Bird assemblage vulnerability depends on the diversity and biogeographic histories of islands

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Biodiversity is widely acknowledged to influence the magnitude and stability of a large array of ecosystem properties, with biodiverse systems thought to be more functionally robust. As such, diverse systems may be safer harbors for vulnerable species, resulting in a positive association between biodiversity and the collective vulnerability of species in an assemblage, or "assemblage vulnerability." We find that, for 35 islands across Northern Melanesia, bird assemblage vulnerability and biodiversity are positively associated. This relationship is highly contingent on Pleistocene connectivity, suggesting that biogeographic history—a factor often overlooked in biodiversity and ecosystem-functioning studies—may influence contemporary ecological processes. In the face of biodiversity loss attributable to anthropogenic drivers, reduced ecosystem functioning may erode the safe harbors of vulnerable assemblages. Paradoxically, these results suggest that biodiverse systems, as more robust systems, may experience greater biodiversity loss over ecological time because they harbor more vulnerable species accumulated over evolutionary time.

biodiversity | ecosystem functioning | historical biogeography | extinction risk | species loss

There is a growing body of evidence that increased levels of biodiversity can impact ecosystem functions in predictable ways. Biodiversity is widely acknowledged to significantly influence the magnitude and stability of a large array of ecosystem properties, with stronger impacts evident when larger scales (1) and multiple functions are considered (2, 3). These findings provide compelling support for biodiverse systems being functionally robust, with greater stability of function (4–6), resistance to invasion (7–10), and resistance to pathogen spread (11). Some of the impacts of higher levels of biodiversity on ecosystem properties that are apparent at ecological timescales (e.g., greater resistance to invasion) may influence evolutionary processes, like extinction rates. In natural assemblages, such a relationship would require the persistent influence of ecosystem functionality on extinction risk across evolutionary time; as such, it may be influenced by biogeographic history.

To quantify the persistent effects of increased ecosystem function in diverse systems, we explore the relationship between biodiversity and an ecosystem property: assemblage vulnerability. Assemblage vulnerability is the composite of the individual vulnerabilities of an assemblage's constituent species based on a suite of geographic, ecological, and anthropogenic factors. We used five indicators of species vulnerability: range size, dispersal ability, clutch size, body size, and International Union for Conservation of Nature (IUCN) threat status. Range size is a strong predictor of extinction risk for birds globally (12). Dispersal ability, body size, and clutch size are species' traits (sensu ref. 13) associated with extinction probability, with poor dispersal, large body size, and low clutch size correlated to elevated extinction risk (14, 15). IUCN threat status represents a widely accepted estimate of vulnerability to human and other contemporary environmental pressures that may not be reflected in ecologically relevant traits. Species vulnerability was considered inversely associated with range size, dispersal ability, and clutch size, and

positively associated with IUCN threat status. Thus, assemblages composed of species with similarly restricted range size, poor dispersal ability, small clutch size, and high IUCN threat status, would have the highest assemblage vulnerability value.

Although often excluded in ecological studies, biogeographic history plays a significant role in determining species composition (16) and, by extension, has the potential to influence properties of species assemblages and the ecosystem functions they govern. Species in an assemblage frequently share diversification histories (17), and when conducting studies across multiple sites at larger scales, it is likely that communities with different assembly histories will be compared (e.g., assemblages characterized by high levels of in situ diversification as opposed to high levels of colonization). Climate-driven sea level change is an example of a key historical biogeographic process that is of particular relevance in island systems. Changes in island connectivity as a result of sea level fluctuation have been invoked to explain relationships between fundamental evolutionary processes (e.g., the relationship between dispersal and diversification rates) (18) and have been related to key evolutionary outcomes (e.g., species richness and endemism) (19). In the Solomon Archipelago, throughout the Pleistocene, fluctuations in sea level have connected and isolated some islands repeatedly, whereas others have remained isolated throughout their histories; these historical connections are clearly evident in the distributions of diversity in the Archipelago, with taxa typically endemic to islands that formed single landmasses at the Last Glacial Maximum (LGM) (20).

Island systems present opportunities to test for the impact of history over evolutionary time on present-day community and

Significance

Biodiversity is broadly thought to be positively associated with a wide array of ecosystem functions and properties. Because these properties may reduce extinction risk, for example, by making functioning more stable and ecosystems less prone to invasion, biodiverse islands have the potential to accumulate species over evolutionary time that are more vulnerable to extinction. We find that bird diversity is positively related to the collective vulnerability of species in a set of assemblages. This relationship is highly contingent on biogeographic history, a factor often overlooked in biodiversity and ecosystem-functioning studies. Our findings expose a paradox: biodiverse systems, as more robust systems, may experience greater biodiversity loss over ecological time because they accumulate more vulnerable species over evolutionary time.

ecosystem properties by providing replicate systems with varied histories. In particular, the Solomon Archipelago has long been recognized as a series of islands that can be divided into two groups based on connectivity at the LGM (21) and, as such, serves as an ideal system for testing hypotheses concerning patterns and processes across ecological, evolutionary, and biogeographical scales (21).

The ability of alternate assembly histories over ecological time to influence biodiversity and ecosystem functioning has been demonstrated experimentally (22), and although the persistence of assembly history's influence on ecological processes over evolutionary time remains relatively unstudied, there is increasing evidence that this may occur (23). As such, it is likely that persistent ecological impacts of assembly history may influence evolutionary processes acting at long timescales (e.g., extinction probability).

To quantify the relationship between diversity and assemblage vulnerability, we use structural equation modeling (SEM) to model the influence of species richness, functional richness, and the distribution of functional traits through trait space on assemblage vulnerability (*Methods* and Fig. 1). We quantify assemblage vulnerability using an index of the individual vulnerabilities of an assemblage's constituent species (i.e., all resident land birds on an island) based on the aforementioned indicators, which we expect to be strongly indicative of species' extinction risks on islands of the Solomon Archipelago (*Methods*). In addition to looking at the relationships between diversity and assemblage vulnerability across all assemblages, following classic studies in the Archipelago (20, 21), we divided the islands into two groups: those that were connected to other major islands at the LGM (land bridge islands), and those that have been isolated throughout their history (isolated islands). By comparing across these alternate histories, we evaluate the influence of biogeographical history on a contemporary relationship between biodiversity and an ecosystem property. This study is a test of hypothetical relationships between biodiversity, assemblage vulnerability, and biogeographic history.

Results

When all islands are analyzed together, regardless of biogeographic history, the model is significantly better than a null model ($n = 35$, $\chi^2 = 38$, df = 5, $P < 0.001$), and species richness is positively associated with assemblage vulnerability (0.47 ± 0.194, $z = 2.4$, $P < 0.05$; Fig. 1). The relationships between functional richness and the distribution of functional traits to assemblage vulnerability were not significant. For this complete dataset, the SEM explained 40% of the variance in assemblage vulnerability. For the land bridge islands, the model was significantly better than a null model ($n = 18$, $\chi^2 = 26.3$, df = 5, $P < 0.001$), but none of the diversity metrics was significantly related to assemblage vulnerability, and the SEM only explained 23% of the variance in assemblage vulnerability (Fig. 2*A*). For the isolated islands, the model was significantly better than a null model ($n = 17$, $\chi^2 = 25.3$, df = 5, $P < 0.001$), the distribution of functional traits was significantly positively related to assemblage vulnerability (0.54 ± 0.22, $z = 2.4$, $P = 0.01$), and functional richness was positively related to assemblage vulnerability, although the relationship was not significant (0.51 ± 0.29, $z = 1.79$, $P = 0.07$; Fig. 2*B*). For the isolated islands, the SEM explained 62% of the variance in assemblage vulnerability. For all three analyses, the covariance of functional richness and SR was consistently high (0.64–0.75) and significant ($P < 0.05$).

The bootstrap analysis to compare the assemblage vulnerability r^2 on isolated islands and land bridge islands showed that the amount of variance in assemblage vulnerability explained by the SEM of the two groups was significantly different ($P < 0.001$; Fig. 3*A*). Our comparison of the island groups to random groups of 18 islands revealed that assemblage vulnerability r^2 for the land bridge islands falls within the lowest 2.5% of the distribution, suggesting it is significantly different from a random grouping. The
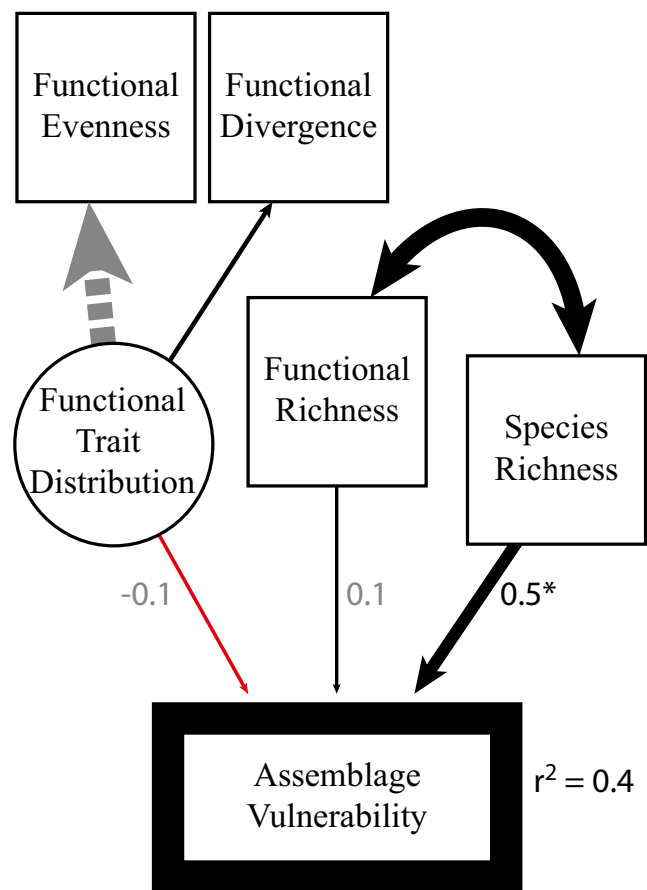

Fig. 1. Assemblages with greater diversity are more vulnerable. A structural equation model of the relationship between the distribution of functional traits, functional richness, and species richness and assemblage vulnerability shows a positive relationship between species richness and assemblage vulnerability. Parameter estimates are standardized, and the paths are scaled to reflect effect size. Significant relationships are denoted with asterisks, and the fixed loading of the distribution of traits on functional evenness is shown as a dashed line. The three dimensions of diversity explain 40% of the variance in assemblage vulnerability.

assemblage vulnerability r^2 of the isolated islands is larger than the mean assemblage vulnerability r^2 for random island groups but does not fall outside of the 95% limits of the distribution (Fig. 3*B*).

Correlations within the vulnerability data (intrinsic biology, range size, and response to anthropogenic pressures) were minimal. Range size and response to anthropogenic pressure (IUCN status) were not significantly correlated, nor were IUCN status and intrinsic biology. Range size was significantly correlated with intrinsic biology ($P < 0.001$); however, the correlation coefficient was low enough (0.3) that all three variables were retained in the calculation of vulnerability scores.

Discussion and Conclusion

Our results demonstrate that across biogeographic groups of islands, increased species richness on islands is associated with more vulnerable avian assemblages in the Solomon Archipelago. We expect that this relationship also exists in nonisland systems, in large part because more diverse continental systems are characterized by higher proportions of rare species, which are likely more vulnerable (24). The expectation that more diverse islands are likely to experience greater rates of species loss is in agreement with predictions based on the theory of island biogeography (25). However, because the accumulation of diversity has been accompanied by an ecological shift toward vulnerable
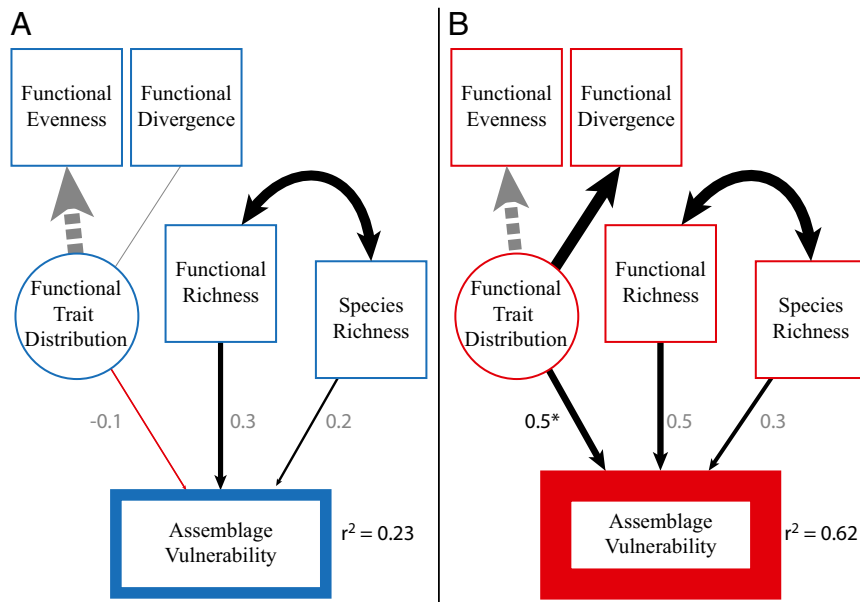
Fig. 2. Alternate histories change the relationships between diversity and assemblage vulnerability. Parameter estimates are standardized, black lines represent positive relationships, red lines represent negative relationships, the paths are scaled to reflect parameter size, significant relationships are denoted with asterisks, and the boxes around assemblage vulnerability are scaled to the amount of variance in assemblage vulnerability explained by the model. For land bridge islands (*A*), the ability of diversity to explain variance in assemblage vulnerability is greatly reduced ($r^2 = 0.23$) and none of the path coefficients is significant. When only isolated islands are considered (*B*), the model has much higher explanatory power (assemblage vulnerability $r^2 = 0.62$) and the relationship between the distribution of functional traits and assemblage vulnerability is significant and positive ($P = 0.01$), and the relationship between functional richness and assemblage vulnerability is positive and nearly significant ($P = 0.07$).

assemblages, our findings suggest that diversity-related ecosystem properties and functions have altered the ecologies of diverse assemblages. This ecological shift has the potential to impact the responses of diverse islands to anthropogenic extinction pressures at shorter timescales, potentially resulting in disequilibrium between colonization and extinction not predicted by island biogeography theory. An additional consideration is the possibility that species richness may be associated with species population sizes, which would further link diversity with assemblage vulnerability. The character of this relationship is likely system specific, with species on more diverse islands potentially having smaller population sizes; however, in some systems, increases in density can compensate for increased species richness (26). The limited data available for the birds of Northern Melanesia suggest that the relationship between species richness and population sizes may have a limited impact on vulnerability, because total bird density increases linearly with species richness (27).

Surprisingly, species richness is a better predictor of assemblage vulnerability than functional diversity when all islands are considered together. This may be because the morphologies of close relatives across this system are relatively highly conserved (i.e., adaptive divergence appears minimal), limiting the variation of functional diversity across the islands; in contrast, speciation drives changes in species richness and has occurred quite rapidly for some groups (e.g., ref. 28). Alternatively, this may be because of conflicting relationships between the different dimensions of diversity and assemblage vulnerability among groups of islands with different biogeographic histories. For example, the relationship between the distribution of functional traits and assemblage vulnerability is positive on isolated islands, and negative on land bridge islands. Species richness, however, is positively related to assemblage vulnerability across island groups.

An important outcome is that the relationship between diversity and assemblage vulnerability is mediated strongly by the Pleistocene connectivity of the islands studied. There is a

significant difference in the amount of variation in assemblage vulnerability explained by the SEM of the two island groups. The stronger relationship between diversity and assemblage vulnerability on isolated islands could be due to the limited opportunities for extirpated populations to be reestablished during periods of low sea level. The accumulation of diversity on isolated islands, which by definition do not have periods of connectivity between islands, may be more dependent on in situ protection of vulnerable species via greater ecosystem functioning as a result of higher diversity. Although historic changes in island size and connectivity have been linked to species richness and proportion of endemic species in an assemblage (19), our findings reveal a distinct example of a contemporary ecological relationship that is highly influenced by an historical biogeographic process.

Our findings suggest that the ecological impacts of community assembly history on contemporary ecological processes may span evolutionary timescales. Therefore, aspects of assembly history that are important at ecological timescales, such as the order of arrival of species to a community (22), warrant further examination in natural systems (e.g., ref. 23). Effects of assembly history that span evolutionary timescales may result in complex interactions with evolutionary processes (e.g., speciation) influencing ecology, and ecology in turn, influencing evolutionary processes (e.g., extinction). More generally, our results suggest that global processes like sea level fluctuations, which influence biogeographic history and community assembly, can influence contemporary ecological processes. This relationship may complicate the comparison of ecological findings across biogeographic areas, providing compelling evidence for the necessity of integrating historical biogeography and ecology.

Our findings have important and surprising implications for conservation, especially for the globally significant biodiversity on islands, which is characterized by significantly higher endemism richness than mainland areas (29). Although biodiverse islands might be expected to have lower background rates of extinction because of their higher ecosystem stability (5, 6),
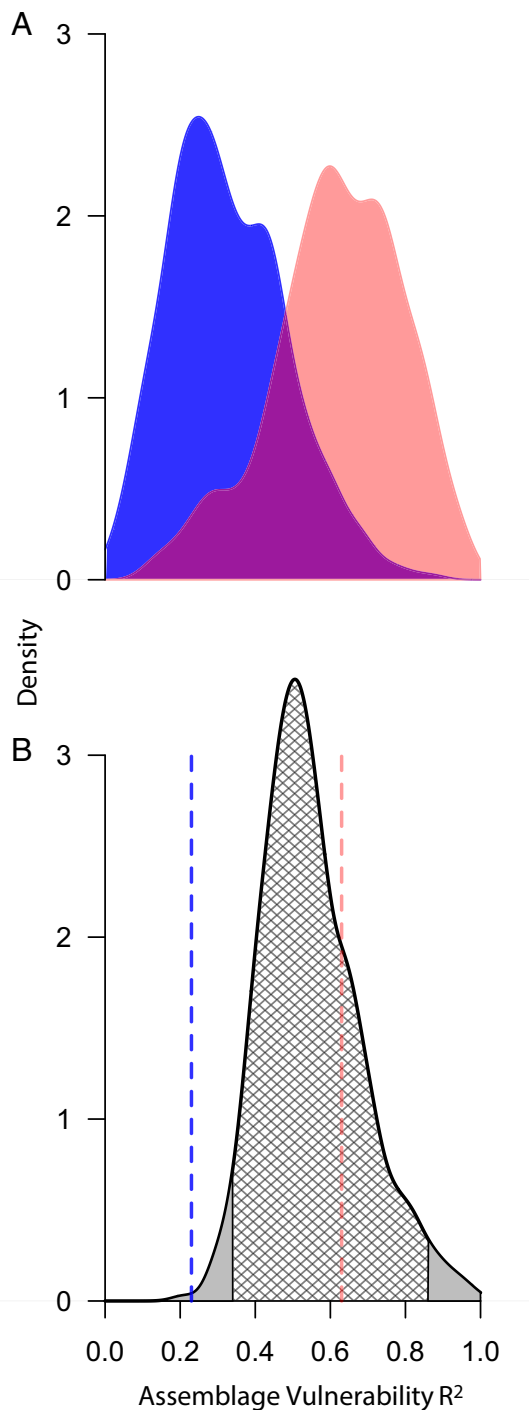
Fig. 3. Robustness to outliers and comparison with random island groupings. When assemblage vulnerability r^2 is calculated across 1,000 bootstrap replicates of 35 islands (*A*), the distributions of variance in assemblage vulnerability explained by the SEM is significantly different ($P < 0.001$), with the assemblage vulnerability r^2 values lower on land bridge islands (blue distribution) than on isolated islands (red distribution). When the island groups based on biogeographic history are compared with random groups (*B*), the assemblage vulnerability r^2 of the land bridge islands (blue dashed line) falls within the lowest 2.5% of the distribution of random groupings, whereas the assemblage vulnerability r^2 of the isolated islands (red dashed lines) lies above the mean of the distribution but does not fall in the top 2.5% of all groups.

resistance to invasion (7–10), and resistance to pathogen spread (11), this prediction is complicated by decreased population-level stability of individual species within diverse communities (30–34). In order for diverse islands to accumulate vulnerable species, the beneficial effects of ecosystem stability and increased ecosystem function that come with greater diversity must out-weigh the costs of increased species-level instability as a result of high diversity. Our results suggest that this is the case, with more diverse assemblages providing the necessary conditions for the accumulation of vulnerable species over evolutionary time, resulting in vulnerable assemblages. As such, more diverse islands are likely to lose species in response to anthropogenic pressures, reducing ecosystem functionality, further reducing their ability to sustain vulnerable species. Predicting changes in the vulnerability of island endemic assemblages can be significantly improved when using historical biogeography to characterize islands. It is clear that diversity and assemblage vulnerability are more tightly coupled on islands with histories of isolation, high-lighting the potential for historical contingency to play a strong role in shaping contemporary ecological processes.

Methods

The biota of Northern Melanesia have been foundational to the development of key theories of community assembly (25, 35, 36). The birds of the Solomon Archipelago continue to serve as the empirical basis for understanding the origins and assembly of diversity within communities (37, 38), making them an ideal system within which to examine the impacts of alternative assembly histories on contemporary ecological relationships.

Our analyses include 35 islands in the Solomon Archipelago that have been used in classic studies in the Archipelago as representatives of this system (20, 21). We included only islands larger than 2.6 km², which is the threshold below which species–area relationships become more complicated for these bird communities (21). Assemblage vulnerability was calculated at the island level, based on the resident land birds that are found on each island (Table S1 and Dataset S1) (20). To calculate assemblage vulnerability, a species-level vulnerability score was calculated for each resident species in the archipelago using hypothesized indicators of vulnerability, and then for each island these species-level scores were combined to create an island-level assemblage vulnerability score.

Species-level vulnerability was quantified, using z scores to standardize across variables, and incorporated intrinsic biology, range size, and response to anthropogenic pressures. Vulnerability as a function of the species' intrinsic biology was calculated as follows:

$$V_s(T) = 1/3\left(-z_{\text{clutch size}} + z_{\text{body size}} - z_{\text{dispersal ability}}\right),\qquad [1.1]$$

where clutch size is the mean number of eggs laid per year, body size is the length of each species (39), and dispersal ability is quantified using the hand–wing index (HWI). HWI is a measure of the aspect ratio of a wing, which is linked to flight efficiency, and is calculated as follows:

$$HWI = 100(WL - SL)/WL,\qquad [1.2]$$

in which WL is the standard measure of wing length, and SL is a measure of the distance from the carpal joint to the tip of the first secondary feather (18, 40). For each species, HWI was based on the measurement of three adult male specimens, when available, at the American Museum of Natural History (AMNH). Vulnerability as a function of each species' range size was calculated as follows:

$$V_s(H) = \left(-z_{\text{total range area}}\right).\qquad [2]$$

Total range area for each species was obtained from BirdLife International (41). Finally, species vulnerability based on the impacts of anthropogenic pressures was estimated as follows:

$$V_s(A) = \left(-z_{\text{IUCN status}}\right),\qquad [3]$$

where IUCN status was converted to a numerical value, with 1 being species of least concern and, and 5 being those species that are critically endangered. These three metrics of species vulnerability were then combined into a single species vulnerability index by taking the unweighted mean:

$$V(S) = 1/3(V_s(T) + V_s(H) + V_s(A)).\qquad [4]$$

To calculate the assemblage vulnerability of the avifauna on each island, we calculated the unweighted mean species scores for the constituent species:

$$F_a(I) = 1/n(V(S)_1 + V(S)_2 \ldots V(S)_n),\qquad[5]$$

where $F_a(I)$ is the assemblage vulnerability for island I, n is the number of species on island I, and $V(S)_n$ is the species vulnerability index for species "n" on the island (as per Eq. **4**).

In addition to assemblage vulnerability, species richness (SR) and functional diversity (FD) were calculated for each island using all of the resident land bird species on each island. For each species, bill length, bill depth, and tarsus length were measured for three adult male specimens, when available, at AMNH. These traits are relevant to the natural histories of birds (42–44). A principal-component analysis (PCA) was used to summarize bill morphology. Functional evenness, functional divergence, and functional richness (45) were calculated using the R package FD (46), based on the functional trait values for all birds on each island (the position of each species on axis 1 and axis 2 of the PCA summary of bill morphology, tarsus length, and body size). These traits were chosen because they are commonly used indicators of resource use and energy constraints (body size) (47, 48), and foraging behavior in birds (bill morphology and tarsus length) (41, 42). SR for each island was calculated using the land birds on each island. To ensure that we were not biasing our metric of assemblage vulnerability by duplicating the same information across aspects of vulnerability (e.g., a high correlation between range size and IUCN status might be expected because changes in range size can drive listing status), correlations between intrinsic biology, range size, and anthropogenic impact scores were examined.

The influence of functional diversity and species richness on assemblage vulnerability was then modeled using SEM, implemented in the R package lavaan (49). The distribution of functional traits through trait space was modeled as a latent variable (which we will call "functional trait distribution"), measured using functional evenness and functional divergence, with the latent variable variance fixed to 1 and the loading on functional evenness constrained to be 1. SR and functional richness were considered exogenous variables. Assemblage vulnerability was regressed onto functional trait distribution, functional richness, and SR (Fig. 1).

To compare the relationship between diversity and vulnerability across biogeographical groupings, the data were divided into two groups of islands: those that were connected to form major land masses at the LGM (land bridge islands), and those that were isolated at the LGM (isolated islands; Fig. 2, Table S1, and Dataset S1) (21). To evaluate the sensitivity of the inter-biogeographical group differences to outliers, we used a bootstrap method in which 1,000 sets of 35 islands were randomly sampled (with replacement) from each of the island groups. The SEM was fit to each random sample, and the assemblage vulnerability r^2 was calculated. The distributions of assemblage vulnerability r^2 values were compared across biogeographic groups using a t test (Fig. 3A). To test whether the groups based on biogeographic history were significantly different from a random subset of the total dataset, we drew 1,000 random samples of 18 islands without replacement, and without regard to their biogeographic history, from the total dataset. We then compared the actual values of assemblage vulnerability r^2 of the biogeographic subsets to the distribution of r^2 values for random groups of islands (Fig. 3B).

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