Interacting Regional-Scale Regime Shifts for Biodiversity and Ecosystem Services

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Current trajectories of global change may lead to regime shifts at regional scales, driving coupled human–environment systems to highly degraded states in terms of biodiversity, ecosystem services, and human well-being. For business-as-usual socioeconomic development pathways, regime shifts are projected to occur within the next several decades, to be difficult to reverse, and to have regional- to global-scale impacts on human society. We provide an overview of ecosystem, socioeconomic, and biophysical mechanisms mediating regime shifts and illustrate how these interact at regional scales by aggregation, synergy, and spreading processes. We give detailed examples of interactions for terrestrial ecosystems of central South America and for marine and coastal ecosystems of Southeast Asia. This analysis suggests that degradation of biodiversity and ecosystem services over the twenty-first century could be far greater than was previously predicted. We identify key policy and management opportunities at regional to global scales to avoid these shifts.

Keywords: biodiversity change, human–environment interactions, tipping points, South America, Southeast Asia

Exploitation of natural resources for the provision of food, fiber, and energy has generally provided increasing social and economic benefits to human society over the last century, despite causing the decline of biodiversity and nonprovisioning ecosystem services (MA 2005). This relationship can break down if it is pushed beyond certain limits, which can lead to regime shifts that are characterized by large and rapid losses of biodiversity; degradation of a wide range of ecosystem services, including provisioning services; and negative consequences for human well-being (Folke et al. 2004, Scheffer 2009). There is growing concern that regime shifts could occur at very large spatial scales over the next several decades as human–environment systems exceed such limits because of powerful and widespread driving forces that often act in combination: climate change, overexploitation of natural resources, pollution, habitat destruction, and the introduction of invasive species (Leadley et al. 2010, Barnosky et al. 2012, Hughes et al. 2013).

Regime shifts have been identified in ecological, socioeconomic, and biophysical systems and are characterized by rapid shifts in the state of the system that are difficult to reverse (Folke et al. 2004, Scheffer 2009, Leadley et al. 2010).

Regime shifts can be driven by a variety of mechanisms that vary in their speed, their spatial extent, and the types of drivers involved. Considerable attention has been paid to regime shifts mediated by tipping points resulting from reinforcing feedbacks that amplify the impacts of the drivers or passing of thresholds that lead to relatively abrupt changes in state (Lenton et al. 2008, Scheffer 2009, Lenton 2013). An important characteristic of tipping points is that they are very difficult to reverse, because feedback loops trap systems in alternative states or because it is difficult to alter the driving forces over policy-relevant timescales. Tipping point mechanisms that are particularly pertinent for this analysis are summarized in tables 1–3.

Regime shifts can also be driven by relatively linear processes that result in smoother transitions than do those driven by tipping point mechanisms. For example, climate change may drive many systems into alternative states that will be difficult to reverse, because of long lag times in socioeconomic systems and in Earth's biophysical systems (Lenton et al. 2008). However, many of these regime shifts lack the nonlinear characteristics and difficult-to-reverse nature of regime shifts mediated by tipping points (Lenton et al. 2008).

Table 1. Mechanisms of ecosystem tipping points.

Mechanism designation	Description	Time (in years)	Size (in kilometers)	References
Fire feedback	Fire maintains or promotes fire-prone vegetation, thus facilitating subsequent fires. Restoring fire-resistant vegetation is slow and may require active fire management.	10–100	1–100	Leadley et al. 2010, Vergara and Scholz 2011, Davidson et al. 2012, Lenton 2013
Forest transition to savanna	The balance between woody and herbaceous vegetation can be tipped by changes in wood harvesting; grazing pressure; fire; climate; and, probably, atmospheric levels (e.g., of carbon dioxide). Large hysteresis in response to drivers can make shifts among states difficult to reverse.	10–100	10–100	Lenton et al. 2008, Vergara and Scholz 2011, Davidson et al. 2012, Lenton 2013
Long-lasting soil degradation	Overgrazing, deforestation, and poor agricultural practices cause degradation of soils. Restoration is challenging because vegetation is difficult to establish on degraded soils and reversing soil degradation is a slow process.	1–100	1–100	Reynolds et al. 2007
Transition to coastal dead zones	Nitrogen arriving in rivers, primarily from fertilizer use, causes algal blooms and subsequent hypoxia zones in coastal areas.	1–10	1–1000	Jackson et al. 2008, Lenton 2013
Marine fisheries collapse	Fishing beyond thresholds causes long-term collapses of marine fish stocks. A variety of mechanisms can inhibit recovery over decades, even when pressures are reduced or removed.	1–10	10–1000	Jackson et al. 2008, Worm et al. 2009
Changes in the structure of marine communities	Marine resources overexploitation combined with moderate eutrophication and additional impacts promote algae and invertebrate-dominated systems. Changes in marine community structure and dynamics make restoration difficult and slow.	10–100	1–100	Jackson et al. 2008

Table 2. Mechanisms of socioeconomic tipping points.

Mechanism designation	Description	Time (in years)	Size (in kilometers)	References
Poverty (marginal resources trap)	Poverty contributes to excessive exploitation of marginal natural resources, especially in periods of unfavorable climate, causing a downward spiral of poverty and environmental degradation.	1–100	10–1000	Reynolds et al. 2007, Foresight 2011
Instability (limited resources trap)	Poor governance, limited resources, and violence beget further social and political instability, permitting unregulated exploitation of natural resources.	1–10	10–1000	Leadley et al. 2010, Foresight 2011
Globalization and natural resource exploitation	Construction of infrastructure to access untapped natural resources provides wealth to build more infrastructure.	10–100	10 to >1000	Walker et al. 2009, Leadley et al. 2010
Amplifying exploitation feedback	The higher demand for and increased economic value of overexploited resources intensifies their exploitation.	1–10	100 to >1000	Cinner et al. 2011

Future regime shifts will have positive and negative effects on human well-being, but our analysis is focused on potentially detrimental regime shifts because of concerns that regime shifts under business-as-usual development pathways will be dominantly deleterious (Lenton et al. 2008). In particular, our analysis suggests that ecosystem, socioeconomic, and biophysical mechanisms could interact to produce widespread, difficult-to-reverse losses of biodiversity, degradation of ecosystem services, and net negative effects on human well-being at regional scales within the twenty-first century. Ecosystem regime shifts are typically related to ecosystem-level feedbacks and thresholds

Table 3. Mechanisms of biophysical tipping points.

Mechanism designation	Description	Time (in years)	Size (in kilometers)	References
Albedo effect	Increased absorption of solar energy by the biosphere, especially due to reduced snow cover, causes local to regional warming.	10–100	100–1000	Lenton et al. 2008, Vuille et al. 2008, Lenton 2013
Evapotranspiration (ET) feedback	Regional cloud formation and rainfall are mediated by vegetation cover and vice versa, which can either be through ET or through the production of cloud condensation nuclei. Deforestation tends to reduce ET and, therefore, increases forest vulnerability to fire and drought.	10–100	100–1000	Avissar and Werth 2005, Ray et al. 2006, Lenton 2013
Greenhouse gases (GHG) feedback	GHG stored in vegetation and soils and released to the atmosphere because of deforestation promote vegetation dieback and facilitate further deforestation.	10–1000	>1000	Lenton et al. 2008, Davidson et al. 2012, Lenton 2013
Tropical coral reef bleaching and decalcification	Ocean warming and acidification are projected to reduce the fitness of tropical corals and the degradation of tropical coral reef ecosystems.	10–100	10–1000	Donner et al. 2005, Hoegh-Guldberg et al. 2007, Pandolfi et al. 2011
Coastal system submersion	If sea-level rise exceeds sedimentation rates, coastal ecosystems will be submerged.	10–1000	1–1000	Gilman et al. 2008, McLeod et al. 2010
Mountain stream disappearance	Declining snowfield and glacier sizes are projected to lead to a reduction of late-summer streamflow and to result in highly nonlinear impacts on biodiversity.	10–100	10–100	Vuille et al. 2008, Jacobsen et al. 2012

within specific ecosystem types (Scheffer 2009; see table 1 for examples of underlying tipping point mechanisms). Socioeconomic regime shifts are related to the vulnerabilities, adaptive capacities, and transformative capabilities of societies in the face of local and global pressures (table 2; Scheffer 2009, Leadley et al. 2010). Biophysical regime shifts are associated with amplifying feedbacks or thresholds in the biosphere–ocean–atmosphere system (table 3; Lenton et al. 2008). The processes underlying deleterious regime shifts can potentially interact to increase the extent or severity of environmental degradation. Our analysis is focused on three types of interaction: (1) *aggregation*, in which regime shifts may co-occur in contiguous areas, which may lead to large areas being affected; (2) *synergy*, in which the processes underlying regime shifts can be synergistic, which can lead to greater degrees of degradation than would occur from a single process; and (3) *spreading*, in which atmospheric transport, movements of organisms, or human migrations can increase the spatial extent or impact of regime shifts.

To illustrate these interactions, we use two examples: the terrestrial ecosystems of central South America and the marine and coastal ecosystems of Southeast Asia (figure 1). Our examples are focused on plausible scenarios with high and rapidly growing rates of resource exploitation, land-use change, and climate change (i.e., business-as-usual scenarios). We then highlight encouraging shifts in recent trends, plausible scenarios of sustainable pathways, and provide policy-relevant examples of measures to reduce pressures and thereby the likelihood of undesirable regime shifts. We also compare projections with observations and experiments and highlight key uncertainties. These regions were chosen because they have very high species diversity (figure 1) and

because quantitative scenarios were available to exemplify how local and global drivers may interact to create regional-scale regime shifts. We also cover, with less detail, other examples of regional-scale regime shifts to illustrate the diversity of mechanisms at play and the potential impacts.

Finally, we argue that most regional- to global-scale studies and assessments of biodiversity have not accounted for the potential impacts of these interactions at regional scales and that analyses focused on single mechanisms or scales may fail to capture synergistic or attenuating effects resulting from those interactions. Therefore, we discuss the need to revise existing scenarios and to update policy recommendations.

Terrestrial and freshwater ecosystem regime shifts in central South America

The central region of South America is dominated by a complex of lowland plains including *cerrado* (a mosaic of grasslands and savanna-type vegetation), *caatinga* (xeric forests and shrublands), and vast agricultural areas to the east; humid tropical forests in the central areas; and montane ecosystems and patchy cultivated areas in the Andes in the west (figure 2). This region is exceptionally rich in both the number and the endemicity of species (figure 1; Pereira et al. 2012). The primary threats to these ecosystems are land-cover conversion and changes in land management, with climate change projected to play an increasingly important role over the next decades (Vergara and Scholz 2011, Davidson et al. 2012).

Widespread degradation of the Amazon humid forest. Widespread degradation of the Amazon forest is a potential regime
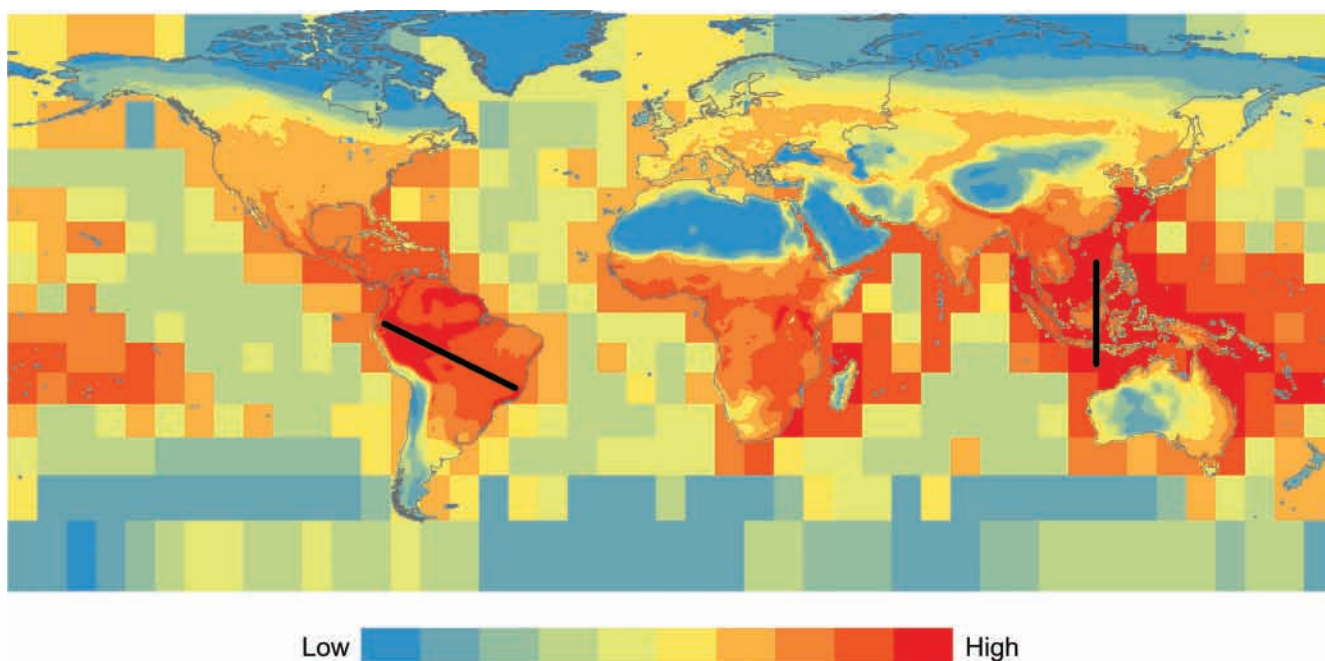
Figure 1. Terrestrial vertebrate diversity (Pereira et al. 2012) and marine diversity (Tittensor et al. 2010). The color gradient represents species richness and uses a geometric scale. The thick black lines indicate the transects used to illustrate regional-scale interactions among regime shifts in terrestrial ecosystems of central South America (figure 2) and marine and coastal ecosystems of Southeast Asia (figure 4). Source: Figure created by Inês S. Martins.

shift mediated by interacting tipping point mechanisms that have been extensively researched. Several modeling studies suggest that synergistic interactions between global climate change and deforestation in the Amazon Basin could cause drought and promote fire, which would lead to the widespread degradation of humid tropical forests and their replacement by savanna-type vegetation or fire-prone secondary forests (figures 2 and 3c, 3d; Lenton et al. 2008, Vergara and Scholz 2011, Davidson et al. 2012). Humid forests, when they are present over large areas, are a key factor in generating the regional rainfall necessary for their own persistence. Models and observations suggest that deforestation alters precipitation patterns and enhances regional drying (Avissar and Werth 2005, Dubreuil et al. 2012, Davidson et al. 2012, Oliveira et al. 2013). In addition, forest fragmentation and the use of fire for deforestation combine with drier climates to make forests more prone to fire (Davidson et al. 2012). Some studies have suggested that, beyond certain thresholds of deforestation and climate change, the feedbacks described above could cause a basin-wide shift to a dry alternative state from which humid tropical forests could not recover. Whether this might occur and the limits beyond which it might occur are subject to great uncertainty (Davidson et al. 2012).

Field observations support the model projections to some extent. Severe droughts in 2005 and 2010 increased the mortality of larger trees and reduced forest carbon sinks (Phillips et al. 2010, Lewis et al. 2011). Experiments have confirmed the susceptibility of larger trees to drought but have also

indicated significant stand-level resistance (Phillips et al. 2010, Davidson et al. 2012). There is great uncertainty in the climate scenarios for this region and in the sensitivity of the humid tropical forests to drought, and recent research suggests that the likelihood of widespread forest replacement by savanna-type vegetation is less than some early studies suggested (Rammig et al. 2010, Vergara and Scholz 2011, Davidson et al. 2012, Huntingford et al. 2013). However, there is a growing consensus that moderate to high rates of deforestation and climate change could cause a shift to degraded, fire-prone forests over substantial areas of the Amazon Basin, especially in the southern and eastern areas (figures 2 and 3c, 3d; Davidson et al. 2012).

Loss of cloud forests in the Andes. Disappearing climates for the cloud forests and *páramo* (i.e., Andean montane vegetation characterized by bunch grasses with scattered rosette, cushion plants, and bogs) ecosystems of the Andes have received considerably less attention than have the lowland Amazon humid forest in terms of regime shifts. The Andes region harbors more species richness per unit area than the Amazon does (figure 1) and is under heavy human pressure (Buytaert et al. 2011). Cloud forest ecosystems depend on the humidity trapped by vegetation for a significant part of their water supply (Ledo et al. 2009). The climate on which these ecosystems depend is projected to disappear during the twenty-first century, with high levels of greenhouse gas emissions resulting from higher temperatures, altered precipitation patterns, and increases in the height of cloud
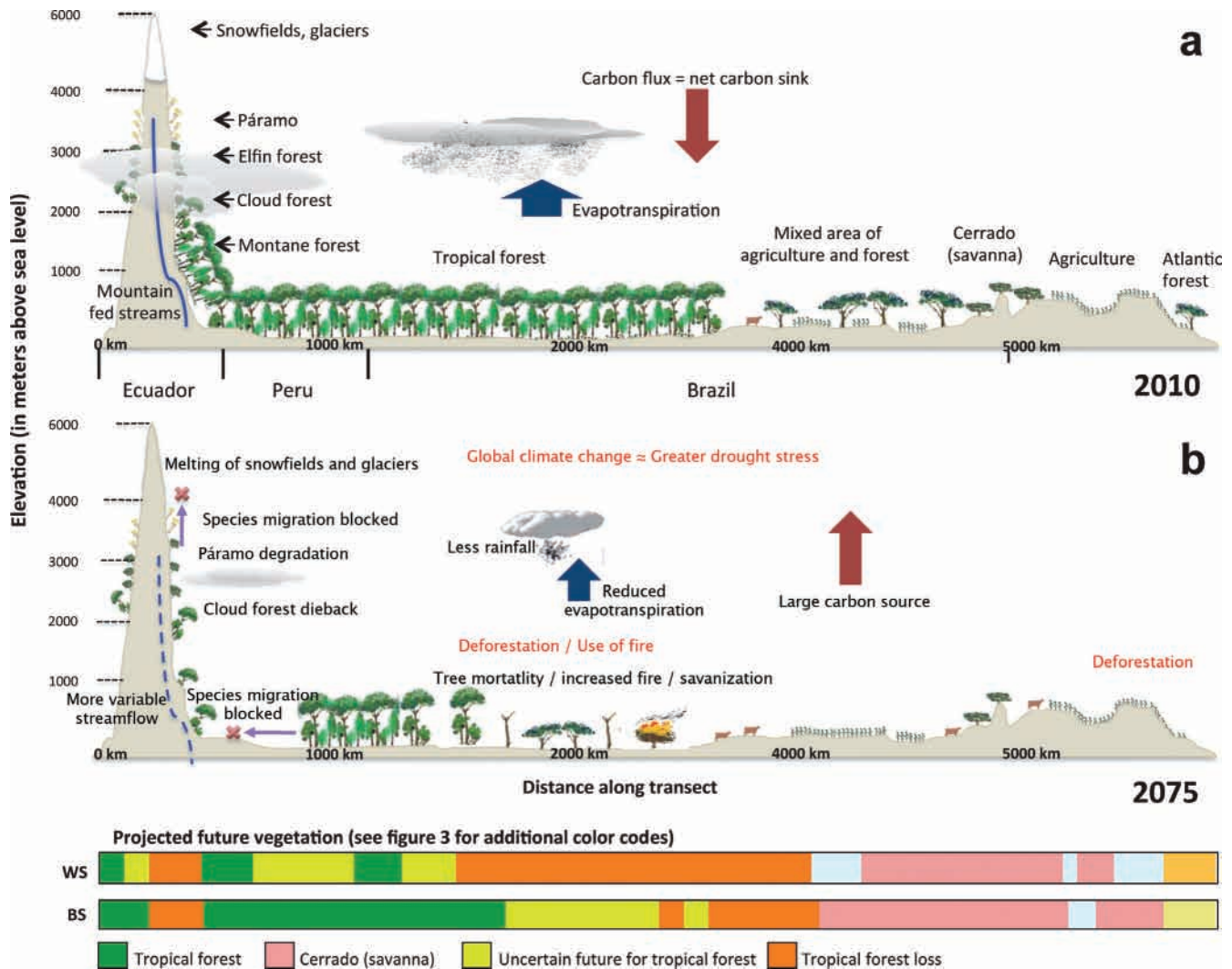
Figure 2. Current (a) and projected (b) cross-sectional profile of the transect across central South America as indicated in figures 1 and 3. The cross-sectional profile was extracted from Google Earth, the illustrations of current vegetation types were based on the Global Land Cover 2000 project, and the illustrations of projected future vegetation types were based on a worst-case scenario in 2075 by Vergara and Scholz (2011; see figure 3c). The bands at the bottom of the figure indicate the projected vegetation types' worst-case (WS) and best-case (BS) scenarios from the transects shown in figure 3c and 3d, respectively. Major drivers of regime shifts are indicated with red text. Abbreviations: km, kilometers; m, meters.

formation, although these projections are highly uncertain (figure 2; Foster 2001, Williams et al. 2007, Minvielle et al. 2011). Land-use changes may strongly interact synergistically with global climate change to drive regime shifts, because deforestation at local and regional scales is projected to enhance the drying out of cloud forests (Ray et al. 2006, Ledo et al. 2009). Continued land conversion to grazing and croplands at higher altitudes may limit the ability of montane forest species to adapt to climate change through upslope migration (figure 2; Feeley and Silman 2010). *Páramo* ecosystems face similar constraints, because they are bounded at higher altitudes by very infertile soils and because upslope migration will result in less available habitat (Buytaert et al. 2011). The spatial heterogeneity of climate

change, especially precipitation, and land-use change may lead to substantial spatial variation in the occurrence and severity of the regime shifts described above.

Snow and glacier melt in the Andes. Streams and rivers in the arid and semiarid regions of the Andes are fed to a great extent by snowfields and glaciers. The majority of glaciers in the Andes are already shrinking, annual snowpacks persist for less time because of recent warming, and models suggest that this trend will accelerate over the coming decades (Vuille et al. 2008). As glaciers retreat and lose mass, there is a temporary increase in stream- and river flow, but once the glacial buffer diminishes, reductions in streamflow are projected during the dry season (Vuille et al. 2008). Reduced
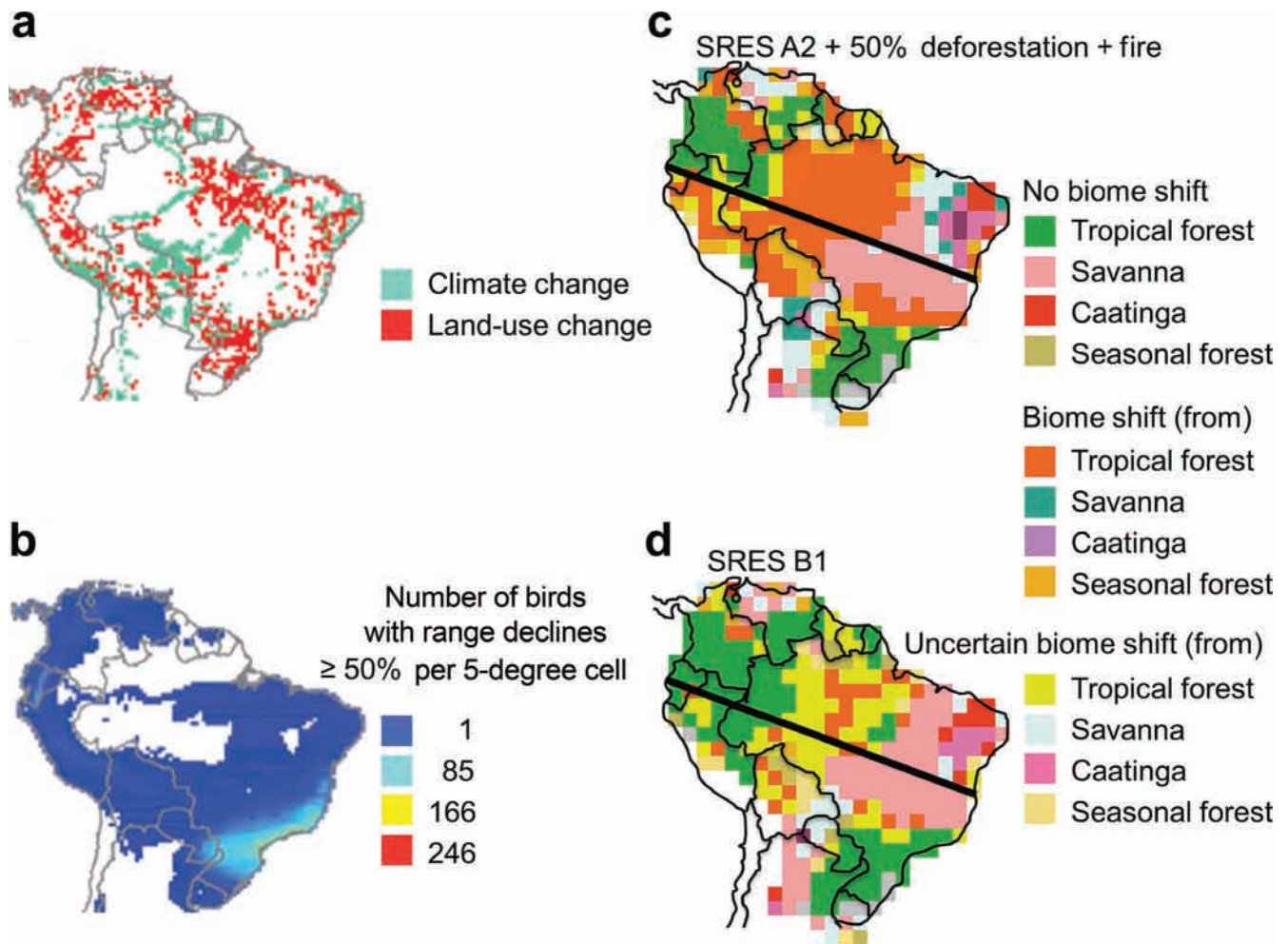
Figure 3. *Projections of (a) biome shifts by 2100 caused by noninteracting land-use change and climate change and (b) bird diversity impacts by 2100 based on these biome shifts (Jetz et al. 2007) in central South America. Projections of (c) a worst-case scenario of biome shifts by 2075 and (d) biome shifts by 2075 in a best-case scenario, both using a model that accounts for key interactions among land use, fire, and climate change. In panels (c) and (d), the biomes were simulated to remain stable, to change (the legend indicates which biome is lost but does not indicate the projected future biome), or to have an uncertain future (fewer than 12 of 15 simulations agreed) by 2075 (Vergara and Scholz 2011). The thick black lines indicate the transects used to illustrate regional-scale interactions among regime shifts in terrestrial ecosystems of central South America. The patterns in panels (a) and (b) are based on the "Order from strength" scenario of the Millennium Ecosystem Assessment, the patterns in panel (c) are based on the Intergovernmental Panel on Climate Change Special Report on Emissions Scenarios (IPCC SRES; Nakićenović et al. 2000) A2 emissions scenario + 50% deforestation + fire, and the patterns in panel (d) are given for the IPCC SRES B1 emissions scenario + 0% deforestation + no fire. Sources: Panels (a) and (b) were adapted from Jetz and colleagues (2007), and panels (c) and (d) were adapted from Vergara and Scholz (2011).*

streamflow from glaciers is projected to have highly non-linear, negative impacts on freshwater species diversity—particularly in headwaters, because species will be unable to migrate to suitable habitats upstream (Jacobsen et al. 2012). Climate change will interact with other drivers of change of stream- and river flow, including water withdrawals that are also reducing streamflow at high altitudes during the dry season (Anderson and Maldonado-Ocampo 2011).

An emerging regional perspective for central South America. Overall, our analysis suggests that moderate to high rates of land-use

change at regional scales could act synergistically with high levels of global climate change to cause habitat loss or severe habitat degradation in natural and seminatural terrestrial and freshwater systems over large areas of central South America (figures 2 and 3). The profile across the region in figure 2 provides pictorial illustrations of regime shifts and their interactions, which are projected to play out across central South America. It illustrates quantitative business-as-usual scenarios for the Amazon forest (figure 3c), as well as more qualitative scenarios for cloud forest, glacier, and snowfield regime shifts. In addition to the synergies among

the drivers described in each of the three regime shifts, aggregation and spreading could lead to regime shifts affecting large areas of the subcontinent.

Long-distance spreading effects are mediated by several mechanisms. First, Amazon deforestation affects rainfall over large regions (figure 2; Avissar and Werth 2005, Dubreuil et al. 2012, Oliveira et al. 2013, Stickler et al. 2013). Observations and models also suggest that ongoing widespread conversion of *cerrado* to croplands could reduce rainfall in the Amazon (figure 2; Costa and Pires 2010) and that deforestation in the western areas of the Amazon Basin and of the lower montane forests of the Andes could alter cloud forest climates in the Andes (figure 2; Ray et al. 2006). Second, socioeconomic interconnections play a key role in deforestation. Logging and land conversion to croplands or pasture in the Amazon Basin in the past few decades have been driven in part by national and global demand for timber, food, and bioenergy (Hecht 2012). Wealth generated by the sales of wood and agricultural products on global markets increases production capacity, which leads to a positive feedback in which access to untapped natural resources (i.e., pristine forests for lumber or land for pastures and crops) provides the capital to further exploit these resources (Walker et al. 2009). Positive feedbacks driven by local actors have also contributed to the spread of deforestation. The use of fire to clear forests and agricultural management practices that rapidly exhaust soil fertility promote further deforestation by small landholders at the forest frontier (Galford et al. 2013). Finally, large-scale movements of species are projected to occur as species try to keep pace with climate change, but habitat fragmentation is projected to substantially impede their ability to do so (figure 2; Feeley and Silman 2010).

These regime shifts, if they occur, could also aggregate spatially to have large negative impacts on a wide range of ecosystem services. In the Amazon, the potential negative impacts on regional-scale ecosystem services include substantial modifications of rainfall at large scales, changes in river flow, reductions in agricultural yields, the loss of carbon stored in trees and soils, and an increased frequency of forest fires (Costa and Pires 2010, Davidson et al. 2012, Oliveira et al. 2013, Stickler et al. 2013). In the Andes, cloud forests and *páramo* ecosystems are essential for the water supply of the watersheds below because of their high water storage and regulation capacity (Buytaert et al. 2011). In the arid and semiarid regions, changes in stream- and river flow due to shrinking glaciers and snowpacks are likely to affect the dry-season supply of water for domestic, agricultural, and industrial use (Vuille et al. 2008, Anderson and Maldonado-Ocampo 2011).

Studies of the effects of global change on biodiversity at the species level in South America have not often accounted for the multiple regional-scale interactions outlined above (e.g., MA 2005, Jetz et al. 2007, Bird et al. 2012, Wearn et al. 2012). These studies may substantially underestimate the upper bound of biodiversity loss in terms of species extinctions and declines in species abundance (but see Bird et al.

2012, Wearn et al. 2012). Analyses using scenarios and models that do not account for these interactions suggest that biodiversity and ecosystem services in central South America, with the exception of Atlantic humid forests, will be relatively unscathed by global change (figure 3a, 3b). This is because the socioeconomic development scenarios and climate change projections that have been used as the basis of most species-level studies, such as the Millennium Ecosystem Assessment scenarios (e.g., MA 2005) and the Intergovernmental Panel on Climate Change (IPCC) *Special Report on Emissions Scenarios* (SRES; Nakićenović et al. 2000), do not include the regional interactions described above. In contrast, figure 3c, 3d shows that substantial biome shifts are projected to occur over much of this region for plausible scenarios of high levels of deforestation, fire, and climate change when models take into account the interactions among these drivers.

Policies to limit the likelihood of regional-scale regime shifts occurring in central South America will have to tackle local land use, freshwater management issues, and global climate change. At the regional scale, the greatest challenges are to reduce the conversion of humid tropical forests and other relatively functionally intact ecosystems to croplands and pastures and to minimize the use of fire (figure 3c, 3d; Davidson et al. 2012). At the global scale, the greatest challenge is to mitigate climate change without increasing pressure on land use for bioenergy.

Changes in laws and law enforcement concerning logging and improved agricultural productivity have substantially reduced large-scale deforestation over the past several years in much of the Amazon Basin (Hecht et al. 2012, Galford et al. 2013). There are also recent trends in woody vegetation gains in the middle elevations in some areas of the Andes, although these do not yet offset forest losses (Aide et al. 2013). It has been suggested that the transition to a lower rate of deforestation in South America could be sustained with appropriate social, economic, technological, and institutional transformations, which include combinations of agricultural intensification, the establishment of protected areas, payments for ecosystem services, effective law enforcement, environmental labeling of forest products, and the development of nonfarm jobs (Hecht 2012, Galford et al. 2013). These transformations may reduce pressures on biodiversity and ecosystem services and may improve the well-being of many actors (Hecht 2012, Galford et al. 2013). However, recent changes in Brazil's forest code and the projected strong global demand for beef, soybean, and wood products suggest that the transformation to low deforestation rates could be fragile (Hecht 2012).

Marine and coastal regime shifts in Southeast Asia

The frontier between the Pacific and Indian Oceans harbors the highest diversity of marine species in the world (figure 1; Tittensor et al. 2010). The marine and coastal ecosystems of this region provide food, tourism income, and physical coastal protection for over 600 million people. In many
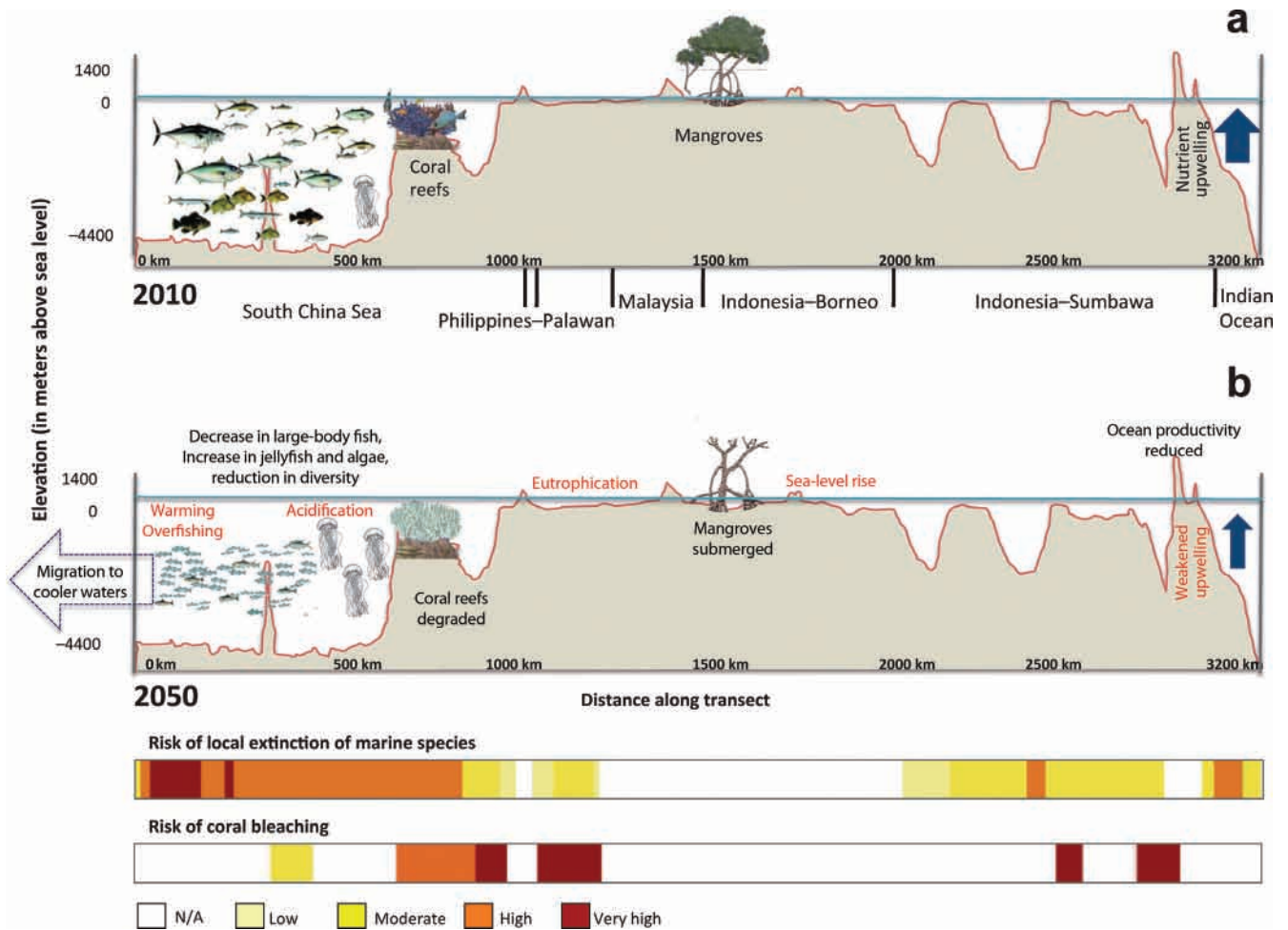
Figure 4. Current (a) and projected (b) cross-sectional profile of the transect across the Indo-Pacific region as indicated in figure 1. The cross-sectional profile was extracted from Google Earth. The illustrations correspond to the mechanisms and impacts described in the text. The bands at the bottom of the figure were extracted from mapped estimates of risk of local extinction of marine species (Cheung et al. 2009), and the projections of risk of coral bleaching are from Donner and colleagues (2005; see figure 5a). Major drivers of regime shifts are indicated with red text. Abbreviation: N/A, not applicable.

parts of this region, marine and coastal ecosystems are being degraded by overfishing, pollution, and habitat destruction, whereas ocean warming and acidification, hypoxia, and sea-level rise are projected to become the major threats over the next few decades (Worm et al. 2009, McLeod et al. 2010, Sumaila et al. 2011). Several mechanisms driving regime shifts have been identified in marine and coastal systems (Jackson 2008) and may interact to aggravate global change impacts in Southeast Asia (figure 4).

Degradation of tropical coral reefs. Degradation of tropical coral reefs due to global warming and ocean acidification tipping points has become a major focus of research in marine ecosystems (Hoegh-Guldberg et al. 2007, Pandolfi et al. 2011). Severe episodes of high sea temperatures are expected to become more frequent and to cause widespread bleaching and death of tropical corals (Donner

et al. 2005, Hoegh-Guldberg et al. 2007, Pandolfi et al. 2011). Ocean acidification caused by rising atmospheric carbon dioxide (CO_2) concentrations may compound global warming effects by reducing the capacity of hard corals to form their carbonate-based skeletons (Pandolfi et al. 2011). Seawater is projected to become too acidic for hard corals in many parts of the world ocean when atmospheric CO_2 concentrations exceed roughly 550 parts per million (Hoegh-Guldberg et al. 2007, Pandolfi et al. 2011). These levels of global warming and CO_2 concentrations are foreseen by midcentury in the most pessimistic scenarios and by the end of the twenty-first century in all but the most optimistic scenarios. Eutrophication, sedimentation, overfishing, and destructive fishing methods are currently the most important causes of coral reef decline and are predicted to interact synergistically with climate change, because they greatly reduce the resistance and resilience of
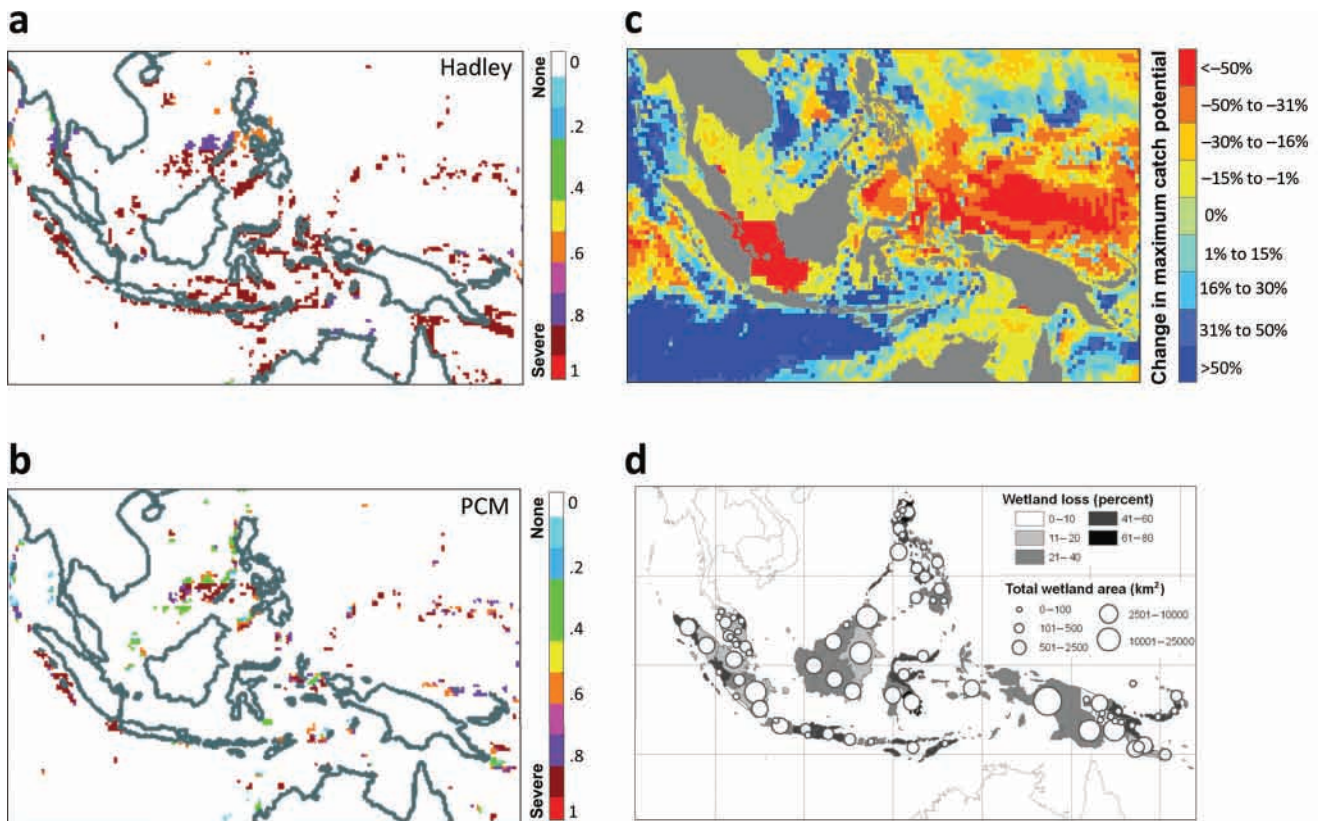
Figure 5. Coral bleaching by 2050 in Southeast Asia due to rising sea temperatures for two different climate models under the Intergovernmental Panel on Climate Change Special Report on Emissions Scenarios (Nakićenović et al. 2000) A2 emissions scenario: (a) the Hadley Centre coupled model, version 3 (Hadley) and (b) the parallel climate model (PCM). Source: Adapted from Donner and colleagues (2005). (c) Projected changes in fisheries catch potential (2005–2055), caused by species migration to cooler waters. Source: Adapted from Cheung and colleagues (2010). (d) Loss of coastal wetlands due to sea-level rise by 2100. Source: Adapted from McLeod and colleagues (2010). Abbreviations: km^2, square kilometers.

corals to high temperatures and acidification (Maina et al. 2011, Gilmour et al. 2013).

Scenarios for the Southeast Asia region project moderate to severe degradation of coral reefs by the mid-twenty-first century due to acidification and warming, with substantial local and regional variability and with the degree of impact depending on the coral reefs' adaptability to thermal stress and the interaction of multiple stressors (figure 5a, 5b; Donner et al. 2005).

Coral reefs in the Southeast Asia region are at elevated risk, because many experience high levels of multiple stressors (Maina et al. 2011). The degradation of coral reefs, including losses of coverage and structural complexity, leads to broader changes in reef communities, including biodiversity declines and species losses, because highly diverse fish and invertebrate communities depend on corals for shelter and feeding (Pandolfi et al. 2011). The impacts of coral reef degradation on ecosystem services and people's livelihoods include declines in locally important fisheries, reduced protection of coasts from storm surges, and the loss of tourism revenues (Hoegh-Guldberg et al. 2007), but these are

observed primarily in very severely degraded reefs and often only after substantial lag times (Pandolfi et al. 2011, Sumaila et al. 2011). There is good evidence that bleaching events have increased in severity and extent because of changing climate in many regions during the last decades and that mass coral extinctions have occurred in the geological past because of natural variation in climate and atmospheric CO_2 concentrations (Pandolfi et al. 2011). Major uncertainties concerning the tipping points for coral reefs include large species-specific differences in responses to climate change and acidification, poorly understood adaptation mechanisms, high levels of spatial heterogeneity in pressures and complex interactions among global change drivers (Maina et al. 2011, Pandolfi et al. 2011).

Overfishing and pollution. Synergistic interactions between overfishing and pollution can lead to well-documented and interacting tipping points in marine ecosystems. Foremost, overfishing can lead to abrupt collapses of fish stocks and can cause indirect collateral effects, such as changes in the physiological traits of populations (Jackson 2008, Worm

et al. 2009). Socioeconomic feedbacks can amplify the ecological mechanisms of collapse, because fishers often respond by increasing fishing effort as catch rates decline (Cinner et al. 2011), and if declines are prolonged, demand and value increase, which increases the incentive to fish. Recovery from a collapse often takes decades, even when fishing is banned or restricted, because of ecological feedbacks that hinder the rebuilding of populations (Jackson 2008, Worm et al. 2009). Moreover, overexploitation of species with disproportionate roles in ecosystem regulation, such as large-body fish at the top of the food chain, alters marine ecosystem food webs, can trigger trophic cascades, and reduces ecosystems' resistance to stressors (Jackson 2008, Worm et al. 2009).

Observations suggest that many marine capture fisheries in the Indo-Pacific region are already overexploited and that the continuation of business-as-usual fishing practices would substantially reduce fish harvests in the future (figure 4; Worm et al. 2009, Muallil et al. 2011, Sumaila et al. 2011). In coastal regions, marine food webs are often also severely disturbed by the effects of large nutrient inputs from terrestrial sources, especially nitrogen, which modifies the marine food web structure and processes through eutrophication and induced hypoxia (Jackson 2008). Nitrogen inputs into coastal areas of the Southeast Asia region are already the highest of any region in the world and are expected to substantially increase over the coming decades (Seitzinger et al. 2010). For example, inorganic nitrogen loads in the rivers of Southeast Asia are expected to rise nearly 20% by 2030 in pessimistic scenarios (Seitzinger et al. 2010). In a growing number of cases, synergistic interactions between eutrophication and overfishing have resulted in the conversion of species-rich, fish-dominated ecosystems to those dominated by resilient species, such as microorganisms and jellyfish (Jackson 2008). These transformations of food webs are often associated with important thresholds, such as the development of low-oxygen "dead zones" that typically take many decades to reverse because of strong hysteresis (Jackson 2008). Southeast Asia is the center of a large and rapidly growing number of sites of coastal hypoxia (*www.wri.org/our-work/project/eutrophication-and-hypoxia*).

Effects of global warming on the distribution of marine organisms. Tropical regions such as the Indo-Pacific are projected to suffer from large net losses of vertebrate and invertebrate species because of climate change as species, especially large-body and pelagic fishes, migrate poleward toward cooler waters, which may result in a high number of local extinctions (figures 4 and 5c; Cheung et al. 2013). Although there are many uncertainties, observations of fish and marine phytoplankton show large shifts toward the poles due to ocean warming over the last two decades (Cheung et al. 2013). Moreover, the metabolism and the timing of biological events for fish and invertebrates are affected by changes in ocean temperature and biogeochemistry (Sumaila et al. 2011, Cheung et al. 2013).

Combinations of these effects of global warming are projected to lead to large reductions in the catch potential in tropical regions, including Southeast Asia (figure 5c; Cheung et al. 2013). Global warming impacts on marine systems lack clear thresholds or amplifying effects, but from policy and management perspectives, these changes in community structure and ecosystem function are projected to be relatively rapid and may be protracted or irreversible over the course of several centuries because of the long lag times in the climate–ocean system (Sumaila et al. 2011).

Sea-level rise in coastal areas. The greatest current threats to coastal wetlands in Southeast Asia are habitat destruction for aquaculture, urbanization, and agriculture (McLeod et al. 2010). Sea-level rise will become a major menace for tidal wetlands, including mangroves, in many regions of the world over the next several decades (figure 5d; Gilman et al. 2008, McLeod et al. 2010). A tipping point for coastal wetlands is when the surface elevation of a coastal ecosystem does not keep pace with the eustatic rise in sea level, which results in a transition from an intertidal to a permanently flooded system (Gilman et al. 2008). Several processes determine the elevation of a coastal ecosystem's surface, including sediment accretion and erosion, soil accretion and erosion, tectonic movement, and coastal subsidence, such as those caused by the extraction of groundwater. Relative sea-level rise is predicted to have the greatest impact on coastal wetlands experiencing net reductions in sediment elevation and where landward migration is hindered by steep slopes or infrastructure. Most mangroves have not been keeping pace with current rates of relative sea-level rise (Gilman et al. 2008). Sea-level rise is projected to contribute about 10%–20% of the total estimated losses of mangroves on Pacific Islands by the end this century (Gilman et al. 2008) and up to 80% of the wetland losses in areas throughout Southeast Asia (figure 5d; McLeod et al. 2010). The impacts on biodiversity from the reduction of coastal ecosystems will result from the loss of nesting, nursery, and feeding habitats for numerous species groups, including fish, invertebrates, birds, and mammals. A reduction of the area and the degradation of coastal ecosystems also result in a decline of coastal ecosystem services, including natural hazard regulation, the regulation of coastal water quality, and carbon storage (Barbier et al. 2011). One of the greatest uncertainties is the magnitude of future sea-level rise. Nevertheless, there is general agreement that sea-level rise in the twenty-first century will be greater than that foreseen by the IPCC in 2007 (McLeod et al. 2010).

An emerging regional perspective. Recent studies for the Southeast Asia region have accounted for the individual mechanisms driving regime shifts (figures 4 and 5), but their interactions have not yet been broadly explored. A qualitative assessment of their interactions for business-as-usual scenarios suggests that the coastal and pelagic areas of this region could undergo widespread transformations that are difficult to reverse and that will significantly reduce

species diversity, lower fish harvests, and cause the degradation of many ecosystem services. These interactions are illustrated in a representative profile across this region in figure 4, which provides pictorial translations of quantitative scenarios of regime shifts and their interactions. Regional interactions are driven by aggregations of regime shifts, synergistic effects of multiple drivers, and spreading. A key synergistic effect of these regime shifts is to reduce the productivity of fisheries in the region more deeply and broadly than would occur because of any single mechanism. In particular, coastal breeding and feeding areas for fish are projected to be reduced in quality and quantity because of the degradation of coral reefs, seagrass beds, mangroves, and other coastal wetlands (figure 4). At the same time, overfishing and eutrophication in business-as-usual scenarios are projected to lead to simplified food webs, with decreased populations of economically important large-body fish (figure 4). Climate change is projected to have similar impacts on fish stocks in the open ocean around the equator and along most coastal areas; it is expected to induce the migration of fish away from the coasts and the equator (figure 5c; Sumaila et al. 2011). This could create synergistic effects that aggravate the impacts of regional drivers, which could lead to large reductions in the catch potential in many areas of this region (figure 4).

These effects are likely to be highly spatially heterogeneous (figure 5), meaning that some regions are projected to face large negative impacts, whereas others will experience minimal or even positive effects of global change when only a single regime shift mechanism is accounted for. For example, climate change effects on fish populations are projected to increase the catch potential in the Indian Ocean on the southern side of the Indonesian island of Java (figure 5c), and this might buffer some of the negative ecological and socioeconomic impacts of projected wetland loss due to rising sea level (figure 5d) and coral reef degradation (figure 5a). In other cases, such as in equatorial areas, the overlap of multiple negative effects of regime shifts may create much greater impacts than any single regime shift. Overall, the combination of regime shifts is foreseen to create a larger aggregate area affected by at least one major regime shift than is projected on the basis of any individual regime shift (figures 4 and 5), but the net effects of interactions among regime shifts remain to be studied.

Unlike the terrestrial example, spreading effects mediated by biophysical processes have not been identified at regional scales for the Southeast Asia marine systems. However, human displacements have been projected to play a potentially important role in spreading regime shifts in this region in the future. For plausible scenarios of low economic growth coupled with high inequity, hundreds of millions of people in this region are expected to become trapped by poverty, rising sea level, and the degradation of ecosystem services, which may lead to unplanned and highly disruptive human migration and increased pressure on coastal systems (Foresight 2011).

Avoiding these regime shifts will require substantial transformation of natural resource exploitation and management at national and regional scales—and a global-scale reduction in greenhouse gas emissions. The establishment of well-designed and properly managed marine protected areas (MPAs), covering a substantial fraction of coastal and pelagic waters, could have many potential benefits, providing that they protect key habitats and help decrease fishing pressure. Coral reefs can recover faster from bleaching events in protected areas, probably because of reduced additional stressors and the presence of keystone fish species (Gilmour et al. 2013). If they are large enough, MPAs could allow fish biodiversity and stocks to be reconstituted within the protected area and could improve the sustainability of the surrounding fisheries (Harrison et al. 2012, but see Hilborn 2013). To move toward ecologically sustainable fisheries, management systems urgently need to implement appropriate spatially explicit controls and rights-based mechanisms to limit exploitation to within ecosystem-level thresholds in order to preserve community structure and processes, to produce multispecies maximum sustainable yields, and to rebuild overexploited and depleted commercial fish stocks and threatened species (Worm et al. 2009). Aquaculture can help meet the rising demand for food from the sea, but aquaculture has its own environmental impacts and productivity limitations (Leadley et al. 2010, Barbier et al. 2011). Scenarios also suggest that the stabilization or reduction of pollution with nitrogen and phosphorus is plausible but will require major efforts to improve organic and inorganic fertilizer management and sewage treatment (Seitzinger et al. 2010). Scenarios including the coordination of regional governance improve the likelihood of managed human migrations and reduced environmental impacts (Foresight 2011). Similarly, coastal wetland, coastal marine, and pelagic systems must be managed at the regional level, because many species move freely across these ecosystems (figure 4). However, local and regional efforts will be far less effective in the long term if they are not accompanied by international efforts to reduce CO_2 emissions and the accompanying global climate change.

Past and current perspectives on regional-scale regime shifts

Regional-scale regime shifts such as those described above have close analogs in the recent past and are already affecting several regions. There are numerous well-documented regime shifts in semiarid regions that have led to negative impacts on human well-being and that involve strong interactions among biophysical, ecological, and socioeconomic mechanisms (Reynolds et al. 2007). For example, a combination of natural climate variability, destruction of natural grass cover, and poorly adapted agricultural practices in the 1930s led to huge dust storms throughout the Great Plains region of the United States (Hornbeck 2012). These storms during the Dust Bowl years removed much of the topsoil in many areas, depositing it over eastern North America and the Atlantic Ocean (Hornbeck 2012). Models suggest that

drought was amplified by the feedback of land degradation on regional climate (Cook et al. 2009). More than a half a million people migrated away from the Great Plains in the 1930s and 1940s, driven by synergistic interactions between drought impacts on agriculture and unfavorable socioeconomic conditions (UNEP 2007). Despite massive investments in tree planting, soil conservation, and social support, there are enduring negative effects on biodiversity, soil fertility, and land values (Hornbeck 2012). "Dust bowls" with similar drivers and consequences have occurred in several semiarid regions over the twentieth century and, for example, are causing large negative environmental and health impacts in China, despite substantial investments in mitigation, including the afforestation of more than 20 million hectares (Cao et al. 2011).

In sub-Saharan Africa, a series of famines coupled with long-term environmental degradation over the last five decades negatively affected the well-being of hundreds of millions people (Foresight 2011). These famines were driven by several interacting factors, including the overuse of marginally productive lands, persistent droughts, poverty traps, armed conflict, and weak governance. The overuse of marginally productive lands has led to lasting degradation in the vegetation and soils of some areas that cannot easily be reversed (Reynolds et al. 2007). In addition, social and political instability in this region promotes the unregulated use of natural resources and drives human migrations to escape poverty or to exploit new natural resources, which often leads to the spread of impacts into areas such as the more intact and highly diverse Guinean forest (Leadley et al. 2010, Foresight 2011). Counteracting these elements, Lenton and colleagues (2008) found that projected future increases in precipitation due to climate change and improved water use efficiency due to rising CO_2 might lead to a "greening of the Sahara/ Sahel [that] is a rare example of a beneficial potential tipping element" (p. 1790). Recent trends in rangeland improvement corresponding to increased rainfall over the last two decades suggest that cautious optimism is warranted if rainfall increases in the future (Hiernaux et al. 2009). However, increased rainfall may be insufficient to create a positive dynamic over the entire region unless it is coupled with improved governance and an end to conflict (Foresight 2011).

These examples from the US Midwest and West Africa illustrate the impacts and risks for human well-being of complex, regional-scale regime shifts, as well as the great difficulty and cost involved in the reversal of degradation. This provides a strong argument for urgent action to prevent regime shifts in regions where signs have been detected or analyses suggest they could occur in the near future.

Uncertainty, scale, and decisionmaking related to tipping point analyses

Large uncertainties are associated with the regime shifts discussed above, especially concerning their magnitude and degree of irreversibility (Leadley et al. 2010). Ecosystem changes in which early warning signs have been detected and

projections are relatively robust include snowfield and glacier melts, coral reef bleaching, coastal degradation due to sea-level rise, the collapse of some fisheries, and migration of species due to climate change. There is only moderate confidence in mechanisms associated with the large-scale degradation of cloud forests of the Andes or the humid tropical forests of the Amazon. The lowest confidence is in the socioeconomic dynamics, because these are very difficult to predict.

Messages about global-scale tipping points and planetary boundaries (Rockström et al. 2009, Barnosky et al. 2012) have helped raise scientific, public, and political awareness about the potential for rapid, irreversible change in human–environment systems. It has been argued, however, that most thresholds and boundaries at the global scale have not yet been clearly identified, that tipping-point mechanisms have been best demonstrated at local and regional scales, and that approaches focused on the global level may not lead to appropriate policy action (De Fries et al. 2012, Brook et al. 2013). In addition, game theory and experiments suggest that multiparty agreements to reduce global change pressures are less likely to be reached when the parties are faced with thresholds characterized by great uncertainty (Barrett and Dannenberg 2012). Therefore, although it is common for scientists to use uncertainty as an argument for applying the precautionary principle (Biggs et al. 2009, Rockström et al. 2009, Leadley et al. 2010, Barnosky et al. 2012), there is a need to better understand the decisionmaking process of stakeholders provided with ambiguous knowledge of thresholds (Polasky et al. 2011, Barrett and Dannenberg 2012).

These considerations suggest that, even though regime shifts and tipping points can be very powerful communications tools, the use of terminology such as *thresholds*, *boundaries*, *tipping points*, and *regime shifts* can lead to confusion about how human–environment systems respond to global change and to inappropriate policy response. This terminology can give the impression that (a) reducing pressures from drivers of global change before thresholds are reached is of little benefit, (b) human–environment systems respond abruptly when global change pressures exceed thresholds, and (c) systems are fully degraded beyond thresholds. Although some systems respond in these ways, our analysis suggests that notions of thresholds or boundaries—which imply that sharply defined changes in state occur at relatively precise levels of global or regional pressures—may not be the best way to describe how most regional regime shifts unfold and may lead to misunderstandings of these mechanisms by scientists, the public, and policymakers. The regional mechanisms that we have identified are projected to unfold over several decades, so they are likely to appear as gradual declines at timescales of a few decades (see also Hughes et al. 2013). In addition, most pressures and impacts are spatially heterogeneous (figures 3 and 5), meaning that increasing global change pressures lead to a greater number of areas undergoing regime shifts, and those changes therefore appear as smoother transitions when analyzed at regional as opposed to local scales (Brook et al. 2013). This effect has

been quantitatively illustrated using a model of regime shifts among grassland, savanna, and forest in Africa. Regime shifts due to climate change and rising CO_2 are foreseen to create abrupt grassland–savanna–forest transitions at local scales, but spatial heterogeneity in the drivers and sensitivity of ecosystems is projected to create asynchrony in the timing of regime shifts, which may lead to smoother transitions at regional scales (Higgins and Scheiter 2012). Finally, many systems have multiple tipping points, each leading to greater levels of degradation and difficulty in restoration (figures 2 and 4; e.g., Hoegh-Guldberg et al. 2007). From a science–policy perspective, all of these considerations mean that reductions in global change pressures are of benefit across a wide range of levels of pressure.

The regional regime shifts that we have identified are driven by interactions among biophysical, ecological, and socioeconomic mechanisms at various scales. Avoiding detrimental regime shifts will require action at local, national, and international levels, and, in some cases, the recent trends in pressures are encouraging. The quantitative analysis of regional-scale regime shifts and means of mitigation and adaptation will require broader, more integrative approaches, instead of treating underlying mechanisms as independent thresholds or boundaries. This means that considerable effort will be required to create a strong evidence-based science–stakeholder dialogue concerning the importance of regime shifts at multiple scales, to identify the actions required to avoid them, and to implement appropriate restoration and adaptation measures if those shifts occur (Reynolds et al. 2007, Leadley et al. 2010, Polasky et al. 2011, DeFries et al. 2012).

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