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Vulnerability of terrestrial island vertebrates to projected sea-level rise

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Abstract

Sea-level rise (SLR) from global warming may have severe consequences for biodiversity; however, a baseline, broad-scale assessment of the potential consequences of SLR for island biodiversity is lacking. Here, we quantify area loss for over 12 900 islands and over 3000 terrestrial vertebrates in the Pacific and Southeast Asia under three different SLR scenarios (1 m, 3 m and 6 m). We used very fine-grained elevation information, which offered >100 times greater spatial detail than previous analyses and allowed us to evaluate thousands of hitherto not assessed small islands. Depending on the SLR scenario, we estimate that 15–62% of islands in our study region will be completely inundated and 19–24% will lose 50–99% of their area. Overall, we project that between 1% and 9% of the total island area in our study region may be lost. We find that Pacific species are 2–3 times more vulnerable than those in the Indomalayan or Australasian region and risk losing 4–22% of range area (1–6 m SLR). Species already listed as *threatened* by IUCN are particularly vulnerable compared with non-threatened species. Under a simple area loss–species loss proportionality assumption, we estimate that 37 island group endemic species in this region risk complete inundation of their current global distribution in the 1 m SLR scenario that is widely anticipated for this century (and 118 species under 3 m SLR). Our analysis provides a first, broad-scale estimate of the potential consequences of SLR for island biodiversity and our findings confirm that islands are extremely vulnerable to sea-level rise even within this century.

Keywords: climate change, conservation, endemic species, island biogeography, range contractions, sea-level rise, threatened species, vertebrates

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Introduction

Climate change is anticipated to have major ecological consequences and difficult challenges for conservation (Dawson *et al.*, 2011), including species geographic range contractions (Parmesan & Yohe, 2003; La Sorte & Jetz, 2010), which increase the risk of extinction of many populations and species (Parmesan, 2006; Thuiller, 2007). The full extent of the impacts from climate change on biodiversity is unclear because many types, even obvious ones, are still not well studied. One such impact is global sea-level rise (SLR). Ocean levels are anticipated to increase significantly due to melting ice and thermal expansion caused by global warming. The large ratio of coastal to interior areas and often large extent of low-lying areas make islands particularly exposed to SLR-induced loss of land (Nicholls & Cazenave, 2010). To date, the consequences of SLR for biodiversity and human inhabitants remain unclear [but see (Aiello-Lammens *et al.*, 2011; Fish *et al.*, 2005; Loucks *et al.*, 2010; Menon *et al.*, 2010)]. Therefore, our goal was to assess the vulnerability of terrestrial vertebrates on islands to current projections of SLR.

Most projections of SLR estimate 0.5–1.9 m elevations will occur during this century (Carlson *et al.*, 2008; Vermeer & Rahmstorf, 2009) and up to 5.5 m rise by 2500 (Jevrejeva *et al.*, 2012), although higher rises are expected if positive feedback loops, such as reduced solar reflection due to ice loss, are included in the analyses (Hansen, 2007). The global or eustatic sea level has already increased significantly during the last century (Kemp *et al.*, 2009), and new data suggest that melting of ice sheets is occurring at twice the rate as previously estimated (Dowdeswell, 2006) and SLR is occurring at 60% faster than the IPCC projections (Rahmstorf *et al.*, 2012). Although there are uncertainties about the rate and extent of SLR in the future, existing projections can be used to consider a range of scenarios, both conservative and liberal, to make assessments of land loss and identify the most vulnerable species (Menon *et al.*, 2010; Wetzel *et al.*, 2012).

The greatest area losses from SLR are expected to occur on small islands and other low-lying coastal regions (Nicholls & Cazenave, 2010; Traill *et al.*, 2011) – and the potential consequences are enormous in these

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areas for human inhabitants (McGranahan *et al.*, 2007) and other species (Fish *et al.*, 2005; Fuentes *et al.*, 2010; Loucks *et al.*, 2010; Aiello-Lammens *et al.*, 2011). For example, a small, 28 cm rise is projected to lead to a 96% reduction in the tiger *Panthera tigris* habitat in the Sundarbans in Bangladesh (Loucks *et al.*, 2010). SLR can also lead to significant loss of seasonally critical habitats: Up to 32% of beach area that Caribbean sea turtles (e.g., *Eretmochelys imbricata, Caretta caretta* or *Lepidochelys kempii*) use as nesting habitat could be lost due to a 0.5 m rise (Fish *et al.*, 2005). Coastal ecosystems are particularly vulnerable, and salt marshes, for example, are projected to decline by 20–45% in this century depending on the IPCC scenario and compensatory ability (Craft *et al.*, 2009). Synergistic effects arising from SLR combined with other factors, such as reduced rainfall, may lead to a complete switch of coastal ecosystem types (Virah-Sawmy *et al.*, 2009) or lead to a gradual loss of mangroves at the seaward fringes (López-Medellín *et al.*, 2011). Thus, the biodiversity on small islands and other low-lying coastal regions appears to be highly vulnerable to SLR, but it is unclear how many species could be lost under existing SLR projections.

Islands are also of concern to conservation biologists because they harbor species with small geographic ranges and high endemicity. The species richness of terrestrial vertebrate endemics, for example, is eight times higher on islands on average than on the mainland (Kier *et al.*, 2009). Around one quarter of all known extant plant species globally are located on islands (Kreft *et al.*, 2008), 10% of mammals, and 12% of birds, despite the fact that islands cover only 2% of the global terrestrial area (Alcover *et al.*, 1998). Moreover, islands have already experienced significant species reductions due to anthropogenic factors, and as many as 80% of all historical extinctions have occurred on islands (Ricketts *et al.*, 2005). In summary, under current SLR projections, large area losses for islands and other low-lying regions can be expected (Menon *et al.*, 2010), which may result in a significant reduction in the earth's overall biodiversity.

In this study, we provide a first broad-scale baseline assessment of SLR and the potential consequences of area loss for island biodiversity. We focus on the islands of the Southeast Asian and Pacific (SEAP), which includes over 12 900 islands, which represents 42% of the global island area. This region contains a large number of endemic terrestrial vertebrates and other species (e.g., Ceballos & Ehrlich, 2006; Catullo *et al.*, 2008) that may be highly vulnerable to SLR. In fact, SLR in this region has already played a surprisingly large role in driving changes in species distributions and extinction (Inger, 1999; Meijaard, 2003; Woodruff, 2010). In our analysis, we used refined, high (90 m) resolution spatial elevation data from Shuttle Radar Topography Mission (SRTM) to estimate area loss, and we show why such high-resolution data are crucial for accurately assessing vulnerability to SLR compared with course-scale data used in previous analyses (Menon *et al.*, 2010). We considered three different SLR scenarios (1 m, 3 m and 6 m) to examine the consequences of both inundation and erosion, and using our SLR projections, we assessed the vulnerability of this region's 3048 endemic terrestrial vertebrates to these SLR scenarios. We compared the vulnerability of different classes of vertebrates and threatened vs. non-threatened species, and we provide a first-order estimation of the area losses from SLR and the contractions of geographic range size for these species.

Material and methods

Study region and islands

Our study area, the SEAP region, covers islands from Southeast Asia (including Philippines, Borneo, Sumatra, Java), Melanesia (New Guinea, New Caledonia), and the Pacific (Micronesia, Polynesia, etc.), which occur in three biogeographic realms (Indo-Malaysia, Australasia, Oceania). We consider 12 983 islands, which are either continental or oceanic in our dataset (see Fig. 1). Continental parts of Southeast Asia and Australia as well as islands below the size of 2.5 ha were excluded. The study region ranged from the Hawaiian Islands in the North to Kermadec Island in the extreme South and from the Andaman Islands in the West to Easter Islands. The islands in our dataset represent a land area of approximately 2.98×10^6 km², i.e., around 42% of the global island area [according to the Digital Elevation Model (DEM) used see below]. They exhibit enormous variation in size, ranging from small atolls of just a few hectares to the world's largest islands over 780 000 km². Their isolation or distance to the nearest continent varies widely from several to >5000 km.

Shuttle Radar Topography Mission (SRTM) Data

To assess island land area and potential area losses due to different degrees of SLR, we used the most recent highly resolved DEM from NASA's SRTM with 90 m spatial resolution (Rodriguez *et al.*, 2005), which provide several important qualitative and quantitative advances compared with datasets used in previous SLR studies (Hastings & Dunbar, 1999) (see summary in Table S1). In particular, the horizontal and vertical resolution and accuracy are significantly greater in SRTM compared with the Global Land One-kilometer Base Elevation (GLOBE) (Hastings & Dunbar, 1999) dataset, used to evaluate SLR effects on coastal area (Li *et al.*, 2009), coastal human populations (Rowley *et al.*, 2007), and ecoregions and endemic species (Menon *et al.*, 2010). The 90 m spatial grain SRTM offers a factor ~120 times finer horizontal spatial resolution compared with the 1 km spatial grain of GLOBE and thus provides a dramatically more detailed topography and realistic representation of changes in coastal elevation. Only coastal regions that have an elevation below the given sea-level rise and that are connected to the ocean will be inundated in our scenarios. The accuracy of inundation models crucially depends on having detailed coastal topography data because fine-scale changes in elevation and barriers that prevent inundation can only be detected with a high-resolution dataset. Future studies will certainly benefit from better vertical spatial resolution than 1 m currently provided by SRTM, although such resolution is not yet available globally. SRTM data also provide a more realistic shoreline than GLOBE, which is crucial for generating accurate models of inundated coastal areas (see Fig. S1 for illustration). Additionally, assessing SLR effects on very small islands is impossible without the high resolution (90 m) DEM data that SRTM offers, as many small islands that are particularly vulnerable are not covered in low-resolution datasets. For example, for the SEAP region, SRTM data provide 12 000 islands whereas with 1 km spatial resolution only around 2700 islands are covered in GTOPO30 data [US Geological Survey's EROS Data Center (EDC) (1996)], which use the same source like GLOBE in this area. Finally, GLOBE does not offer comparable quantitative assessments of its statistical uncertainty, which precludes error estimation. A previous comparison suggested that GLOBE data overestimate inundated areas in comparison with high-resolution LIDAR (light detection and ranging) data, whereas SRTM data underestimated inundated area (Gesch, 2009). Thus, although erosion is included in our models, our SRTM-based study provides a conservative assessment of SLR effects.

Quality control of SRTM data

As the original SRTM dataset contains voids, we used an improved version of the SRTM v.4 DEM of the Consultative Group on International Agricultural Research (CGIAR) (Jarvis *et al.*, 2008), in which spatial filtering methods to correct this phenomenon were used (Gorokhovich & Voustianiouk, 2006). We transformed the raster data into vector data (by using an ArcGIS raster to polygon conversion along the cell boarders) and projected the data using a regional Lambert equal area

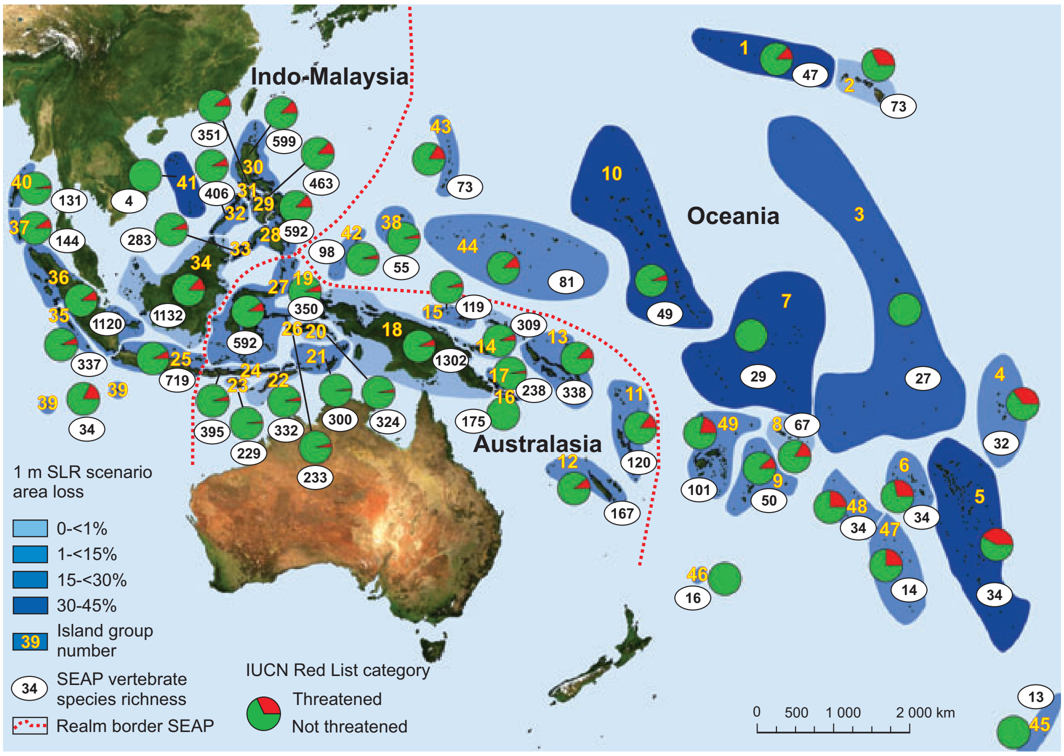

Fig. 1 Vulnerability of island groups due to a 1 m sea-level rise (SLR) and SEAP terrestrial vertebrate richness in coastal and close-to-coast regions (highland and montane regions excluded; Lambert Equal Area projection). Island group number: 1. Northwestern Hawaii and Midway Islands, 2. Hawaii, 3. Central Polynesia, 4. Marquesas Archipelago, 5. Tuamotu Archipelago, 6. Society Islands, 7. Western Polynesian Islands, 8. Samoa, 9.Tonga, 10. Eastern Micronesia, 11. Vanuatu, 12. New Caledonia, 13. Solomon Islands, 14. New Britain and New Ireland, 15. Admiralty Islands, 16. Louisiade Archipelago, 17. Trobriand Islands, 18. New Guinea, 19. Halmahera, 20. Seram, 21. Banda Sea Islands, 22. Timor and Wetar, 23. Sumba, 24. Lesser Sunda Islands, 25. Java and Bali, 26. Buru, 27. Sulawesi, 28. Mindanao, 29. Western Visayas, 30. Luzon, 31. Mindoro, 32. Palawan, 33. Sulu Archipelago, 34. Borneo, 35. Mentawai Islands, 36. Sumatra, 37. Nicobar Islands, 38. Yap islands, 39. Christmas and Cocos Islands, 40. Andaman Islands, 41. South China Sea Islands (Paracel, Spratly), 42. Palau Islands, 43. Mariana Islands, 44. Caroline Islands, 45. Easter Island, 46. Kermadec Island, 47. Tubuai, 48. Cook Islands, 49. Fiji.

projection for Southeast Asia and the Pacific. For quantifying island area loss, we based our assessments on the improved SRTM v.4 DEM. The DEM dataset was clipped along coastlines by applying the 'Shorelines and Water Bodies Database', which is very detailed along shorelines and contains small islands [Kropáček *et al.*, 2011; see also US Geological Survey's EROS Data Center (EDC) (2009)]. Furthermore, to avoid the interpretation of SRTM artifacts as small islands, the islands were also validated by visual cross-checking the results with high-resolution satellite imagery (from the period 1990–2005 on Bing maps and Google Earth, depending on the location as data come from various sources). We eliminated over 700 (6%) of apparent islands that we identified as artifacts, such as jetties, docks, or data voids (Fig. S2). We used this refined 90 m spatial resolution DEM to estimate potential area losses on islands due to different degrees of sea-level rise, and the corrected DEM layer is available from the authors upon request. Our absolute SLR-driven area loss estimates are within the statistical uncertainty of SRTM data and will probably be modified as more accurate DEMs become available in the future.

SLR scenarios and island area loss calculation

We simulated future inundation and erosion by applying a range of different possible sea-level rise scenarios (1 m, 3 m, and 6 m SLR) and integrated a scenario-specific erosion-rate into our model. We considered coastal areas that are connected to the ocean with SRTM elevation values equal to and below the sea level of the respective scenario as flooded. These SLR scenarios were chosen because they cover the range from existing estimates, which include the most conservative 0.5–1 m SLR (e.g., 18–59 cm, IPCC, 2007b) to more liberal ones. The 0.5–1 m SLR projections have been criticized as being too conservative (Dowdeswell, 2006) and one of these projections (Siddall *et al.*, 2010) has subsequently been retracted for similar reasons. Other studies forecast an SLR of 1.3–1.4 m (Rahmstorf, 2007; Carlson *et al.*, 2008), 0.7–1.9 m (Vermeer & Rahmstorf, 2009) in this century or up to 3 m by 2300 (Schaeffer *et al.*, 2012) or more (Schubert *et al.*, 2006) in subsequent centuries, including a 5.5 m rise by 2500 (Jevrejeva *et al.*, 2012). Thus, our study covers both conservative and liberal estimates of SLR. The Greenland ice-sheet alone holds enough water for a 7 m rise (Gregory *et al.*, 2004), and Greenland and the Antarctica together hold enough for a 70-m rise (Alley *et al.*, 2005), but we did not cover these worst-case scenarios.

SLR-driven land erosion may significantly exacerbate direct area loss from SLR and therefore we included an estimate of potential area loss from erosion in our model (Stive, 2004; Zhang *et al.*, 2004). As detailed data on local lithology are not available, we used a simple formula based on distance to shore as first-order estimate of horizontal erosion. Specifically, the latest IPCC report suggested that horizontal shoreline recession due to erosion can be expected to be in the range of 50–200 times the vertical rise of sea level (IPCC, 2007a), and for this study, we chose the slightly conservative factor of 100. Specifically, for the 1 m SLR scenario this translated into a 100 m buffer zone adjacent to shore to be severely impacted by erosion and thus considered inundated (300 m for the 3 m SLR). To avoid overestimation of inundated inland area, we limited this erosion buffer to the coastal zone, as defined by an elevation <20 m above current sea level and a distance to ocean of <100 km. Areas in the hinterland with no connection to the ocean and with potential barriers that prevent flooding were thus not considered inundated.

Sea-level rise across biogeographic island groups

For a first-order assessment, we grouped islands into 85 ecoregions, broadly following Olson and colleagues (2001), which are characterized by distinct geography, habitats, and communities (Olson *et al.*, 2001). We excluded 12 ecoregions in the island interiors far away from coastal zones (Hawaii tropical high shrublands, New Britain-New Ireland montane rain forests, Central Range montane rain forests, Central Range subalpine grasslands, Sulawesi montane rain forests, Mindanao montane rain forests, Luzon montane rain forests, Luzon tropical pine forests, Borneo montane rain forests, Kinabalu montane alpine meadows, Sumatran montane rain forests, Sumatran tropical pine forests). Subsequently, we merged ecoregions on larger islands into a single island group, resulting in a total of 49 island groups that represent either one whole or several islands and that cover all islands in the SEAP area (see also Fig. 1). The Sunda Shelf mangroves and Sundaland heath forest ecoregions extend over both to Sumatra and Borneo and delineation between these two island groups is not possible. However, this classification does not affect our analyses, as no island group endemic species are included, and so there is no double-counting of island group-specific species.

Potential loss in biodiversity

To assess the potential biodiversity impacts of SLR, we derived species occurrence for terrestrial vertebrates (Amphibia, Aves, Mammalia, and Reptilia) for each island group from the Wildfinder database version 01.06 (WWF, 2006). Following the exclusion of montane or subalpine ecoregions (see above), the island group x species matrix for analysis did not include highland habitat specialists, and we further excluded all marine bird species, resulting in a total of 4465 vertebrate species. In our approach, we calculated range loss only for bird species where the coastal area is their main habitat. To simplify interpretation, we excluded 37 bird species whose main feeding habitat is water or inundated areas, due to the unclear impact SLR will have on their main feeding and nesting sites. A total of 3048 species are globally restricted to the 49 island groups (i.e., region-endemic) and we focus on them to calculate area loss in relation to their entire distribution. A total of 2578 species in the analysis are strict endemics, i.e., species occurring on only one island group. All else being equal, island groups are expected to vary in potential biodiversity loss from SLR due to differences in proportional area loss and the richness of all or region-endemic species. To integrate these effects and identify most impacted island groups, we calculate a simple score of island–region-specific SLR biodiversity impact as biodiversity impact score $S_{1m} = S_{0m}\left(1 - \frac{A_{1m}}{A_{0m}}\right)$, where S is species richness and A is the area at current (0 m) and future conditions for e.g., 1 m SLR. The impact score represents the number of species extinctions per island group (global extinctions in the case of island region endemic species) for the likely unrealistic scenario of fraction area lost resulting in an identical fraction of species lost. It is equivalent to setting $z = 1$ in a species loss prediction based on a power-law species (or endemics) area model: $S_{1m} = S_{0m}\left(1 - \left(\frac{A_{1m}}{A_{0m}}\right)^{Z}\right)$. For comparison, we also provide impact scores for $z = 0.25$ and $z = 0.1$, which may approach the slope values for empirically observed species– or endemics–area relationships on the mainland [see He & Hubbell (2011) for recent discussion of caveats and the discussion section in this article]. The absence of fine-scale information on within-island group species distributions prevents quantifying appropriate island group-specific extinction rates and z values. We therefore interpret the impact score simply as integrative measure to compare islands. Actual extinction rates will be affected by the spatial and between-species variation in geographic range occupancy within island groups (Storch *et al.*, 2003).

Estimating SLR-driven geographic range contractions

We analyzed the 3048 region-endemic terrestrial vertebrate species for relative potential loss in geographic range due to SLR-driven area loss. For each species, we calculated current-day maximum geographic range size, R_{0m}, as the sum of the areas, A_{0m}, of the island groups it currently occupies. We estimated projected range size for a given e.g., 1 m SLR scenario, R_{1m}, as the sum of all the projected sizes, A_{1m}, of the same island groups. Proportional loss in geographic range size was then given as $R_{1m} = \left(1 - \frac{R_{1m}}{R_{0m}}\right)100$. This loss estimate assumes that species do not show trends in how occupancy varies within the geographic range, e.g., as in the extreme (and unrealistic) case of there being no unsuitable habitat within the range. This assumption is not probably upheld as ecoregional and expert-based range maps strongly overestimate species actual fine-scale distribution and, certainly at scales finer than 100 km, incur high errors of commission (Hurlbert & White, 2005; Hurlbert & Jetz, 2007; Jetz *et al.*, 2008). Thus, to achieve more realistic estimates of geographic range size and to assess the sensitivity of range loss projections to distribution data type, we randomly selected 61 mammal, amphibian and bird species endemic to the Oceanic region for manual refinement (see Table S2a). Specifically, we used species habitat preference information provided by the IUCN assessment (http://www.iucnredlist.org) to identify clearly unsuitable land-cover types, as categorized by the GlobCover 2.2 global land-cover classification (ESA, 2008) (Table S2b). For detecting differences in SLR in different island groups, taxonomic groups or between threatened and not threatened species, we analyzed the data using General Linear Models after arcsine transforming percentage data. We analyzed the effects of SLR on the full geographic range of endemic species and we excluded species occurring in two or three realms for the realm-specific comparison of average area loss. Evaluation of whether species are currently threatened or not was based on the IUCN Red List Database (IUCN, 2009). Species considered 'critically endangered', 'vulnerable', or 'endangered' were subsumed in our study as 'threatened', and 'near threatened', and 'least concern' species were considered 'not threatened'. All spatial analyses in this study were conducted with spatial data projected using Lambert Equal Area projection, based on the WGS84 Ellipsoid.

Results

Area loss from SLR

Under the 1 m or 3 m sea-level rise scenarios, our findings indicate a loss of terrestrial land area in the SEAP region of ca. 28–116 × 10^3 km², which comprises 0.9–3.9% of total island area (276 × 10^3 km² and 9.3% for the 6 m scenario, Table 1). Approximately 15–42% of all islands in the 1 m and 3 m scenarios are expected to become completely inundated and vanish (62% for the 6 m scenario), with around 20% of the islands losing 50–99% of their area (Table 2). Island groups ($n = 49$) with smaller areas, such as in the Oceanic realm, are made up of many low-lying islands (i.e., islands with a low mean island elevation) and thus they are particularly vulnerable to SLR [correlation between mean island group area and elevation: Spearman's r (r_s) = 0.69, $P < 0.01$]. As expected, SLR-induced area loss increases with decreasing island group area (1 m SLR scenario: $r_s = -0.81$, $P < 0.01$). This geomorphic variability results in significant regional differences in SLR-induced land area loss among the three different biogeographic realms, with the Oceanic realm as most and the Australasian realm as least vulnerable (Table 1; Fig. 1). Oceanic islands will potentially lose 2–4 times

Table 1 Disparate losses of island areas (km^2) in the three study realms under three sea-level rise (SLR) scenarios

		1 m SLR loss		3 m SLR loss		6 m SLR loss	
Region	Island area km²	km²	%	km²	%	km²	%
AA	1 279 655	7436	0.6	28 266	2.2	81 960	6.4
IM	1 648 721	19 043	1.2	82 620	5.0	186 955	11.3
OC	48 356	1907	3.9	4869	10.1	7007	14.5
Total	2 976 732	28 385	1.0	115 755	3.9	275 922	9.3

AA, Australasia; IM, Indo-Malaysia; OC, Oceania.

Table 2 Disparate loss of numbers of islands in the SEAP region

	1 m SLR loss		3 m SLR loss		6 m SLR loss	
	number	%	number	%	number	%
Islands lost	1910	14.7	5440	41.9	8005	61.7
Islands losing 50–99% of area	2454	18.9	3051	23.5	2662	20.5

more area than Australasian islands, and up to three times more than the Indomalayan. However, due to the large differences in total island area within these three realms, absolute area loss will be greatest in Indo-Malaysia (e.g., 3 m SLR will lead to an area loss of 82.6×10^3 km^2 in Indo-Malaysia compared to 4.9×10^3 km^2 in Oceania). These differences in area loss are magnified at the level of the 49 island groups: the six most vulnerable will potentially lose 28–92% of their island area, whereas the three least vulnerable only lose less than 1% under a 1 m and 3 m SLR scenario (Fig. 1; Table S3).

Impacts on island terrestrial vertebrate diversity

The 49 island groups with 12 983 islands making up the study region represent over 40% of the world's island area, and they harbor a total of 4465 terrestrial vertebrate species (>15% of global diversity; 544 amphibians, 2115 birds, 768 mammals, and 1038 reptiles), with over 2/3 restricted (endemic) to the study region. The region is also home to a surprisingly large proportion (1184/6666 or 18%) of the world's strict endemic species (according to WWF definition; species that occur only in one ecoregion, see also WWF, 2006), especially for mammals (23% of all) and birds (33% of all). Island groups vary considerably in vertebrate richness (Fig. 1), and richness strongly increases with island group area ($r_s = 0.74$, $P < 0.01$). Large island groups tend to have the least relative SLR-induced area loss, and consequently, we find that the number of endemics decreases with increasing area loss (Fig. 2a, c, $r_s = -0.57$ for SEAP vertebrates, $r_s = -0.70$ for island group endemics, $P < 0.01$).

To identify island groups with the potentially greatest loss of biodiversity, we calculated a biodiversity impact score that integrates the area loss and species richness of an island group in a comparable way (Fig. 2a, c; Table 3a, b, and Table S3). The metric identifies both, expansive archipelagos made up of many low-lying islands such as the Sulu archipelago, Northwestern Hawaii - Midway Islands, and Eastern Micronesia, as well as large high-diversity islands, e.g., Java-Bali and Sumatra as regions with the greatest SLR impact on biodiversity (Fig. 2b, d; Table 3a, Table S3). For Sulu archipelago, currently home to 283 vertebrate species, an area loss of around 27% is expected under a 3 m SLR. Our assessment indicates that SLR will have potentially devastating consequences for species in this region and its inhabitants. The biodiversity impact score for Sulu archipelago is 78 for all vertebrates (assuming a simple species loss–area loss proportionality), which means that 78 species may lose all habitable area in the region ($z = 1$, see methods). The same metric for island region endemics (which are species only found in the Sulu archipelago), is 1–4 species (for the 1–6 m scenario, $z = 1$). A more conservative assumption of the relationship between area loss and species loss ($z = 0.25$, $z = 0.01$) may still result in substantial impacts (impact scores of 22, 9, respectively). In places such as Tuamotu and Sulawesi island, group endemics are particularly strongly affected (biodiversity impact scores for endemic species ≥ 3, Fig. 2d). In contrast, other island groups have biodiversity impact scores that are 0 for island group endemic species, such as Samoa and Easter Islands (for a 1 and 3 m scenario, $z = 1$). Overall, we identify 33 island groups with an impact score for all SEAP vertebrate species of at least 8 given a 3 m SLR (and $z = 1$).

High impact scores for island group endemic species are of greatest conservation concern, as they may most strongly indicate potential for global extinction. The ten most vulnerable island regions have impact scores between 13 (1 m SLR) and 67 (6 m SLR) for island endemic species ($z = 1$). For island group endemic species, the summed impact score ($z = 1$) for all 49 island groups and the 3 m SLR scenario is 118. This finding suggests that under the simple species loss–area loss proportionality assumption, approximately 118 species are vulnerable to extinction in the only island group they occupy due to area loss from SLR in this region (and our estimate increases from 37 species for a 1 m SLR scenario to 246 species for a 6 m SLR scenario).

Impacts on species range sizes

To assess species-level threats, we evaluated potential SLR-induced contractions in global range size of the 3048 SEAP-restricted terrestrial vertebrate species by region, vertebrate class, and IUCN Red List category. For a preliminary baseline comparison, we make the simplifying assumption that all species range area losses are proportional to island group area loss. Under this assumption, we find that endemic vertebrates occurring in Oceania will probably lose the highest share of their range (4–22%, 1–6 m scenario), with those in the Indomalayan realm as much as 1–10% (1–6 m

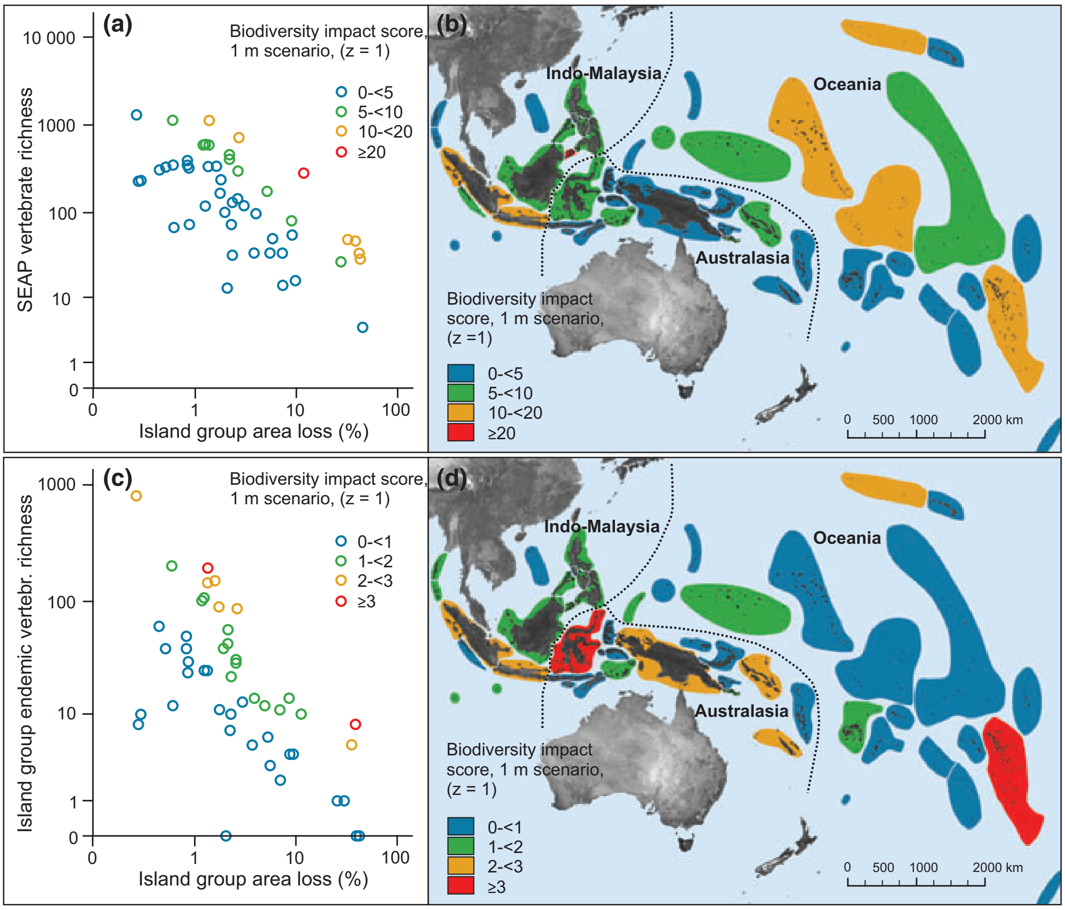

Fig. 2 Sea-level rise-induced loss of dry land, the variation in species richness, and potential biodiversity impact among island groups for (a, b) all vertebrates and (c, d) island group endemics. The figure also shows a map representing the biodiversity impact score for each island group for all vertebrates (b) and island group endemics (d). Results are for a 1 m SLR scenario and biodiversity impact score given $z = 1$, see methods. The biodiversity impact score provides an integrative measure of the potential impact of the area loss on biodiversity in island groups.

scenario, Fig. 3a). Endemic species living on islands in the Australasian biogeographic realm are expected to incur the least area loss (1–7%, Fig. 3a). As a consequence of their differing biogeography in the region (Fig. S3), some vertebrate classes appear much more vulnerable than others. Birds appear particularly at risk due to their occurrence on small, remote oceanic islands that are projected to see particularly high proportional SLR-induced area loss.

We find that species already threatened (IUCN, 2009) are significantly more vulnerable to SLR than other species (Fig. 3b). Already threatened species will lose on average more area than nonthreatened ones, e.g., 6.6% vs. 3.8% of total range on average in a 3 m scenario (11.6% vs. 8.5% in a 6 m scenario). This means that species already vulnerable to extinction will probably lose around 30–50% more area on average than other species. Threatened species will be particularly vulnerable in island groups where high area losses due to SLR will take place: these island groups will be of special conservation concern (see geographic patterns of threatened species per island group, Fig. 1).

Few species in the analysis are likely to occur equally in both potentially inundated and noninundated parts of an island region, as our analysis assumes. To assess the sensitivity of our results to this assumption, we repeated the analysis of the 61 most vulnerable species in Oceania after performing a careful habitat refinement of their range (see Fig. S4 for an example species and a comparison of the habitat-refined and nonrefined range model). We find slightly greater range loss compared with unrefined range data, on average between 5% for a 1 m SLR scenario and 12% for a 3 m scenario (compared to 2% and 8%, Table S4). As expected, the reanalysis with refined range data reveals substantial between-species variation in area loss depending on the elevation and proximity of ranges to coastal areas. From the specific overlap between fine-scale geographic range and SLR-induced area loss, some

Table 3 The top 10 (out of 49) island groups with the potentially greatest SLR-induced SEAP biodiversity impact scores (for 1 m inundation) (a) and summarized values for the top ten and all island groups (b). Area gives total current-day terrestrial area for the island group and area loss quantifies the loss projected under different scenarios. The SEAP vertebrates and island group endemic vertebrate species richness is listed together with biodiversity impact scores (S) for 1 m, 3 m, and 6 m SLR. The biodiversity impact score (I) estimates potential species loss under different hypothetical and uniform values of z (z = 1, 0.25, 0.1) for the relationship between island group area loss and species loss (see methods for details). Island group names, realm (AA, Australasia; IM, Indo-Malaysia; OC, Oceania), and region ID (see also Fig. 1) is given

					Area loss%			SEAP vertebrates										Island group endemic vertebrates									
									S_{1m}, z =			S_{3m}, z =			S_{6m}, z =				S_{1m}, z =			S_{3m}, z =			S_{6m}, z =		
Rank	ID	Island group	Realm	Area km²	1 m	3 m	6 m	No.	1	0.25	0.1	1	0.25	0.1	1	0.25	0.1	No.	1	0.25	0.1	1	0.25	0.1	1	0.25	0.1
(a)																											
1	3	Sulu Arch.	IM	2530	12	27	40	283	34	9	4	78	22	9	112	34	14	10	1	0	0	3	1	0	4	1	0
2	25	Java and Bali	IM	138 282	3	7	11	719	19	5	2	49	13	5	80	21	8	87	2	1	0	6	2	1	10	3	1
3	1	NW Hawaii & Midway Isl.	OC	13	38	79	98	47	18	5	2	37	15	7	46	29	15	5	2	1	0	4	2	1	5	3	2
4	10	E Micronesia	OC	690	32	73	97	49	16	5	2	36	14	6	47	28	14	1	0	0	0	1	0	0	1	1	0
5	36	Sumatra	IM	460 613	1	7	16	1120	15	4	2	81	21	8	178	47	19	145	2	0	0	10	3	1	23	6	2
6	5	Tuamotu Arch.	OC	1518	42	73	80	34	14	4	2	25	10	4	27	11	5	8	3	1	0	6	2	1	6	3	1
7	7	W Polyn. Isl.	OC	107	43	84	96	29	12	4	2	24	11	5	28	16	8	0	0	0	0	0	0	0	0	0	0
8	29	W Visayas	IM	34 916	2	7	12	463	10	3	1	31	8	3	55	14	6	43	1	0	0	3	1	0	5	1	1
9	16	Louisiade Arch.	AA	1809	5	13	20	175	9	2	1	23	6	2	35	9	4	12	1	0	0	2	0	0	2	1	0
10	32	Palawan	IM	14 508	2	9	19	406	9	2	1	37	9	4	76	20	8	57	1	0	0	5	1	1	11	3	1

		Area loss%			Island group endemic vertebrates									
						S_{1m}, z =			S_{3m}, z =			S_{6m}, z =		
Region	Area km²	1 m	3 m	6 m	No.	1	0.25	0.1	1	0.25	0.1	1	0.25	0.1
(b)														
10 most vulnerable island groups	654 986	2	7	15	368	13	3	0	40	12	5	67	22	8
All island groups	2 976 732	1	4	9	2578	37	10	4	118	32	13	246	68	28

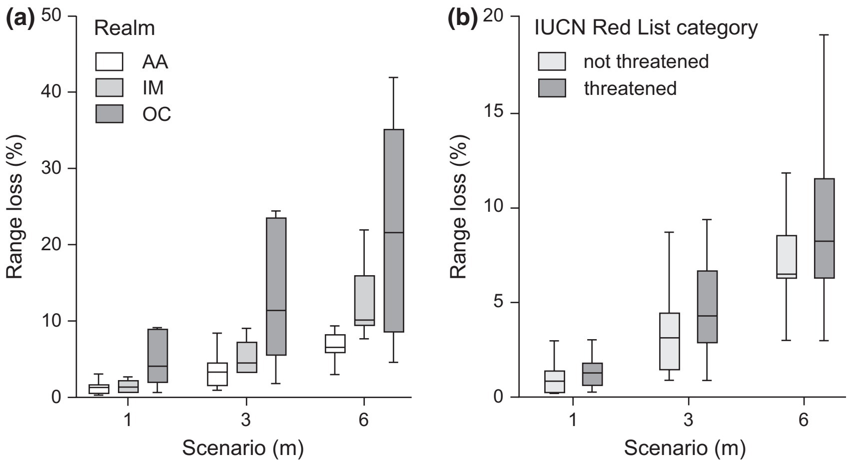

Fig. 3 Potential contractions of geographic ranges of endemic terrestrial vertebrate species under different SLR scenarios, according to (a) realm (AA, Australasia; IM, Indo-Malaysia; OC, Oceania) and (b) current IUCN Red List category. Boxes give the interquartile range, whiskers the highest and lowest values.

species are ultimately expected to go extinct. The sensitivity analysis regarding the range occupancy assumption suggests that region-wide range loss estimates (Fig. 3) may in fact be conservative (Fig. S5).

Discussion

Area loss from SLR

We found that SLR is likely to result in large and significant loss of area on islands in Southeast Asia and the Pacific due to inundation and erosion and some ecoregions risk losing significant parts of their area even under a 1 m SLR. We estimate that the total area lost in this region will be approximately the size of Haiti, Iceland, and New Zealand, under the 1 m, 3 m, and 6 m scenarios, respectively. Of all regions, islands are expected to experience the largest relative impacts of sea-level rise and the largest increase in the spatial heterogeneous sea-level rise (since 1993) could be detected in the SEAP region (Nicholls & Cazenave, 2010). Our results show that the SEAP region and thus their island endemics are highly vulnerable. We found enormous variation in vulnerability of islands to SLR at different scales (realms, island groups, and islands) due to geographic difference in size (which is broadly associated with elevation and coastline length) and topographic structure of islands (Stoddart, 1992). Islands of the Oceanic realm will lose most of their area compared with islands of the other realms, 2–4 times more than on Australasian islands, and up to three times more than in the Indomalayan realm. This result shows that effects on coastal species from inundation will be most severe and particularly in the realm with the lowest human population densities (Wetzel *et al.*, 2012). Atolls are particularly endangered from sea-level rise, whereas islands with high elevations may provide refuges for some species (Baker *et al.*, 2006). In addition to the coastal regions, low-lying central areas of atolls are vulnerable and will be inundated with increasing SLR (Woodroffe, 2007). The most disturbing of our findings is the likely complete disappearance of 15–62% of islands, mainly small ones (and 19–24% of islands will lose 50–99% of their area), under the 1–6 m scenarios we considered. This significant land loss will lead to reduced habitat connectivity at a significant rate and reduced gene flow between populations.

Area loss and island biodiversity

We found that the 49 island groups vary tremendously in their vulnerability to SLR (Table 3a, Table S3). Some island ecoregions lose more than one-third of their areas, whereas others will experience only minor area losses under a 1 m SLR, due to the stark differences in island topography and the complex regional biogeography. Many islands in the region already experienced dramatic species extinctions after human arrival, which has resulted in the loss of around 2000 bird species on tropical Pacific islands (Steadman & Martin, 2003) and substantial impacts on their ecological structure (Boyer & Jetz, 2010) and SLR will impact species also on islands with relatively low human population densities (Wetzel *et al.*, 2012). Many low-lying islands and archipelagos harbor a number of range-restricted species, such as in Oceania, and our results show that these islands are particularly vulnerable to SLR effects. Depending on the actual relationship between loss of area and loss of species, which probably varies along geographic, environmental, and ecological gradients, the 10 most vulnerable island groups are expected to lose up to 13 under a 1 m scenario and 67 species under a 6 m SLR scenario. Menon and colleagues (2010) previously suggested that Southeast Asia and nearby islands are one of the regions where SLR effects are likely to be most prominent. Using 1 km spatial resolution GLOBE data, they estimated global area loss of 0.7% due to a 1 m SLR rise and a subsequent loss of 181 species (out of 18 628) when assuming regional *z*-values, where the loss is highest in tropical regions. They cautioned that their inferences were limited by a lack of high-resolution biodiversity data, although they did not appear to appreciate the limitations of the GLOBE data to assess vulnerability of coasts and islands to SLR. Nevertheless, our results confirm that the islands of Southeast Asia and the Pacific and their biodiversity are highly vulnerable to SLR, and around 37–118 strict endemic species (out of 2578) may face the threat of extinction, under a 1 m SLR–3 m SLR, respectively. While we focused on island species, many taxa inhabiting continental coasts may be equally or even more threatened by SLR. Unless they are able to adapt to rising sea levels, mangroves along the mainland coast (habitat of many specialized vertebrates like the Sundarbans of Bangladesh) might largely disappear even with SLR below 1 m (Loucks *et al.*, 2010). Many vulnerable coastal areas are located in Asia and Africa (Nicholls & Cazenave, 2010). Finally, the effects of SLR extend to nonterrestrial vertebrates such as turtles and fishes for which coastal island habitats are vital for reproduction (Fish *et al.*, 2005).

Preliminary estimates of the specific SLR threat to species emerge from our analyses on potential range contractions. A substantial number of species are expected to lose over 50% or even 90% of their range due to inundation under a 3 m SLR scenario applying a refined species range model, which would greatly increase their risk of extinction. These high levels of range loss are supported by our sensitivity analysis with habitat-refined data. We found for all SLR scenarios that endemic species already endangered will suffer more range losses than nonthreatened species. SLR will therefore increase the already higher extinction risk on islands compared with the mainland due to invasive species, land-use change, and poaching (Boyer, 2010), which makes island species a primary conservation concern (Ricketts *et al.*, 2005). Threatened species tend to have smaller geographic ranges than other species (Cardillo *et al.*, 2008; Lee & Jetz, 2008), which is also the case for threatened species in the SEAP region (median range of threatened species 84 × 10^3 km^2 vs. 280 × 10^3 km^2 for nonthreatened species). For narrow-ranged species, the loss of an even small area and resulting range fragmentation may have a substantial effect on a populations' viability, as observed for narrow-range species in forest 'islands' (Harris & Pimm, 2008). Populations on small islands tend to exhibit lower genetic diversity than other populations (Frankham, 1997; Spielman *et al.*, 2004), which also increases their extinction risk (Frankham, 1997). Thus, area loss from SLR would be expected to add to the already greater vulnerability to extinction of island populations. Several caveats should be considered when translating area loss into biodiversity loss in the context of global change (e.g., Pimm & Raven, 2000; Oertli *et al.*, 2002; Lewis, 2006; Guilhaumon *et al.*, 2008; He & Hubbell, 2011; Storch *et al.*, 2012). We here use an 'impact score' related to the species–area relationship for different z levels (that we assume to not vary within an island region) to simply bookend first-order estimates of likely threats to biodiversity. However, actual species extinction risk may be much more severe than our results imply; for instance, a study on a sandy-coast bird species has shown that populations might decline more rapidly than predicted by area loss alone (Aiello-Lammens *et al.*, 2011).

Additional threats. There are several reasons to expect our estimates are conservative, and that SLR impacts will probably be exacerbated by other aspects of global change (Traill *et al.*, 2011). First, we only considered SLR and we ignored rising temperatures and the other impacts anticipated from climate change, including invasions of predators and infectious diseases (Hof *et al.*, 2011). Future work will benefit from more dynamically incorporating and combining at species level the disparate sources of future extinction risk of which SLR-induced area loss is only one many factors. Second, we only examined effects from inundation and erosion on reducing island area, but SLR will have many additional geophysical consequences, such as seawater intrusion into river deltas or near-coastal groundwater reservoirs (Schubert *et al.*, 2006), which will probably have adverse effects on many species. Third, we only considered terrestrial vertebrates in our study, and more accurate estimates of effects on biodiversity need to consider other groups, including aquatic taxa. For example, many aquatic organisms are expected to become highly threatened from the alterations SLR will cause to coral reefs, estuaries, mangroves, and other aquatic habitats (Ellison & Stoddart, 1991), with additional harmful economic consequences for local communities (McManus, 1997). Fourth, we did not consider increases in human population density or anthropogenic impacts [accelerated land-use change (Brooks *et al.*, 1997; Bomhard *et al.*, 2005; Kier *et al.*, 2009), forest fires, bush meat hunting, and wildlife trade (Sodhi *et al.*, 2004)] that are likely to exacerbate estimated SLR-driven biodiversity loss, as a study on magpie geese shows (Traill *et al*., 2010). Also, we did not consider how SLR can magnify human impacts on species and habitat *outside of coastal regions*: by forcing humans to move to higher elevations or other islands, flood refugees will probably cause additional habitat loss, especially in the hinterland of populated coastal regions (Wetzel *et al*., 2012). We recognize that some species could undergo geographic range shifts and may be partially buffered from range loss, and indeed such climate change-induced shifts have already been observed on the mainland. However, given the large separation distance in our island regions, there is likely little scope for range expansion. Further range shifts and resulting island invasions, should they occur, will probably have a more devastating effect on islands than mainland, given the greater relative importance of biotic process structuring their communities (Buckley & Jetz, 2007). More work is necessary to better understand and, if possible, incorporate these additional factors to make more accurate projections.

Our projections indicate that SLR will cause large habitat loss on islands, especially on the low-lying islands and even in the 1 m scenario. We also find that these area losses from SLR will increase the risk of extinction for many animals, and especially for endemic species in the Pacific realm and species already considered threatened. Overall, habitat loss due to SLR can lead to a significant range loss for endemic species on islands and is likely to be an influential driver affecting future extinction risk of threatened species in coastal regions. These findings have important implications for all low-lying islands and coastal regions with far-reaching consequences for future conservation planning. Conservation efforts will benefit from a stronger integration of SLR effects in the planning of reserves or landscape connectivity, as previously suggested for other climate change effects (Hannah *et al*., 2002; Heller & Zavaleta, 2009). Assessments of climate change effects on biodiversity and pinpointing centers of imminent extinctions (Ricketts *et al*., 2005) would be greatly improved with more extensive and finer scale species distribution data (Jetz *et al*., 2012), as the detail of our biogeographic knowledge in the region is surprisingly limited. Finally, additional fieldwork is required to better understand the perturbations and loss of ecological functions as first SLR-driven species extinctions set in.

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Author contributions

Florian Wetzel, Helmut Beissmann, Dustin Penn, and Walter Jetz designed the research. Florian Wetzel and Walter Jetz collected the data and performed the analyses. Florian Wetzel, Dustin Penn, Helmut Beissmann, and Walter Jetz wrote the manuscript.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Comparison of SRTM (90 m spatial resolution) vs. GTOPO30 (1 km spatial resolution) regarding coastline, shape, and number of islands.
Fig. S2. Example for SRTM coastline inaccuracies and island misinterpretation.
Fig. S3. Vulnerability of island groups due to a 1 m sea-level rise (SLR) and share of SEAP terrestrial vertebrate classes in coastal and close-to-coast regions.
Fig. S4. Example for the sea-level rise-driven area loss: Influence on the habitat-refined range of the bat *Pteropus yapensis* (Yap flying fox).
Fig. S5. Range loss due to three SLR scenarios for the 61 mammal, amphibian, and bird species in Oceania after range refinement.
Table S1. Comparison of GLOBE Elevation Model in a 1 km horizontal resolution vs. SRTM Digital Elevation Model in a 90 m horizontal resolution.
Table S2. Habitat-refined species in Oceania and excluded unsuitable habitat. (a) 61 habitat-refined species in Oceania and their unsuitable habitat types (b) Description of habitat (land-cover) types identified as unsuitable in Table S2a.
Table S3. The 49 island groups of the SEAP region with the potential SLR-induced biodiversity impact scores. Islands are ranked by S_{1m} for SEAP vertebrates.
Table S4. Sensitivity analysis**:** Area loss for 61 endemic vertebrates in Oceania according to three range models.