Conservation Biology

Contributed Paper

Benefits to Poorly Studied Taxa of Conservation of Bird and Mammal Diversity on Islands

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Abstract: *Protected area delineation and conservation action are urgently needed on marine islands, but the potential biodiversity benefits of these activities can be difficult to assess due to lack of species diversity information for lesser known taxa. We used linear mixed effects modeling and simple spatial analyses to investigate whether conservation activities based on the diversity of well-known insular taxa (birds and mammals) are likely to also capture the diversity of lesser known taxa (reptiles, amphibians, vascular land plants, ants, land snails, butterflies, and tenebrionid beetles). We assembled total, threatened, and endemic diversity data for both well-known and lesser known taxa and combined these with physical island biogeography characteristics for 1190 islands from 109 archipelagos. Among physical island biogeography factors, island area was the best indicator of diversity of both well-known and little-known taxa. Among taxonomic factors, total mammal species richness was the best indicator of total diversity of lesser known taxa, and the combination of threatened mammal and threatened bird diversity was the best indicator of lesser known endemic richness. The results of other intertaxon diversity comparisons were highly variable, however. Based on our results, we suggest that protecting islands above a certain minimum threshold area may be the most efficient use of conservation resources. For example, using our island database, if the threshold were set at 10 km^2 and the smallest 10% of islands greater than this threshold were protected, 119 islands would be protected. The islands would range in size from 10 to 29 km^2 and would include 268 lesser known species endemic to a single island, along with 11 bird and mammal species endemic to a single island. Our results suggest that for islands of equivalent size, prioritization based on total or threatened bird and mammal diversity may also capture opportunities to protect lesser known species endemic to islands.*

Keywords: conservation prioritization, endemic species, mixed effects model, spatial analysis, species richness, threatened species

Beneficios de los Taxa Poco Estudiados para la Conservación de la Diversidad de Aves y Mamíferos en Islas

Resumen: *Las islas marinas necesitan urgentemente de acciones de conservación y delimitación de áreas protegidas pero los beneficios potenciales de estas actividades para la biodiversidad pueden ser difíciles de evaluar debido a la falta de información sobre la diversidad de especies para taxa menos conocidos. Usamos modelos de efectos lineales mixtos y análisis espaciales simples para investigar si las actividades de conservación basadas en la diversidad de taxa insulares bien conocidos (aves y mamíferos) tienen la probabilidad de capturar la diversidad de taxa menos conocidos (reptiles, anfibios, plantas vasculares terrestres, hormigas, caracoles terrestres, mariposas y escarabajos tenebriónidos). Ensamblamos datos de diversidad totales, amenazados y endémicos para los taxa bien conocidos y los poco conocidos y los combinamos con las características biogeográficas de las islas físicas para 1190 islas de 109 archipiélagos. Entre los factores biogeográficos de las islas físicas, el área de las islas fue el mejor indicador para la diversidad de los taxa poco conocidos y los bien conocidos. Entre los factores taxonómicos, la riqueza total de especies de mamíferos fue el mejor indicador para la diversidad total de taxa menos conocidos, y la combinación de la diversidad de mamíferos amenazados y aves amenazadas fue el mejor indicador de la riqueza endémica de los taxa menos*

Paper submitted November 23, 2013; revised manuscript accepted April 7, 2014.

Conservation Biology, Volume 00, No. 0, 1–10

DOI: 10.1111/cobi.12354

conocidos. Sin embargo, los resultados de otras comparaciones de diversidad entre taxa fueron altamente variables. Con base en nuestros resultados, sugerimos que proteger a las islas por encima de un área de cierto umbral mínimo puede ser el uso más eficiente de los recursos de conservación. Por ejemplo, usando nuestra base de datos de islas, si el umbral estuviese puesto en 10 Km^2 y el 10% más pequeño de islas mayores a este umbral estuviera protegido, 119 islas estarían protegidas. Las islas variarían en tamaño entre 10 y 29 Km^2 e incluirían 268 especies endémicas de taxa menos conocidos en una sola isla, junto con 11 especies endémicas de aves y mamíferos en una sola isla. Nuestros resultados sugieren que para las islas de tamaño equivalente, la priorización basada en la diversidad total o amenazada de aves y mamíferos también puede capturar oportunidades para proteger especies menos conocidas endémicas a islas.

Palabras Clave: análisis espacial, especies amenazadas, especies endémicas, modelo de efectos mixtos, priorización de la conservación, riqueza de especies

Introduction

Habitat loss, biological invasions, direct exploitation of species, and climate change interact to threaten species in every taxonomic group (Brook et al. 2008). As these landscape-scale extinction drivers create widespread environmental change, it is likely that many unknown species are vanishing (Peres 2005). For this reason, protecting geographic areas often appears preferable to protecting individual species (Bruner et al. 2001; Moritz 2002). In recent years, conservation attention has focused on biodiversity hotspots, geographic regions high in both extinction risk and diversity of target taxa (Myers et al. 2000; Myers 2003). To identify such hotspots, researchers have examined multiple taxa simultaneously, searching for parts of the globe where high diversities of different groups (e.g., plants and vertebrates) overlap (Myers et al. 2000).

Because we lack species richness assessments for most locations for lesser known groups, it is hard to assess how much of their diversity will be captured within identified hotspots (Samways & Grant 2007). Although very large scale diversity patterns are common across taxa (e.g., diversity peaks in tropical regions [Mittelbach et al. 2007]), the degree of congruency in diversity patterns of different taxa at the scale of protected areas on continents is highly variable (Heino et al. 2005). For example, taxonomic groups in Finnish streams respond independently to environmental factors; no group is a reliable indicator of other groups (Heino et al. 2005). Similarly, there is little congruence in species richness of 6 different terrestrial taxa in a reserve in Greece (Kati et al. 2004), among 3 invertebrate taxa in a region of the Swiss Alps (Oertli et al. 2005), or between plants and fungi in Swedish grasslands (Öster 2008). In contrast, diversity of Californian butterflies and plants show congruent peaks (Hawkins & Porter 2003), whereas diversity of large moths is a fairly reliable indicator of other taxonomic groups in Denmark (Lund & Rahbek 2002) and carabid beetle diversity is an indicator of plant and vertebrate diversity in China (Schuldt et al. 2009). Diversity of vascular plants and terrestrial vertebrate taxa show strong convergence across a wide range of geographic locations (Qian & Ricklefs 2008). Although species richness of plants and herbivores is positively associated at various scales, diversity peaks are largely nonoverlapping (Jetz et al. 2009). A meta-analysis of 237 species richness correlations showed an overall positive but weak congruency among taxa (Wolters et al. 2006).

Marine islands are both centers of endemism, of particular importance to global biodiversity, and epicenters of extinction (Loope et al. 1988; Kier et al. 2009). Island populations are necessarily limited in size (Burkey 1995; Frankham 1998) and exhibit a tendency toward vulnerable forms (Paulay 1994). For example, island plants are less likely to possess thorns or toxins than mainland plants (Vitousek 1988). As a result of these vulnerabilities, islands are considered hotspots and are targeted by conservation efforts (Maunder et al. 1997; Brummitt & Lughadha 2003; Caujapé-Castells et al. 2010). There is currently high interest in the identification of island hotspots that may be targeted for conservation (Chown et al. 2001; Olson & Dinerstein 2002). As on continents, existing island conservation prioritization schemes are biased toward well-known taxa (Brooks et al. 2006). For most islands, understanding of bird and mammal diversity is fairly complete (IUCN 2013). Whereas botanical knowledge is also extensive (Purvis & Hector 2000), botanical diversity is so high that new species continue to be discovered with relative frequency. By contrast, the species richness of invertebrate groups on most islands is completely unknown, and the richness of reptiles and amphibians is often only partially explored (Glaw & Vences 2000). Basic species inventories are rare and unbalanced across geographies (Ahrends et al. 2011). It is thus difficult to assess confidently how well high diversity of well-known taxa coincides with that of lesser known taxa.

Well-known and lesser known taxa may track each other on marine islands according to island biogeography theory (IBT). The theory predicts that species richness on islands should be driven by the combination of island size and isolation from the mainland, which influence immigration and extinction rates (MacArthur & Wilson 1967). Islands that are far from the mainland or small should have lower immigration rates than islands that are near the mainland or large, due to a lower chance of species' arrival on the island (MacArthur & Wilson 1967). Small islands should exhibit elevated extinction (i.e., high species turnover) because population sizes will of necessity be smaller (MacArthur & Wilson 1967). Recent refinements of IBT argue that large islands or islands far from the mainland should have elevated speciation due to wider availability of open niches (Whittaker et al. 2008); islands with higher maximum elevation should have greater species richness due to greater habitat diversity (Kalmar & Currie 2006); and islands lower in latitude should have greater diversity due to tropical diversity effects (Kalmar & Currie 2007).

Because IBT predicts that physical characteristics of islands are key to species diversity, it may be that well-known and lesser known taxa track each other fairly well if both respond independently and in the same manner to physical drivers. However, taxonomic differences in speciation rates, transport modes, range sizes, and habitat requirements could confound these patterns and lead to disjunct diversity curves (Brown & Lomolino 2000; Cowie & Holland 2006). Furthermore, site-specific diversity is characterized by disequilibrium, which violates a basic premise of IBT (Brown & Lomolino 2000).

A number of studies have examined the factors driving diversity across different insular taxa. Large area and island age are indicators of high diversity of various taxa for the Azore, Canary, Galapagos, Marquesas, and Hawaiian Islands (Whittaker et al. 2008); high diversity of land snails across 8 oceanic archipelagoes (Cameron et al. 2013); and high diversity of 17 animal groups in the Aeolian Islands (Fattorini 2009). Large area and low isolation are indicators of high plant species richness for more than 400 islands globally (Weigelt & Kreft 2013). Although area is a significant predictor of bird, bat, butterfly, and herpetofauna diversity in the Lesser Antilles, the relationship between species diversity and area and habitat diversity varies across taxa (Ricklefs & Bermingham 2001). Island area, elevation, and isolation are indicators of plant diversity and endemism across 6 oceanic archipelagoes (Chiarucci et al. 2011). Island area, age, elevation, and isolation are indicators of spider diversity in Macaronesia (Cardoso et al. 2010), and increased habitat diversity correlates with increased species diversity across a wide set of islands (Hortal et al. 2009). Island elevation is a significant predictor of endemic species diversity in the Canary Islands (Steinbauer et al. 2012).

We adapted linear mixed effects modeling techniques used in such studies to explore how well diversity of well-known taxa (landbirds and mammals) predicts the diversity of several groups of lesser known taxa. We hypothesized that diversity patterns of lesser known taxa are indicated by those of well-known taxa, which in turn are largely determined by the combined effects of physical island characteristics (area, latitude, distance from mainland and nearest large island, and maximum elevation). We also used biodiversity information to assess and compare practical approaches to protected area selection. Our ultimate goal was to test whether land protection targeting the well-known taxa will effectively capture lesser known taxa as well. Although we focused here on islands, these methods could also be used for continental regions with clearly defined areas and unusually high biodiversity, such as mountain sky islands (e.g., Samways et al. 2010, 2011).

Methods

Data Collection

To compare diversity of well-known and lesser known taxa across islands, we developed a database containing global marine island information. We began with the Threatened Island Biodiversity (TIB) database (TIB Partners 2012). The TIB contains comprehensive threatened vertebrate diversity data for its islands. We conducted an extensive literature search in Web of Science and in the University of Arizona library to add data for nonthreatened well-known vertebrates and all lesser known taxa. We searched for the following terms: *island* combined with, in succession, *species richness*, *species diversity*, *endemic*, *amphibian*, *reptile*, *plant*, *insect*, *arthropod*, and *mollusc*. The search netted 623 sources, from which we extracted data on species richness and endemism for lesser known taxa on each island (not all islands contained complete data for all lesser known taxa). We then examined our database to determine which lesser known taxonomic groups or subgroups contained sufficient data (data for over 100 islands) for our quantitative analyses. These groups were amphibians, reptiles, vascular plants, tenebrionid beetles, butterflies, ants, and land snails. We filled as many database gaps as possible by searching library sources and field guides for these particular taxonomic groups. The final island database contained 1190 islands, representing 109 archipelagos, for which complete diversity data existed for at least one lesser known taxonomic group.

We downloaded spatial data for all mammal species from the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN 2013) (Supporting Information). We used ArcGIS to examine the shapefiles for each island in our database in order to count total species richness and number of single-island endemic (SIE) mammal species. The IUCN spatial data were the most comprehensive mammal diversity data set we could find, although it has certain key limitations. First, the shapefile resolution was poor, and small islands in particular were difficult to discern. Shapefiles for each mammal species delineate the best possible estimate of each species' range, but researchers have not completed thorough mammal surveys on every island. It may be that some mammals occur on islands for which they have not yet been reported.

For landbird diversity, the IUCN spatial data are not available in a searchable format. So, for each archipelago in turn, we used library and Internet resources (primarily field guides, peer-reviewed scientific literature, and Avibase [Lepage 2013]). Bird lists from professional or amateur birdwatchers are available for most large and midsized islands. However, such lists are often presented without assessment of the search effort upon which the list is based. The bird diversity data in our database likely span a spectrum of quality. Where possible, we eliminated accidental and non-native species from our diversity estimates.

We used library sources, Internet references, and Google Earth (Google 2013) measurements to gather island biogeography data (area, latitude, longitude, maximum elevation, distance to a mainland, and distance to the nearest large island) for each island in the database.

Linear Mixed Effects Model Construction

We applied a linear mixed effects model followed by a spatial analysis to each lesser known taxon in turn. We examined the following relationships (summarized with sample sizes in Table 1): total species richness for each lesser known taxon versus total bird species richness; species richness of each SIE lesser known taxon versus species richness of threatened birds; species richness of each SIE lesser known taxon versus species richness of SIE birds; total species richness of each lesser known taxon versus total mammal species richness; species richness of each SIE lesser known taxon versus threatened mammal species richness; and species richness of each SIE lesser known taxon versus species richness of SIE mammals.

We combined bird and mammal richness, because data on birds and mammals are the most available diversity information for most islands and island conservation organizations currently base many of their prioritization decisions on the combined diversity of birds and mammals, and examined the following relationships: total species richness of each lesser known taxon versus total combined bird and mammal species richness; species richness of each SIE lesser known taxon versus combined threatened bird and threatened mammal species richness; and species richness of each SIE lesser known taxon versus combined SIE bird and mammal species richness.

Finally, we assessed the following additional relationships: threatened bird species richness versus physical island biogeography factors; threatened mammal species richness versus physical island biogeography factors; combined threatened bird and threatened mammal species richness versus physical island biogeography factors; and species richness of SIE lesser known taxon versus physical island biogeography factors. Because few islands have been examined for all focal taxa, we used a unique set of islands for each analysis (i.e., only those islands for which necessary data were available) (Table 1).

For the mixed effects model, fixed effects included species richness of the well-known taxon, log-transformed area, latitude, distance to the mainland, distance to the nearest large island, and maximum elevation. Island, archipelago, and region were random effects, and their spatial structure was defined in the model. Species richness of the lesser known taxa was the response variable. For every lesser known and well-known species combination, all fixed effects and their interactions were included in the initial model. We applied model simplification techniques (Crawley 2007) to reduce the number of tested effects to a biologically meaningful subset. We eliminated fixed effect interactions from each model in a stepwise fashion, beginning with 5-way, then 4-way, etc. Each model simplification step was accepted if its Akaike information criterion (AIC) value was at least 2 points lower than the AIC of the previous model (Crawley 2007). Once the model had been simplified as far as possible, P values of remaining variables were examined for detection of significant relationships.

To supplement the mixed model, we applied a simple spatial model to each lesser known and well-known taxon pair. Using analysis of variance with archipelago as block, we fitted latitude and longitude as covariates and examined only the well-known taxon richness variable as a predictor within that framework (Crawley 2007).

Practical Conservation Approach Analyses

We conducted a practical conservation approach analysis by considering in turn the 3 factors that emerged in the mixed models as the best predictors of lesser known taxon diversity: total mammal diversity, the combination of threatened bird and threatened mammal diversity, and island area. We assessed the number of species and the land area that would receive protection under different practical conservation scenarios.

The strongly significant and positive relationships between area and both mammal and bird diversity demonstrated that prioritizing conservation by any of these factors would result in conservation actions directed toward the largest islands (Fig. 1). However, conservation of large islands is often infeasible. Conservation actions applied to very small islands, by contrast, are relatively feasible. For example, invasive vertebrates can be completely removed from very small islands (e.g., Nogales et al. 2004; Campbell & Donlan 2005; Howald et al. 2007). Based on these practical considerations, we examined our database to assess the combined land area represented and number

Table 1. Matrix of results (*P* values) of island taxon diversity pattern comparisons tested via linear mixed effects modeling.*

		Mammals			*Birds*			*Mammals + birds*					
LKT		*SR*	*thr*	*SIE*	*SR*	*thr*	*SIE*	*SR*	*thr*	*SIE*	*Area*	*Dist.*	*Elev.*
Reptiles	SR	<0.001 (351)			NR (306)			NR (306)					
	SIE		<0.001 (163)	0.799 (163)		<0.001 (220)	<0.001 (220)		<0.001 (139)	<0.001 (144)	<0.001 (163)	NR (163)	NR (163)
Amphibians	SR	<0.001 (302)			<0.001 (272)			<0.001 (272)					
	SIE		0.008 (100)	0.224 (100)		<0.001 (109)	0.559 (109)		<0.001 (97)	0.22 (99)	NR (100)	NR (100)	<0.001 (100)
Plants	SR	<0.001 (459)			<0.001 (307)			<0.001 (307)					
	SIE		0.113 (101)	0.033 (116)		0.037 (183)	0.529 (183)		0.003 (98)	<0.001 (108)	<0.001 (115)	<0.001 (115)	NR (115)
Ants	SR	<0.001 (202)			NR (132)			NR (132)					
	SIE		NR (28)	0.159 (29)		NR (46)	<0.001 (46)		NR (28)	<0.001 (29)	0.743 (29)	NR (29)	NR (29)
Tenebrionid beetles	SR	<0.001 (85)			0.001 (122)			<0.001 (122)					
	SIE		0.001 (65)	0.001 (98)		<0.001 (103)	NR (103)		<0.001 (84)	<0.001 (85)	0.001 (98)	NR (98)	NR (98)
Snails	SR	<0.001 (195)			NR (148)			NR (148)					
	SIE		0.437 (39)	0.772 (39)		<0.001 (54)	0.844 (54)		0.016 (31)	0.499 (30)	0.081 (38)	0.082 (38)	NR (38)
Butterflies	SR	<0.001 (173)			NR (167)			NR (167)					
	SIE		0.022 (59)	0.123 (59)		NR (66)	NR (66)		0.026 (51)	<0.001 (52)	<0.001 (59)	NR (59)	NR (59)
Island area			<0.001 (583)			<0.001 (839)			<0.001 (475)				
Dist.			NR (583)			NR (839)			NR (475)				
Elev.			NR (583)			NR (839)			NR (475)				

**Sample sizes for each comparison (i.e., the unique set of islands for which we found number of species/biogeographic information for that comparison) are shown in parentheses.*
Abbreviations: SR, species richness; SIE, single island endemic; LKT, lesser known taxa; area, island area; dist., distance to mainland; elev., maximum island elevation. Because model simplification was used, NR means no relationship was examined in the final, simplified model.

of SIE species conserved if islands were protected according to the following criteria: smallest island prioritization, smallest 25% of islands in the database by land area; endemism prioritization, 10% of database islands with highest occurrence of SIE birds and SIE mammals; threatened species prioritization (because conservation funding is often tied to threat status), 10% of database islands with highest combined occurrence of threatened birds and threatened mammals. Then, because on the smallest islands the number of SIE species is very low, we assessed the conservation efficiency of a threshold minimal area approach: prioritization of the smallest 10% and 25% of islands above a threshold land area of 10 km^2, beyond which occurrence of SIEs increased for most taxa (see Results).

All statistical analyses were performed in R version 2.14.1 (R Development Core Team 2012).

Results

Linear Mixed Effects Models

In island biogeography models, island area was the most common significant variable. It predicted species richness of threatened mammals and birds and SIE reptiles, plants, tenebrionid beetles, and butterflies (Table 1).

Endemic species richness for lesser known taxa was significantly predicted by threatened bird plus threatened mammal richness for all groups except ants (Table 1). Total mammal species richness significantly predicted total species richness for all 7 lesser-known taxa (Table 1).

Spatial Analyses

When spatial structure was taken into account, land area was a significant predictor of all lesser known taxa except

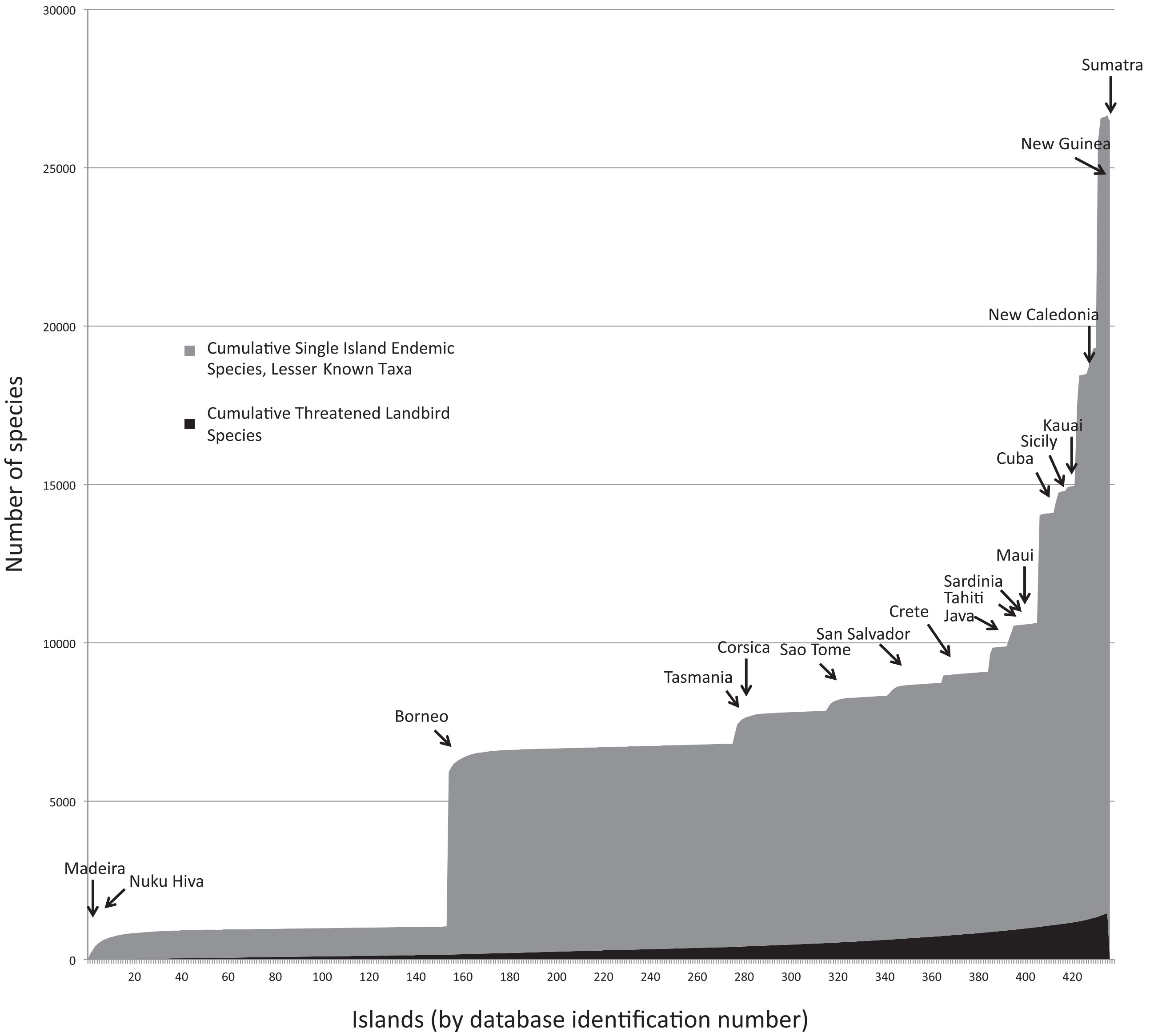

Figure 1. Cumulative number of single-island endemic species in lesser known taxonomic groups captured by hypothetical conservation efforts targeted at an increasing number of threatened landbird species. Only islands with single-island endemic, lesser known taxa are included in this figure. All rapid increases in number of lesser known taxon species indicate the addition of large islands to the set of conserved islands.

ants and land snails (Supporting Information). Total mammal species richness again predicted total species richness of all lesser known taxa (Supporting Information). Threatened mammal + bird richness was a significant predictor of endemic diversity of all lesser known taxa except ants (Supporting Information).

Practical Conservation Approach Analyses

Islands selected for conservation action based on the best predictors of lesser known taxon diversity (i.e., high total diversity of mammals or high combined diversity of threatened birds and mammals) captured lesser known taxa reasonably well (Table 2; Fig. 2). The size of conserved area under scenarios based entirely on diversity became extremely large (Table 2). Selecting the smallest 10% or 25% of islands ≥10 km^2 in area as conservation priorities (based on the most common area value at which numbers of endemic species begin to climb in diversity vs. area graphs [Supporting Information]) generated intermediate values of both land conserved and diversity captured.

Table 2. Land area represented and the number of single-island endemic species captured by conservation scenarios based on bird and mammal endemism, diversity of threatened species, and minimum island area beyond which species diversity increases.

	Conservation scenario[a]					
	smallest	*endemism*		*threatened species*	*threshold minimal area*	
	island	*birds*	*mammals*	*birds + mammals*	*10%*	*25%*
Land area protected (km^2)	21.93	3,661,526	1,675,379	2,705,717	2016	14,984
No. islands protected	297	119	119	119	119	297
SIE species protected[b]						
mammals	1 (0.4)	186 (79.1)	235 (100)	192 (81.7)	6 (2.6)	19 (8.1)
birds	0 (0.0)	1022 (99.6)	466 (45.4)	333 (32.6)	5 (0.5)	78 (7.6)
reptiles	1 (0.2)	347 (80.4)	351 (84.8)	339 (81.9)	9 (2.2)	34 (8.2)
amphibians	0 (0.0)	146 (94.8)	151 (98.1)	153 (99.4)	0 (0.0)	2 (1.3)
plants	30 (0.1)	22,319 (90.9)	15,459 (63.0)	15,642 (63.8)	227 (0.9)	883 (3.6)
ants	0 (0.0)	801 (99.8)	793 (98.8)	801 (99.8)	0 (0.0)	0 (0.0)
tenebrionids	0 (0.0)	9 (9.4)	44 (45.8)	31 (32.3)	1 (1.0)	16 (16.7)
land snails	2 (0.2)	863 (77.0)	769 (68.6)	777 (69.3)	31 (2.8)	158 (14.1)
butterflies	0 (0.0)	1 (5.9)	12 (70.6)	10 (58.8)	0 (0.0)	0 (0.0)

[a] *Scenario definitions: smallest island, conserve smallest 25% of islands, by land area, in the database; endemism, conserve 10% of database islands with highest occurrence of single-island endemic birds and mammals; threatened species, conserve 10% of database islands with highest occurrence of threatened birds plus threatened mammals; threshold minimal area, conserve smallest 10% and 25% of islands above the threshold land area of 10 km^2.*

[b] *Single-island endemic (SIE) species values are presented as numbers of species followed by parenthetical percentages of all SIE species for that taxon in the database.*

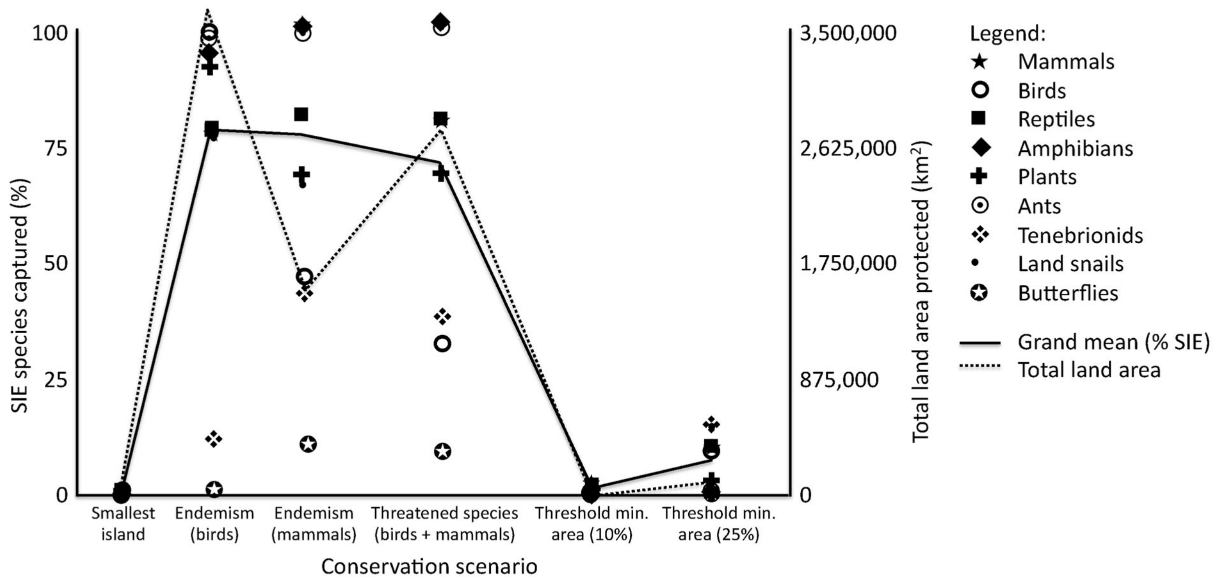

Figure 2. Conservation efficiency of various conservation scenarios applied to the island biodiversity database (smallest island, conserve smallest 25% of database islands by land area; endemism, conserve 10% of database islands with highest occurrence of single-island endemic [SIE] birds or mammals; threatened species, conserve 10% of database islands with highest occurrence of threatened birds plus mammals; threshold minimal area, conserve smallest 10% and 25% of islands above a threshold area of 10 km^2). Scenarios that conserve high percentages of the single-island endemic (SIE) species richness for each taxon or for all taxa combined (grand mean) also represent protection of enormous land area and are therefore unlikely to be practical.

Discussion

Total mammal diversity was the best indicator of total lesser known taxa diversity (Table 1), and the combination of threatened mammal plus threatened bird diversity was the best indicator of lesser known taxon endemic diversity. Threatened bird and mammal occurrence data are available for a large percentage of the world's islands (TIB Partners 2012). Furthermore, much existing conservation prioritization is based on threatened species occurrences (e.g., the Small Islands, Big Difference campaign [Ricketts et al. 2005; Langhammer et al. 2007; Rondinini et al. 2011]).

Examining quantitative diversity patterns together with practical conservation scenarios enabled us to explore options for conservation efficiency that neither approach would permit alone. Selecting islands above a threshold minimal area served as an example of a potentially reasonable approach. Within our database, protection of the smallest 10% of islands larger than 10 km^2 captured 119 islands that ranged in size from 10 to 29 km^2 and totaled 2016 km^2. This set of islands contained 11 SIE birds and mammals and 268 SIE species of lesser known taxa. This method could also be used for a specific set of islands of different sizes, such as the Caribbean Islands. Within this set, the smallest 10% of islands larger than 10 km^2 would be assessed for protection, and islands high in bird and mammal diversity would receive priority. Methods such as these generate candidate island portfolios that are feasible to protect. Then, bird and mammal diversity can be used to identify islands within the group that are likely to have disproportionately high biodiversity (given their size). The islands protected will be small, but some extremely small islands support important biodiversity (Samways et al. 2010), and these methods may help conservation organizations pinpoint them.

Idiosyncratic Diversity Patterns and Dispersal Mode

Relationships among taxonomic groups are multifaceted, implying that basic island biogeography is not the sole explanation of diversity patterns. Diversity of threatened bird species and threatened mammals did a better job than biogeography at predicting endemic richness of lesser known taxa. High threat levels are often indicative of small population size (IUCN 2013), which may in turn reflect habitat specialization, topographic diversity, and other factors that could drive high diversification and endemism (Peck et al. 1999). Diversity of single-island, endemic, well-known taxa, however, was in general a poor predictor of endemic lesser known taxon diversity. This could in part reflect differences in speciation rate between vertebrates and invertebrates (Valentine et al. 1991; Thomas et al. 2006; Hendry et al. 2007) and between homeotherms and poikilotherms (Martin & Palumbi 1993).

Lack of association between endemism rates could also reflect trait differences among taxa. Total mammal diversity was the most reliable of all tested predictors: it was significantly related to total species richness for all 7 investigated lesser known taxa. We conjecture that this derives from a combination of shared physical biogeographical experiences and similarities in dispersal rate. Most of the species of mammals and lesser known taxa we examined are largely limited by the boundaries of each island. Dispersal between islands occurs for all taxa, but the rate of dispersal of birds is generally greater than even mammals that can fly, such as bats, or lesser known taxa such as butterflies.

Quantitative Diversity Patterns and On-The-Ground Practicality

Protected areas established to protect threatened mammals and birds may also protect endemic species of at least plants, reptiles, amphibians, tenebrionid beetles, butterflies, and land snails. This is encouraging because much conservation action is already directed toward threatened birds and mammals. However, there is no indication that protected areas based on threatened birds and mammals will include high diversity regions for ants. If many more taxonomic groups were included in our analysis, we would expect at least some of them to be similarly distinct in their diversity patterns.

In general, ants exhibited the least congruent patterns of all examined groups. As a taxonomic group with a generally limited flight stage (the nuptial flight of queens), ant dispersal is limited and may more closely mimic that of mammals than birds. An additional factor perhaps limiting speciation rates is the unusually long generation time typical of ants relative to other invertebrates (Keller & Genoud 1997). Finally, ant diversity studies on islands (and elsewhere) are highly spotty and frequently incomplete (D. Holway, personal communication; Fisher 2005), which suggest pervasive lack of information may limit the power of our analyses.

Due to data constraints, we selected lesser known taxa that had been studied enough for a minimal sample size. Because diversity patterns differed even among the 7 focal lesser known taxa we selected, we could not make generalizations to specific taxa we did not examine. However, our results suggest that, for islands of equivalent size, conservation prioritization based on bird and mammal threat levels or total mammal diversity is likely to capture diversity peaks of at least some other taxonomic groups. Because conservation funding is often tied to threat status, it is encouraging that threatened birds and mammals can thus be used as indicators for a variety of other taxa. However, we recognize that not all species of conservation concern will be captured by these methods; there are many endemic or remarkable species that occur on islands otherwise low in diversity or small in size. Species-specific conservation will still be necessary and must go hand in hand with the landscape view we present here. We caution that the concept of umbrella species is subject to debate and continual revisitation (Roberge & Angelstam 2004; Branton & Richardson 2011). The contrasting ecological requirements of different taxonomic groups can exclude some species from conservation benefits when they fail to meet the criteria used to select umbrella species (Seddon & Leech 2008). Correct selection of umbrella species can be difficult (Branton & Richardson 2011). Although our focus here on broad diversity of birds and mammals, rather than on individual species, may allay some concerns, it is still impossible for island conservation groups to determine with certainty how many species they are protecting and how many they are failing to protect. Undiscovered species outside protected areas will continue to become extinct. Inventories of biodiversity are the only means by which one can fully assess conservation effectiveness.

Acknowledgments

We thank K. Newton for her gracious assistance with the TIB Database and for generously offering early advice and guidance on data collection strategies. We are deeply grateful to M. Balman, S. Butchart, R. Cowie, D. Holway, M. J. Nogales Hidalgo, R. Rundell, and M. Seddon for providing us with essential species diversity information.

Supporting Information

Map of total mammal species richness on islands examined (Appendix S1), spatial model outputs (Appendix S2), and plots of main comparisons (Appendix S3) are available on-line. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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