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Avian Dispersal Ability Shapes Species–Area Relationships on Islands Worldwide

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ABSTRACT

Island biogeography theory provides key insights into biodiversity patterns across islands species–area relationships and conservation. However, classical island biogeography theory assumes that species are ecologically equivalent in terms of their dispersal ability. We evaluated the role of a key trait (hand-wing index, a proxy for dispersal ability in birds) in shaping species-area relationships of avifauna spanning 6706 species on 3894 islands. High community-weighted mean (CWM) dispersal ability in regional species pools had widespread but context-dependent effects on island species-area relationships. Among island archipelagos at smaller spatial extents, high CWM dispersal ability was associated with steeper species-area relationships. Among zoogeographical realms at larger spatial extents high CWM dispersal ability was associated with shallower species-area relationships and higher local species richness on small islands. Our study reveals that geographic variation in species' dispersal traits has strong effects on island species-area relationships and likely plays an important role in non-neutral community assembly.

1 | Introduction

'Why do some islands harbor more species than others?' is a fundamental and enduring question in ecology (Losos and Ricklefs 2010). Fifty years ago, MacArthur and Wilson (1963, 1967) developed the Theory of Island Biogeography to explain patterns of species diversity on islands, a foundational theory that continues to provoke scientific interest across disciplines (Gilbert 1980; Warren et al. 2015; Patiño et al. 2017; Matthews, Triantis, and Whittaker 2021). Two observations are central to core island biogeography theory. First, more isolated islands have lower species richness due to reduced immigration rates (dispersal limitation). Second, larger islands have higher species richness due to reduced extinction rates, an observation that gives rise to the canonical island species–area relationship (ISAR). The log–log ISAR describes how species richness changes with island area via two parameters: the intercept ($\log(c)$) and slope (z): $\log(N_{\text{island}}) = \log(c) + z \times \log(\text{Area}_{\text{island}})$ (Type IV ISAR *sensu* Scheiner 2003). In turn, variation in the slope (z) of the ISAR among ecosystems, regions and taxa can provide important insights into the ecological and evolutionary causes of biodiversity change across spatial scales (Drakare, Lennon, and Hillebrand 2006; Jacquet et al. 2017; Gooriah et al. 2021).

Although powerful in its simplicity, core island biogeography theory assumes that species are ecologically equivalent in terms of their dispersal, mortality and reproductive rates. Nevertheless, MacArthur and Wilson (1967) emphasised the importance of variation in dispersal ability but noted there was 'no information available at this time with which to evaluate the matter [of interspecific variation in dispersal] in a

quantitative fashion' (1967, 132). Recent advances in macro-ecological synthesis echo these calls to unpack the assumption of species equivalence by explicitly integrating species traits into community ecology (Sidlauskas et al. 2010; McGill et al. 2019; Spasojevic et al. 2018). For example, meta-analyses and empirical studies have revealed notable effects of species body mass in explaining variation in ISAR characteristics (e.g., Finlay, Esteban, and Fenchel 1998; Hillebrand et al. 2001; Drakare, Lennon, and Hillebrand 2006; Jacquet et al. 2017). In these studies, body mass has been considered a proxy for dispersal ability. However, body mass has multifarious other impacts on selective processes that can simultaneously constrain species distributions and impact ISARs. For example, larger body mass also increases intraspecific and interspecific competitive ability (Leyequién, De Boer, and Cleef 2007; Miller et al. 2017), cold tolerance (Bergmann 1847) and fasting endurance (Calder 1974). Other studies have used discrete functional or phylogenetic groups in lieu of a continuous measure of dispersal ability (e.g., forest-interior birds vs. widespread birds, herbivores vs. predators; Aranda et al. 2013; Wu et al. 2016; Jacquet et al. 2017). However, like body mass, these proxy variables are often only loosely tied to dispersal ability and instead highly correlated with other aspects of life history (Pigot et al. 2020). Thus, it remains unclear to what extent variation in dispersal ability *alone* can impact ISARs.

Global macroecological databases on birds offer a unique opportunity to evaluate the contribution of a key dispersal-related trait to ISARs. Sheard et al. (2020) compiled morphological measurements of the Hand-Wing Index (HWI) for ca. 10,000 species of birds, covering nearly all Aves. HWI is an appropriate measure of dispersal ability in birds with mechanistic links to biodiversity patterns: variation in HWI has been linked to increased natal dispersal distances (Claramunt 2021; Chu and Claramunt 2023), gap-crossing ability in fragmented landscapes (Claramunt, Hong, and Bravo 2022), geographic range size (Sheard et al. 2020) and ability to track elevational range shifts (Neate-Clegg et al. 2021). In the context of island biogeography theory and ISARs, island communities within regions that contain species with greater dispersal ability (e.g., higher HWI) should generally have higher rates of immigration, lower spatial aggregation of species and higher local species richness as high dispersal ability allows species to move farther across landscapes (Figure S1). Empirical studies at small and intermediate scales have generally found positive effects of dispersal on SAR intercepts (Aranda et al. 2013; Finlay, Esteban, and Fenchel 1998; Hillebrand et al. 2001; Walentowitz et al. 2022) or slopes (Drakare, Lennon, and Hillebrand 2006; Wu et al. 2016), although ISARs can exhibit scale-dependence (Drakare, Lennon, and Hillebrand 2006; McGill 2011). However, it remains unclear how dispersal impacts ISARs at local and global scales.

In this study, we evaluated the role of a key dispersal trait (HWI) in shaping bird ISARs worldwide. We tested how dispersal ability influences ISAR slopes and intercepts using two independent datasets and a recent study of HWI across birds (Sheard et al. 2020). First, we used data from a recent meta-analysis of ISARs estimated for archipelagos at smaller spatial extents (Matthews et al. 2019) and combined these data from a recent study of HWI across birds (Sheard et al. 2020). Second, we constructed a new database of avian island biodiversity, inspired by Kalmar and Currie (2006), which we used to calculate new
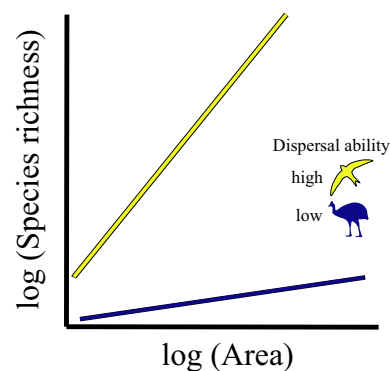

FIGURE 1 | Prediction of effects of dispersal on the island species–area relationship (ISAR). Island communities within a region that contains species with greater dispersal ability (yellow ISAR) have a higher intercept and steeper slope compared to a region that contains species with lower dispersal ability (blue ISAR).

ISARs at larger spatial extents for all zoogeographical realms worldwide (Holt et al. 2013) while accounting for geographical and climatic characteristics of islands. To characterise dispersal ability, we calculated the community-weighted mean (CWM) HWI at varying levels of biological organisation (Lavorel et al. 2008; Spasojevic et al. 2018), from communities of co-occurring breeding birds on islands to global zoogeographical realms (Holt et al. 2013). If higher CWM(HWI) in a regional species spool increases dispersal into local communities and decreases spatial aggregation of species, we predicted that higher CWM(HWI) in a region increases the ISAR slope and intercept (Figure 1, Figure S1).

2 | Methods

We tested our prediction (Figure 1, Figure S1) using two independent databases. To test whether dispersal ability influences the ISAR at smaller spatial extents (hereafter 'small scale'), we used data from a recently published database of ISARs for 21 island archipelagos where island area ranged from 4963 to 150,000 km^2, (Matthews et al. 2019). We tested whether these ISAR intercepts and slopes vary according to the dispersal ability of birds in their corresponding realms (described below). To expand our tests to larger spatial extents (within and across zoogeographical realms, hereafter 'large scale'), we constructed a new database of global terrestrial avifauna spanning 3894 islands from all 11 zoogeographical realms worldwide where island areas ranged from 4963 to 785,750 km^2. We then tested whether these newly estimated ISAR intercepts and slopes vary according to the dispersal ability of birds in their corresponding realms. The large-scale dataset only captured 139 of the 375 islands used for the small-scale dataset. For the 128 islands in both datasets that had species richness available, richness estimates were highly correlated ($t = 26.211$, df $= 126$, p-value < 0.01, Rho $= 0.919$), validating the use of the large-scale dataset (Figure S2). As additional geographic and climatic factors also explain variation in species richness, we performed one additional test of our prediction at the large scale with nine ecological factors using multiple regression. This analysis tested for an additive effect of dispersal ability on island species richness (i.e., effect on

ISAR intercept) as well as an interaction between island area and realm-dispersal ability (i.e., modulating effect of dispersal ability on ISAR slope). R code for all analyses is provided in the Supporting Information on Zenodo. A detailed methods section is provided in Supporting Information S1.

2.1 | Effects of Dispersal Ability on Island Species–Area Relationships at Smaller Spatial Extents

For the small-scale analysis, we compiled data from a recent meta-analysis of factors influencing smaller-scale ISARs within island archipelagos (Matthews et al. 2019). We chose only the studies that reported ISARs of birds on islands ($N = 21$ island groups in nine different zoogeographical realms), extracted their log(c) and z parameters and assigned each island group to a zoogeographical realm that its islands intersected with following Holt et al. (2013). We then combined realm and HWI data from Sheard et al. (2020) and estimated the dispersal ability of the zoogeographical realm by calculating the CWM of the HWI as the average dispersal ability of all species in the zoogeographical realm ('realm CWM(HWI)', Figure S3). However, our metric of realm dispersal ability is an imperfect proxy variable that is influenced by whether and how to weight CWMs by species abundance (ter Braak 2019; Zelený 2018; Miller, Damschen, and Ives 2019; Zheng et al. 2022) and uncertainty in estimates of global population sizes of birds (Callaghan, Nakagawa, and Cornwell 2021; Robinson et al. 2022). Therefore, we present unweighted CWMs of HWI, and acknowledge that the inferences drawn from our approach are likely sensitive to variation in global and local population size estimates.

Our approach adopts a broad definition of the 'regional species pool', where dispersal within but not across zoogeographical realms is plausible. Thus, our approach conservatively defines a regional species pool as equivalent to the biota of a zoogeographical realm. This approach makes several assumptions (Si et al. 2022; Triantis et al. 2022): (1) regional pools are defined using current species distributions despite changing over time (e.g., islands are routinely connected to mainlands during glaciation cycles; Siddall et al. 2003), (2) all species in the regional pool are able to disperse to and successfully establish in local communities and (3) regional pools are constructed at the species level instead of higher taxonomic levels. This definition of the regional pool makes tractable the geographic variation in the relative contributions of high-dispersal taxa to a region's avifauna.

Finally, we fitted spatial regression models (detailed below) with realm CWM(HWI) as the predictor of ISAR parameters (slope and intercept) to test the prediction that higher dispersal ability in the regional pool increases slopes of ISARs at small spatial scales within zoogeographical realms (Figure 1). Weighted regression models with the number of islands as weights as well as mixed effects models with lmerTest (Kuznetsova, Brockhoff, and Christensen 2017) using realm as a random intercept revealed qualitatively identical results. Last, we performed a robustness analysis to evaluate the contributions of three additional archipelago-level variables from Matthews et al. (2019).

2.2 | Effects of Dispersal Ability on Island Species–Area Relationships at Larger Spatial Extents

For the large-scale analysis, we tested the effect of dispersal ability on ISARs by expanding our analyses to encompass more and larger islands. Because the species identities used to construct the small-scale ISARs were not available in Matthews et al. (2019), we constructed new ISARs using species for which dispersal ability was available. Following Kalmar and Currie (2006), we constructed a global database of bird species on islands and calculated one ISAR for each of the 11 zoogeographical realms worldwide. We used a global database of coastlines (South 2017) to trace and polygonise island perimeters, which yielded 4080 islands worldwide. We estimated the species richness on each island by finding the intersection of the terrestrial species' breeding ranges from Birdlife International (2018) and each island/polygon.

We then assigned each island to a zoogeographical realm by determining, for each island, the realm with which most of its area intersected, or its nearest zoogeographical realm if no intersections were found (Figure S4). This yielded 3894 islands that were inhabited by at least one terrestrial bird's breeding range. Then, we calculated one ISAR for each of the 11 zoogeographical realms separately by regressing the natural logarithm of the species richness on islands as a function of the natural logarithm of island area and extracting the log(C) and z parameters. Following the same approach for the small-scale analysis, we fitted spatial and weighted linear regression models with realm CWM(HWI) as the predictor of the newly calculated ISAR parameters to test how greater dispersal ability in the regional pool influences intercepts and slopes of ISARs. Last, we explored the robustness of our results to uncertainty in the ISAR parameter estimates and outliers and our findings remained qualitatively unchanged (Supporting Information S1).

2.3 | Effects of Dispersal Ability on Island Species–Area Relationships Using Speciose Families

As HWI also varies phylogenetically and with foraging ecology (Sheard et al. 2020), we stratified our large-scale analysis by family and used speciose avian families as replicates within zoogeographical realms. We constructed 248 ISARs, one for each family within a realm. For each family in each realm, we also calculated the CWM(HWI) by averaging the HWI of all confamilial species in the realm (Figure S5). We retained all ISARs that had a minimum of 30 species per family in the insular avifauna and regional pool (Supporting Information S2), as this represented a good balance between data quantity and quality (Figure S6). We then ran weighted linear regression (wLR) models to explore the effect of log-transformed CWM(HWI) on the ISAR's intercept and slope, using the number of islands in each ISAR as weights. We also used weighted phylogenetic linear mixed models (wPGLMM) to account for the repeated sampling of families across realms and the phylogenetic relatedness of families. We fitted the phylogenetic models in brms (Bürkner 2017, 2024) and calculated phylogenetic signal (λ). We examined the robustness of our results by running both wLR and wPGLMM models on two additional subsets of the novel realm-family ISARs (minimum of 10 or 50 species per family). Ten out of these twelve models yielded qualitatively identical conclusions.

2.4 | Additional Drivers of Island Bird Diversity at the Global Scale

Species richness is also governed by climatic and geological variables. Therefore, we tested our prediction at a large scale in a complementary analysis using multiple regression and 3574 islands as sampling units. We first measured the dispersal ability of each island's avifauna by calculating the island CWM(HWI) of all its terrestrial breeding birds (Figure S7). For each island, we then determined an index of terrestrial isolation (Kalmar and Currie 2006), elevational ranges (Hollister et al. 2020) and climate heterogeneity (Fristoe, Iwaniuk, and Botero 2017). Using six climate variables (mean, within-year-variance and predictability of temperature and precipitation) from an over 100-year-long time series, we performed a principal component analysis (Revelle 2021), which reduced these data down to two major environmental raster layers: PC1 (52% proportion variance) characterised temperature harshness and PC2 (37% proportion variance) characterised xeric harshness (Table S1). For each island, we selected the values of PC1 and PC2 covered by its coastline and calculated their mean and standard deviation. Climate heterogeneity was defined as the sum of intra-island standard deviations in PC1 and PC2. We then fitted spatial regression models of log-island diversity as a function of scaled and centred predictor variables, which had been log-transformed when necessary. As many islands belong to the same realm, we also performed a mixed effects regression model using lmerTest (Kuznetsova, Brockhoff, and Christensen 2017) using realm as a random effect, which revealed qualitatively similar results.

2.5 | Contributions of Migratory Species and Passerines

We also evaluated the contribution of migratory species, as seasonal migration is a life-history strategy to 'remain in place' during the breeding season by departing towards wintering grounds when conditions become unfavourable (Winger et al. 2019). Migrants, therefore, contribute ephemerally to species richness, especially in temperate zones (Sheard et al. 2020). Despite this potential correlation between climate and island dispersal ability, predictors in multiple regression models were sufficiently independent (Table S2). Next, we examined the validity of our results by repeating the main analyses within two speciose taxonomic clades, the perching birds (order Passeriformes, $N = 7841$ species) and all others (non-passerines, $N = 5201$ species in BirdLife taxonomy), which covered comparable ranges of dispersal ability (range HWI Passeriformes: 1.98–58.43; range HWI Non-passeriformes: 0.01–74.28). Last, we reran all analyses using standardised HWI values by centring HWI on each order's mean HWI. For simplicity, we present the raw HWI values in the main text.

2.6 | Contributions of Range Size

Species with large range sizes might disproportionately contribute to local diversity and inflate ISAR intercepts, especially in the temperate zone. For example, larger range polygons

could increase the chance of false presences on islands. Therefore, we evaluated the relative contributions of dispersal ability and range size in three robustness analyses. First, we calculated CWM of range size (Sheard et al. 2020) at realm and island levels, reran all analyses using CWM(log(range size + 1)) instead of CWM(HWI) at realm and island levels and compared measures of model fit. Next, we added CWMs of range size as additional predictors in all models. Finally, we recalculated CWMs of HWI while weighting by range size and reran all analyses.

Following Freckleton and Jetz (2009) and Cardillo and Skeels (2016), we refitted each final regression model with a spatial regression model while accounting for inter-centroid spatial distances (of islands, archipelagos and realms) to inform the variance–covariance matrices of each spatial regression model (Figures S8–S10). Results from spatial and non-spatial regression models were qualitatively identical.

3 | Results

ISARs varied substantially worldwide with ISAR slopes (z) ranging from −0.055 to 0.388 among zoogeographic realms at the large scale (Figure 2). At the small scale, ISAR slopes from Matthews et al. (2019) ranged from 0.066 to 0.544. Mean dispersal ability, the CWM(HWI) of a realm, also varied substantially across realms (mean = 27.41, SD = 2.95, range: 23.27–32.77). Mean dispersal ability was highest in the Palearctic and Nearctic realms and lowest in the Afrotropical and Oriental realms (Figure S3).

3.1 | Effects of Dispersal Ability on Island Species–Area Relationships at Smaller Spatial Extents

At the small scale, dispersal ability (realm CWM(HWI)) had no significant effect on the intercept (estimate = 0.156, SE = 0.094, $t = 1.652$, $p = 0.116$, Figure 3A) and a significant positive effect on the slope of the ISAR (estimate = 0.026, SE = 0.011, $t = 2.452$, $p = 0.025$, Figure 3B). Mixed effects models, weighted regression and spatial regression confirmed these results (Table S3). Considering additional predictors from Matthews et al. (2019) confirmed that realm CWM(HWI) had no effect on intercepts and a positive effect on slopes (Table S4). Additionally, this revealed a significant negative effect of isolation on ISAR intercepts (estimate = −0.618, SE = 0.249, $t = −2.487$, $p = 0.022$, Table S4).

3.2 | Effects of Dispersal Ability on Island Species–Area Relationships at Larger Spatial Extents

At the large scale, dispersal ability had a significant positive effect on the intercept of the ISAR (estimate = 0.634, SE = 0.189, $t = 3.356$, $p = 0.0008$, Figure 3C) and a significant negative effect on the slope (estimate = −0.034, SE = 0.010, $t = −3.590$, $p = 0.0071$, Figure 3D). These effects were qualitatively robust to incorporating weights, independent observation errors in CWM(HWI) and ISAR parameters in a Bayesian metaregression
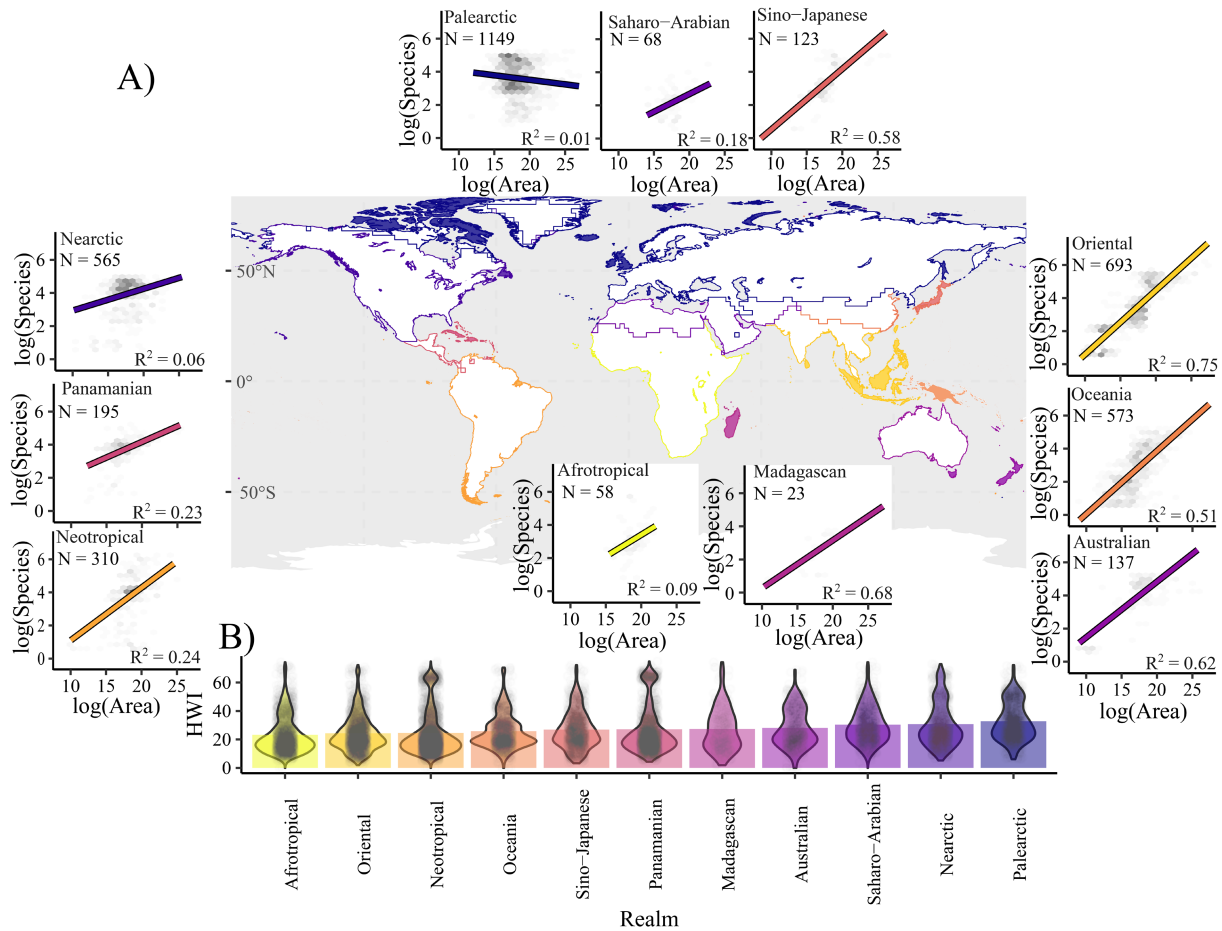
FIGURE 2 | Avian dispersal abilities and island species–area relationships (ISARs) in the large-scale analysis of zoogeographical realms. (A) ISARs vary across zoogeographic realms worldwide. Map shows realm delimitation following Holt et al. (2013) with continental landmasses and realm borders coloured by dispersal ability, calculated as the community-weighted mean Hand-Wing Index of the species in a realm (CWM(HWI)). Islands in our analysis are coloured by the rank of their realm's CWM(HWI). Panels show realm-specific ISARs, sample sizes of islands and goodness of fit. Dark cells show higher counts of islands. (B) Realms are ordered and coloured by the rank of their CWM(HWI).

framework, as well as to the removal of the Palearctic's extreme ISAR values (Tables S3 and S5, Figures S11–S13).

3.3 | Effects of Dispersal Ability on Island Species–Area Relationships Using Speciose Families

At the large scale, the 71 ISARs from avian families showed wide variation in ISAR intercepts (range: −3.381—4.073) and slopes (range: −0.130—0.293; Supporting Information S2). Distantly related families from different zoogeographical realms had similar dispersal abilities (e.g., Palearctic Hawks CWM(HWI) = 40.37 and Panamanian Parrots CWM(HWI) = 38.88; Figure S5). Dispersal ability significantly increased intercepts (wLR: estimate = 1.229, SE = 0.405, Z = 3.033, p = 0.003; Figure 4A) and decreased slopes (wLR: estimate = −0.053, SE = 0.022, Z = −2.444, p = 0.017; Figure 4B). These effects remained qualitatively identical in 10 out of 12 robustness analyses using different subsets of data (minimum 10, 30 and 50 species per family) and two analysis methods (with and without incorporating phylogeny; Tables S6 and S7; Figure S14). Phylogenetic signal of ISAR parameters (i.e., intra-class correlation coefficient) was high for all models (range λ: 0.90–0.94; Table S7).

3.4 | Additional Drivers of Island Bird Diversity at the Global Scale

Island species richness was also influenced by island isolation, environmental conditions, dispersal ability within islands and interactions among explanatory variables. Island area had a significant positive effect on species richness (coefficient = 0.163, SE = 0.019, p < 0.001; Table 1; Figure 5A) but showed a significant negative interaction with realm CWM(HWI) (interaction coefficient = −0.152, SE = 0.013, p < 0.001; Figure 5B). Moreover, islands that were more isolated and farther from the nearest zoogeographical realm also had significantly lower species richness (coefficient = −0.350, SE = 0.022, p < 0.001). Xeric harshness (coefficient = −0.258, SE = 0.013, p < 0.001) and elevational range (coefficient = −0.144, SE = 0.015, p < 0.001) had negative effects on species richness and temperature harshness had no effect on species richness (coefficient = 0.027, SE = 0.022, p = 0.213). Contrary to expectations, the negative effect of isolation increased with realm CWM(HWI) (interaction coefficient = −0.237, SE = 0.026, p < 0.001). Last, islands with high CWM(HWI) within island avifauna also had lower species richness (coefficient = −0.771, SE = 0.015, p < 0.001),
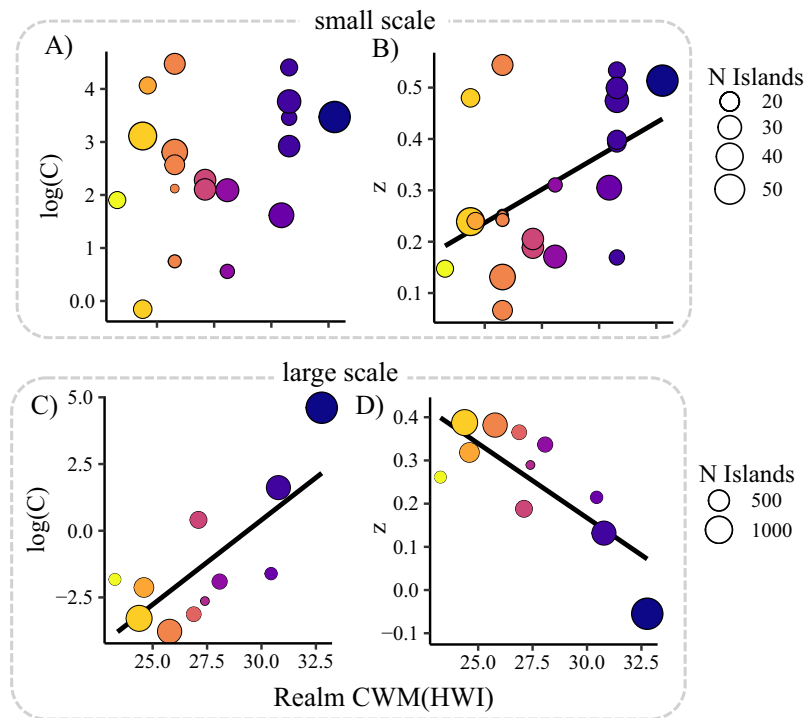
FIGURE 3 | Effects of dispersal ability on island species–area relationship (ISAR) intercepts ($\log(C)$) and slopes (z) at small and large scales. Smaller spatial extent realm CWM(HWI) has no effect on intercepts (A) but increases slopes (B) among the 21 island archipelagos in the database from Matthews et al. (2019). Realm CWM(HWI) increases intercepts (C) and decreases slopes (D) among the 11 zoogeographical realms in Figure 2. Significant effects from spatial regression models are shown with black lines. Point colour reflects realm membership (Figure 2). Point size shows a number of islands used to estimate each ISAR.

suggesting evidence of a dispersal filter against species with low dispersal ability. Spatial and mixed regression models supported similar conclusions (Table 1; Table S8).

3.5 | Contributions of Migratory Species

Surprisingly, excluding migratory species had only minor effects on our main results (Figures S13 and S15). Although migratory species contributed heavily to distributions of dispersal ability among zoogeographical realms and islands, especially in high latitudes (Figure S16), the larger-scale ISARs across realms were only weakly affected by their absence (Figure S17). Excluding migrants also prohibited convergence in the spatial regression models of ISAR parameters, so we reported the standard regression models instead. In these non-spatial regression models, the effect of realm dispersal ability on ISARs remained significant even after excluding migrants ($\log(C)$: $t = 2.642$, $p = 0.027$; (z): $t = -2.501$, $p = 0.034$; p-values from non-spatial regression; Figures S13 and S15). Finally, the exclusion of migratory species had weak effects on the significance, direction, and magnitude of predictors in multiple regression analyses (Figure S18) with two notable exceptions. First, when migrants were included, temperature harshness was associated with a non-significant increase in island species richness, but when migrants were excluded, temperature harshness had a significant negative effect on island species richness (coefficient = -0.342, SE = 0.019, $p < 0.001$; Figure S18; Table 1; Table S9). Second, when migrants were included, the interaction between realm dispersal ability

and isolation was significant and negative, but when migrants were excluded, the interaction between realm dispersal ability and isolation on island species richness became significant and positive (coefficient = 0.346, SE = 0.047, $p < 0.001$; Figure S18; Table 1; Table S9).

3.6 | Effects of Passerines Range Size and Standardised HWI

The direction of the effect of HWI on ISAR parameters remained constant and the magnitude and uncertainty showed only slight variation across major robustness analyses (Figures S13, S19–S22). Our results remained qualitatively identical when repeating all steps with only passerine birds (Figure S19) and non-passerine birds (Figure S20). At the small scale, dispersal ability had a positive effect on the ISAR slope for both raw and standardised HWI values (Figures S13B and S21B). At the large scale, the significant effects of dispersal ability on the ISAR intercept and slope using raw HWI values became non-significant using standardised HWI values (Figures S13C,D and S21C,D), despite similar effects of raw and standardised HWI values on island species richness (Figure S21E). Range size explained little variation when used in place of HWI (Table S10) or in addition to HWI (Tables S11–S13). However, when weighting CWM(HWI) by range size, the effect sizes of realm-level dispersal became non-significant, but they retained the same direction of effects as in the main analyses (Figures S13 and S22).
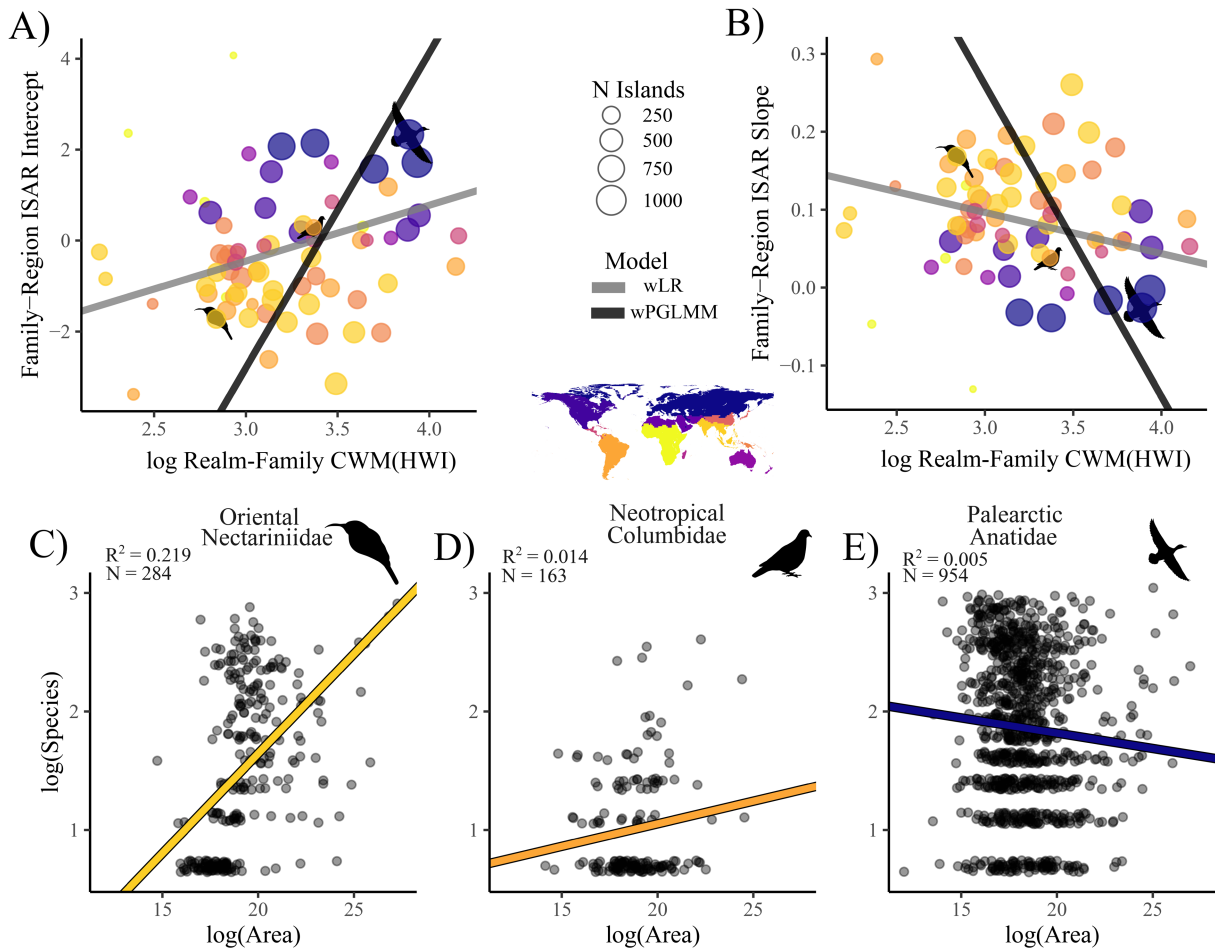
FIGURE 4 | Effects of dispersal ability on island species–area relationships (ISARs) for well-sampled avian families at the large spatial scale. When 71 ISARs are estimated using individual speciose families (> 30 species per family) within single zoogeographical realms, the CWM(HWI) of confamilial species in the realm increases ISAR intercepts (A) and decreases slopes (B). Significant effects from weighted linear regression (wLR) and weighted phylogenetic generalised linear mixed models (wPGLMM) are shown with solid grey and black lines. Point colour reflects realm membership (Figure 2) and size indicates a number of islands used to estimate ISARs. Icons show examples of ISAR parameters for three avian families from panels (C)–(E).

TABLE 1 | Coefficients of spatial regression model of global bird richness on islands ($N = 3574$). $\Phi = 2.626653\text{e-}06$.

| Parameter	Estimate	Standard error	*Z* statistic	*p*
Intercept	3.426	0.015	233.315	< 0.001
Island CWM(HWI)	−0.771	0.015	−52.381	< 0.001
Xeric harshness	−0.258	0.013	−20.04	< 0.001
Isolation	−0.35	0.022	−15.89	< 0.001
Log(distance from realm)	−0.231	0.016	−14.028	< 0.001
Realm CWM(HWI)	0.283	0.022	13.125	< 0.001
Log(area):realm CWM(HWI)	−0.152	0.013	−11.273	< 0.001
Log(elevational range)	−0.144	0.015	−9.629	< 0.001
Isolation:realm CWM(HWI)	−0.237	0.026	−8.978	< 0.001
Log(area)	0.163	0.019	8.437	< 0.001
Log(climate heterogeneity)	0.026	0.013	2.081	0.037
Temperature harshness	0.027	0.022	1.246	0.213
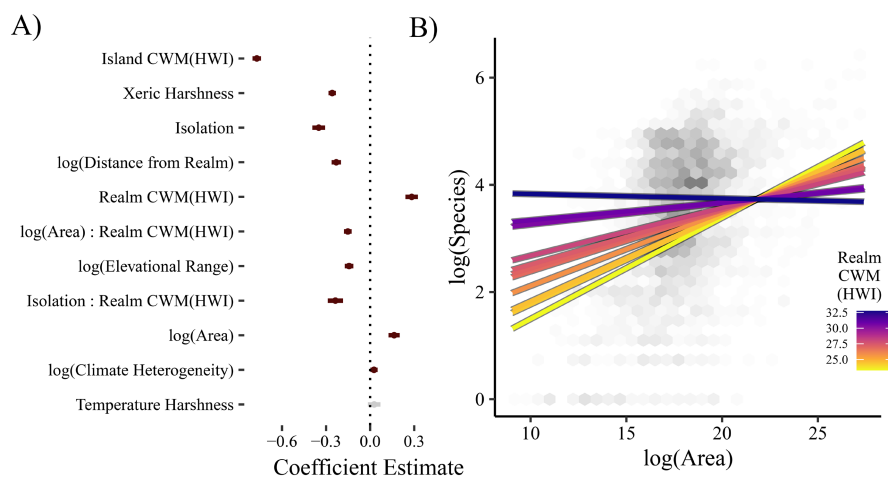
FIGURE 5 | Additional ecological drivers of island species richness at the large spatial scale. (A) Coefficient plot of global spatial regression models of island bird species richness with migratory species shows significant factors in black and non-significant factors in grey and ':' denotes interactions. (B) The CWM(HWI) of species in the realm (Realm CWM(HWI)) influenced ISARs through a positive effect on species richness and via a negative interaction with island area. Lines show predicted means for each realm (coloured by realm dispersal ability rank). Dark cells show higher counts of islands. Coefficient values are from spatial regression models.

4 | Discussion

We found widespread but context-dependent effects of dispersal ability on ISARs. Interestingly, increased dispersal ability in realms steepened ISAR slopes at small spatial extents (Figure 3B) but flattened ISAR slopes and increased ISAR intercepts at large spatial extents (Figure 3C,D). We validated our findings by stratifying our analyses across well-sampled families (Figure 4, Figure S8). Our results were robust to the effects of other ecological drivers of avian island biodiversity (Figure 5), additional uncertainty in ISAR parameters (Figures S11 and S13), outliers (Figures S12 and S13), the exclusion of migratory species (Figures S13, S15–S18), broad-scale taxonomic variation in dispersal ability (Figures S13, S19 and S20) and the effects of range size (Figure S22, Tables S10–S13). Our results reveal how a key dispersal trait can shape fundamental biodiversity patterns and island biogeography across scales.

To date, most studies have focused on how geographic factors such as area and isolation influence ISARs (Connor and McCoy 1979; Drakare, Lennon, and Hillebrand 2006; Matthews et al. 2019, 2021). Our results highlight the importance of trait differences among species, specifically traits related to dispersal ability, in shaping ISARs across spatial scales. Two separate mechanisms might act simultaneously to explain how dispersal ability influences ISARs. First, dispersal ability might have an indirect effect on ISARs, via a primary effect on species range size, as species with higher dispersal ability have larger geographic ranges (Sheard et al. 2020; Pegan and Winger 2020). In this scenario, latitudinal variation in range size (e.g., Rapoport's rule, Stevens 1989) could be a major driver of latitudinal variation in ISAR slopes (Figure 2; Drakare, Lennon, and Hillebrand 2006), as larger range sizes can lead to decreased spatial turnover, giving rise to flatter ISARs (Amarasekare and Nisbet 2001; Hubbell 2001). Second, dispersal ability could also directly impact ISARs by increasing propagule pressure from mainland species pools as well as increasing dispersal among islands. This direct effect of dispersal could conceivably operate

without impacting range size and seems potentially plausible, as increased dispersal ability confers increased natal dispersal distances (Claramunt 2021; Chu and Claramunt 2023), increased abilities to overcome geographic barriers (Claramunt, Hong, and Bravo 2022) and greater gene flow (Claramunt et al. 2012). Regardless of how dispersal influences ISARs, we acknowledge that it is currently challenging to remove the influence of variation in geographic range size from correlated factors in macroecological studies (Quintero and Jetz 2018). Our results highlight the importance of considering how variation in species' dispersal traits among regions contributes to geographic variation in ISARs (Connor and McCoy 1979; Drakare, Lennon, and Hillebrand 2006; Matthews et al. 2019, 2021).

When considering additional ecological drivers of island species richness, we found contrasting effects of realm-level and island-level dispersal ability (Table 1): increased dispersal ability in the realm elevated species richness, whereas dispersal ability on islands decreased species richness (Figure 5A). This apparent paradox can be resolved when considering that island-level ecological characteristics might prohibit colonisation by low-dispersal taxa, such that frequent colonisation events would be necessary for low-dispersal taxa to establish populations on islands. We found that species-poor islands were comprised of species with high dispersal abilities (high island CWM(HWI)), suggesting that high-dispersal taxa seem to be more successful at passing through the filter of island community assembly (Burns 2005; Kraft and Ackerly 2014). One established, high-dispersal taxa that arrive early in the colonisation process might additionally exclude late-arriving, low-dispersal taxa via priority effects (Chase 2003). Interestingly, island-dwelling species of birds have been shown to have increased HWI (Sheard et al. 2020) and island communities have converged on high-dispersal assemblages (Triantis et al. 2022). This supports the hypothesis that spatially varying selection can operate on the dispersal process itself (Vellend 2016), and leave predictable signatures in community trait distributions among the successful colonists. From an evolutionary perspective, this

might be surprising, as plants (Cody and Overton 1996), insects (Roff 1990) and birds (Wright, Steadman, and Witt 2016; Gaspar, Gibb, and Trewick 2020), have repeatedly lost dispersal ability on small, isolated islands. As we found that species-poor islands were occupied by high-dispersal species, we suspect such evolutionary changes in dispersal ability might yield weak effects on community-level patterns of dispersal traits.

Like previous studies in birds (e.g., Kalmar and Currie 2006), we also found strong roles of ecological correlates of diversity. In line with the predictions of core island biogeography theory, island species richness was decreased on islands that were smaller, more isolated, and farther from the nearest zoogeographical realm (Table 1). Climate harshness also was important, as increasing xeric harshness, which captures trends in productivity (Table S1), decreased species richness in line with the 'species-energy hypothesis' (Wright 1983). In contrast, temperature harshness had no effect on species richness. While this might seem counter-intuitive, the regions of the earth with high-temperature harshness tend to be temperate regions, which are also inhabited by migrant species, but only for a portion of the year. Thus, excluding migrants revealed a strong negative effect of temperature harshness on island richness (Table S9, Figure S18), suggesting another environmental filter.

Our results were largely robust to a variety of analytical choices, but analyses controlling for phylogenetic variation in HWI revealed variable outcomes: when standardising HWI on the order's mean value, the direction of all major effects remained but only one out of three significant effects were recovered (Figure S13). Instead, when we stratified our large-scale analyses by families and accounted for phylogenetic relationships, we saw a strong role of phylogeny ($\lambda > 0.9$) and concordant, significant effects of dispersal ability across families and realms (Figure 4, Figure S8, Tables S6 and S7).

One possible explanation for the scale-dependent effect of dispersal could come from theoretical studies on dispersal and nested species–area relationships (Chave, Muller-Landau, and Levin 2002; He and Legendre 2002; Figure S23). However, it remains unknown if and under which circumstances these theoretical predictions apply to non-nested, Type IV ISARs such as the ones we examined here (Scheiner 2003). Our results suggest avenues for further research. Importantly, future simulation studies of the role of dispersal on ISARs should account for core processes such as extinction (Cabral, Valente, and Hartig 2017) and explore interactive effects of dispersal and extinction (e.g., rescue effects, Gotelli 1991) as well as dispersal and competition (e.g., priority effects; Chase 2003). Moreover, theoretical work could explore how scale-dependent effects of dispersal interact with increasing spatial extent and grain size, and identify the spatial scale(s) at which the effects of dispersal may reverse, e.g., by treating spatial scale as a continuous parameter.

In conclusion, we critically examined a core tenet of core island biogeography, namely the assumption of species equivalence in dispersal ability. We showed that global variation in a key dispersal trait has scale-dependent effects on ISARs. Our results illustrate the importance of dispersal as a major process governing island community ecology with implications for fundamental

patterns of diversity distributions, community assembly and species–area relationships (Vellend 2010, 2016). In the context of increased global dispersal, invasive species and accelerating global change, a better understanding of dispersal patterns and processes can ultimately aid conservation efforts and improve our ability to understand island biodiversity and its responses to rapid anthropogenic changes (Weigelt et al. 2016).

Data Availability Statement

All data are open-access and all code is archived on Zenodo: https://zenodo.org/records/12741516.

Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.70020.

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Supporting Information

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