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Future climate change driven sea-level rise: secondary consequences from human displacement for island biodiversity

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Abstract

Sea-level rise (SLR) due to global warming will result in the loss of many coastal areas. The direct or primary effects due to inundation and erosion from SLR are currently being assessed; however, the indirect or secondary ecological effects, such as changes caused by the displacement of human populations, have not been previously evaluated. We examined the potential ecological consequences of future SLR on >1,200 islands in the Southeast Asian and the Pacific region. Using three SLR scenarios (1, 3, and 6 m elevation, where 1 m approximates most predictions by the end of this century), we assessed the consequences of primary and secondary SLR effects from human displacement on habitat availability and distributions of selected mammal species. We estimate that between 3–32% of the coastal zone of these islands could be lost from primary effects, and consequently 8–52 million people would become SLR refugees. Assuming that inundated urban and intensive agricultural areas will be relocated with an equal area of habitat loss in the hinterland, we project that secondary SLR effects can lead to an equal or even higher percent range loss than primary effects for at least 10–18% of the sample mammals in a moderate range loss scenario and for 22–46% in a maximum range loss scenario. In addition, we found some species to be more vulnerable to secondary than primary effects. Finally, we found high spatial variation in vulnerability: species on islands in Oceania are more vulnerable to primary SLR effects, whereas species on islands in Indo-Malaysia, with potentially 7–48 million SLR refugees, are more vulnerable to secondary effects. Our findings show that primary and secondary SLR effects can have enormous consequences for human inhabitants and island biodiversity, and that both need to be incorporated into ecological risk assessment, conservation, and regional planning.

Keywords: conservation priorities, extinction risk, global change, human migration, human settlements, Indo-Malaysia, insular biodiversity, range contractions, sea-level change

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Introduction

Global warming will cause sea-level rise (SLR) due to melting ice and thermal expansion of oceans (Church & White, 2006; Rahmstorf, 2010). Current predictions of SLR vary from 0.5 to several meters before the end of this century (Hansen *et al.*, 2006; Schubert *et al.*, 2006; IPCC, 2007a; Carlson *et al.*, 2008), and show the strong increase in SLR due to climate change (Robinson *et al.*, 2012). Studies are beginning to evaluate potential SLR effects on coastal wetlands, but general assessments of the consequences for coastal and terrestrial biodiversity across large regions remain scarce. Future SLR will inundate coastal areas and thus lead to an area loss in coastal regions, and even moderate SLR can have surprisingly large ecological impacts, especially for low-lying coastal zones and deltas (Nicholls & Cazenave, 2010). Studies have examined the potential consequences of SLR for biodiversity on a few marine species (e.g. in turtles; Fish *et al.*, 2005; Fuentes *et al.*, 2010). However, there are only few terrestrial studies available and these focus on coastal ecosystems (Virah-Sawmy *et al.*, 2009; Kirwan *et al.*, 2010) or examine just a few individual species such as tigers (*Panthera tigris*, Loucks *et al.*, 2010) or use coarse data (Menon *et al.*, 2010). Thus, comprehensive assessments of SLR effects on terrestrial biodiversity are lacking. Such analyses are particularly urgent for low-lying islands and coastal areas which are considered to be major hotspots of vulnerability to future SLR (IPCC, 2007b; Cazenave & Llovel, 2010; Nicholls & Cazenave, 2010). Moreover, in addition to area losses from inundation and erosion (primary effects), SLR is also likely to cause a variety of

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downstream or secondary effects, such as ecological impacts due to the displacement and relocation of human populations from low-lying coastal regions (McGranahan *et al.*, 2007; Rowley *et al.*, 2007; Nicholls & Cazenave, 2010) into the hinterland (Dasgupta *et al.*, 2009). Secondary effects are generally ignored or overlooked, yet they can be even more important than primary ones, such as the unexpected high rates of mortality from infectious diseases following wars and armed conflicts (Ghoborah *et al.*, 2003) and increased bush meat hunting resulting from fish declines (Brashares *et al.*, 2004). However, until now, human displacement and other secondary effects have escaped the attention of ecological assessments of climate change driven sea-level rise.

We aimed to assess the consequences of future SLR for species distributions and terrestrial biodiversity on islands — incorporating both the primary and secondary effects from human displacement. We focused our study on >1,200 islands in the Southeast Asian and the Pacific region (SEAP, Fig. 1), with an area of approximately 2.97 × 10^6 km². The SEAP is a global biodiversity hotspot of high conservation priority (Myers *et al.*, 2000), as it has a high concentration of endemics and range-restricted species (Catullo *et al.*, 2008), but also burgeoning urban areas along coastal regions and deltas (Nicholls & Cazenave, 2010). In our first analyses, we quantified the primary and secondary effects for all 1,287 islands where secondary effects can occur. In our second analyses, we quantified the potential habitat losses and range contractions for all mammal species that are vulnerable to secondary effects on a subset of 106 Indo-Malaysian islands (where reliable high-resolution information on species distribution is available). Rather than assuming that urban and agricultural areas inundated just vanish, we examined the potential ecological impacts on island biodiversity caused by human displacement and relocation. We assumed that urban and agricultural areas lost to SLR will be relocated to the hinterland and encroach on wildlife, such that an area of habitat of equal size (and an arbitrarily chosen location) is removed from the existing range of mammal species ('secondary effects'). Our analyses specifically addressed the following questions: (1) How much of the coastal zone of these islands could be lost due to SLR and how many people are likely to become SLR refugees; (2) What are the relative importance of primary vs. secondary effects from SLR; (3) To what extent do primary and secondary SLR effects vary among species and biogeographic regions? To our knowledge, our analysis is the first to quantify the potential secondary effects due to displaced human activities under SLR.

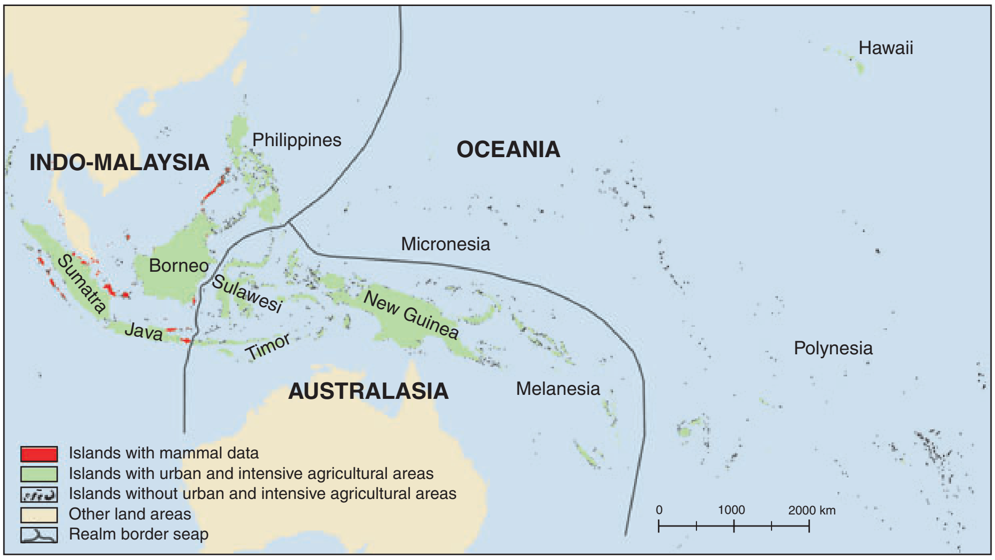


Fig. 1 The Southeast Asian and Pacific (SEAP) region with associated islands. The study region ranges from the Hawaiian islands in the North to the Kermadec Island in the extreme South, and from the Andaman Islands in the East to the Easter Islands in the West (with a bounding box 28.4°N to 30.5°S and 92.2°E to 105.4°W). For analyzing primary and secondary sea-level rise effects on islands, we used all 1,287 SEAP islands with urban and intensive agricultural areas (green), but excluded all islands with no such areas. For analyzing secondary effects on species distributions, we used the 106 Indo-Malaysian islands where reliable distribution data of mammal species are available (red).

Materials and Methods

Study region

Our study focused on the SEAP region (Fig. 1), the largest insular region in the world covering islands of Southeast Asia (including Philippines, Borneo, Sumatra, Java), Melanesia (New Guinea, New Caledonia), and the Pacific (Micronesian and Polynesian archipelagos). It can be divided into three distinct biogeographical realms, Australasia, Oceania, and Indo-Malaysia (Olson *et al.*, 2001), and we used these realms for comparing SLR effects among regions. Our island dataset is based on the Digital Elevation Model (DEM) from NASA's Shuttle Radar Topography Mission (SRTM) with 90 m resolution (Jarvis *et al.*, 2008). To avoid the misclassification of SRTM artifacts, such as small islands, we additionally validated the islands by visually comparing the island dataset with satellite imagery (Microsoft Bing Maps and Google Earth). Our validated and improved island dataset covered 12 983 islands, of which we excluded all islands with a total area of ≤ 3.5 km^2 (i.e., the lowest quantile regarding island area size). These very small islands were excluded because (1) they are of minor relevance for the spatial extent of species' habitats (covering only 0.2% of the total island area) and (2) many of them will be completely inundated (for example 32% of the islands in the 1 m scenario and 90% in the 6 m scenario). We additionally excluded all islands without urban settlements or intensive agricultural land because they are not exposed to secondary SLR effects. Our study finally included 1,287 islands with a total area of ca. 2.96 million km^2, covering 99% of the total island area in the SEAP region.

The Southeast Asian region is considered globally to be one of the major hotspots of vulnerability to future SLR (Cazenave & Llovel, 2010; Nicholls & Cazenave, 2010). In particular, there is a large number of people vulnerable to coastal flooding (IPCC, 2007b). Recent studies on sea-level changes over the last two decades show increases across the region (Nicholls & Cazenave, 2010). For instance, there has been a relatively high sea-level increase in the Philippines and in New Guinea and a lower increase in the area of the Andaman Islands. Analyses of recent SLR show that Southeast Asia will be more strongly affected than other regions globally. For example, the sea-level in the gulf of Thailand is rising faster than on the global average (Trisirisatayawong *et al.*, 2011). Trends in the Pacific also indicate that the western tropical Pacific might be more affected by SLR than the eastern Pacific, particularly near North America (Merrifield, 2011). Overall, these findings indicate that our study region will be strongly affected by SLR in the coming decades.

SLR scenarios

We considered three SLR scenarios (1 m, 3 m, and 6 m) based on the SRTM DEM (see above), and then calculated the area of land loss due to inundation. We included a scenario-dependent erosion rate as erosion increases with rising sea-level (Stive, 2004; Zhang *et al.*, 2004). To estimate effects of coastal erosion in addition to inundation, we used a rough estimate based on the current IPCC report that suggests shoreline recession to be in the range of 50–200 times of the rise in relative sea-level (IPCC, 2007b). In the absence of a detailed model for coastal erosion based on local lithology and geomorphology, this simple rule should provide a first-order estimation of possible effects from erosion on areas vulnerable to temporal inundation. Thus, in addition to a simple inundation effect we also included a horizontal erosion effect. To avoid overestimating the rate of erosion, we restricted the erosion effect by applying a vertical and horizontal threshold (erosion is limited to a maximum of 20 m above mean sea-level vertically and to the coastal zone 100 km horizontally). Our three implemented scenarios cover a range of projections, including forecasts that estimate SLR to be around 0.5 m IPCC (2007a), 1.3–1.4 m (Rahmstorf, 2007; Carlson *et al.*, 2008), 0.7–1.9 m (Vermeer & Rahmstorf, 2009), up to 2 m (Grinsted *et al.*, 2010), or several meters in the next century or the coming centuries (Schubert *et al.*, 2006).

More precise SLR scenarios (i.e., below a ± 1 m accuracy) are not yet available because data on local lithology and geomorphology for the whole SEAP region are lacking. There have been attempts to reconstruct past sea-level rise in the SEAP region (Woodroffe & Horton, 2005) and the implications for terrestrial area availability (Voris, 2000). Sea-level fluctuations in the past 50 years in the Southeast Asian region show a heterogeneous rise (IPCC, 2007a), including a decadal regional variability in the region (cf. years 1993–2003 vs. 1955–2003). Future SLR is also likely to be heterogeneous (Cazenave & Llovel, 2010); however, we did not extrapolate such heterogeneities into the future because uncertainties are very high (Bamber *et al.*, 2009) and because spatially explicit datasets for future rise in the SEAP region are unavailable. Due to the resolution of the SRTM dataset (1 m elevation steps), modifying the SLR scenarios by regional uplift or subsidence does not improve the accuracy of the dataset. Estimates of SLR change consider uplift or subsidence to be a minor factor, at least over the past 17 000 years (cf. Voris, 2000). Hence, we did not include regional uplift or subsidence in our scenarios, and instead, we assume a simple, homogenous increase across the region. Overall, our scenarios cover the range from the most common SLR estimate in this century to higher ones for the forthcoming century, and we do not consider more liberal estimates or the worst-case scenarios (i.e., Greenland and the Antarctic together hold enough water to elevate the sea-level up to 70 m; Gregory *et al.*, 2004; Alley *et al.*, 2005).

Primary and secondary SLR effects on islands in the SEAP region

For calculating primary effects, we estimated the inundated and eroded area of the coastal zone according to our three SLR scenarios. The coastal zone was defined according to the Millennium Ecosystem Assessment as the area along the coasts with a maximum elevation of 50 m above mean sea-level and an inland distance of maximum 100 km. In this coastal zone, we identified urban and intensive agricultural areas and distinguished these from potential areas of habitat for wildlife. For the extent of intensively used agricultural

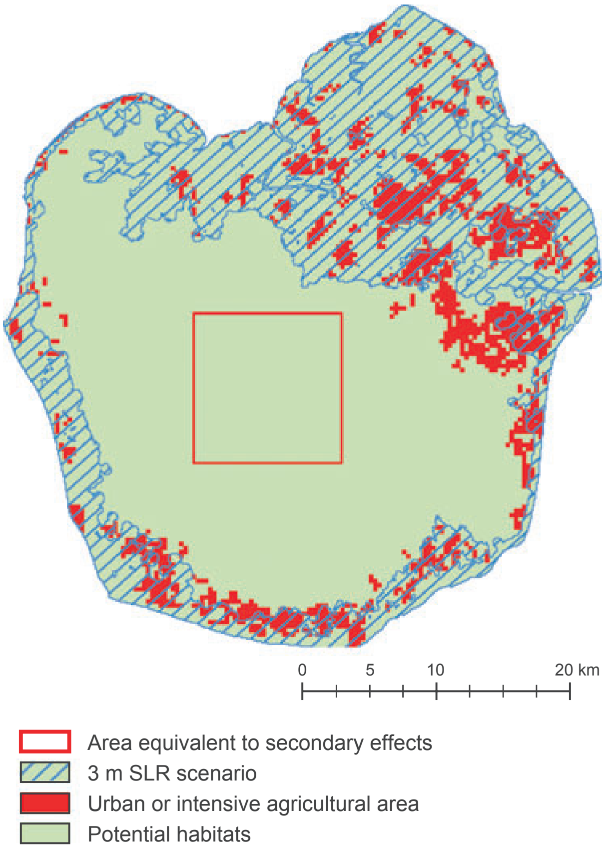


Fig. 2 An example of how primary and secondary sea-level rise effects can be estimated on islands (here exemplified for the Southeast Asian island of Rupat, northeastern coast of Sumatra, Indonesia, 1.901008 N, 101.585252 E). Projected inundation (blue dashed areas, 3 m scenario) affects both potential habitats (light green) and areas of urban and intensive agriculture (red) via primary effects. Areas of urban and intensive agriculture are likely to lead to land-conversion in the hinterland (secondary effects). The red rectangle symbolizes the area size which had to be reclaimed if land-conversion in the hinterland is equal to area loss of urban and intensive agriculture.

area, we used the land-cover classes from the GlobCover 2.2 land-cover data (300 m resolution; ESA, 2008), which covers the most intensive farming types ("post-flooding or irrigated croplands" and "rainfed croplands"). Areas not covered by urban or intensive agricultural land were defined as "potential habitats" (light green in Fig. 2). These areas represent potentially suitable habitats for those species that avoid urbanized or intensively used land. To assess the magnitude of secondary SLR effects, we calculated the area of inundated urban and agricultural areas according to a 1 m, 3 m, and 6 m rise above present-day sea-level and assumed that inundation leads to an equal area replacement in the hinterland (example in Fig. 2). We could not include more explicit spatial projections of human displacement because integrated models including socio-economic factors and their constraints on migration destinations are highly complex, and currently do not exist at this scale of analysis (Findlay, 2011; Piguet *et al.*, 2011). Furthermore, as the number of people who will potentially be forced to migrate remains unclear and controversial (Gemenne, 2011), we did not add such uncertainty into our analyses. For the spatial distribution of human population density we used the data from the Gridded Population of the World dataset (CIESIN, 2004), a global spatial dataset on human population numbers and densities.

Potential consequences of primary and secondary SLR effects for species distributions

For assessing potential primary and secondary SLR effects on species distributions, we used the mammal species distribution data on Indo-Malaysian islands from the detailed evaluation of Meijaard (2003). This datasets provides reliable high-resolution information on species distribution in this region, contrary to many global datasets. For each species, we estimated the potential range loss due to primary SLR effects, i.e., the habitat inundated and eroded in a 1 m, 3 m, or 6 m SLR scenario (across all islands of the Meijaard study). We could assign 109 species from this dataset to 106 islands (see Data S1 and S2). Of these, 54 species avoid urbanized or intensively used land-cover types and are therefore vulnerable to secondary effects. Avoidance of urbanized or intensively used land-cover types was derived for each species from habitat preference data from the IUCN Red List database (2009). As the presence of a species on an island only represents its extent of occurrence (EOO) and hence overestimates its area of occupancy (AOO) (Gaston & Fuller, 2009), we further refined the species distribution data by using species' habitat data from the IUCN (2009). For each species, we linked the habitat types from the IUCN Habitats Classification Scheme (version 3.0) to the spatial explicit land-cover classes from the GlobCover 2.2 land-cover classification (ESA, 2008; Data S3), and then refined the species distributions by clipping those landcover types that are definitely unsuitable for the species (cf. Jetz *et al.*, 2007). This results in AOO maps where species presence is constrained to suitable landcover types within the EOO. We further refined the species distributions by clipping off (unsuitable) elevations outside the maximum or minimum observed for the species (Catullo *et al.*, 2008) based on information from the Southeast Asian Mammal Database (IEA, 2010). These refined species distribution data provided a conservative estimation of the AOO of a species and allowed estimating species-specific habitat loss due to primary and secondary SLR effects.

For evaluating secondary effects, we assumed an equal-area land-conversion of inundated coastal urban and intensive agricultural areas in the hinterland (compare red rectangle in Fig. 2), and the range of a species was reduced proportionally to the size of the range in the hinterland (see formula below). For example, this means that if a species range covers 30% of the remaining island area, 30% of the area of land-conversion will be located there and consequently lead to a range reduction. Therefore, the percent range loss of a species (pRL) due to secondary effects across all islands (where present) was calculated as follows ('moderate range loss model'):

$$\mathrm{pRL_{mod}} = \frac{\sum_{i=1}^{106} \mathrm{UIA}f_i \times \sum_{i=1}^{106} \frac{\mathrm{AOOu}_i}{\mathrm{Au}_i}}{\sum_{i=1}^{106} \mathrm{AOO}_i} \times 100 \qquad [1]$$

where i is the island index (island 1–106), UIAf is the urban area and intensive agricultural area loss per island (in km^2), AOO is the total area of occupancy per island (in km^2), AOOu is the area of occupancy per island which is unaffected by SLR (in km^2), and Au is the remaining island area (in km^2) unaffected by SLR (but not urban or intensive agriculture).

Note that this model provides a moderate estimation of the range loss due to SLR as an equal-area land-conversion is assumed; hence the model is a conservative estimate of secondary effects on species distributions. Range loss could be greater if the relocated area falls completely within a species' habitat (maximum effects model). We illustrate this point with a comparison between the moderate range loss model (above) and a maximum effects model (see Data S4). A minimum effects model would assume that land-conversion in the hinterland takes place first outside a species' AOO, which could occur in some particular (and possibly rare) circumstances; but is unlikely to be a general pattern across species and islands. All results shown below refer to the moderate range loss model unless otherwise stated. Our assessment should be highly conservative because we do not include the increased resources, which would be required to relocate and rebuild urban and agricultural areas or the consumption due to increased population growth anticipated in these regions.

Results

Area loss from primary and secondary SLR effects

Our analyses indicate that primary effects due to inundation and erosion from SLR will result in large area losses of the coastal zone throughout the entire SEAP region, and we find large differences among geographic regions (Table 1; Fig. 3). We estimate that on average, 3% of the coastal area will be inundated in a 1 m scenario, 13% in a 3 m scenario, and 32% will be lost in a 6 m SLR scenario across all 1,287 islands with urban and intensive agricultural area (see Table 1; Fig. 3, for a comprehensive quantitative comparison of the potential land loss with and without erosion see Data S5). Islands within the Oceanic realm are most vulnerable to inundation (7–46% area loss; 1–6 m SLR scenario), followed by the islands of Indo-Malaysia (4–35%) and the islands of Australasia (2–25%). In addition, the amount of inundated urban and intensive agricultural land (which determines the amount of land-conversion in the hinterland, i.e., secondary SLR effects) varies. A high percentage of urban and intensive agricultural land is projected to become inundated on islands in Indo-Malaysia (around 30%; 1–6 m scenario, Table 1, Fig. 3) and Oceania (20–35%; 1–6 m scenario, Table 1, Fig. 3), the other inundated area consist of potential habitat area. In contrast, only 12–16% of the inundated coasts on islands in Australasia are urban or intensive agricultural land (1–6 m scenario), consequently, 84–88% will be area loss of potential habitat area that causes no secondary effects (Table 1; Fig. 3). This finding indicates tremendous spatial variation in the relative importance of primary vs. secondary effects, with primary effects predominating in Oceania and secondary effects being more pronounced in Indo-Malaysia (Fig. 3). Also, many Oceanic islands will not be affected by secondary effects, as only 5% are covered with urban or intensive agricultural areas. The loss from secondary effects is much greater on Australasian (14%) or

Table 1 Projected area loss in the coastal zones of the 1,287 islands in the Southeast Asian and Pacific (SEAP) region due to inundation and erosion (i.e., primary sea-level rise effects). Amount of inundated urban and intensive agricultural areas (UIA) and potential habitat area (PH) in the coastal zone are also given. Estimates are for each of the three realms of the study region and the whole SEAP region. The coastal zone is defined as ≤ 50 m above mean sea-level and ≤ 100 km inland. SLR, sea-level rise; IM, Indo-Malaysia; AA, Australasia; OC, Oceania

	Total		1 m SLR scenario			3 m SLR scenario			6 m SLR scenario		
Realm	Coastal Area (km²)	Coastal UIA (km²)	Coastal area loss (%, km²)	Thereof UIA loss (%, km²)	Thereof PH loss (%, km²)	Coastal area loss (%, km²)	Thereof UIA loss (%, km²)	Thereof PH loss (%, km²)	Coastal area loss (%, km²)	Thereof UIA loss (%, km²)	Thereof PH loss (%, km²)
IM	524,486	134,287	3.5	32.4	67.6	15.6	32.0	68.0	35.4	28.5	71.5
			18,432	5,976	12,456	81,577	26,073	55,504	185,692	52,985	132,707
AA	317,602	45,027	2.1	11.9	88.1	8.4	15.8	84.2	25.2	16.1	83.9
			6,550	781	5,769	26,710	4,216	22,495	79,931	12,900	67,031
OC	8,019	3,098	7.3	21.1	78.9	26.4	31.6	68.4	45.6	35.4	64.6
			585	123	462	2,117	669	1,448	3,660	1,296	2,364
SEAP region	850,107	182,412	3.0	26.9	73.1	13.0	17.0	43.6	31.7	36.8	75.1
			25,567	6,880	18,687	110,404	30,957	79,447	269,283	67,181	202,102

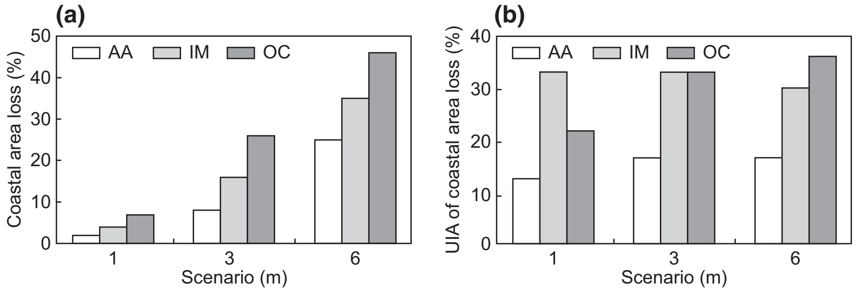


Fig. 3 Projected area loss of the coastal zone for 1,287 islands with urban and intensive agricultural areas (UIA) in the Southeast Asian and Pacific region. (a) Total area loss due to inundation and erosion, i.e., *primary sea-level rise effects* (in % coastal area) and (b) inundated and eroded intensive urban and agricultural area potentially causing *secondary effects* (% urban and intensive agricultural areas within the coastal zone). Estimates cover the three geographic realms of the study region, AA, Australasia; OC, Oceania; IM, Indo-Malaysia.

Indo-Malaysian (18%) islands compared with Oceanic islands. However, most of the islands with no urban or intensive agricultural area are very small, and cover only 1% of whole island area. Around 4–27% of the human coastal population in SEAP are expected to migrate (for the 1–6 m SLR scenario, Table 2), i.e., 8–52 million people. On islands in Indo-Malaysia, a particularly high percentage of humans will be forced to migrate (4–28%, 1–6 m scenario, Table 2), whereas populations on Oceanic or Australasian islands (2–16%) will be less vulnerable. The total number of SLR refugees in Indo-Malaysia for a 3 m SLR is estimated to be 26 million, whereas in Oceania less than half a million refugees are anticipated (Table 2).

SLR will thus lead to a dramatic loss of potential habitat for terrestrial species, especially on SEAP islands with urban or intensive agricultural areas (Table 1; Fig. 3). Islands are projected to lose 11–15% (1 m scenario), 25–31% (3 m scenario), and 39–45% (6 m SLR scenario) of their potential habitat due to inundation and erosion of coastal areas (primary effects) (Fig. 4a). As expected, the secondary effects are particularly pronounced on islands with a high degree of urban and intensive agricultural areas (fourth quartile; Fig. 4b). Furthermore, the increase in secondary effects from the 1 to the 3 and the 6 m scenario is much steeper for the fourth quantile (i.e., islands with highest percentage of urban and intensive agricultural area) than for the first to third quantile. This means that SLR (i.e., coastal area loss) in regions with a high amount of urban and agricultural areas relative to island size will be more severe than in regions with a low percentage of urban and agricultural area. Hence, islands which already have a large ecological impact from human populations will lose 6–24% of habitat area due to secondary effects, additional to the 13–44% based on primary effects (Fig. 4). In contrast, islands with a low coverage of urban and intensive agricultural areas will suffer a relatively minor area loss from secondary effects (0–1%; Fig. 4b). Interestingly, for primary SLR effects the increase in habitat loss due to scenario strength is of similar magnitude for all islands (compare parallel

Table 2 Projected potential effects on human population size based on three scenarios (1 m, 3 m, and 6 m) of sea-level rise (SLR). Estimates are separated for the three realms and the whole study region. IM, Indo-Malaysia; AA, Australasia; OC, Oceania

	Total	1 m SLR scenario	3 m SLR scenario	6 m SLR scenario
Realm	Coastal human population (number)	Coastal human population (%, number)	Coastal human population (%, number)	Coastal human population (%, number)
IM	167,839,190	4.4 7,452,477	15.6 26,224,778	28.5 47,763,899
AA	20,778,920	2.2 458,662	7.9 1,643,182	16.4 3,413,777
OC	2,904,344	2.0 57,707	9.3 270,989	16.4 475,131
whole SEAP region	191,522,454	4.2 7,968,846	14.7 28,138,949	27.0 51,652,807

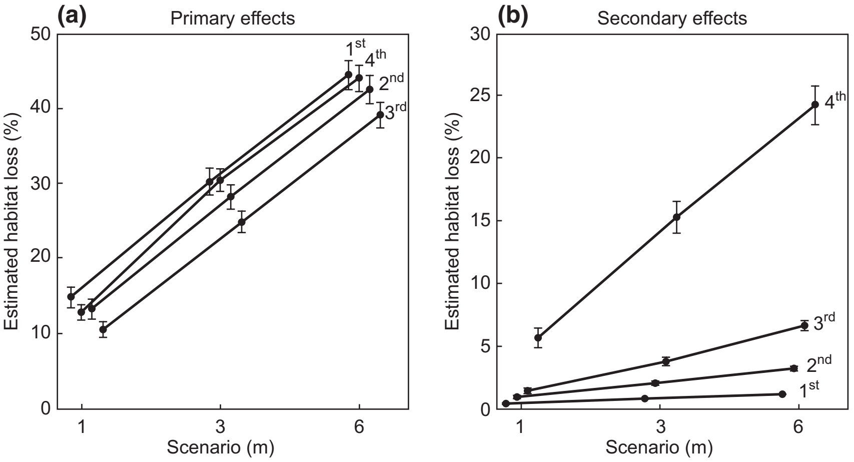


Fig. 4 Potential loss of habitat availability on 1,287 islands with urban and intensive agricultural land due to (a) primary and (b) secondary sea-level rise (SLR) effects given three SLR scenarios (1 m, 3 m, and 6 m) on 1,287 islands (>3.5 ha) in Southeast Asia and the Pacific region. Islands were subdivided into quartiles according to the percentage of area covered by urban and intensive agricultural land (first quartile = lowest percentage of urban and intensive agricultural land area, fourth quartile = highest percentage, whiskers indicate the standard error). Note that for primary effects, a larger SLR scenario leads to a proportional increase in habitat loss across all quartiles (parallel lines in (a)), whereas for secondary effects, (b) the islands with the largest urban and intensive agricultural land areas (fourth quartile) show a proportional stronger habitat loss than islands with a small urban and intensive agricultural land area (quartiles 1–3).

lines in Fig. 4a), whereas for secondary SLR effects the increase in habitat loss due to scenario strength is much stronger for islands with a high coverage of urban and intensive agricultural areas (Fig. 4b). Overall, the relative impact of SLR on potential habitat loss *per se* is dependent on island area size: the smaller the island, the greater the relative impact of SLR on its habitat (Data S7).

Potential consequences of SLR effects for biodiversity

Using a dataset of reliable, high-resolution information on species distributions, we estimated the percent area loss of habitat-refined ranges for 54 mammals on 106 Indo-Malaysian islands. The estimated range loss due to secondary effects is greater than for primary effects for at least 10–18% of the selected mammals in a moderate range loss scenario and for 22–46% in a maximum range loss scenario because most of their range is located in the hinterland where SLR driven land-conversion takes place. Some species (5 of 54 or 9%) are only vulnerable to secondary effects. Overall, including secondary effects increases the percent range loss in all SLR scenarios (Data S6). Interestingly, we find that secondary effects are important for assessing the variance, as well as average effects: when secondary effects are included, then the minimum and maximum values of estimated percent range losses are higher compared to assessing primary effects alone (Fig. 5, Data S6). This result indicates that the neglect of secondary effects of SLR can lead to significant underestimates of habitat loss not only on average but also in the extremes (minimum and maximum) for individual species. However, our study only evaluates relatively small islands when compared with Borneo or New Guinea, for example, and as such smaller islands are likely to be exposed to relatively more SLR impact when compared with larger islands (Data S7), the secondary SLR effects on biodiversity are expected to be less important for larger islands.

To illustrate the variation in SLR effects among species and SLR scenarios, we chose three mammal species which show contrasting vulnerabilities to primary vs. secondary effects (Fig. 6, for species habitat requirements see Data S8). First, for the endangered Smoky Flying Squirrel (*Pteromyscus pulverulentus*), the projected range loss due to primary effects is small (1–3%, 1–6 m SLR scenario), whereas range loss due to secondary effects is considerably stronger (2–60%), especially for a 6 m SLR scenario (Fig. 6a, Data S6). Second, for species such as the rodent Rajah Sundaic Maxomys (*Maxomys rajah;* Fig. 6b), primary SLR effects are more important than secondary ones, and the increasing trend of primary and secondary effects with increasing magnitude of SLR scenarios remains similar. Third, other species, such as the Java Mouse-deer (*Tragulus javanicus;* Fig. 6c, Data S6), are also more vulnerable to primary than secondary effects, but the increase in vulnerability to primary effects with increasing magnitude of SLR scenarios is proportionally stronger than those

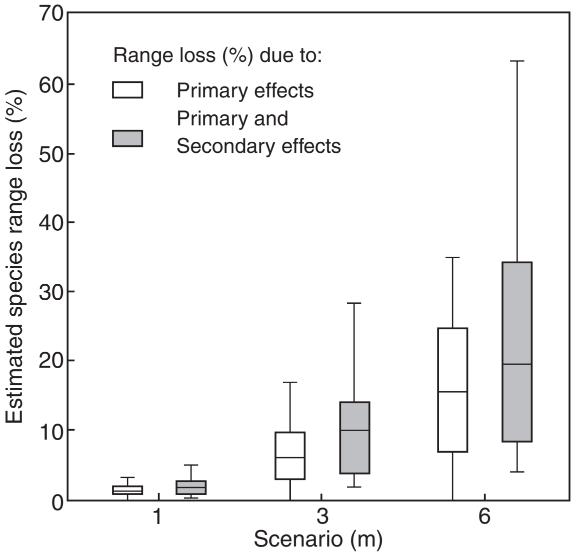


Fig. 5 Estimated percent range loss of mammal species due to primary (white boxes), and primary and secondary (gray boxes) sea-level rise (SLR) effects. Data summarize the SLR effects on the estimated area of occupancy of 54 mammals on 106 Southeast Asian islands. Boxes represent the interquartile range (IQR), horizontal lines within the boxes represent medians, and whiskers extend to 1.5 times the IQR. Note that including secondary effects not only increases the median but also the minimum and maximum values of estimated percent range loss indicating that SLR effects on individual species distributions might be dramatically underestimated if secondary effects are not taken into account.

of secondary effects (Fig. 6c, Data S6). These examples illustrate how primary and secondary SLR effects are expected to differ among different species depending upon their geographical distribution and proximity to human populations.

Discussion

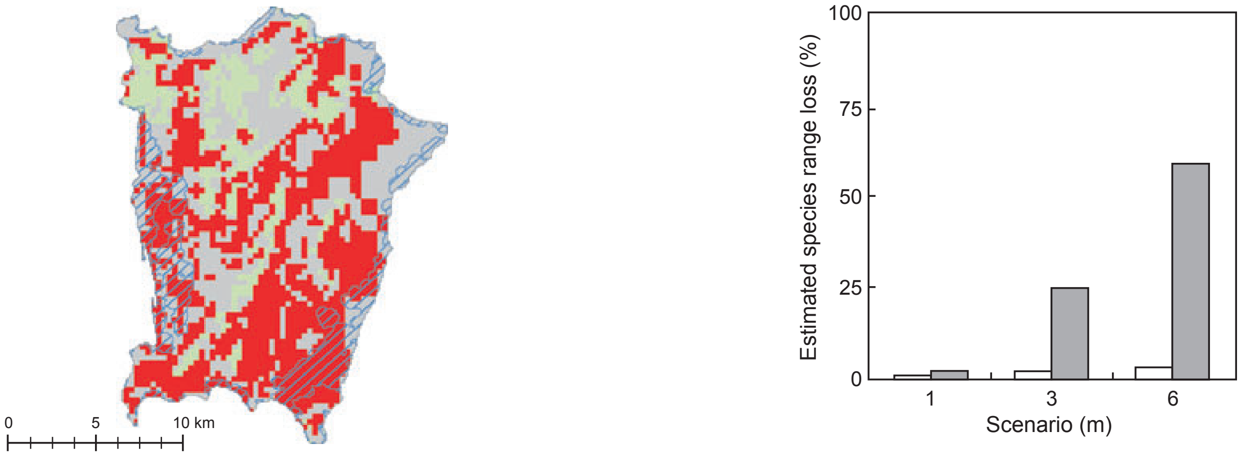
Our results provide several novel and important implications for assessing the potential consequences of SLR for human populations and biodiversity on islands, which mainly include the following: (1) The primary effects from SLR alone will be potentially devastating in the SEAP region, and we estimate that 3–32% of the coastal zone of islands could be lost in the future, depending upon the scenario. Moreover, 15–27% of the human coastal population (8–52 million people) are likely to become SLR refugees; (2) The secondary SLR effects on biodiversity from human refugees can be even more devastating than from primary effects and increase estimates of overall habitat loss depending upon the region; (3) The relative importance of primary vs. secondary effects differs enormously among geographic regions. Islands with less urban and intensive agricultural land area, as in Oceania, are more vulnerable to primary effects, whereas biodiversity on more densely populated islands, as in Indo-Malaysia, are more vulnerable to secondary effects; and (4) Some species are more vulnerable to secondary than primary effects, and secondary effects of SLR can potentially have a large impact coastal and on non-coastal species. Below we address the main findings in more detail, and explain how our results call for a new agenda in climate change research that aims to provide comprehensive ecological assessments that include secondary effects from human displacement caused by sea-level rise.

Our findings indicate that the primary SLR effects due to inundation and erosion will have major impacts on human populations and biodiversity on islands for all SLR scenarios, including the 1 m SLR scenario currently predicted at the end of this century. Inundation from SLR will lead to massive migrations of coastal populations (McGranahan *et al.*, 2007; Reuveny, 2007). Although the magnitude and relocation of human refugees (Small & Nicholls, 2003) and land-conversion of undisturbed areas in the hinterlands remains unclear, our analyses indicate potentially devastating ecological consequences if urban and intensive agricultural areas in the coastal zones of islands are forced to be relocated to the hinterland.

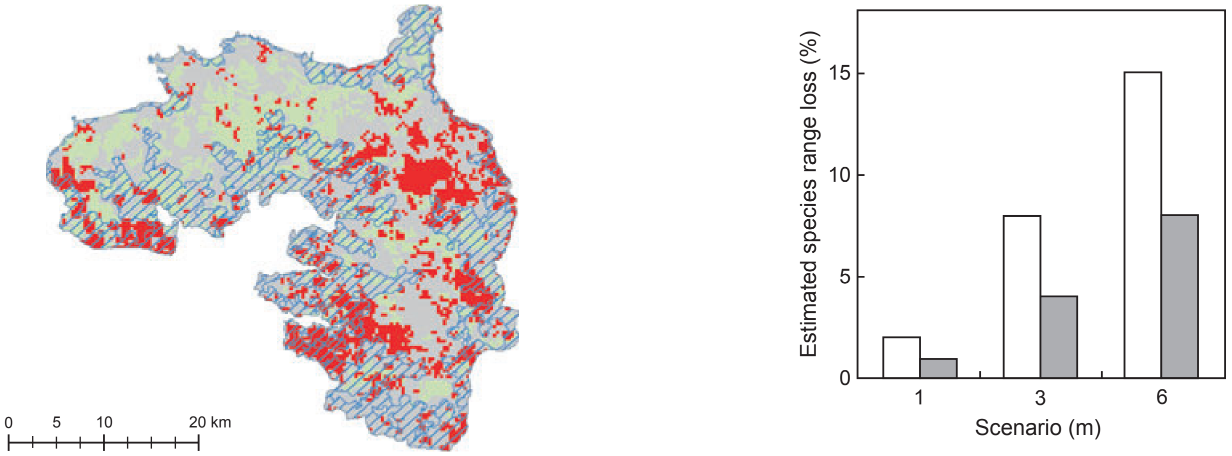
Our most surprising findings are that the ecological impacts from SLR can be even greater for secondary than primary effects, and their relative importance differs dramatically among geographic regions. The mag-

Fig. 6 Illustrative examples of potential range losses (%) of three select mammal species in the Southeast Asian region (Indonesia, Malaysia), given estimated primary vs. secondary effects. Maps (left) show potential effects due to sea-level rise (SLR, 3 m scenario, blue dashed areas), urban and intensive agricultural area (red), and suitability of habitats (green = suitable, gray = unsuitable), whereas barplots (right) show estimated percentages of range loss due to primary (white) and secondary (gray) effects. (a) Smoky Flying Squirrel (*Pteromyscus pulverulentus*) showing higher secondary effects than primary effects (the species occurs only on one island in this region, i.e., Pulau Pinang, 5° 23′ N, 100° 15′ E. (b) Rajah Sundaic Maxomys (*Maxomys rajah*) showing equally strong primary and secondary effects (the species occurs regionally on 26 islands, map exemplifies Pulau Bintan, 1.009167 N, 104.549167 E, whereas barplots summarize range loss across all 26 islands), and (c) Java Mouse-deer (*Tragulus javanicus*) showing higher primary effects than secondary effects (the species occurs on 41 islands, map exemplifies Pulau Bengkalis, 1.498750 N, 102.254167 E, and barplots summarize range loss across all 41 islands).

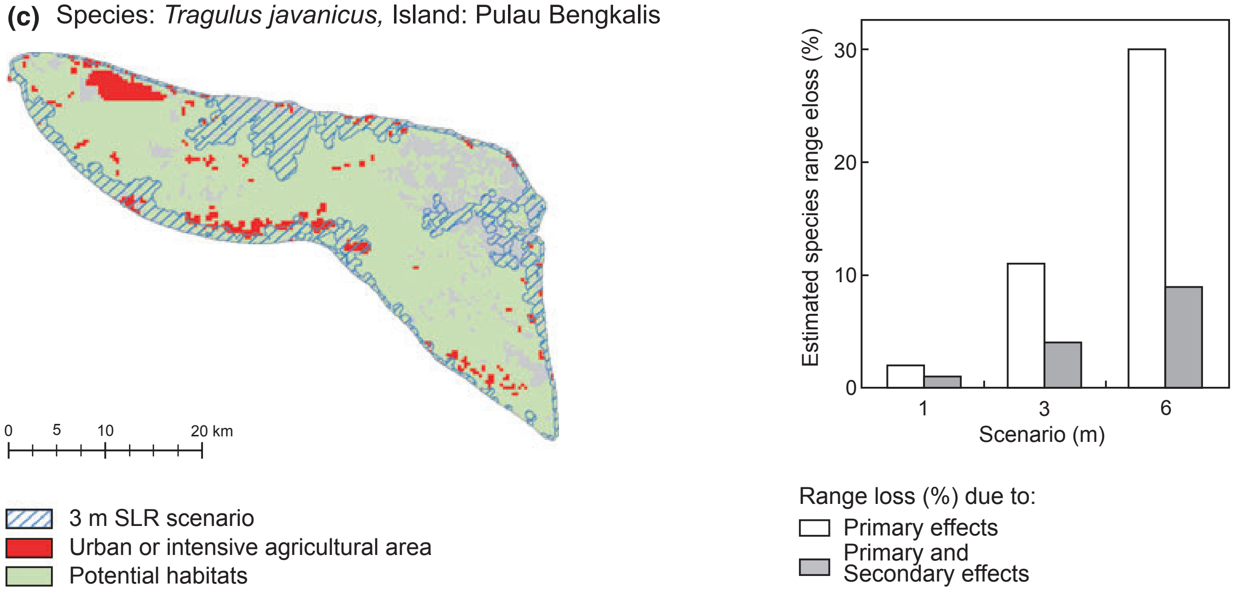
(a) Species: *Ptermomyscus pulverulentes,* Island: Pulau Pinang



(b) Species: *Maxomis rajah,* Island: Pulau Bintan



(c) Species: *Tragulus javanicus,* Island: Pulau Bengkalis



nitude of impacts from primary effects depends largely on the geomorphology of the coastal zone (i.e., the lower the elevation of the coastal areas the more area will be affected). Therefore, the primary SLR effects in Oceania are likely to be more important than secondary ones because low-lying islands (e.g. atolls) predominate in this region and because levels of urbanization are relatively low (McGranahan *et al.*, 2007). In contrast, the magnitude of secondary effects depends on the spatial configuration and composition of converted lands: the higher the share of urban and intensive agricultural areas, the more pronounced are the secondary effects of SLR on potential habitat in the hinterlands. Consequently, the secondary effects of SLR in Indo-Malaysia and many other regions in Southeast Asia will likely have more important consequences for biodiversity than primary ones because coastal areas have very high human population densities (Small & Nicholls, 2003; Rowley *et al.*, 2007) and large areas of urban and intensive agricultural land that will be inundated. The magnitude of effects also depends on how much the sea-level will rise (reflected in our scenarios): in higher SLR scenarios, more area will be affected and more people will have to migrate. As people have already caused large losses of undisturbed habitat in Southeast Asia (Sodhi *et al.*, 2004), additional land-use change would be expected to have particularly severe consequences for biodiversity. Therefore, many species and populations are already threatened and are vulnerable to further land loss. Furthermore, there are high population densities and growing urban areas in Southeast Asia along coastal regions and deltas (Nicholls & Cazenave, 2010), so in addition to increased land-use changes, there will be additional pressure from increased population numbers. These geographic differences in vulnerability to primary vs. secondary SLR effects suggest that more studies are needed that use spatially-explicit models to assess the impact of climate change on biodiversity and human populations.

Our results indicate that the inclusion of secondary SLR effects on species distributions increases the estimated range losses for almost all of our selected mammal species (Data S6). We find that some species are more vulnerable to primary effects, whereas other species are more vulnerable to secondary effects. Our models for a set of 54 mammal species and their habitat refined ranges on 106 islands in the Indo-Malaysian region suggest that range losses are greater for secondary than for primary effects for approximately 10–18% of the selected species in the moderate range loss model (depending on the SLR scenario) and for 22–46% of the species in the maximum range loss model (see also Data S6). Some species that exclusively live in the hinterland, and are not vulnerable to primary effects from SLR, can become severely affected by secondary effects from human displacement. Furthermore, any habitat reduction and partial range loss can have severe consequences for species survival, particularly for species that are vulnerable to land-use change (Stork *et al.*, 2009) or for those species that are already threatened (Brooks *et al.*, 1997; Purvis *et al.*, 2000; Cardillo *et al.*, 2005). The SEAP region contains a high concentration of such species (Ceballos & Ehrlich, 2006; Catullo *et al.*, 2008), and many of these species would be expected to suffer additional population declines and are at risk of extinction if they are unable to respond to habitat loss by dispersal. Furthermore, other climate change effects, such as temperature or precipitation change, are expected to cause problems for many species by themselves (Virah-Sawmy *et al.*, 2009; Greaver & Sternberg, 2010). Even moderate habitat destruction can potentially lead to a time-delayed extinction over longer periods of time (Tilman *et al.*, 1994). Overall, our findings thus indicate that climate change-driven SLR effects will have severe ecological consequences on the distribution of mammals in the SEAP region, possibly leading to extinctions and severe range reductions for a large number of species.

We raise the caveat that mammals may not provide a representative sample to assess the effects of SLR on island biodiversity in general. Studies on species richness suggest that cross-taxon congruence is sometimes low (Grenyer *et al.*, 2006), especially among vertebrates and invertebrates (Wolters *et al.*, 2006). In Southeast Asia, geographic patterns of vertebrate species richness also vary considerably, including the percentage of endemics (Sodhi *et al.*, 2004). Cross-taxon congruence also depends on the spatial scale of sampling units (Qian & Kissling, 2010). Thus, the vulnerability of species to primary and secondary SLR effects may differ in other vertebrate classes or taxonomic groups, and additional studies are therefore needed before our results can be extrapolated to other taxonomic classes or spatial scales. Nevertheless, we expect threatened or endemic species of all taxonomic groups to be particularly vulnerable. In Southeast Asian mammals, hotspots of endemics are often located in mountain regions and on small islands (Catullo *et al.*, 2008). The former might be particularly vulnerable to secondary effects, whereas the latter are likely to be affected by both primary and secondary effects. Thus, our results suggest that primary effects are relatively high for taxa that predominantly occur in coastal regions or low lying islands, whereas secondary effects might be more pronounced for species in mountainous regions. Also, endemic and threatened species might be particularly vulnerable to secondary SLR, as island regions containing high numbers of endemics (Orme *et al.*, 2005; Kier *et al.*, 2009). Mammals and amphibians might be particularly vulnerable to SLR, as they have a high percentage of threatened species (Sodhi *et al.*, 2010) and high rates of endemism in the area (Sodhi *et al.*, 2004). Furthermore, we note that our results from the SEAP region should not be extrapolated to assess the risk for terrestrial vertebrate species globally.

We emphasize that our assessment of the magnitude of the ecological consequences of SLR are rough estimates, although our findings may be overly conservative for several reasons. First, we used a moderate range loss model, which assumes a range loss proportional to range size in the hinterland, although additional analyses (Data S4) show that secondary effects can be much greater if the relocated area falls completely within a species' range or habitat. Second, we only included the most intensive farming types, although many other forms of land-conversion will also impact biodiversity. Third, we excluded the smallest islands from our analysis (those with the lowest altitudes, e.g. atolls), which are most prone to inundation and SLR. Any species living only on those islands will go extinct if SLR is pronounced and habitat loss cannot be compensated by dispersal. Fourth, we only considered three SLR scenarios (1 m, 3 m, and 6 m) and we do not consider more liberal estimates or the worst-case scenarios (Gregory *et al.*, 2004; Alley *et al.*, 2005). Fifth, we did not include increases in population growth or resource extraction by humans, which will likely be required by relocation of urban and agricultural areas that are inundated by SLR. Finally, we did not consider the consequences of other ecological interactions, such as increased interspecific competition due to the migration of coastal species (Klanderud, 2005; Ahola *et al.*, 2007), in addition to human refugees, or changes in temperature, rainfall, or other consequences anticipated from climate change. It is likely that some species will benefit from sea-level rise and other aspects of climate change (there will be winners, as well as losers); however, it appears safe to assume that a reduction in habitat area from SLR will reduce the capacity of islands to sustain terrestrial biodiversity. The consequences of SLR for the distributions and habitats for taxa other than mammals still need to be evaluated, and population models should be used to assess a wider range of impacts from SLR (Aiello-Lammens *et al.*, 2011). Nevertheless, our findings are consistent with previous studies on some individual species (Fish *et al.*, 2005; Loucks *et al.*, 2010), which indicate that SLR even much smaller than in our scenarios can have a large ecological impact.

In summary, our study provides further evidence that the SLR anticipated from global warming will have major consequences for biodiversity and species distributions on islands due to land and habitat loss (primary effects), and the first evidence that the secondary effects due to land-conversion and human migration to the hinterland can be even more important than primary effects in many regions. Our findings provide strong support for the suggestion that the incorporation of human behavior and movements in response to climate change are urgently needed to accurately evaluate the possible consequences of global change for biodiversity and ecosystem functioning (Myers, 2002). Furthermore, our results suggest the need for developing a new research agenda that explicitly aims to provide quantitative forecasts of secondary SLR effects on biodiversity and human populations. Human displacement from SLR has enormous economic, political, and medical implications (Piguet *et al.*, 2011) and our results indicate that they will also place enormous pressures on natural areas in the hinterlands, including protected areas and national parks. While the current protected area network can serve as important and cost effective feature for species conservation (Balmford *et al.*, 2002), any reduction in protected areas is likely to lead to increased extinction risks (Woodroffe & Ginsberg, 1998). Conservation and regional planning of the future management of natural and protected areas need to take both primary and secondary SLR effects into account. However, current approaches to assess future impacts on island biodiversity or to select priority areas for future conservation networks (Kremen *et al.*, 2008) do not even include the primary effects of sea-level rise. We are unaware of any study that has specifically assessed the potential consequences of including secondary SLR effects in conservation planning of future protected area networks, and there is an urgent need to include such factors in research and conservation science in the future.

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Supporting Information

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

Data S1. Map with 106 Indo-Malaysian sample islands with presence of mammal species (numbers related to island name, see Data S2).

Data S2. The 106 Indo-Malaysian islands with presence of select mammal species, basic data and consequences of sea-level rise (SLR) scenarios (alphabetical order, island number based on Meijaard evaluation (2003), island area according to Lambert Equal Area projection, coordinates in decimal degrees, and primary and secondary SLR effects as percent loss of potential habitat, i.e., not urban or intensive agricultural areas).

Data S3. The 54 mammal study species and suitable/unsuitable habitat types regarding ESA landcover data (ESA, 2008) within the study region. Suitable habitat for a species = 1, unsuitable habitat = 0. Unsuitable habitat was excluded by (a) identifying habitat preferences based on IUCN (2009) and then linking them to ESA-landcover data and (b) excluding unsuitable ESA-landcover types from the extent of occurrence of species.

Data S4. Comparison of species' range loss due to different secondary effect scenarios assuming an equal area replacement of inundated urban and agricultural areas in the hinterland. (a) Relocation scenario$_{\text{moderate}}$: A moderate scenario assuming that land-conversion will be evenly distributed over the remaining island area. (b) Relocation scenario$_{\text{maximum}}$: A worst-case scenario assuming that all land-conversion takes first place within the area of occupancy of a species.

Data S5. Projected area loss in the coastal zones of the 1,287 islands in the Southeast Asian and Pacific (SEAP) region due to inundation and erosion, and inundation without erosion. Estimates are for each of the three realms of the study region and the whole SEAP region. The coastal zone is defined as ≤ 50 m above mean sea-level and ≤ 100 km inland. SLR, sea-level rise; IM, Indo-Malaysia; AA, Australasia; OC, Oceania.

Data S6. List of 54 mammals species on Indo-Malaysian islands and range loss due to primary and secondary sea-level rise effects (data according to 1 m, 3 m, and 6 m sea-level rise scenarios, range loss calculations are based on refined range maps, species presence on islands according to Meijaard (2003)).

Data S7. Sea-level rise (SLR) and its impact on potential habitats (loss of undisturbed area), depending on island area size: (a) 1 m SLR (b) 3 m SLR (c) 6 m SLR. Island area classes: 1: ≤ 1 km², 10: 1–<10 km², 100: 10–<100 km², 1000: 100–<1000 km², and ≥ 1000: ≥ 1000 km².

Data S8. List of the three sample mammal species and their habitat requirements where contrasting trends of primary and secondary effects habitat loss were exemplified. The table indicates suitable habitat according to the IUCN evaluation (IUCN, 2009) and the minimum and maximum elevation of the species regarding the Southeast Asian Mammal Database (IEA, 2010).