study by Barnagaud et al. (2014). These results strongly suggested that both historical and ecological processes regulate the species coexistence of island bird assemblages. The findings on the effects of island climate and isolations were consistent with our expectations: species on warmer, wetter, more stable and isolated islands and long-distance dispersers had more clustered phylogenetic fields, supporting that in-situ speciation and dispersal limitation shape geographical patterns of species co-occurrence. On the other hand, most of the ecological traits had unexpected effects: the overdispersed phylogenetic fields were found in granivores and species inhabiting wetland or coastal habitats, while frugivores showed a phylogenetic clustering; body size was positively correlated with phylogenetic clustering. These unexpected results may suggest that particular species traits have general effects on species assembly at global scale, which have never been found.

In this study, we discovered some island-specific patterns in phylogenetic fields. Substantially high phylogenetic clustering was seen on northern species-poor islands and on tropical species-rich islands, indicating two distinct mechanisms. Only a small number of clades could colonize the high-latitude islands, while other taxa failed due to distributional constraints or unstable and harsh climate (i.e., niche conservatism hypothesis, Hawkins, Diniz-Filho, Jaramillo, & Soeller, 2006; Kissling et al., 2012). On the other hand, on tropical islands, high rates of in-situ speciation likely cause extreme phylogenetic clustering (i.e., diversification rate hypothesis, Cabral et al., 2014, Rohde, 1992; Wright, Keeling, & Gillman, 2006). These findings were consistent with our expectations: species on warmer, wetter, more stable and isolated islands and long-distance dispersers had more

clustered phylogenetic fields, supporting that dispersal limitation and in-situ speciation, respectively, shape geographical patterns of species co-occurrence. Sandel et al. (2011) showed that low climate-change velocity and low climatic seasonality were associated with the high endemism, hence showing the prevalence of local speciation for amphibians, mammals and birds globally. Villalobos et al. (2013) also found a similar pattern in Neotropical bat species, which showed clustered phylogenetic fields at equatorial and species-rich regions, which suggests higher speciation rates on islands at lower latitudes. In-situ speciation would also be more pronounced on remote and isolated islands because infrequent colonization events give the opportunity to the evolution of new species to fill the available ecological space within islands (Emerson & Gillespie, 2008; Gillespie & Baldwin, 2009; MacArthur & Wilson, 1967).

Habitat preference and dietary guild also affected the phylogenetic fields of island bird species, suggesting that major drivers of species assembly would differ depending on species' ecological strategies. As for the habitat preference, only the wetland- or coastal-specific species showed biased phylogenetic fields of overdispersion. We predicted that species inhabiting harsh environmental conditions exhibit clustered phylogenetic field. This prediction was not supported with the species on harsh habitat, that is, rocky and desert, did not showing any clustered phylogenetic fields. Among the foraging guilds, granivores showed overdispersed phylogenetic fields, whereas frugivores tend to have clustered phylogenetic fields. For the other diet guilds, none of the biased phylogenetic fields were observed. Although the effects of habitat preferences or dietary guild on phylogenetic structure of bird assemblages were rarely examine, several studies showed higher population fluctuation (Barshep et al., 2017) and also population decline (Virkkala & Lehikoinen, 2017) for the bird species in wetland. Kissling, Sekercioglu, and Jetz (2011) reported that global distribution of bird species richness showed pronounced differences between foraging guilds. These all suggested the function of differential drivers, for example, evolutionary innovations in dietary preferences or environmental constraints on distribution, at the species assembly of island bird species, which could be a subject of future studies.

Phylogenetic clustering on the islands are the other features of the phylogenetic fields of island bird species. In the present study, because long-distance dispersal showed only a weak phylogenetic signal (Table 1, Figure 1b), the main driver of phylogenetic clustering on the islands may not dispersal limitation but in-situ speciation (Emerson & Gillespie, 2008). Moreover, large-scale latitudinal migration, which showed a weak phylogenetic signal, had a considerable influence on the clustering of species' phylogenetic fields. This indicates that migrants may co-occur with close sedentary relatives, which is consistent with the finding of Rolland et al. (2014) who showed that settling down of seasonal migrants in newly colonized areas promotes diversification. Body size was phylogenetically highly conserved and negatively correlated with phylogenetic clustering in the present study. This suggests the influence of competitive exclusion on smaller-bodied species in insular bird assemblages. Indeed, Leyequién, Boer, and Cleef (2006) demonstrated that competition strength increased with body mass similarity in bird species. We should note that a coarse categorization of these traits might be inadequate to detect phylogenetic signals. For example, out of 5,161 species we classified only 304 species as long-distance dispersers after leaving the nest. Further studies using more quantitative trait measures, for example, wing shape (Claramunt, Derryberry, Remsen, & Brumfield, 2012), might be needed to effectively test the effect of mobility on phylogenetic structure. We detected only weak effects of geographical features, such as island area or elevational range (Table 2), although, on the islands characterized by large area and/or complex physiognomy, increased in-situ speciation rates and decreased extinction rates have been shown (Ackerman, Trejo-Torres, & Crespo-Chuy, 2007; Kisel & Barraclough, 2010; Losos & Schluter, 2000). Note that we included only present size of the islands in this study, but paleogeographical features such as paleo-area at the LGM may be more important for some islands (Norder et al., 2018; Rijsdijk et al., 2014; Weigelt, Steinbauer, Cabral, & Kreft, 2016).

From a taxon-specific perspective, we can see extensive radiations of several tropical bird species, which showed highly clustered phylogenetic fields, such as *Meliphaga* honeyeaters (e.g., *M. aruensis*, *M. orientalis*, *M. albonotata*) and *Sericornis* scrubwrens (*S. spilodera*, *S. papuensis*, *S. arfakianus* and *S. perspicillatus*; Norman, Rheindt, Rowe, & Christidis, 2007; Norman, Christidis, & Schodde, 2018) in New Guinea. Extreme clustered phylogenetic fields were also seen in pigeons living on small northern islands such as the Faroe Islands (e.g., *Columba livia*, *C. palumbus*, *Streptopelia decaocto*). These pigeon species are widely distributed across Europe (BirdLife International & NatureServe, 2015). For buntings, finches and waxbills (Emberizidae, Fringillidae and Estrildidae) comprising the majority of granivores, the higher levels of competition could also explain the observed phylogenetic overdispersion (Cadena & Loiselle, 2007; Moulton & Lockwood, 1992).

Our results confirm the value of the phylogenetic field approach in island systems. While many island studies focused only on island characteristics (Kalmar & Currie, 2006; Weigelt et al., 2015) or analyzed island

characteristics and species traits separately to test the roles of dispersal and habitat filtering (Carvajal-Endara, Hendry, Emery, & Davies, 2017), the use of phylogenetic fields allow us to directly compare the effects of environments and ecological traits on the co-occurrence patterns of birds on islands worldwide. Moreover, we found the positive effects of body size and temperature on phylogenetic fields, which were opposite from the results of Barnagaud et al. (2014). This indicates that several different processes may shape species co-occurrence patterns on islands versus continents. More comparison between insular and continental assemblages would help to understand what makes island assemblages so unique. In addition, because species traits can influence extinction risk (Heinen, van Loon, Hansen, & Kissling, 2017), using a species-based approach to evaluate non-random extinctions is also important for conservation science (Sobral, Lees, & Cianciaruso, 2016).

In conclusion, combining the species-based approach of phylogenetic fields (Villalobos et al., 2013) and the island as the model ecosystem (MacArthur & Wilson, 1967; Whittaker et al., 2017), we showed that ecological traits and environmental variables jointly influenced the co-occurrence patterns of island birds worldwide. In particular, phylogenetic clustering was strongly determined by tropical climate and island isolation. This could indicate that climatic and biogeographic characteristics were the main drivers of ecological diversification and in shaping species assemblages on islands. Furthermore, we found that ecological traits had substantial effects on species-co-occurrence, even after accounting for abiotic factors; granivorous, wetlands or coastal birds might be sorted phylogenetically through competitive exclusion or extinction. Our study demonstrates that the species-based phylogenetic field, which integrates the role of functional traits in a species-specific geographic range, is a promising approach to better understand ecological and historical processes driving large-scale biodiversity patterns.

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