Reconsidering Terrestrial Biological Conservation Towards Balancing between Biodiversity and Ecosystem Services

A DISSERTATION PRESENTED BY

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TO THE GRADUATE SCHOOL OF ENVIRONMENT

AND INFORMATION SCIENCES

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF

DOCTOR OF ENVIRONMENTAL SCIENCE

IN THE SUBJECT OF

ECOLOGY

YOKOHAMA NATIONAL UNIVERSITY
MARCH 2020

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Abstract

Halting the loss of global biodiversity is one of the most urgent and challenging tasks facing global human society. Because species do not recognize political borders, multilateral and regional forms of cooperation, entailing careful consideration of economic and cultural relationships are necessary to conserve biodiversity. The framing of international goals for defining policy norms and shaping the behaviors of individuals and organizations is critical for the strengthening of such cooperation. In October 2020, future global biodiversity conservation goals will be formulated at the 15th meeting of the Conference of the Parties to the Convention on Biological Diversity in Kunming, China. This study explores the practical implications of the new goals relating to terrestrial biodiversity conservation, focusing specifically on the following two questions. (1) How can existing biodiversity conservation schemes be improved? (2) How can a balance be achieved between the protection of biodiversity and ecosystem services?

Whereas almost all biologists have advocated the expansion of protected areas, some have also pointed to the necessity of improving existing ones to maximize conservation gains. In Chapter 2, I present a case study that provides inputs for improving the quality of conservation through a reconsideration of criteria for biodiversity hotspot. I initially identified possible biodiversity hotspot and subsequently compared the rate of historical land-use change in the identified regions and in existing biodiversity hotspots. The results showed that the rate of land-use change in biodiversity hotspots was significantly lower than the rates in the identified regions, suggesting that rapid land-use change accentuates the threat posed to endemic plant diversity. Thus, it is likely that biodiversity hotspots support many species vulnerable to the rate of land-use change (i.e., species with low dispersal abilities or high sensitivity to invasive alien species) and that suppression of rapid land-use change and specialized protection of such vulnerable species increase the efficiency of conservation.

The concept of ecosystem services is often considered a competing approach in relation to traditional biodiversity conservation, resulting in ethical and practical conflicts between these two environmental management frameworks (i.e., human-centered vs. nature-centered conservation). In light of my review of the literature, in Chapter 3, I explore a potential strategy for balancing biodiversity conservation and the protection of ecosystem services that entails the subdivision of ecosystem services into global-public and local-public services. I show that in the case of local-public ecosystem services, the introduction of a bottom-up biodiversity conservation regime, wherein beneficiaries identify the source area and protect biodiversity to keep the quality of these services has significant potential for achieving the balance. Global-public ecosystem services, by contrast, are highly compatible and consistent with the application of traditional conservation frameworks. Moreover, consideration for the services is likely to lead to higher-level ecosystem management in a changing world.

Currently, bottom-up conservation focusing on local-public ecosystem services is rarely applied because links with nature are not generally recognized. In Chapter 4, as a preliminary step toward promoting recognition of these links, I visualize spatially limited areas of five ecosystem services in Japanese forests: edible wild plants, crop pollination, water purification, noise attenuation, and flood control. My findings indicate that while there were considerable variations in the spatial limitations by the services, which ranged from 3.3% to 93.1%, there were no cases of zero limitations. Further, existing protected areas tended to be located in areas that were spatially limited with regard to edible wild plants and crop pollination. These findings indicated that the application of ecosystem services values within decision-making processes without considering social perspectives could result in the overlooking of locations where human well-being is strongly connected with ecosystems.

Finally, in Chapter 5, I outline some of the implications and give suggestions for post-2020 conservation targets. First, efforts should be made to improve conservation planning and design within existing protected areas based not only on monitoring results but also on the application of the latest data and scientific evidence. Second, it needs to create a transparent conceptual framework and a system for classifying ecosystem services. Third, the dissemination of bottom-up biodiversity conservation and biodiversity-friendly agriculture and forestry should be encouraged to ensure the sustainable use of local-public and global-private ecosystem services, respectively.

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Contributing Authors

Kei-ichi Okada and Akira S. Mori contributed to Chapter 2, and Akira S. Mori contributed to Chapters 3 and 4.

Acknowledgements

First, I would like to express my deep gratitude to my advisor, Prof. Akira S. Mori, for his continuous support throughout my doctoral program. He constantly encouraged and motivated me while I was conducting research. Thanks to his frank, caring, and timely responses, my five-year doctoral program was enjoyable and meaningful. I look forward to continuing to work with him.

I would also like to thank my advisors at Yokohama National University: Prof. Hiroyuki Matsuda, Prof. Akiko Sakai, Prof. Takehiro Sasaki, Prof. Hiroki Oikawa, and Prof. Maiko Kagami for their insightful comments and encouragement. I am grateful to Prof. Tomoya Iwata, who was my advisor during my undergraduate program at Yamanashi University.

I extend my sincere thanks to Keita Nishizawa, Yashuko Yamada, and Satoshi Miyazaki, who are special colleagues and peers. I further express my deep gratitude to my wonderful colleagues, Dr. Kei-ichi Okada, Dr. Ryo Kitagawa, Dr. Tatsumi Shinichi, Dr. Shota Mashumoto, and Dr. Shinya Hayashi, whose sense of humor made this work so enjoyable. Moreover, I would like to thank the members and supporting staff at the Mori, Sakai, and Sasaki Laboratories.

This research was supported through a scholarship awarded by the Japan Securities Scholarship Foundation and through a Sasakawa Scientific Research Grant awarded by the Japan Science Society. In addition, support for my work was provided by the Japan Student Services Organization, through the Technology Development Fund of the Japanese Ministry of the Environment (S-14), and through a KAKENHI grant awarded by the Japan Society for the Promotion of Science (JP 19J15582).

Last, I would like to thank my wonderful family, friends, and concerned individuals in Kijitei, including Kazuhiro Sato and Mieko Kobayashi, for their patience and support throughout my doctoral studies.

1

General Introduction

Phenomenally diverse life forms have evolved on earth over a long history spanning 3.8 billion years. The genes, traits, and behaviors of all living organisms vary, and these differences are constitutive of biological diversity (hereinafter referred to as "biodiversity"). According to Primack (2014), biodiversity can be defined as "the complete range of species and biological communities, as well as the genetic variation within species and all ecosystem processes." As shown in Figure 1.1, three levels of biodiversity: genetic, species, and ecosystem diversity can be derived from this defiinition.

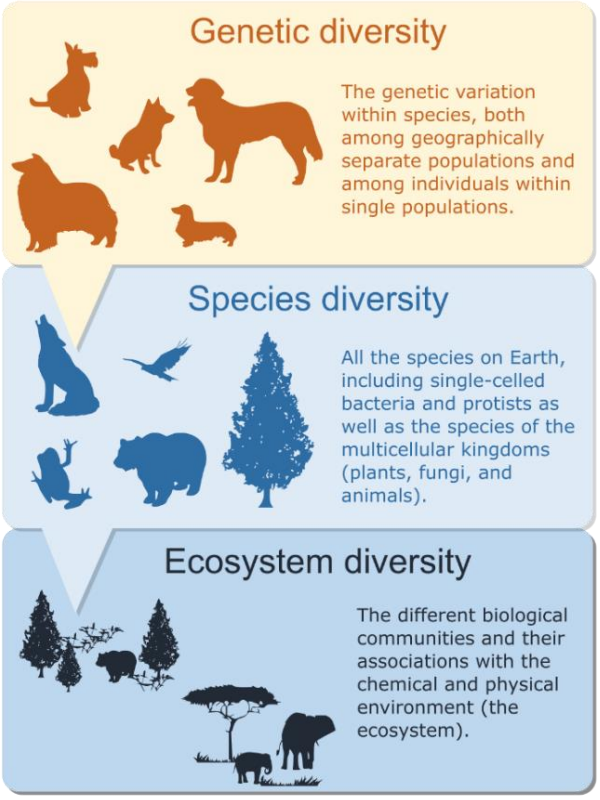


Figure 1.1: The three levels of biodiversity and their definitions.

Benefits derived from biodiversity have supported humanity. For example, the increased global demand for food associated with population growth has been met through increased crop and livestock production resulting from breeding and genetic manipulation of various wild plant and animal species (Diamond, 1999). These species have also contributed to the development of new products, such as pharmaceuticals, botanical medicines, cosmetics, manufacturing, and construction (Beatiie et al., 2005). Moreover, technologies have advanced in the field of biomimicry or biomimetics, which entails emulating species' structure and functions (Snell-Rood, 2016). Very few species provide such benefits directly, and most still have potential value for present and future generations. For instance, the Food and Agriculture Organization of the United Nations (2019) reported that around 6,000 out of 382,000 vascular plant species are cultivated for food production, of which only 200 are major species upon which human societies are heavily dependent.

Since the term biodiversity was first introduced by Walter G. Rosen in the 1980s, it has attracted considerable attention globally. It is widely used not only by politicians, researchers, and conservationists but also by the public at large. A key factor underlying the generalized usage of this term is the prevailing uneasiness evoked by the unprecedented rate of loss of global biodiversity. This loss can be attributed to deteriorating environments resulting from land-use changes, climate change, pollution, and overexploitation (Tilman et al., 2017). Among these anthropogenic drivers, land-use change, which is directly linked to habitat loss, has had the greatest impact (Figure 1.2; Newbold et al., 2015).

Figure 1.2: An Oil Palm Plantation near the Deramakot Forest Reserve in Sabah, Malaysia. Source: Kei-ichi Okada.

Since ancient times, humans have been transforming natural ecosystems into anthropogenic landscapes (Harari, 2014). Currently, more than half of the primary vegetation has been lost (Figure 1.3; Hurtt et al., 2011). Fossil records reveal that mass extinction events have occurred five times to date. The last one to occur was the Cretaceous–Paleogene extinction event (K–Pg extinction), caused by an asteroid collision. During this event, approximately 75% of all species became extinct (Raup and Sepkoski, 1982). The current high extinction rate of mammals and birds, beginning in the twentieth century, which has been attributed to human activities, has been identified as a sixth mass extinction event (McCallum, 2015).

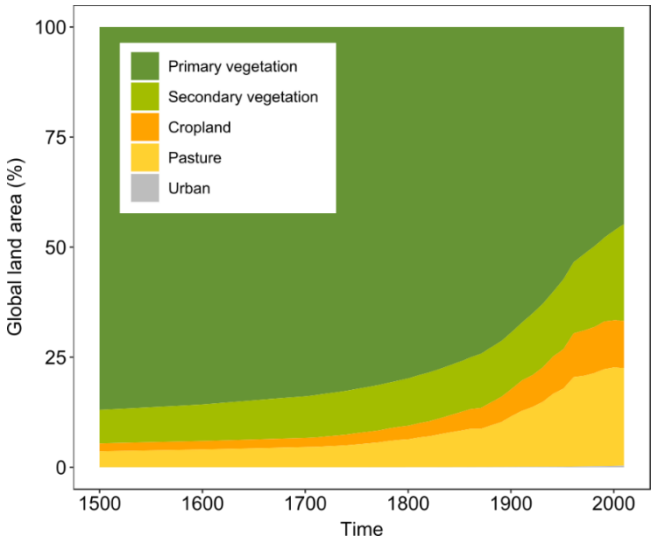


Figure 1.3: Time series of the fraction of global land-use excluding ice and open water. Data were extracted from Hurtt et al. (2011).

For instance, on May 6, 2019, it was reported at the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) meeting in Paris that one million species[1] could become extinct within decades because of excessive human pressures (Tollefson, 2019). A meta-analysis of 320,924 instances of occurrence data compiled globally and covering 11,525 sites revealed that more than 10% of global biodiversity has been lost as a result of land-use changes (Newbold et al., 2015). Usubiaga-Liaño et al. (2019) showed that the current rate of expansion of cropland (12.1%) and pasture (25%) exceed the thresholds at which biodiversity can be secured at a minimum level to support human well-being (cropland: 11.2%, pasture: 15.7%). Apart from these estimates, a large number of scientific papers have confirmed the decline of biodiversity at regional scales extending to the global scale (e.g., Butchart et al., 2010; Pimm et al., 2014; Japan Biodiversity Outlook Science Committee, 2015; Seibold et al., 2019). It is noteworthy that some of these analyses have shown that at local scales, the number of species evidencing decrease or increase trends is balanced (e.g., Schipper et al., 2016; Inger et al., 2015; Dornelas et al., 2019).

Against this backdrop, various approaches for avoiding or mitigating biodiversity loss at local-to-global scales have been explored. These approaches entail *in-situ* conservation (e.g., limiting human access and use of biodiversity, restoring degraded areas, and excluding invasive species) and *ex-situ* conservation (e.g., storing seeds, pollen, tissue, and embryos and breeding threatened species in botanical or zoological gardens) (Primack, 2014). The creation of protected areas is a standard strategy deployed to safeguard biodiversity effectively at or beyond the landscape scale. Definitions of protected areas vary among researchers. However, I would define a protected area as a geographical space that is managed through legal or other effective means (see Dudley, 2008). As of July 2018, 238,563 protected areas had been listed by the International Union for Conservation of Nature (IUCN) (Figure 1.4; UNEP-WCMC, IUCN, NGS, 2018). Of these protected areas, 14.9% comprise terrestrial land surfaces and 7.3% of them are sea- or ocean-based. In addition, some NGOs have applied their own criteria to identify unique high-priority areas at regional and national scales and have introduced active conservation, including biodiversity hotspots (see Figure 2.1 in Chapter 2), key biodiversity areas, important bird areas, and "last of the wild" sites (Schmitt, 2011).

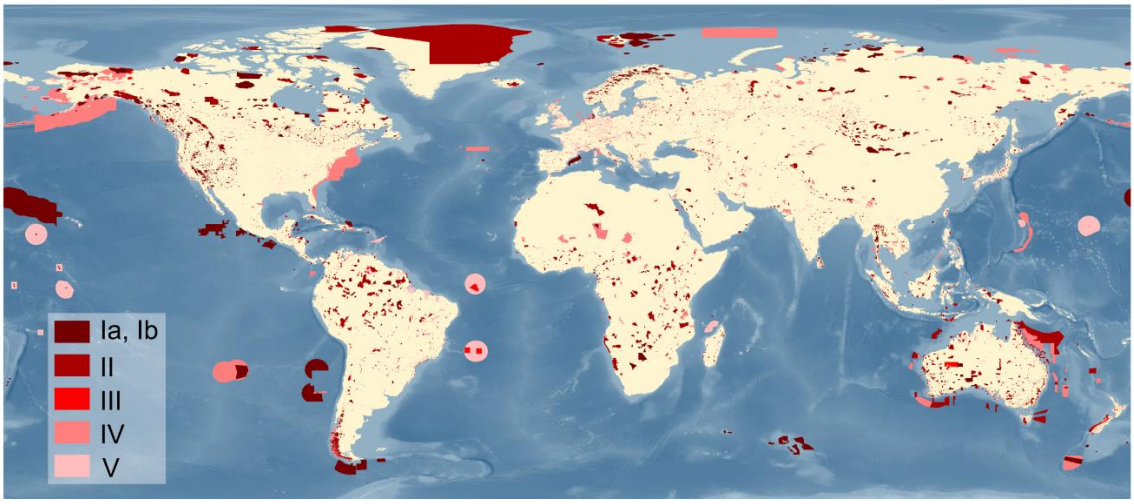


Figure 1.4: A map of protected areas across the world. Ia: strict nature reserve, Ib: wilderness area, II: national park, III: natural monument or feature, IV: habitat/species management area, V: protected landscape/seascape. Source: https://www.protectedplanet.net/ (accessed on October 19, 2019). Please refer to Dudley (2008) for detailed descriptions of the categories.

The human population is projected to reach 11 billion by 2100 (United Nations Department of Economic and Social Affairs, Population Division, 2019). Moreover, as a result of increasing income levels, most people worldwide will move out of poverty within a few decades (Rosling et al., 2018). While these projected trends are evidently positive ones, they will require the expansion of agricultural land (WWF, 2018). To address the increasing such threats posed to biodiversity, global conservation goals will be formulated at the 15th meeting of the Conference of the Parties to the Convention on Biological Diversity to be held in Kunming, China, in October 2020 (CBD; https://www.cbd.int/). The setting of these new international goals has, however, raised some concerns that relate, for example, to their compatibility with other international frameworks[2] (Ohsawa et al., 2019), differentiated responsibilities of individual countries depending on their development or income levels (Marques et al., 2019), and the quantifiability or measurability of targets (Butchart et al., 2016). In this thesis, I take up two prevailing debates on biodiversity conservation at the landscape scale. The first relates to the question of whether the focus should be on establishing new protected areas or on strengthening existing ones (e.g., Wilson, 2016; Büscher et al., 2017; Barnes et al., 2018; Adams et al., 2019). The second debate centers on the critical question of how the concept of ecosystem services can be incorporated into biodiversity conservation (e.g., Ridder, 2008; Naidoo et al., 2008; Vira and Adams, 2009). Chapter 2 addresses the first question. Here I examine ways of improving the quality of biodiversity conservation, focusing on historical land-use changes in biodiversity hotspots. The second question is examined in Chapter 3, where I identify notable characteristics of ecosystem services and outline practical methods for balancing the two dimensions of conservation relating to biodiversity and ecosystem services. I further visualized areas within Japanese forests where the uses of ecosystem services are limited as an initial step toward implementing both dimensions of conservation, in Chapter 4. Lastly, in Chapter 5, I outline some of the implications of my findings for the framing of the new biodiversity targets and future biological studies.

1. Although the number of threatened species (one million) reported by the IPBES needs more consideration in the future, there is no doubt that many species are on the verge of extinction.
2. Examples include the Sustainable Development Goals (SDGs), the Sendai Framework for Disaster Risk Reduction 2015-2030, and the Paris Agreement.

2

Reconsidering Biodiversity Hotspots based on the Rate of Historical Land-Use Change

2.1 Introduction

The Quantity versus the Quality of Biodiversity Conservation

Many conservation biologists have advocated the establishment of new protected areas. The main reasons for this advocacy are increasing threats posed to biodiversity (Noss et al., 2012; Wuerthner et al., 2015; Willson, 2016), discrepancies between existing protected areas and areas of high importance identified on the basis of newly developed biodiversity indicators (e.g., functional and phylogenetic diversity; Pollock et al., 2017), and the flaws of traditional conservation framing approaches (Jenkins et al., 2013; Betts et al., 2017). In 2010, the 193 parties to the Convention on Biological Diversity (CBD) adopted the 20 Aichi Biodiversity Targets for 2020 in support of an overall goal of human society living in harmony with nature (https://www.cbd.int/sp/targets/). Of these targets, the eleventh prescribes effective and equitable conservation of 17 percent of the terrestrial land surface. While the achievement of the goal by 2020 appears to be infeasible, there has been an increase in the number of protected areas (UNEP-WCMC, IUCN, NGS, 2018).

Such quantity-based targets and the subsequent increase in the number of protected areas have nevertheless raised concerns relating to the designation, in name only, of unmanaged protected areas (i.e., "paper parks"), the chronic shortfalls of staff and money attributed to resource dilution, and the discounting of small habitats (Fukuda-Parr, 2014; Venter et al., 2014; Pressey et al., 2017). Some researchers have contended that there should be a shift in focus from a quantity-based to a quality-based approach (e.g., Barnes et al., 2018; Adams et al., 2019). For instance, based on their analysis using a non-spatial dynamic landscape model, Adams et al. (2019) found that increased investments in the management of existing protected areas, rather in the expansion of new protected areas, would be effective in mitigating global biodiversity loss.

The main types of protected areas, as defined by the IUCN, comprise national parks, nature reserves, wilderness areas, wildlife management areas, and landscape protected areas (Dudley, 2008). The purpose as well as the associated land identification process and management system for each of these categories differ (Dudley, 2008). In light of these differences, a widely used approach for improving the quality of protected areas is adaptive management. This approach entails an iterative process of adjusting behavior, decisions, and actions to improve conservation gains on the basis of the evaluation of monitoring outcomes (e.g., Berkes et al., 2003; Williams and Brown, 2016). However, the implementation of adaptive management in more than 40,000 protected areas is unfeasible given constraints of finances, monitoring data, and expertise. Because alternative methods do not exist, the formulation of guidelines based on scientific evidence is imperative (Barnes et al., 2018). To get inputs and explore some implications for this challenging issue, in this chapter, I will give an example of the improvement of the conservation quality in biodiversity hotspots through the reconsideration of these criteria relating to conservation priority, focusing on historical land-use changes. It should be noted that as the following section shows, although not formally defined as protected areas, biodiversity hotspots are regions that are of high priority for global biodiversity conservation. I chose to include biodiversity hotspots in my study because they are identified using similar criteria to those used for existing protected areas and are associated with rich biological data (e.g., Brooks et al., 2006; Dudley, 2008; Schmitt, 2011). Therefore, the findings of this study and their implications are applicable to protected areas, worldwide.

Biodiversity Hotspots and Land-Use Changes

Myers et al. (2000) define a biodiversity hotspot as a biogeographic region that (1) contains more than 1,500 endemic vascular plant species and (2) has lost at least 70% of its primary vegetation (Figure 2.1). These explicit and quantitative criteria have contributed to raising awareness of the importance of biodiversity conservation (Marchese, 2015) and have prompted conservation-related actions supported by many international organizations over the last 25 years. These organizations and funding mechanisms include the Critical Ecosystem Partnership Fund, Conservation International, World Wildlife Fund, and Birdlife International (CEPF, http://www.cepf.net).

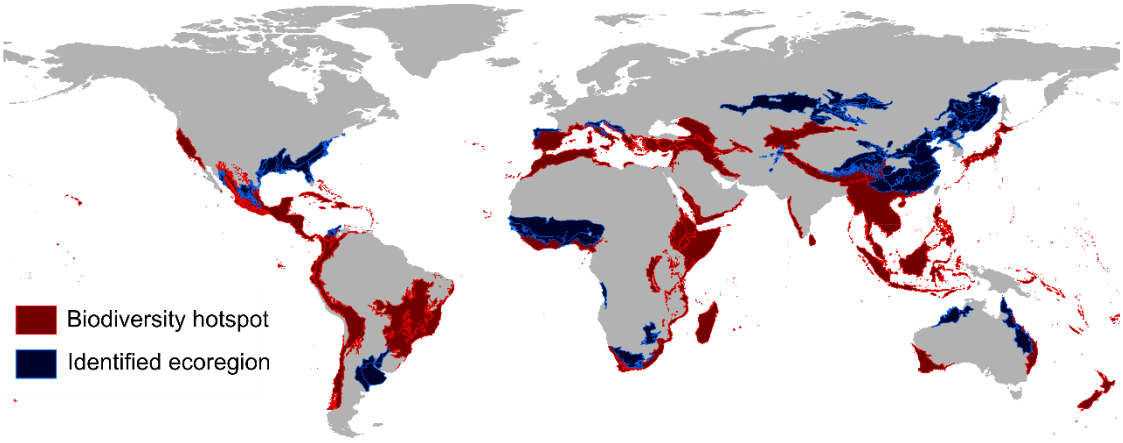


Figure 2.1: Global map of biodiversity hotspots (red, n = 35) and identified ecoregions (navy, n = 66). In this study, the number of biodiversity hotspots follows Mittermeier et al. (2011), but the North American Coastal Plain (NACP) was identified as the 36th biodiversity hotspot in 2016 (see Figure 2.7a). Source: Kobayashi et al. (2019).

To address the reconsiderations, I focused on the historical rate of land-use change in biodiversity hotspots. Land-use change usually causes declines in biodiversity, but the magnitude of such declines depends on the patterns of land-use change, such as the type (e.g., Sodhi et al., 2009; Newbold et al., 2015), intensity (e.g., Allan et al., 2014; Newbold et al., 2015), and spatial configuration of land-use change (e.g., With and King, 2001; Fahrig, 2003). Despite an increasing body of empirical and theoretical knowledge regarding the effects of these spatial patterns on biodiversity, the temporal aspects (e.g., the

rate/duration of land-use change) remain unclear due to the lack of long-term observations of historical land-use change and biodiversity over the course of a century (Ellis et al., 2013; Dornelas et al., 2018). However, biodiversity loss largely depends on the temporal patterns of environmental change; for instance, rapid climate change beyond the speed of species migration leads to species extinction (Pearson, 2006; Dawson et al., 2011). Therefore, a high rate of land-use change would also have a negative impact on biodiversity (Ordonez et al., 2013).

Given that biodiversity hotspots still host a large number of endemic species although they have experienced a severe loss of primary vegetation, land-use change in biodiversity hotspots might have occurred at a slow pace. This historical aspect of land-use change is expected to provide meaningful ecological implications that are relevant to policy and management for conservation within and perhaps outside biodiversity hotspots. Here, I created a new index describing the rate of land-use change (RLUC) every ten years from 1500 to 2010 across a $0.25^\circ \times 0.25^\circ$ grid that represents the rate of land-use transitions from primary and secondary vegetation to three anthropogenic land-use types (cropland, pasture, and urban land) while also accounting for differential impacts on biodiversity on the basis of the type of land-use change. Second, I identified regions that have lost more than 70% of their primary vegetation and had higher endemic plant species richness before the land-use change as biodiversity hotspots (i.e., regions that had a possibility to be biodiversity hotspots). Third, I compared the RLUC of the biodiversity hotspots and that of the identified regions. Finally, I discuss the significance of conservation in biodiversity hotspots based on the results of this analysis.

2.2 Materials and methods

Rate of Land-Use Change Index

The RLUC index is based on the Land-Use Harmonization dataset (LUH2 v2h), which provides information on past land-use transitions among 12 land-use types across a $0.25^\circ \times 0.25^\circ$ grid for the years 850-2015 (Hurtt et al., 2011). This dataset was downloaded from http://luh.umd.edu/index.shtml (accessed 23

December 2016). To simplify the calculation, I categorized the 12 land-use types into 5 groups: primary vegetation (forested primary land and nonforested primary land), secondary vegetation (potentially forested secondary land and potentially nonforested secondary land), cropland (C3 annual crops, C3 perennial crops, C4 annual crops, C4 perennial crops, and C3 nitrogen-fixing crops), pasture (managed pasture and rangeland), and urban land.

The decadal rate of land-use change to urban land (ΔU_{it}) in year t and grid cell i was calculated as

$$\Delta U_{it} = \frac{\sum_{k=t}^{t+9}(OU_{ik} + \alpha_{it} \cdot NSU_{ik})}{O_{it} + \alpha_{it} \cdot S_{it}} \quad (1)$$

and

$$NSU_{ik} = \begin{cases} SU_{ik} - US_{ik} & (SU_{ik} > US_{ik}) \\ 0 & (SU_{ik} < US_{ik}) \end{cases} \quad (2)$$

where O_{it} and S_{it} are the fractions of primary and secondary vegetation, respectively, and OU_{ik} represents the transition from primary vegetation to urban land in year k, which runs from t to $t + 9$. For the secondary vegetation, there are annual transitions from urban land (US_{ik}) and to urban land (SU_{ik}); thus, I calculated the net annual transition from secondary vegetation to urban land (NSU_{ik}) as in Eq. (2). α_{it} is a constant for considering the variability in the habitat quality of the secondary vegetation (see next section). In the same way, I calculated the decadal rates of land-use change to cropland (ΔC) and to pasture (ΔP) from primary and secondary vegetation. I omitted grid cells in which the fraction of primary and secondary vegetation was less than 5% to reduce uncertainty in the RLUC value attributed to calculation errors.

The LUH2 v2h dataset assumes that secondary vegetation never returns to primary vegetation. Although secondary vegetation does not host the same number of faunal and floral species as primary vegetation, the species composition in such areas becomes closer to that in primary vegetation with maturity (Dent and Write, 2009). To incorporate this variability in habitat quality into the RLUC index, I modeled the maturity of the secondary vegetation, β_{it}, as shown in Eq. (3) using the secondary vegetation biomass density (SB_{it}, kg C/m^2) and potential biomass density of the primary vegetation (PtB_i, kg C/m^2), which

were obtained from the LUH2 v2h dataset. Next, I modeled the habitat quality of the secondary vegetation, α_{it}, as shown in Eq. (4) using β_{it} and a weighted constant, σ, which represents the proportional decrease in bird species richness in tropical forests attributed to land-use change following Koh and Ghazoul (2010): secondary vegetation (σ_s=0.25), cropland (σ_c=0.68), pasture (σ_p =0.68), and urban land (σ_u=1). This focus was chosen because 1) birds have been used as an indicator of habitat quality due to their sensitive and rapid responses to environmental change (Canterbury et al., 2000; Gardali et al., 2006; Chambers, 2008; Alexandrino et al., 2016), and 2) tropical forests exhibit the highest terrestrial bird biodiversity and thus include various functional traits in response to land-use change (Karp et al., 2011; Mori et al., 2013; Newbold et al., 2014), enabling us to widely quantify the degradation of habitat quality in ecological communities.

$$\beta_{it} = \begin{cases} 1 & (SB_{it} > PtB_i) \\ \dfrac{SB_{it}}{PtB_i} & (SB_{it} < PtB_i) \end{cases} \quad (3)$$

$$\alpha_{it} = (1 - \sigma_s) \cdot \beta_{it} \quad (4)$$

To incorporate the habitat quality of urban land, cropland, and pasture, the rates of each type of land-use change were multiplied by each σ value and aggregated as shown in Eq. (5). The square-root transformation was applied to improve the normality of the RLUC data.

$$RLUC_{it} = \sqrt{\sigma_u \cdot \Delta U_{it} + \sigma_c \cdot \Delta C_{it} + \sigma_p \cdot \Delta P_{it}} \quad (5)$$

In total, 51 RLUC maps for 1500-2010 (i.e., 1500s, 1510s … 2000s) were created (Figure 2.2 and Appendix 1). Please note that the RLUC index does not consider several factors that could cause biodiversity decline: 1) the transition in land use from primary vegetation to secondary vegetation and 2) land-use intensity, fragmentation and habitat restoration.

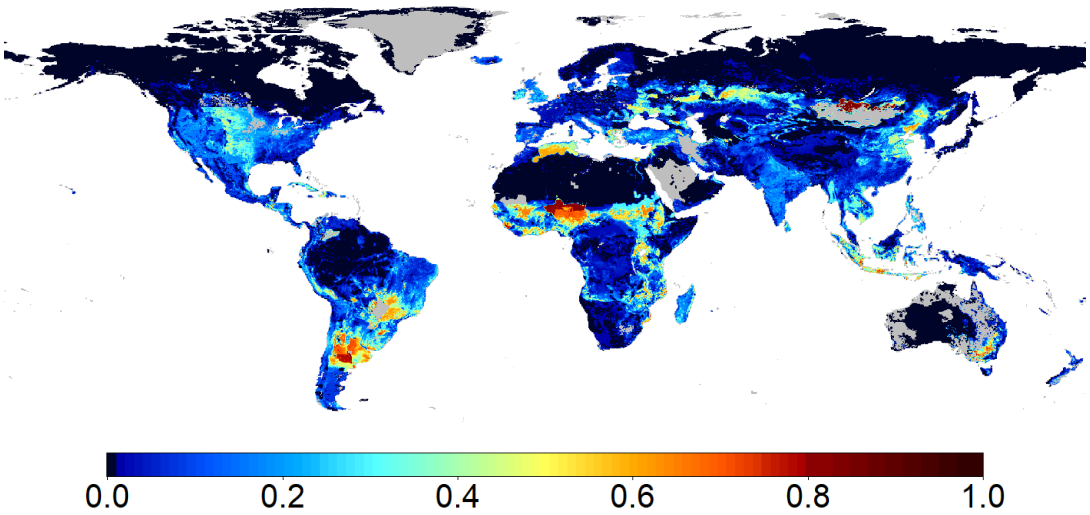


Figure 2.2: RLUC maps at a grid scale of 0.25° × 0.25° for the 2000s. The color gradient and gray coloration denote the RLUC and the cells in which the fraction of primary and secondary vegetation is less than 5%, respectively. Source: Kobayashi et al. (2019).

Identification of Ecoregions for RLUC Comparison

To identify regions that have lost 70% of their primary vegetation and may have at one time contained at least 1500 endemic plant species, the minimum value to be considered a biodiversity hotspot, I used the terrestrial ecoregion (Olson et al., 2001) as a fundamental unit because the boundaries of biodiversity hotspots correspond to clusters of several ecoregions (except for the Caucasus, Eastern Afromontane, and Maputaland-Pondoland-Albany hotspots). GIS data for the ecoregions in vector format were downloaded from https://www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world (accessed 15 January 2016). I created an ecoregion raster map with a 0.25° × 0.25° grid and calculated the fractions of primary vegetation in 2010 for 867 ecoregions using the LUH2 v2h dataset. Twenty-eight ecoregions did not be identified at the 0.25° resolution of this ecoregion map. I excluded 635 ecoregions in which the remaining primary vegetation exceeded 30% or in which biodiversity hotspots are already present (204 ecoregions remained; Figure 2.3).

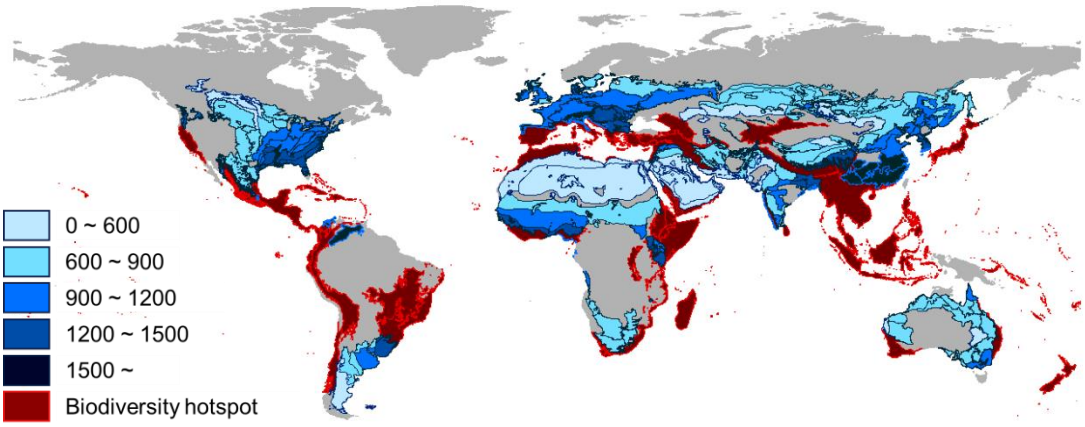


Figure 2.3: Global map of 204 ecoregions in which the primary vegetation was less than 30% in 2010. The blue gradient shows the predicted vascular plant species richness. Red represents the biodiversity hotspots. Source: Kobayashi et al. (2019).

Next, I evaluated the endemic plant species richness before land-use change based on the predicted vascular plant species richness and the percentage of endemic vascular plant species. The predicted vascular plant species richness was obtained from a map that shows the putative vascular plant richness gradient across a 7,800 km^2 hexagonal grid based on evapotranspiration, number of wet days per year, topographic and habitat heterogeneity, and vegetation complexity (i.e., without anthropogenic variables, such as land-use change; Kreft and Jetz, 2007; Ellis et al., 2012). I downloaded the map from http://ecotope.org /anthromes/biodiversity/plants/data/ (accessed 21 July 2016) and resampled it to a 0.25° × 0.25° grid. The values of vascular plant richness were averaged across both the biodiversity hotspots and remaining ecoregions. The resolution of the map is too coarse for some small/island biogeographic regions; thus, I excluded three biodiversity hotspots (the East Melanesian Islands, New Caledonia, and Polynesia-Micronesia) and 21 ecoregions in which the number of map cells was less than 5 following this procedure. I also excluded 61 ecoregions in which the predicted species richness was lower than that in the least species-rich biodiversity hotspot, that is, the Horn of Africa, which contains an estimated number of 733 species (Appendix 5). Note that the predicted vascular plant species richness does not represent the γ diversity for each biogeographic region but instead represents the average α diversity.

Third, data regarding the percentages of endemic vascular plant species (hereafter called the "percentages of endemics") in the biodiversity hotspots and remaining ecoregions were collected from the literature and online sources (Appendix 5). For 70 ecoregions, I adopted the national or regional values (e.g., the percentage of endemics in the Altai-Sayan Montane Forests was applied to 6 composed ecoregions; http://wwf.panda.org/about_our_earth/ecoregions/altaisayan_montane_forests.cfm, accessed 13 September 2016). I avoided adopting the percentages of endemics in extremely large countries, such as Russia and Australia. For African ecoregions, categorical values were available (i.e., very high, high, medium, and low numbers of endemics; Burgess et al., 2004). I excluded 62 ecoregions in which the percentage of endemics was lower than 10% (for African ecoregions, I excluded medium and low) and 15 ecoregions for which the percentage of endemics could not be found. In total, 66 ecoregions were identified as regions that had the possibility to be biodiversity hotspots (hereafter called "identified ecoregions"; Figure 2.1 and Appendix 5).

Data Analysis

I averaged the RLUC index values across both the biodiversity hotspots and identified ecoregions. Student's t-test was used to test the null hypotheses that there are no differences in the most rapid rates of historical land-use change between 1500 and 2010 (maximum RLUC) and the cumulative rates of historical land-use change (accumulated RLUC) between the biodiversity hotspots (n=35) and identified ecoregions (n=66).

The historical land-use change in the LUH2 v2h dataset was estimated based on population growth (Goldewijk et al., 2011; Hurtt et al., 2011); thus, the RLUC index exhibits spatiotemporal uncertainty, including national data gaps and abrupt decreases (Appendix 6). I excluded some biodiversity hotspots and identified ecoregions that are in countries with data anomalies (Appendix 6) and then compared the RLUC values of the biodiversity hotspots and identified ecoregions.

The RLUC index applied the same σ values estimated on the basis of the loss of bird species richness in tropical forest to all biomes even if almost all of the surface area was nonforested primary land (Figure 2.4 and Appendix 7). To address this assumption, I recalculated the RLUC index using lower (σ_s=0.13, σ_u =0.5, σ_c =0.13, σ_p =0.13) and higher σ values (σ_s =0.38, σ_u =1, σ_c =0.92,

σ_p=0.92). Next, I compared the original and new RLUC values in the biodiversity hotspots and identified ecoregions in which the coverage of nonforested primary land in 850 (i.e., the first year of the LUH2 v2h dataset) was higher than 10, 30, or 50%.

In the identification of ecoregions, I used 10% as a threshold for the percentage of endemics, even though the minimum value in biodiversity hotspots is 15% (Wallacea). This is because corrected percentages of endemics were estimated from the current state of the ecosystems (i.e., after land-use change), and the past percentages of endemics are likely higher than the present ones. To address this assumption, I conducted the same analysis to identify the ecoregions but set the threshold at 5% (n = 86) and 15% (n = 50). In this study, all geostatistical and statistical analyses were performed with the ArcGIS ver. 10.3 (ESRI, Redlands, CA, USA) and R software 3.0.2 (R Core Team, 2013).

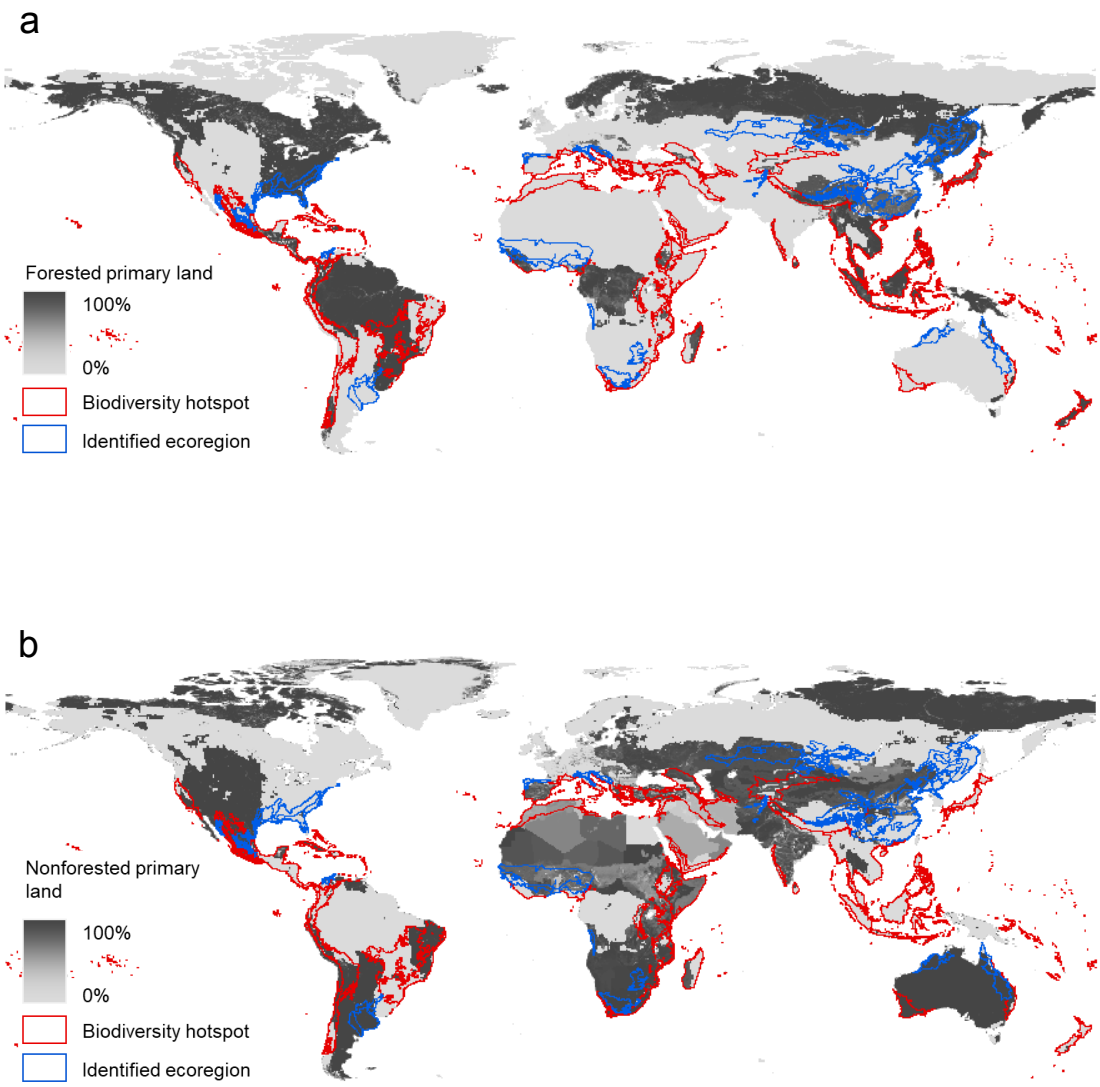


Figure 2.4: Maps of forested primary land (a) and nonforested primary land (b) in 850. The gray gradient shows the percentage of forested or nonforested primary land. The red and blue borders indicate biodiversity hotspots and identified ecoregions, respectively. Source: Kobayashi et al. (2019).

2.3 Results

The most rapid land-use change around the globe occurred in the 1950s ($RLUC_{1950s}$ = 0.16). The continental difference in the maximum RLUC was low in all areas except for Oceania (Appendix 2). The most rapid land-use change across five of the continents occurred from 1940 to 1960, while Europe experienced that in the 1900s ($RLUC_{1900s}$ = 0.20). In addition, Europe is characterized as having a high percentage of areas in which the fraction of primary and secondary vegetation was already less than 5% in the sixteenth century (Appendix 1).

The time series of the RLUC data for the biodiversity hotspots and identified ecoregions is shown in Figure 2.5. Our comparisons show that average maximum and accumulated RLUC during 1500-2010 in the biodiversity hotspots (n = 35, maximum RLUC = 0.32 ± 0.14, accumulated RLUC = 3.35 ± 1.1; Figure 2.6) are significantly lower than those in the identified ecoregions (n = 66, maximum RLUC = 0.42 ± 0.17, accumulated RLUC = 3.97 ± 1.19; Figure 2.6 and Table 2.1). I obtained the same significant results related to the maximum and accumulated RLUC even when I changed the σ values in the RLUC or the thresholds for the fraction of nonforested primary land or the percentage of endemics in the identification of ecoregions (Table 2.1).

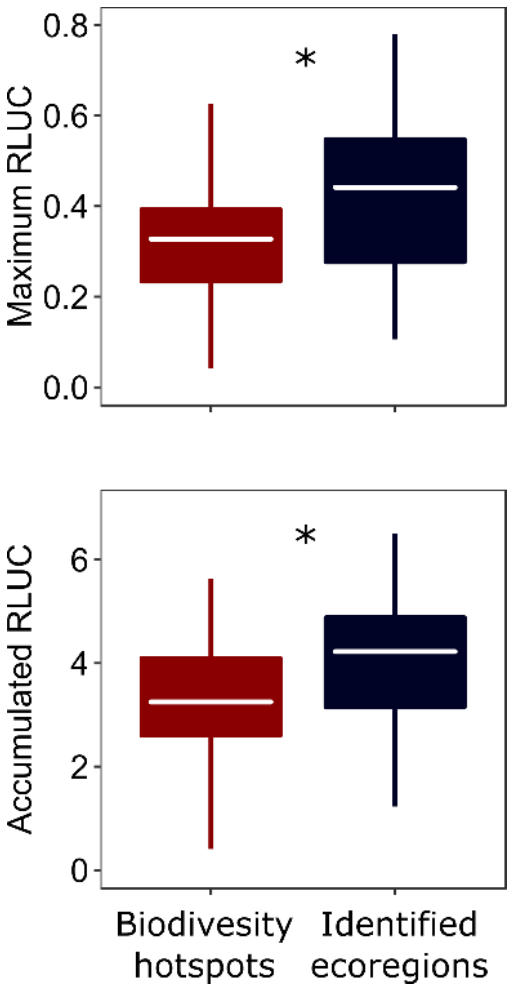


Figure 2.6: Comparison of the RLUC between biodiversity hotspots (n = 35, red) and identified ecoregions (n = 66, navy). The top and bottom panels show the maximum RLUC and accumulated RLUC, respectively. Asterisks indicate significant differences according to Student's t-test ($p < 0.05$). Source: Kobayashi et al. (2019).

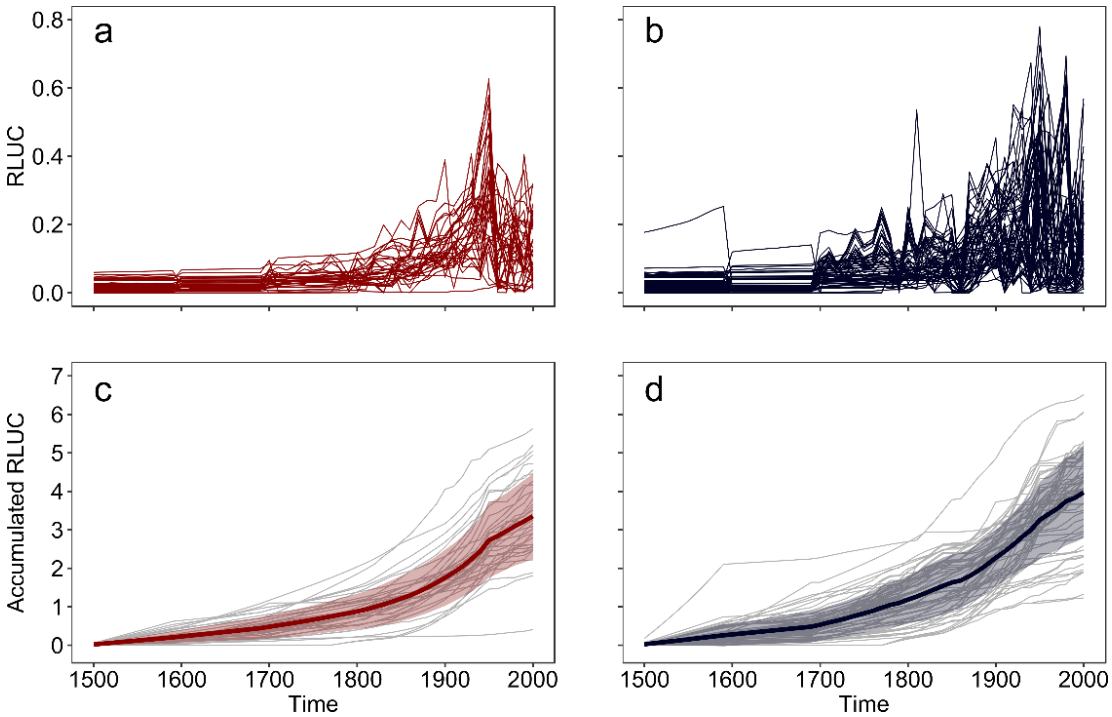


Figure 2.5: Time series of the RLUC data for 1500-2010 in the biodiversity hotspots (n = 35) and identified ecoregions (n = 66). The top panels show the transitions in the RLUC in the biodiversity hotspots (a) and identified ecoregions (b), and the bottom panels show the transitions in the accumulated RLUC in the biodiversity hotspots (c) and identified ecoregions (d). Gray lines, thick lines, and shaded polygons in panels c and d denote transitions in the accumulated RLUC, the average accumulated RLUC, and the 95% confidence intervals for each biodiversity hotspot and identified ecoregion, respectively. Source: Kobayashi et al. (2019).

Table 2.1: Results of the comparison of the maximum and accumulated RLUC in biodiversity hotspots and identified ecoregions. Source: Kobayashi et al. (2019).

Index	Threshold of the percentage of endemics (%)	Threshold of nonforested primary land (%)	No. of biodiversity hotspots /identified ecoregions	Maximum RLUC for 1500-2010			Accumulated RLUC for 1500-2010		
				Biodiversity hotspots, mean ± s.d.	Identified ecoregions, mean ± s.d.	*p*-value	Biodiversity hotspots, mean ± s.d.	Identified ecoregions, mean ± s.d.	*p*-value
RLUC	10	-	35/66	0.32 ± 0.14	0.42 ± 0.17	**< 0.01**	3.35 ± 1.1	3.97 ± 1.19	**0.01**
RLUC	10	-	26/34*	0.32 ± 0.15	0.43 ± 0.17	**0.01**	3.25 ± 1.14	4.05 ± 1.24	**0.01**
RLUC low†	10	-	35/66	0.23 ± 0.1	0.3 ± 0.12	**< 0.01**	2.37 ± 0.78	2.81 ± 0.84	**0.01**
RLUC high‡	10	-	35/66	0.37 ± 0.16	0.49 ± 0.2	**< 0.01**	3.9 ± 1.28	4.61 ± 1.39	**0.01**
RLUC	10	>10	32/51	0.32 ± 0.14	0.46 ± 0.15	**< 0.01**	3.41 ± 1.13	4.28 ± 1.02	**< 0.01**
RLUC	10	>30	23/41	0.37 ± 0.12	0.51 ± 0.12	**< 0.01**	3.75 ± 0.92	4.46 ± 0.77	**< 0.01**
RLUC	10	>50	16/37	0.4 ± 0.12	0.51 ± 0.12	**< 0.01**	3.93 ± 1	4.53 ± 0.68	**0.01**
RLUC	5	-	35/86	0.32 ± 0.14	0.39 ± 0.17	**0.04**	3.35 ± 1.1	4.09 ± 1.16	**< 0.01**
RLUC	15	-	35/50	0.32 ± 0.14	0.41 ± 0.17	**0.01**	3.35 ± 1.1	3.92 ± 1.17	**0.03**

* I excluded 9 biodiversity hotspots and 32 identified ecoregions that occur in countries with data anomalies (see Appendix 6).

† RLUC in which the σ (habitat quality) values were changed to lower values ($\sigma_s = 0.13$, $\sigma_u = 0.5$, $\sigma_c = 0.34$, $\sigma_p = 0.34$).

‡ RLUC in which the σ (habitat quality) values were changed to higher values ($\sigma_s = 0.38$, $\sigma_u = 1$, $\sigma_c = 0.92$, $\sigma_p = 0.92$).

2.4 Discussion

The Effects of the Rate of Land-Use Change on Biodiversity

The maximum and accumulated RLUC values in the biodiversity hotspots were relatively lower than those in the identified ecoregions (Figure 2.6), suggesting that land-use change in the biodiversity hotspots has occurred at relatively slower pace than that in other biodiverse regions and that the higher rate of land-use change likely accelerates species diversity loss. The environmental conditions suitable for the local persistence of species fluctuate on timescales of decades to millennia and according to long-term natural climate cycles and natural/anthropogenic disturbances (Davis and Shaw, 2001; Colwell et al., 2008; Lenoir et al., 2008). The changes in regional species diversity associated with these habitat suitability changes are generally determined by the rates of species immigration and extinction (Jackson, 2010). Land-use change that occurs at a rate beyond the speed of species migration would make the persistence of species populations difficult and lead to decreased biodiversity (Ordonez et al., 2014). Given that species with small ranges often have small population sizes and weak dispersal abilities (Dynesius and Jansson, 2000; Gaston, 2003; Jansson, 2003), endemic species seem to be highly sensitive to the rate of land-use change. Indeed, Sandel et al. (2011) provided convincing evidence showing that areas that experienced rapid climate change were associated with the absence of endemic species.

Rapid land-use change leads to a high frequency of contact between people and nature and thus will increase the risk of invasion by alien species that can pose a threat to native species (Von Der Lippe and Kowarik, 2007; Helmus et al., 2014). Endemic species are usually vulnerable to alien species because of their low ability to compete for resources (Messing and Wright, 2006; Reaser et al., 2007); for example, the main reason for endemic species loss in the Galapagos Island was invasion by Lantana camara (Mauchamp et al., 1998). Given these effects on native biological communities, biodiversity hotspots might have maintained many species with high vulnerability to rapid land-use changes. Although the concept of biodiversity hotspots is not entirely free from criticism, the specific vulnerability attributed to historical human activity is an important ecological feature supporting the advantages of prioritizing biodiversity hotspots for conservation.

Human impacts were already one of the main reasons for species extinctions in the sixteenth century (Baillie et al., 2004), but the RLUC was low worldwide during that period (Appendix 2). The rapid destruction of natural and seminatural habitats began in the middle of the nineteenth century in Europe and in the eastern United States (see animation file: https://doi.org/10.6084/m9.figshare.7794485.v1). The explosive human population growth attributed to an increase in the food supply has facilitated massive land-use changes at the global scale since the beginning of the twentieth century (Goldewijk, 2001, DeFries, 2014). The global RLUC increased starting in the 1900s and peaked from 1940 to 1960 (Appendix 2), which coincides with the period of human population growth called the "green revolution". The rapid land-use changes in Oceania and Africa (Appendix 2) are reflected in the massive agricultural land expansion that occurred in Australia starting in the late nineteenth century (Laut, 1988) and the transition of Sub-Saharan dry shrubland to pasture and cropland, respectively.

As reflected by the latest RLUC recorded for the 2000s, the worldwide rate of land-use change remains high (Appendix 1 and Appendix 2) due to excessive land-use changes in the Middle East, South America, and Africa. These regions include many biodiversity hotspots, such as the Cerrado, Tropical Andes, and Horn of Africa. Note that the calculation of the RLUC does not consider the suppression of land-use change by the identification of conservation priority areas. Given that the identification of biodiversity hotspots began in 1988 (Mittermeier et al., 2011), the actual rates of land-use change in biodiversity hotspots might be low. However, I need to note that further rapid land-use change will cause the disappearance of vulnerable endemic species and thus lead to the disqualification of biodiversity hotspots as having hotspot status.

Unrecognized Biodiversity Hotspots

Biodiversity hotspots were identified based on the evaluation of independent data sources (Myer et al., 2000), and thus unrecognized hotspots are likely to exist due to biogeographic information biases (Noss et al., 2015). Some identified ecoregions have a low RLUC, suggesting that these ecoregions have not experienced rapid land-use changes and thus still may potentially be biodiversity hotspots. I identified 18 identified ecoregions in which the maximum and accumulated RLUC were lower than the average maximum and accumulated RLUC among the biodiversity hotspots (Figure 2.7 and Appendix 7).

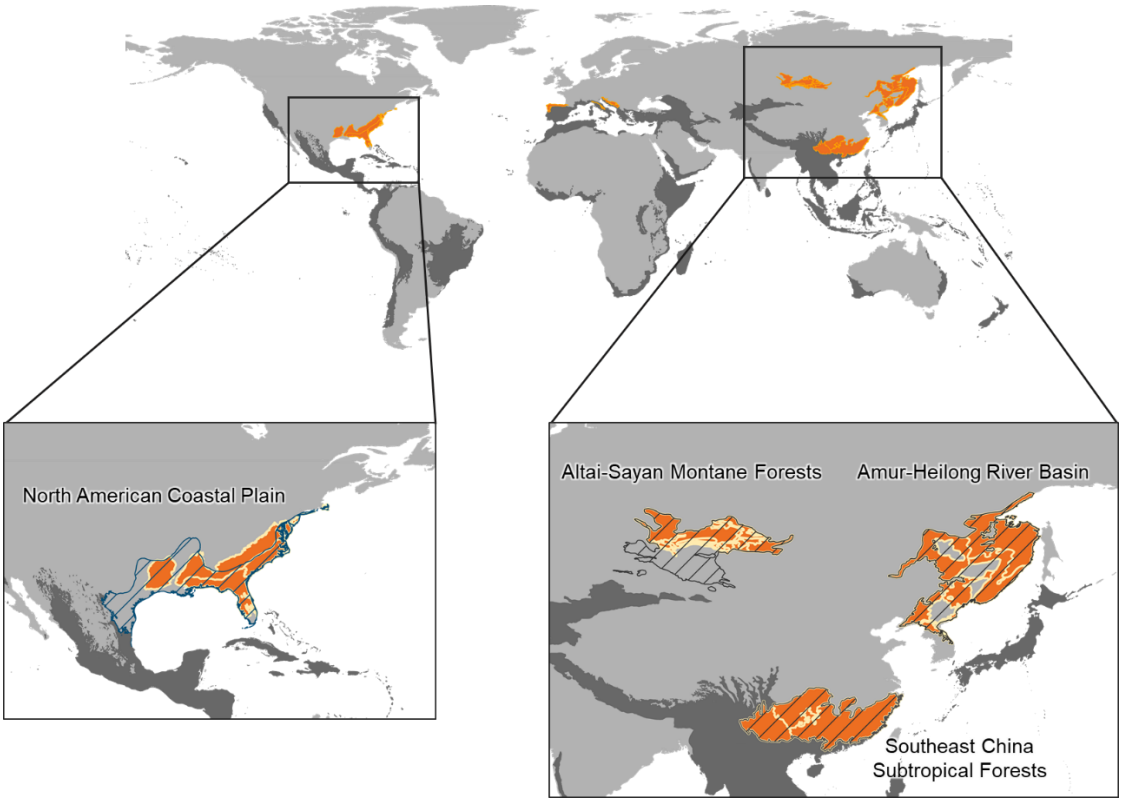


Figure 2.7: Global map of ecoregions in which the maximum and accumulated RLUC are lower than the average maximum and accumulated RLUC in biodiversity hotspots (orange) and the biodiversity hotspots themselves (dark gray). The blue hatched area in denotes the NACP, which was identified as the 36th biodiversity hotspot in 2016. The black hatched areas denote the candidate areas of new biodiversity hotspots. Source: Kobayashi et al. (2019).

I propose three regions as new candidate biodiversity hotspots considering the clusters of identified ecoregions that have a low RLUC and other biodiverse ecoregions. The first is the Altai-Sayan Montane Forests (Figure 2.8; Kokorin et al., 2001), consisting of six ecoregions (three of them are identified ecoregions with a low RLUC; Figure 2.7 and Appendix 7). This

Figure 2.9: Argali mountain sheep (*Ovis ammon*). Source: Belovodchenko Anton (Shutterstock).

region hosts more than 3700 vascular plant species and a large number of endemic plant species (Kokorin et al., 2001) and was designated a Global 200 Ecoregion (G200) because of its outstanding ecological features (e.g., biodiversity, unusual ecological or evolutionary phenomena, and global rarity of habitats; Olson and Dinerstein, 2002). Its faunal diversity is especially unique, and it is well known as the habitat of the snow leopard (*Panthera uncia*) and argali mountain sheep (Figure 2.9; *Ovis ammon*).

Figure 2.8: Landscape of the Altai-Sayan Montane Forests. Source: Valerii M (Shutterstock).

The second is the Amur-Heilong River Basin (Figure 2.10), consisting of six ecoregions (three of them are identified ecoregions with a low RLUC; Figure 2.7 and Appendix 7). Ussuri broad-leaf and mixed forests are designated a G200 because of their abundance of endemic fauna and flora (Olson and Dinerstein, 2002; WWF, http://wwf.panda.org/about_our_earth/ecoregions/russian_

Figure 2.11: Amur tiger (*Panthera tigris altaica*). Source: Ondrej Prosicky (Shutterstock).

fareast_temperate_forests.cfm, accessed 28 September 2017). Acting as a refuge during the last ice age, this ecoregion still maintains populations of unique and abundant species. It is also famously the habitat of the Amur tiger (Figure 2.11; *Panthera tigris altaica*), which is protected in many formal reserves while being simultaneously exposed to threats such as deforestation, habitat conversion to agriculture, and poaching.

Figure 2.10: Landscape of the Amur-Heilong River Basin. Source: Konstantin Baidin (Shutterstock).

The third is the Southeast China Subtropical Forests (Figure 2.12), consisting of three identified ecoregions with low RLUC values (Guizhou Plateau broadleaf and mixed forests, Jian Nan subtropical evergreen forests, and Yunnan Plateau subtropical evergreen forests). Jian Nan subtropical evergreen forests, as an example, is rich in birds and mammals, including endangered species, such as the

Figure 2.13: White-headed leaf monkey (*Trachypithecus polioceph-alus*). Source: iceeyes198369 (Shutterstock).

silver oriole (*Oriolus mellianus*), white-headed leaf monkey (Figure 2.13; *Trachypithecus poliocephalus*), and Chinese pangolin (*Manis pentadactyla*) and is identified as a G200 (Olson and Dinerstein, 2002; WWF, http://wwf.panda.org/about_our_earth/ecoregions/sechina_hainan_ moist_forests2.cfm, accessed 28 September 2017). Among these three candidate regions, the Southeast China Subtropical Forests have the highest priority for conservation. This is because the average human footprint, which is an index of human pressure on the environment (Venter et al., 2016), is high in this region (12.8, see Appendix 3). This value is comparable to those in the Caribbean Islands (13.1, Appendix 3) and Mediterranean Basin (13.4, Appendix 3).

Figure 2.12: Landscape of the Southeast China Subtropical Forests. Source: Cyril Hou (Shutterstock).

Interestingly, I was able to identify many ecoregions located on the NACP (Figure 2.7) as potential biodiversity hotspots. The NACP had previously been assumed to accommodate low levels of biodiversity due to historical misconceptions regarding its climatic and environmental characteristics. Nevertheless, the NACP was found to meet the criteria for designation as a biodiversity hotspot by Noss et al. (2015) and was identified as the 36th biodiversity hotspot in 2016 (CEPF, http://www.cepf.net/resources/

hotspots/Pages/default.aspx, accessed 28 September 2017). While this fact supports the reliability of our identification of unrecognized biodiversity hotspots, I do not have enough evidence to prove that the three candidate regions meet the criteria of biodiversity hotspots due to the limited available biogeographical information in English, importantly emphasizing the need for more detailed surveys.

Uncertainty of the Results

Some caveats exist regarding this study. First, the RLUC index does not consider the spatial and taxonomic variation in biodiversity decline (i.e., the same σ values were applied to all biomes). A species richness model constructed from an ecological assemblage dataset from 11,525 sites around the world did not show significant taxonomic differences in biodiversity declines by type of land-use change (Newbold et al., 2015). It also showed that the relative magnitude of the effect of land-use change on biodiversity (i.e., secondary vegetation < cropland ≈ pasture < urban land) does not change even if specific biomes are excluded from the dataset (tenfold geographical cross-validation, Newbold et al., 2015). The RLUC index can therefore be effectively used to suggest that rapid land-use change has a negative impact on biodiversity. This statement is also supported by our results from an additional analysis showing that the RLUC in biodiversity hotspots was relatively low even if I changed the σ values or set specific thresholds in nonforested primary land (Table 2. 1).

Second, the transition from primary forested land to secondary nonforested land or from nonforested land to forested land were not incorporated into the calculation of the RLUC. Such vegetation changes associated with climate change, grazing/browsing, and fire regimes have been one of the main threats to native species (Archer, 2009; Ratajczak et al., 2012). However, these changes have occurred over a long period of time at a relatively slow pace (Barger et al., 2011), and thus do not strongly raise the RLUC, which represents the decadal rate of land-use change. For instance, in semiarid grasslands in northern Texas, USA, the rate of wood-cover increase was 0.15% per year at 400 km2 (1937-1999, Anser et al., 2003).

Third, I have possibly overlooked some ecoregions in the identification process because 1) small ecoregions were excluded before the fraction of primary vegetation or the vascular plant species richness was evaluated, 2) the

percentages of endemics were obtained from independent literature and online sources, and 3) I used the average α diversity as the predicted vascular plant species richness (Appendix 5). Given that the results were robust in response to a change in the number of identified ecoregions (Table 2.1), the omission of identified ecoregions is unlikely to change our conclusions, but the number of ecoregions that are possible biodiversity hotspots would increase. I excluded many island ecoregions having usually high endemic diversity (Kier et al., 2009), including the Cocos Islands, the Queen Charlotte Islands, and Taiwan. If these regions have lost a large amount of their primary vegetation, they are likely to be recognized as new biodiversity hotspots.

Fourth, there are inherent spatiotemporal errors and data biases associated with the LUH2 v2h dataset, and I may have overlooked some data anomalies that were not identified in Appendix 6. The suitable starting point from which to examine the relationship between historical land-use change and biodiversity was unclear, and I thus used the LUH2 v2h dataset primarily because of the length of the time period covered by this dataset rather than on the basis of predictability. The mechanisms underlying how the rate of land-use change affects biodiversity also remain unclear. As an important suggestion, Appendix 2 and the animation file show that rapid land-use change has occurred since the 1940s at the global scale (excluding the EU), indicating the possibility of revealing the mechanisms in further studies, especially in developed countries, including Japan, North America, and Australia, where excessive land-use changes have occurred in modern times (i.e., the time period during which reliable historical land-use data can be obtained).

Implications

Reducing the rate of land-use change may lead to preferable consequences of biodiversity loss even if the fraction of natural habitat loss remains the same. The suppression of rapid land-use change represents an effective approach to protecting biodiversity, especially in biodiversity hotspots and the three candidate hotspot regions. However, I must ensure that such suppression does not encourage land-use development or intensification in other areas. The expansion of anthropogenic landscapes is necessary to meet the increasing demand attributed to future population growth (Popp et al., 2017). Given that many biodiversity hotspots and the three candidate hotspot regions are located

in developing countries (Figure 2.7), there should be great emphasis on formulating conservation strategies specialized to mitigate the effects of rapid land-use change (e.g., identifying and protecting species that are vulnerable to the rate of land-use change and controlling invasive alien species).

The future loss of primary vegetation was predicted in all of the representative concentration pathways (RCPs, Hurtt et al., 2011) in the three candidate hotspot regions. To face this threat, the identification of new biodiversity hotspots will greatly contribute to the effective protection of global biodiversity. However, note that our results do not prove that the three candidate regions meet the criteria for the designation of biodiversity hotspots. More biogeological information and surveys are needed, such as in the Forests of East Australia (Williams et al., 2011) and the NACP (Noss et al., 2015), which are 35th and 36th biodiversity hotspots identified in 2011 and 2016, respectively. Such information will also contribute to reducing systematic biases regarding historical biogeography (Noss et al., 2015) and inequality in conservation efforts.

Tracing historical human activities is one of the most effective approaches for determining site-specific vulnerability and note that this approach is not limited to biodiversity hotspots. Most of the identified ecoregions have unfortunately experienced rapid land-use change, including ecologically and evolutionarily outstanding ecoregions, such as the West Sudanian Savanna (Burgess et al., 2004), Cape York Peninsula Tropical Savanna (Hitchcock et al., 2013) and Nama Karoo (Burgess et al., 2004). However, these ecoregions may have not experienced other specific land-use change (e.g., those related to high land-use intensity and frequent/long-term land-use change). Identifying such site-specific vulnerabilities will greatly contribute to improving the quality and efficacy of biodiversity conservation at the landscape level.

Data Availability

The global RLUC maps for 1500-2010 are stored as GeoTIFF data at https://doi.org/10.6084/m9.figshare.7794485.v1. Note that careful consideration of the uncertainty in the RLUC attributed to the LUH2 v2h dataset and our assumptions of habitat quality (σ) is needed, especially when these data are used at a small scale.

3

How to Protect both Biodiversity and Ecosystem Services

3.1 Introduction

The History of Biological Conservation

In the field of environmental ethics, seminal works published in the 1960s (e.g., Carson, 1962; Boulding, 1966; White, 1967; Fuller, 1969) prompted debates on the underlying reasons the protection of nature. Light and Katz (1996) identified key positions within these debates, notably anthropocentrism vs. non-anthropocentrism, instrumental vs. intrinsic value, individualism vs. holism, and pluralism vs. monism. A consensus that appears to have emerged within discussions encompassing a wide variety of positions[1] is that non-anthropocentrism, intrinsic values, moral monism, and holism are integral components of environmental ethics (Light and Katz, 1996). Prior to 2000, biodiversity conservation was implemented in a manner that was aligned with this consensus, whereby wilderness and intact natural habitats (*nature for itself*) were prioritized or protecting threatened species or habitats in light of human pressures (*nature despite people*) was foregrounded (Mace, 2014).

Contrasting with this nature-based perspective is one that espouses ecosystem services, introduced through two influential studies published in 1997 (Daily, 1997; Costanza, 1997). These studies prompted an explosion of related research in the field of ecology and environmental economics (Figure 3.1; e.g., Seppelt et al., 2011; Boerma et al., 2017; Acharya et al., 2019). Although the definition of ecosystem services continues to be debated (Díaz et al., 2018; Braat, 2018; Kadykalo et al., 2019), it is generally defined as the benefits that people obtain from ecosystems (Millennium Ecosystem Assessment, 2005). The protection of ecosystem services is now a standard objective[2] for biological conservation and is sometimes referred to as the *new conservation*[3]. However, the definition, which is closely affiliated with the concepts of sustainable development and natural capital, seems to go against the consensus relating to non-anthropocentrism and the intrinsic value of nature. Indeed, some experts have strongly opposed this movement, sometimes adopting a hostile tone in their critiques (e.g., McCauley, 2006; Sagoff, 2008; Redford and Adams, 2009; Soulé, 2013).

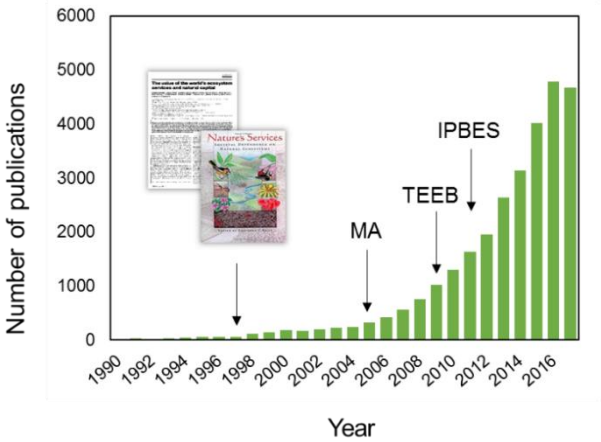


Figure 3.1: Trends in the number of publications in which the term "ecosystem services" appeared between 1990 and 2016. Data were obtained from the ISI Web of Science database. Arrows in the figure denote the inception years of the Millennium Ecosystem Assessment (MA), the Economics of Ecosystem and Biodiversity (TEEB), the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), and the year of publication (1997) of the papers by Daily and Costanza et al.

The conflicts relating to fundamentally different motives for protecting nature have also highlighted practical problems (Schröter et al., 2014). Considering criteria such as wilderness, vulnerability, and representativeness (Schmitt, 2011), advocates of traditional conservation accord priority to areas that are isolated and are not subject to anthropogenic pressure. By contrast, advocates of the new conservation focus on social-ecological relationships and bundles and

interlinkages (i.e., trade-offs and synergies) of ecosystem services (de Groot et al., 2010; Burkhard and Maes, 2017). Such differences in emphasis result in discrepancies in critical areas and management schemes aimed at expanding protected areas (Ridder, 2008; Naidoo et al., 2008; Vira and Adams, 2009). In this chapter, drawing on the findings of a review of the literature, I explore potential approaches for balancing the protection of both biodiversity and ecosystem services. As a prelude to my presentation, I will introduce three notable characteristics of ecosystem services in the following section.

The Concept of Ecosystem Services

Notwithstanding global recognition of the term ecosystem services, its interpretation has differed among researchers and institutions (Daily 1997; Hooper et al. 2005; Boyd and Banzhaf 2007; La Notte et al., 2017). Consequently, as shown in Box 1, diverse conceptual frameworks for ecosystem services have been proposed. These frameworks have subtle differences in their terminologies, but they also exhibit a standard common feature. Specifically, they bracket together goods and services entailing different characteristics, such as rivalry (rival vs. non-rival), excludability (excludable vs. non-excludable), and scale of beneficiaries (local vs. global) as ecosystem services.

A rival is someone whose consumption of products (e.g., crops and timber) reduces the quantities of these products that are available for others' use (Fisher et al., 2009). Something like outdoor recreation is considered excludable if it is possible to prevent or limit consumers (Fisher et al., 2009). In general, rival and excludable ecosystem services (hereinafter called "private ecosystem services") are automatically priced on the basis of the balancing of supply and demand and are traded in conventional markets (Costanza et al., 1997). By contrast, it is difficult to set prices for a second set of ecosystem services (hereinafter called "public ecosystem services"[4]), which have not been traded in markets.

There are two scales of beneficiaries (Syrbe and Walz, 2012). In the first case is one that the benefits extend to people throughout the world (hereinafter called "global ecosystem services"), like as climate regulation services through the absorption of carbon dioxide. However, the benefits of a second category of ecosystem services (hereinafter called "local ecosystem services) are area-specific. For example, the benefits of flood mitigation are only realized by people living downstream. In light of these characteristics, and following La Notte et al. (2019),

I re-classified ecosystem services into three categories as shown in Table 3.1: global-private, global-public, and local-public ecosystem services.

Table 3.1: A descriptive summary of ecosystem services. In Chapter 3, I do not identify the types of ecosystem services. Please refer to Chapter 4.

Ecosystem services	Rivalry	Excludability	Type
Global-private ecosystem services			
Biomass growing for timber provision	Rival	Excludable	Source-productivity (*in-situ*)
Global-public ecosystem services			
Global climate regulation	Non-rival	Non-excludable	Sink (*omnidirectional*)
Local-public ecosystem services			
Crop pollination	Non-rival	Non-excludable	Source-suitability (*omnidirectional*)
Pest control	Non-rival	Non-excludable	Source-suitability (*omnidirectional*)
Disease control	Non-rival	Non-excludable	Source-suitability (*omnidirectional*)
Air filtration	Non-rival	Non-excludable	Sink (*omnidirectional*)
Microclimate regulation	Non-rival	Non-excludable	Sink (*omnidirectional*)
Water purification	Non-rival	Non-excludable	Sink (*directional with dependency on a slope*)
Noise attenuation	Non-rival	Non-excludable	Buffer (*directional*)
Mass stabilization	Non-rival	Non-excludable	Buffer (*directional with dependency on a slope*)
Flood protection	Non-rival	Non-excludable	Buffer (*directional with dependency on a slope*)

Education	Non-rival	Non-excludable*	Information (*in-situ*)
Outdoor recreation	Non-rival	Non-excludable*	Information (*in-situ*)
Aesthetic beauty	Non-rival	Non-excludable*	Information (*omnidirectional*)

*It can be "excludable" depending on the location

3.2 Conservation for Protecting Biodiversity and Ecosystem Services

Local-Public Ecosystem Services

Most ecosystem services are categorized as local-public (Table 3.1). However, the protection of these services within high-priority areas using existing biodiversity-centered conservation frameworks poses challenges for the following reasons. First, potential flows relating to these services are not necessarily correlated with biodiversity (e.g., Anderson et al., 2009; Xu et al., 2017). Second, as discussed in Chapter 4, the consumption or experience of these services is associated with spatial, legal, and cultural limitations. A bottom-up biodiversity conservation system wherein beneficiaries of local-public ecosystem services identify the source area of these services and protect biodiversity to improve or keep their quality, as a technique, has significant potential for addressing both of these conservations. Accumulated ecological evidence confirm that biodiversity is associated with the increased quantity and stability of ecosystem services (see Appendix 8; Cardinale et al., 2012; Isbell et al., 2017). Even if the source area of local ecosystem services is not accorded high priority in relation to criteria such as wilderness or representativeness, protecting its biodiversity is a rational approach for maintaining and optimizing public-local ecosystem services.

There is no strict definition of bottom-up biodiversity conservation and no widely accepted method for implementing it; rather, it is realized through various approaches, such as private land conservation (Capano et al., 2019), privately protected areas (Mitchell et al., 2018), and other effective area-based conservation measures (Donald et al., 2019). Moreover, given inequalities in investments of public funds into the conservation of locally consumed ecosystem

services (e.g., through taxes and donations), entrusting the protection of these services to the beneficiaries is a desirable option (Villamagna et al., 2017). The adverse effects of the loss or degradation of an ecosystem, which is the source of public-local ecosystem services, are not dispersed as in the case of global climate regulation (Syrbe and Walz, 2012); rather, they directly impact on the lives of beneficiaries. Consequently, by all rights, conservation initiatives should be undertaken spontaneously in the absence of official interventions. However, at present, bottom-up conservation approaches are rarely implemented because of the prevalence of a lack of recognition of the connections between humans and nature (e.g., Castro et al., 2011; Muhamad et al., 2014; Zhang et al., 2016).

Kitoh (1996), a Japanese environmental philosopher, has argued that whereas humans are both passively and actively connected to nature, most people are not aware of the linkages (and sometimes made these to be weak). From the perspective of ecosystem services, the link corresponds to step by which an ecosystem contributes to human well-being (Box 1, Figure b; see also Potschin and Haines-Young, 2017). In ancient communities, the links were explicit and narrow in scope. However, with the development of economies and trade, they have expanded globally and have become increasingly complicated and diverse, especially in the case of private-global ecosystem services (Figure 3.2). While it is difficult or even impossible to capture all of the links relating to global-private ecosystem services (Figure 3.2a), those associated with public-local ecosystem services are relatively simple to recognize (Figure 3.2b).

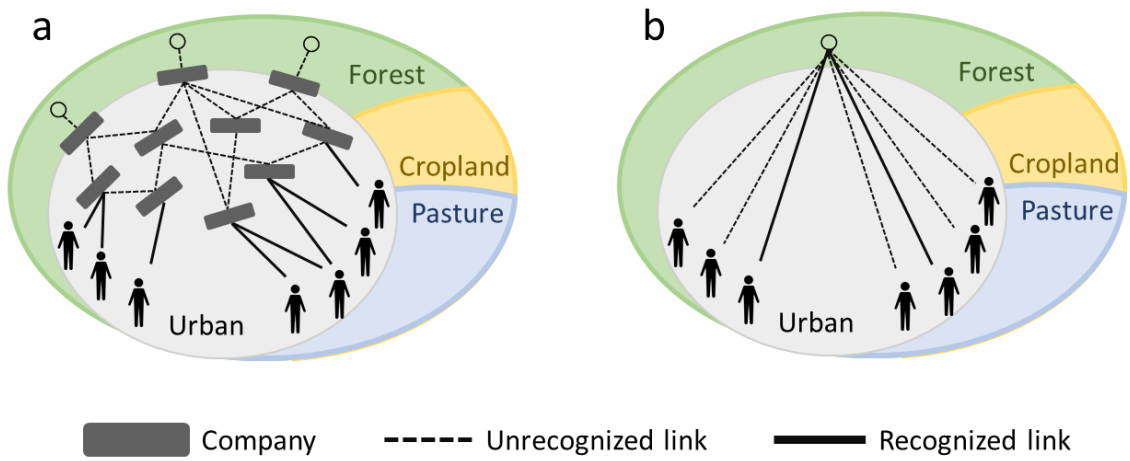


Figure 3.2: The links between human societies and nature relating the global-private ecosystem services (a) and local-public ecosystem services (b). The solid and dashed lines denote recognized and unrecognized links, respectively.

For example, the Japanese public is aware of strong cultural links associated with some of the forests remaining in the vicinity of temples or shrines (Figure 3.3), and these areas have often been managed more strictly than protected areas (Kadoya et al., 2017). The findings of a questionnaire-based survey conducted by Imai et al. (2013) that was administered to 5,225 Japanese responded revealed that public awareness of ecosystem services (especially cultural services) promotes behavioral intentions that are supportive of environmental conservation. I argue that the visualization and quantification of these links in future studies are essential for promoting bottom-up biodiversity conservation. Accordingly, Chapter 4 focuses on an examination of the actual uses of ecosystem services.

Figure 3.3: Secondary forest in Meiji Shrine (http://www.meijijingu.or.jp/english/about/1.html). Source: Songquan Deng (Shutterstock).

Global and Public Ecosystem Services

Conservation for protecting and maintaining global-public ecosystem services (i.e., global climate regulation) is consistent or highly compatible with traditional conservation measures for the following reasons. First, no spatial, legal, or cultural limitations apply because the benefits extend to people throughout the world (Syrbe and Walz, 2012). Second, biodiversity has a strong association with carbon storage (e.g., Strassburg et al., 2010; Bai et al., 2011; Labrière et al., 2016). Indeed, in some types of biological conservation activities centered on the mitigation of climate change, such as reducing emissions from deforestation and forest degradation (REDD+), biodiversity conservation has been performed without critical contradictions relating to management and land identification (e.g., Busch et al., 2011; Gardner et al., 2012; Kettle, 2012). Furthermore, incorporating human-centered perspectives into traditional conservation, and vice versa, entail advantages.

The composition, structure, and function of ecosystems undergo a continuous process of dynamic reconfiguration. The main driver of this process is disturbance, referring to a relatively discrete event in time that disrupts ecosystems. Examples include wind, droughts, floods, fires, and disease outbreaks (Figure 3.4; Pickett and White 1985). Such natural disturbances and the subsequent process of vegetation recovery are inherent and integral for maintaining biodiversity and ecosystem services (Mori, 2012). Here, I posit that a disturbance would be expected within an ecosystem that has a high aesthetic value. From a nature-centered perspective, such a disturbance would be acceptable. However, from a human-centered perspective, eliminating or mitigating the disturbance would be prioritized. The decision on the appropriate response requires scientific evidence because the temporal dynamics of most ecosystems are subject to anthropogenic environmental change (e.g., de Jong et al., 2013; Wårlind et al., 2014). For example, climate change has altered the frequency and intensity of disturbances worldwide (Seidl et al., 2017). Anthropogenically intensified disturbances may cause catastrophic damage to an ecosystem. If the ecosystem does not have sufficient areas to absorb the damage, then the disturbance may lead to irreversible ecosystem changes (Mori, 2012). The existing diversity of individual perspectives on this topic has generated debates that have sparked people's interest in ecological assessments and forecasts and is likely to lead to higher-level measures based on scientific evidence.

Figure 3.4: Natural disturbances in primary forests within Shiretoko National Park, Japan. A shallow landslide (a), and wind disturbance (b). Source: Yuta Kobayashi.

3.3 Ethics and Biodiversity

Because contrasting ethical theories such as anthropocentrism and non-anthropocentrism can be comprehended by the general public, individual positions are not categorically dichotomized. Even if individuals are not familiar with both theories, they can intuitively make moral judgments, condemning actions entailing the unnecessary destruction of nature (Wilson, 1984; Kaplan and Kaplan, 1989). Moreover, they can understand the importance of protecting/managing nature because regardless of their income and knowledge levels, they rely on ecosystem services. Indeed, Sandbrooks et al. (2019), who analyzed data from a survey administered among 9,264 conservationists from 149 countries, found that while personal perspectives were diverse, they were not partitioned based on the categories of new or traditional conservation. By contrast, new and traditional conservation are presented as mutually exclusive within debates, and ethical discussions on this topic have been widespread, focusing on esoteric wording known only to native English researchers. The lack of attention to Asian and African societies may have undermined reasonable global biodiversity conservation because the unique relationships of certain Asian and African communities with nature have been overlooked.

For example, as shown in Figure 3.5, *satoyama* ecosystems, entailing a mixed mosaic pattern of farmland and secondary forest, are found in Japan. This type of ecosystem serves as a refuge against past natural developments and continues to harbor high levels of biodiversity (Biodiversity Center of Japan, 2010). One of the reasons for biodiversity loss within these ecosystems is a decrease in human interventions. Many Japanese people recognize the intrinsic value of secondary as well as primary/intact forests, leading to active conservation. Another example is the *Chiloé* agricultural system, an *in-situ* agro-biodiversity reserve that has existed for millennia in Chile and continues to produce more than 200 endemic

Figure 3.5: The satoyama landscape in Nagano, Japan. Source: Norikazu (Shutterstock).

varieties of potato (FAO, http://www.fao.org/family-farming/detail/en/c/283015/). The existence of such semi-natural or agricultural ecosystems[5] wherein biodiversity requires human activities to thrive contravenes the views espoused in earlier discussions on new and traditional conservation. My aim is not to criticize these views; rather, I argue that exclusive wording should be avoided, and moral diversity should be respected to strengthen the path toward convergence.

Bryan G. Norton, an American environmental pragmatist, posited that environmental policies serving the interests of the human species as a whole, and in the long run, also serve the interests of nature. According to this convergence hypothesis, a desirable policy will inevitably entail a convergence of differing perspectives, such as anthropocentrism, and non-anthropocentrism (Norton, 1991). Once individuals know the meaning of biodiversity, they will be able to envision an ideal state of nature along a biodiversity axis. The implication of my argument is that if people also understand the role of biodiversity within ecosystem services, then ideal states of biodiversity will be similar. Although Norton intentionally used the phrase 'in the long run' as a prelude to his hypothesis, it is also possible to achieve a balance between ecosystem services and biodiversity conservation in the short run by categorizing ecosystem services on the basis of the following criteria: rivalry, excludability, and the scale of beneficiaries.

1. Examples include deep ecology (Næss, 1973; Devall and Sessions, 1985), ecofeminism (Griffin, 1978; Merchant, 1980), and bioregionalism (Berg and Dasmann, 1978).
2. Aichi Biodiversity Target 11 states that: "By 2020, at least 17 per cent of terrestrial and inland water areas and 10 per cent of coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem services, are conserved through effectively and equitably managed, ecologically representative and well-connected systems of protected areas and other effective area-based conservation measures, and integrated into the wider landscape and seascape."

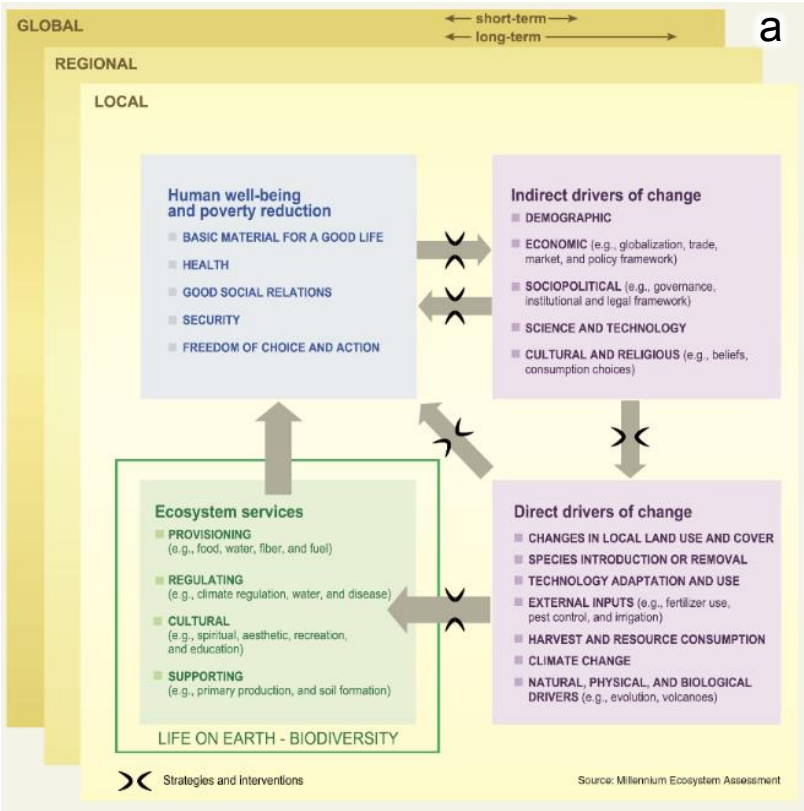
   Sustainable Development Goal 15 is to "Protect, restore and promote sustainable use of terrestrial ecosystems, sustainably manage forests, combat desertification, and halt and reverse land degradation and halt biodiversity loss."
3. It refers to human-centered conservation that is aimed at protecting biodiversity because of its importance to people. For this type of conservation, partnerships with corporations, the natural capital approach, and the use of market-based tools such as payments for

ecosystem services are emphasized (Kareiva and Marvier, 2012; Sandbrook et al., 2019).

4. Public ecosystem services encompass *club goods* that are non-rival/excludable, *open access* goods that are rival/non-excludable, and *pure public* goods that are non-rival/non-excludable. See Fisher et al. (2009) for detailed explanations of these terms.
5. Examples include *shimbue juu kihamba* agroforestry practices in Tanzania, the *kuttanad* farming system in India that is below sea level, and China's traditional tea agro-system, known as *pu'er* (Agricultural Heritage, https://www.agriculturalheritage.com/).

Box 1

Fisher et al. (2009) acknowledged the educational value of the system developed within the Millennium Ecosystem Assessment for classifying ecosystem services (Figure a). Accordingly, four core ecosystem services have been identified: provisioning, regulating, cultural, and supporting ecosystem services. However, these authors also criticized this system because the associated evaluation process entails the risk of double counting. In its place, they recommended the cascade model, which differentiates between capacity, flow and the benefits provided from nature (Figure b; Potschin and Haines-Young, 2017). However, Costanza et al. (2017) pointed out that socio-ecological relationships were oversimplified in the cascade model and consequently proposed a new conceptual framework, as shown in Figure c. Recently, a novel and comprehensive concept was introduced by some members of the IPBES. They defined nature's contributions to human societies as all of the positive contributions and detriments that humans obtain from nature (Figure d; Díaz et al., 2015; Díaz et al., 2018). In addition, various conceptual frameworks have been proposed (e.g., Wallace, 2007; Rounsevell et al., 2010; Mace et al., 2012; Smith et al., 2013)



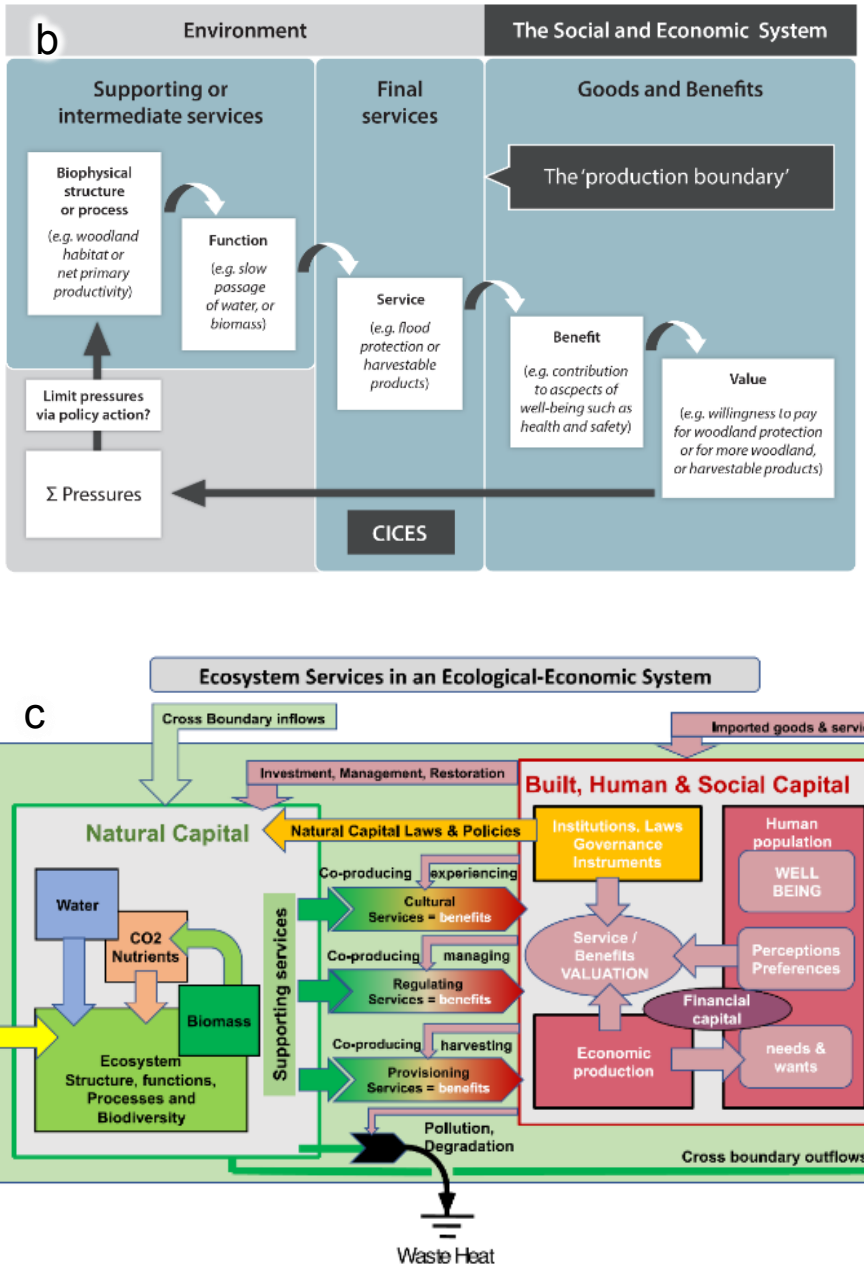


Figure: Conceptual models of ecosystem services proposed in the Millennium Ecosystem Assessment (2005) (a), by Potschin and Haines-Young (2017) (b), and by Costanza et al. (2017) (c). See the original articles, cited here, for detailed descriptions of these models.

4

Spatial Limitations Relating to the Use of Ecosystem Services

4.1 Introduction

Potential and Actual Flow of Ecosystem Services

As mentioned in Chapter 3, I explore the actual uses of local-public ecosystem services as a preliminary step toward promoting recognition of the links between people and nature and subsequent bottom-up biodiversity conservation. With reference to La Notte et al. (2019) and Potschin and Haines-Young (2017), I define the terminologies used for this study: an ecosystem generates potentially useful matter, energy, and information irrespective of human demand. This capability of nature as capital is designated as *ecosystem service potential* (hereinafter 'ES potential'). An actual use of ecosystem services such as harvest, consumption, or experience occurs when the ES potential interacts with human demand, and the amount of service flow is called the *actual flow of ecosystem services* (hereinafter 'actual flow'). For instance, forests continuously purify water through nutrient uptake by plants, but if no actual use of the water occurs (e.g., taking and transporting it to a city or cropland), the actual flow is zero (i.e., no benefit is provided to people).

In general, the ES potential is positively related to biodiversity because 1) primary and intact habitats with high biodiversity are built on dynamic and complex biophysical and chemical processes, and 2) biodiversity itself can increase the quality or quantity of ecosystem functions (Appendix 9; Cardinale et al., 2012; Isbell et al., 2017; Tilman et al., 2014). Nevertheless, the evidence does not show that biological conservation can simultaneously protect both biodiversity and ecosystem services (Watson et al., 2019) because actual use is limited in current social systems by spatiotemporal availability, by regional, national and cultural background, and by legal prohibition. In other words, the actual flow is not necessarily correlated to biodiversity. Many studies related to ecosystem services have specifically emphasized the ES potential. Moreover, they have often confused the ES potential and actual flow (Boerema et al., 2016). If the actual uses are constrained, then the lack of socio-ecological perspective might lead to failure of reasonable decision-making by counting the value of unavailable natural resources and overlooking locations for which human well-being is connected firmly to the ecosystem (Xu et al., 2017; Watson et al., 2019; Zoderer et al., 2019). The objective of our study is to provide quantitative evidence of spatial limitations of actual uses, and to elucidate the importance of incorporating social perspectives into ES research, with specific examination of forest-derived ecosystem services in Japan (Figure 4.1).

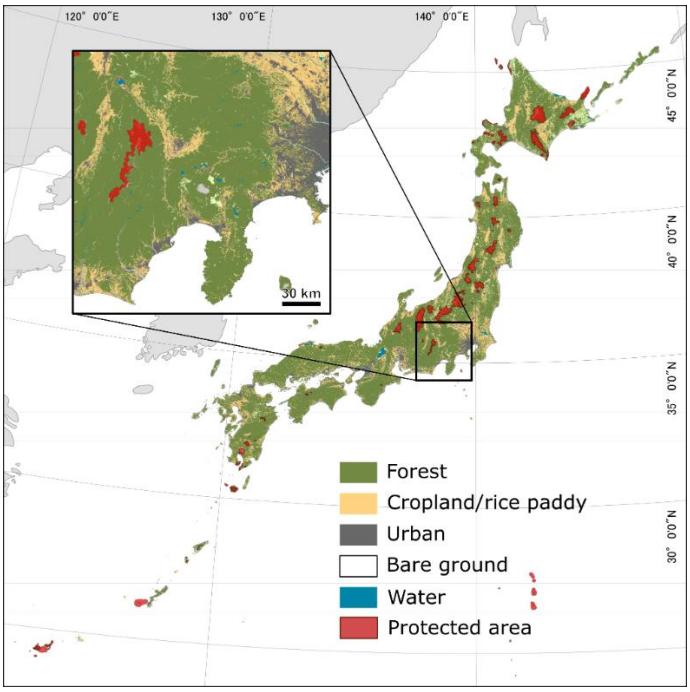


Figure 4.1: Land use classification map in Japan at 50 × 50 m². Transparent red shows protected areas that are categorized as Ia (strict nature reserve), Ib (wilderness area), or II (national park) by the International Union for Conservation of Nature. Figure 4.3 presents results for the area in the upper left panel.

Evaluation of the actual uses requires the identification of spatial characteristics of ecosystem services. Several classifications have been reported. La Notte et al., (2019) classified ecosystem services into five groups according to the fate of energy, biomass, and information: source-productivity, source-suitability, sink, buffer, and information. Syrbe and Walz (2012) classified spatial characteristics of ecosystem services into four groups based on spatial relations of areas in which the service occurs and where the related benefit is realized: *in-situ, omnidirectional, directional, and directional with dependency on a slope*. Both ideas are straightforward and crucially important to evaluate the spatial limitations. I subdivided the classification presented by La Notte et al., (2019) based on the spatial relations and re-classified them into eight types.

New Classification System of Ecosystem Services

Provisioning services including timber production, wild plants, and wild animals are classified as source-productivity (*in-situ*), in which ecosystems act as sources of matter or energy in the form of biomass (Figure 4.2). Harvest or collection of timber and non-timber forest products occurs in areas that people can visit. Therefore, accessibility (e.g., distance from a road, slope, blockage by a river or lake) limits the actual uses of this services.

Pollination and control of pests and diseases are classified as source-suitability (*omnidirectional*), by which ecosystems provide matter and energy which increase habitat suitability for specific species living in or cultivated in the other ecosystem (Figure 4.2). The actual flow is the contribution to crop yield by forest-dependent pollinators, predators, and parasitoids. Consequently, no actual use in forests occurs where croplands are not within a foraging range of beneficial species. Sink and buffer services are separated into several types: *omnidirectional*, *directional*, and *directional with dependence on a slope*. Carbon storage and air filtration are sink (*omnidirectional*), which ecosystems act as sinks to store or absorb matter, and the benefit extends to surrounding areas without directional bias (Figure 4.2).

No spatial limitation applies because widely diverse people can receive a benefit. Noise attenuation and smell reduction are classified as buffers (*directional*), which ecosystems act as transformers, changing the magnitude of flows of matter or energy, and the benefit is realized in specific areas (Figure 4.2). Distributions of forests, sources of noises or smells and the beneficiaries

are limited to the actual use. Water purification (sink), flood control (buffer), and soil erosion prevention (buffer) are available as *directional with dependency on a slope* (Figure 4.2). The spatial limitations are determined by the directions of the potentially useful things and their usage. For instance, the actual flow of flood control is zero if there is no artificial landscape (e.g., urban and cropland) downstream. Cultural services are classified as information, which ecosystems act as sources of information, and which are separable into two types: *in-situ* and *omnidirectional* (Figure 4.2). Outdoor recreation and education are categorized as information (*in-situ*). The actual use is limited by accessibility such as source-productivity. Aesthetic beauty is information (*omnidirectional*). No spatial limitation exists because the ES potential equals the actual flow; i.e. the existence of nature itself produces the benefits. See also Table 3.1.

Among these types, I selected five forest-derived ecosystem services: wild plants (source-suitability, *in-situ*), crop pollination (source-suitability, *omnidirectional*), water purification (sink, *directional with dependency on a slope*), noise attenuation (buffer, *directional*), and flood control (buffer, *directional with dependency on a slope*). I assumed that all Japanese forests have the ES potentials of the five ecosystem services, irrespective of these intensities. Then I quantified the spatial limitations of the actual uses.

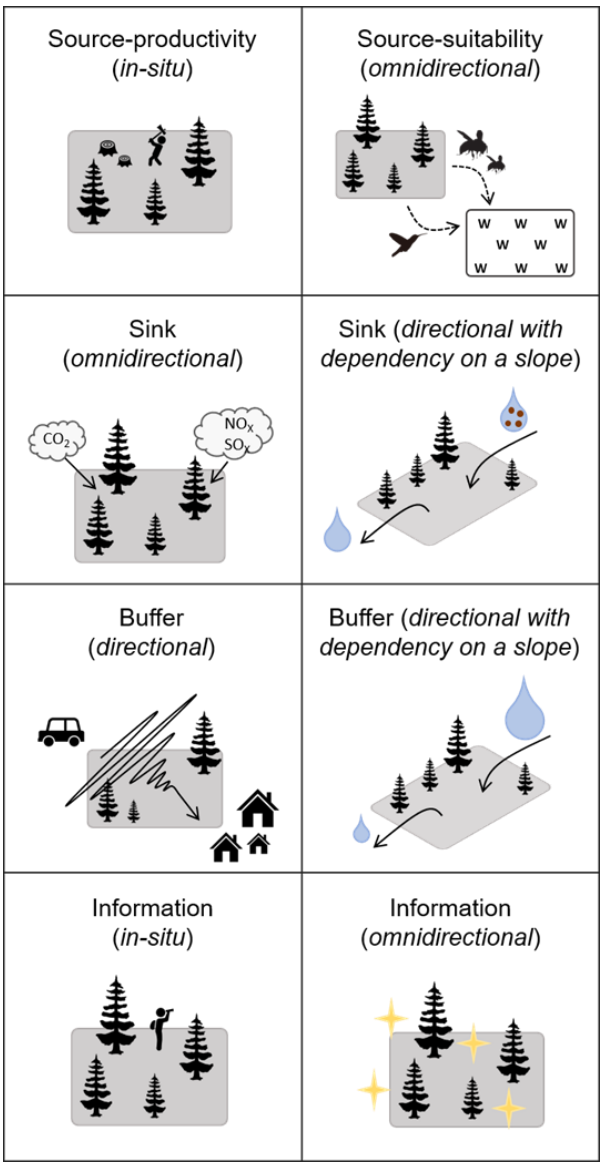


Figure 4.2: Types of ecosystem services. Based on reports of studies by La Notte et al., (2019) and by Syrbe and Walz (2012), I classified ecosystem services into eight types: '*in-situ*', by which the potentially useful thing is provided, with the benefit realized in the same area; '*omnidirectional*', by which a potentially useful thing is provided and extended omnidirectionally, with the benefit realized in surrounding areas; '*directional with dependency on a slope*', by which the potentially useful thing is provided after which it gravitationally flows down, with the benefit realized downstream; '*directional*', by which A potentially useful thing is provided and extended with directional bias, with the benefit realized in a specific area. A detailed description related to classification presented by La Notte et al., is included in the main text.

4.2 Materials and Methods

Wild Plants

We evaluated accessibility of an area based on the degree of slope of its ground surface and its distance from a road. First, we calculated the degree of a slope using an elevation map at 50 × 50 m^2 resolution (Japan Map Center, Tokyo, Japan) and extracted cells that exceed 30 degrees (Appendix 9, Figure 1). An interview survey conducted on the Noto peninsula, Japan showed that collection of edible mushrooms and plants does not occur in forests 3 km or more from a road (Nakazawa et al., 2014). We therefore extracted cells that are separated by 3 km or more from a road (Appendix 9, Figure 2). Road data were downloaded from the Ministry of Land, Infrastructure, Transport, and Tourism of Japan in vector format (MLIT; https://fgd.gsi.go.jp/download/menu.php, accessed 9 June 2019). Next, both maps were merged and then masked by a forest map at 50 × 50 m^2 grid (Figure 4.1) to visualize the spatial limit of the actual use of wild plants (Figure 4.3a and Appendix 9, Figure 3). The forest map was created from a land-use/land-cover map downloaded from the Japan Aerospace Exploration Agency (JAXA; http://www.eorc.jaxa.jp/ALOS/lulc/jlulc_jpn.htm, accessed 31 Oct 2017).

Crop Pollination

Diverse crops depend on wild pollinators and reared honeybees and bumblebees in Japan (Konuma and Okubo, 2015). This study specifically addressed crop pollination by forest-dependent wild pollinators. A typical and important crop pollination species is *Apis cerana*, a generalist honeybee that contributes to the pollination of various crops, including apple, cauliflower, cabbage, radish, litchi, and cardamom (Taki et al., 2011). The foraging range of *A. cerana* has been reported as approximately 2 km (Dyer and Seeley, 1991). We assumed that forests within 2 km of cropland actually contributed to crop yields. First, we created a cropland map from the land-use/land-cover map at a 50 × 50 m^2 grid. We extracted cells separated by 2 km or more from cropland (Appendix 9, Figure 4) and masked it with the forest map (Figure 4.3b and Appendix 9, Figure 5).

Water Purification

We targeted public waterworks that supply surface water to more than 5000 people. The names of rivers and lakes of water sources were collected from the Japan Waterworks Association (2013). If the river length was less than 50 km, then we assumed its intermediate point as an intake point. For the remaining rivers (length > 50 km) and lakes, we collected the locations of the intake points from online sources. In all, 1,406 intake points were identified, but 42 points could not be found. We created watershed polygons by setting the intake points as pour points on a 50 × 50 m^2 grid (Appendix 9, Figure 6) using software (Spatial Analyst Hydrology Tools, ArcGIS ver. 10.3; ESRI, Redlands, USA) and the elevation map. Then we extracted forests that are not covered by the watersheds (Figure 4.3c and Appendix 9, Figure 7).

Noise Attenuation

Sound pressure level (*SPL*, dB) at distance *R* (m) is modeled as for a point sound source

$$SPL = SPL_0 - 20\log_{10}\frac{R}{R_0}$$

and for a line sound source,

$$SPL = SPL_0 - 10\log_{10}\frac{R}{R_0}$$

where SPL_0 is a reference sound pressure level at distance R_0 (Fukuhara, 2003). This study treated two point sound sources (airport and industrial area) and two line sound sources (road and railway), with the assumption that each sound source generates the sound shown in Table 4.2 at 1 m (Fukuhara, 2003). First, we calculated the sound decay length required for each sound to be 40 dB, which is the level at which people feel no discomfort (Table 4.1). Second, we created buffers around roads, railways, airports, and industrial areas based on the respective sound decay lengths (Appendix 9, Figure 8). GIS data of sound sources were downloaded from MLIT (road: https://fgd.gsi.go.jp/download/menu.php;

railway airport and industrial area: http://nlftp.mlit.go.jp/ksj/, accessed 9 June 2019). Third, we created buffers around urban areas based on each buffer length (Appendix 9, Figure 9). Fourth, we extracted cells for which both buffer maps overlapped and masked the cells with a forest map (Figure 4.3d and Appendix 9, Figure 10).

Table 4.1: Summary of sound sources.

Sound source	*SPL* at 1 m (dB)	Distance necessary to reach 40 dB (m)
Point		
Airport	120	3162
Industrial area	100	316
Line		
Road	70	100
Railway	80	1000

Flood Control

We created artificial land-use maps (urban, cropland, and rice paddy) from the land-use/land-cover map. Then, we created watershed polygons by setting the artificial land-use cells as pour points (Appendix 9, Figure 11) using software (Spatial Analyst Hydrology Tools of ArcGIS ver. 10.3; ESRI, Redlands, USA) and the elevation map. We overlaid the map with the forest maps and extracted forests that are not covered by the watershed (Figure 4.3e and Appendix 9, Figure 12).

Spatial Analysis

We downloaded a map of protected areas in Japan (Protected Planet, https://www.protectedplanet.net/country/JP, accessed 27 Jan 2018) and extracted terrestrial protected areas that are categorized as Ia (strict nature reserve), Ib (wilderness area), or II (national park) by the International Union for Conservation of Nature (Figure 4.1). Then, we calculated the coverage of the spatially limited areas in protected areas.

4.3 Results

A high-density network of roads with total distance of 1,278,184 km is maintained in Japan. For that reason, 98.9% of forests are within 3 km of a road (Appendix 9, Figure 2). However, 16.1% of forests are on the steep slopes (>30°) of Japanese mountains, reflecting its high relief topography (Appendix 9, Figure 1). Collection of wild plants is limited to 17.5% of forests (Figure 4.3a and Appendix 9, Figure 3). Croplands occupy 6% of the Japanese land surface, but they are scattered (Appendix 9, Figure 4), leading that 23.7% of forests are not used for crop pollination (i.e., > 2 km from cropland, Figure 4.3b and Appendix 9, Figure 5). Both water purification and flood control are water-related directional services, but their respective spatial limitations are extremely different. Because artificial landscapes have spread near large river estuaries, 96.8% of forests contribute to flood control (Figure 3e and Appendix 9, Figure 12). However, most potable water is taken upstream and is sent to cities. Therefore, 41.2% of forests are not used for water purification (Figure 4.3c and Appendix 9, Figure 7). Half of the forests (55.4%) are distant from noise sources and do not contribute to noise attenuation. Also, 37.0% of

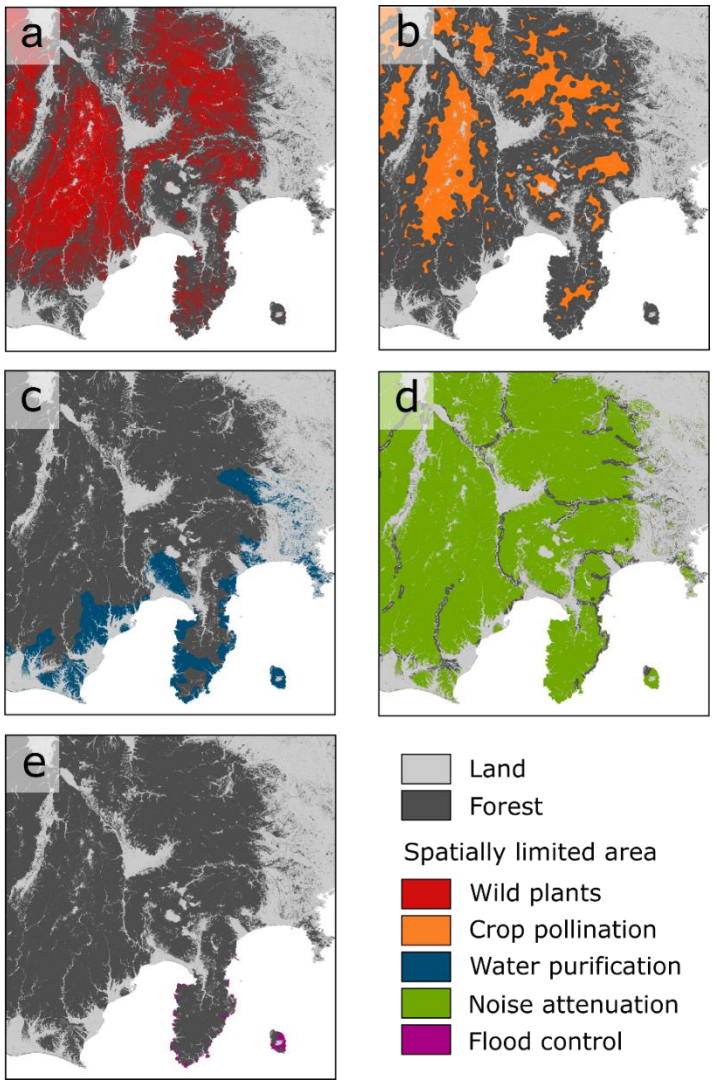


Figure 4.3: Map of area of actual uses that are spatially limited: wild plants (a), crop pollination (b), water purification (c), noise attenuation (d), and flood control (e).

forests attenuate noise, but no beneficiary exists. The actual use of noise attenuation was found to be spatially limited in 93.1% of forests (Figure 4.3d and Appendix 9, Figure 10). The coverage of protected areas in the five spatially limited areas described above are presented in Figure 4.4. For wild plants, crop pollination, and noise attenuation, those values were higher than the rates of the respective spatially limited areas: 35.7, 67.3, and 99.2% (i.e., existing protected areas tend to be in spatially limited areas).

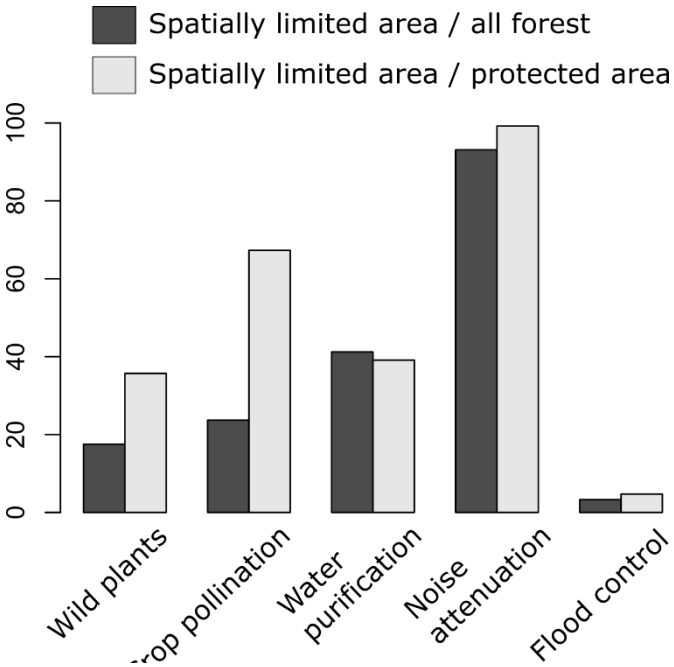


Figure 4.4: Coverages of spatially limited areas of five ecosystem services in all Japanese forests (dark gray) and in protected areas (light gray).

4.4 Discussion

Spatial limitations of actual used areas vary widely by the type of ecosystem service (3.3% to 93.1%), but none was zero, suggesting that the quantitative and monetary nature values reported to date might be overestimates in the context of the actual flow. Japan is a heavily forested country, with a high degree of biodiversity (Biodiversity Center of Japan, 2010). Nevertheless, primary vegetation accounts for only 20% of the terrestrial surface and has remained mainly in areas that are less susceptible to human influence (e.g., low road and population density, and steep slopes). Protected areas were identified in such intact areas, which tend to be in spatially limited areas for wild plants, crop pollination, and noise attenuation (Figure 4.4). Areas with high biological importance for conservation do not necessarily provide benefits to humans under the current social system. Today, the ES potential can be assessed even without exclusive or technical knowledge using valuation tools and open data (e.g.,

InVEST, TESSA, ARIES; Dunford et al., 2017). Although the same results are unlikely to be obtained in other regions, considering estimates of the ES potentials during decision-making with no consideration of the limitations of actual use will likely engender unexpected outcomes for both biodiversity and ecosystem services conservation. In this regard, we recommend the application of our methods to assessments in other countries.

Given expectations for future population growth and concentration (Popp et al., 2017), human demand for ecosystem services can be expected to increase. Meeting such demand requires an increase in the amount of the actual flow by intensifying existing human interactions (Cumming et al., 2014). A threshold of sustainability is crucially important: the maximum actual flow ensuring the provision of potentially useful services through time without causing degradation of other ecosystems (La Notte et al., 2019; Rockström et al., 2009). For instance, changes in water flow regimes caused by

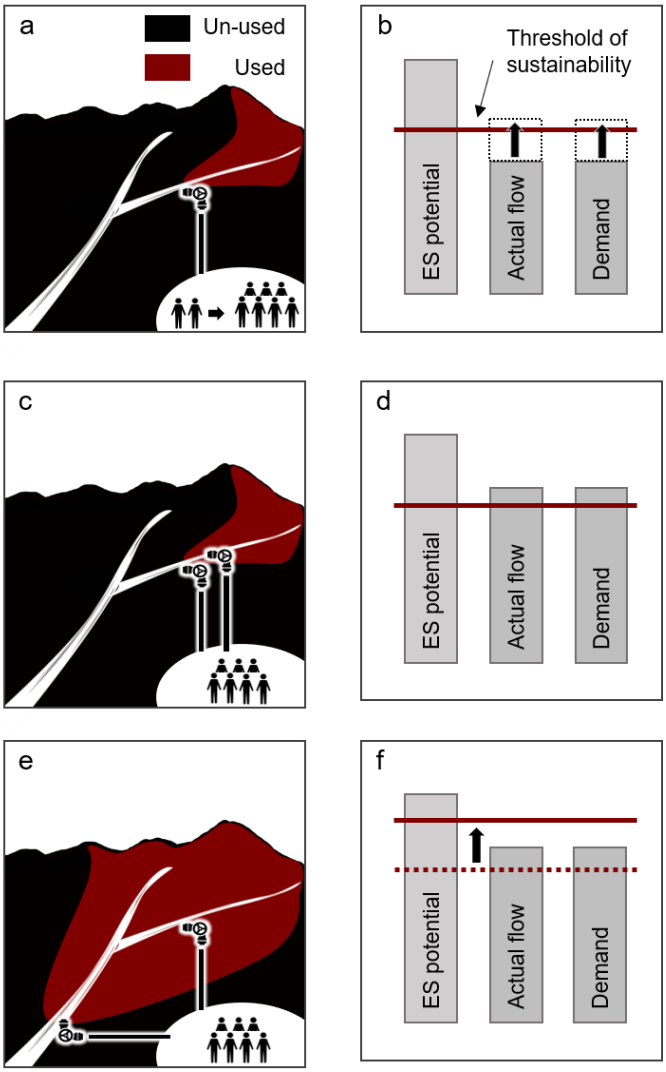


Figure 4.5: Approaches to increasing the actual flow of water purification and water provision. Current use of the water for drinking is conducted under the threshold of sustainability, but water intake must be increased because of population growth (a, b). Approach 1: water intake increases by intensifying existing human interaction (c), but it entails the risk of becoming greater than the threshold (d). Approach 2: water intake increases under the threshold by building a new water facility in another place that had been previously unused (e, f).

excessive water intake (i.e., overuse of ecosystem services) engender degradation of the fluvial ecosystem (Bunn and Arthington, 2006). Shedding light on spatial limitations of the actual use by this approach is useful to visualize unused natural resources that can be used under the threshold (Figure 4.5). Such expanded use can also contribute to the reduction of risks of unexpected depletion or irreversible degradation of natural resources by diversifying the sources of benefits, even while confronting climate change, pollution, and overexploitation (Alvarez et al., 2017).

Application of our results raises some caveats. First, the cropland map includes non-entomophilous plants. Therefore, spatially limited areas are larger than those shown in Figure S5. Second, we were unable to consider waterworks that provide water to populations of less than 5000 and which use groundwater as a water resource because of data limitations. Consequently, the actual limitation for water purification should be less than that shown in Figure S7. Third, we did not consider legal prohibitions against the actual uses. Ecosystem services that have either rival-ness or excludability, including source-productivity and information types, are subject to legal restrictions. As described above, quantifying or visualizing the actual flow or use requires social data that cannot be obtained by individual researchers or groups. For example, high-resolution and well-classified land-use maps are needed for source-suitability type services given the narrow foraging range of pollinators or predators, but currently available ones include cropland to produce one category (e.g., GLC30, http://www. globallandcover.com/GLC30Download/index.aspx; USGS, https://landcover. usgs.gov/global_climatology.php). To fill these data gaps, one must 1) assert the importance of such data to national and international organizations and 2) seek creative methods such as ecosystem service evaluations using Google Street View (Richards and Edwards, 2017), worldwide outdoor game data (Cord et al., 2015), and downscaling of statistical data (Verkerk et al., 2015).

Various constraints can affect biodiversity conservation in national or regional administrative governments, including limited budgets (Adams et al., 2012), inherent tradeoffs with other societal needs (e.g., expansion of urban and agricultural landscapes; Hurtt et al., 2011), and distributions of species beyond administrative boundaries (Kobayashi et al., 2019). In many ecosystem services (source-suitability, sink, buffer), potentially useful things leave the source ecosystem (Figure 4.2), but the benefits are then realized in other areas and

perhaps in other countries. Our results do not indicate that conservation of both biodiversity and ecosystem services is impossible. Instead, our results highlight the necessity of resource management across the national border with careful consideration of the spatial patterns of the ES potential, actual flow, and human demand, as well as biodiversity. Detection of the spatial limitations of the actual uses can clarify the connection of countries and regions which must cooperate. To date, several studies have been pursued as attempts to calculate actual flows (Verkerk et al., 2015; Watson et al., 2019), but the complex and nonlinear relations of coupled ecological and social systems remain unclear (Villa et al., 2014), leading to controversy over the definition of ecosystem services (the new concept of "nature's contributions to people" has been introduced; Díaz et al., 2018; Braat, 2018). Although we do not declare the definitions that will eventually be suitable, it is readily apparent that ecosystem services studies which include social perspectives are great challenges that must be assigned priority.

5

General Discussion

Many indicators support a view that human societies are progressing across the world. Examples of this progress include the increasing rates of literacy and of access to electricity and safe drinking water, and, conversely, decreasing rates of child labor, malnutrition, and deaths from disaster along with shrinking nuclear arsenals (Rosling et al., 2018). However, almost all biological studies show that biodiversity is deteriorating globally (Pimm et al., 2014; Newbold et al., 2015; Tollefson, 2019). Because floral and faunal species do not recognize political borders (IUCN, https://www.iucnredlist.org/), multilateral and regional cooperation, entailing careful consideration of economic and cultural relationships are required for the effective conservation of biodiversity (Wilson and Burnie, 2001; Dowie, 2009; Lehmann et al., 2018; Marques et al., 2019). By defining policy norms and shaping the behaviors of researchers, companies, and organizations, international biodiversity conservation goals play a key role in facilitating such cooperation (Tittensor et al., 2014; Visconti et al., 2019). In this concluding chapter, I trace the implications of my research and give some suggestions for future biological conservation studies and for the development of a post-2020 framework aimed at balancing the protection of ecosystem services and biodiversity, with reference to the Aichi Biodiversity Targets 7, 11, and 14.

Target 7: *By 2020 areas under agriculture, aquaculture and forestry are managed*

sustainably, ensuring conservation of biodiversity.

Target 11: *By 2020, at least 17 per cent of terrestrial and inland water areas and 10 per cent of coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem services, are conserved through effectively and equitably managed, ecologically representative and well-connected systems of protected areas and other effective area-based conservation measures, and integrated into the wider landscape and seascape.*

Target 14: *By 2020, ecosystems that provide essential services, including services related to water, and contribute to health, livelihoods and well-being, are restored and safeguarded, taking into account the needs of women, indigenous and local communities, and the poor and vulnerable.*

A Numerical Goal for Expansion of Protected Areas

Scholars have argued that the wording of global goals must be clear and measurable (e.g., Butchart et al., 2016; Ohsawa et al., 2019). Accordingly, Aichi Biodiversity Target 11 appears to meet both of these requirements. Although there are some concerns relating to quantity-based approaches (Di Minin and Toivonen, 2015; Barnes et al., 2018), insightful and constructive analyses of Target 11 have been conducted from various perspectives (e.g., Kadoya et al., 2014; Pouzols et al., 2014; Larsen et al., 2015; O'Leary, 2016) rather than other vague targets (Amako et al., 2019). Indeed, a zero draft of the post-2020 targets is aimed at protecting at least 30 percent of land and marine surfaces (SCBD, 2020).

As my first suggestion, efforts should be made to improve conservation planning and design within existing protected areas. While adaptive management should be encouraged, other approaches can also be attempted. Applying the new land-use data generated in 2011 (Hurtt et al., 2011), I conducted a case study that entailed a reconsideration of biodiversity hotspots that were proposed over three decades ago (Myers, 1988). The findings of the case study have critical implications for achieving effective biodiversity conservation (i.e., protecting species with low dispersal ability and controlling invasive alien species). This reconsideration of biodiversity hotspots was accomplished in the absence of *in-situ* monitoring data and expert interventions. This approach is therefore appropriate in the context of initiatives to develop and expand new protected

areas that are constrained by shortfalls of staff and money attributed to resource dilution (Barnes et al., 2018).

Second, a transparent conceptual framework should be created for ecosystem services. The assumption underlying Aichi Biodiversity Target 11 is that the simultaneous protection of ecosystem services and biodiversity to equal degrees at the same location and measure leads to ethical and practical conflicts (Doak et al., 2014). As I showed in Chapter 3, such conflicts could be alleviated by subdividing ecosystem services into global-public and local-public services. In the absence of a consensus on the definition and classification of ecosystem services, and of associated indicators (La Notte et al., 2017), a new and integrative conceptual model is required in which articulate notable characteristics of ecosystem services (e.g., rivalry, excludability, and the scale of beneficiaries) and include a summary of previous models and terminologies (see Box 1 in Chapter 3). Moreover, as discussed in Chapter 4, efforts to advance social-ecological research can support and strengthen bottom-up biodiversity conservation at the source areas of local-public ecosystem services.

Global-Private Ecosystem Services

In Chapter 3, I did not discuss global-private ecosystem services that are already traded in markets. Efforts to balance the protection of biodiversity and global-private ecosystem services are not easily accomplished because these benefits are not maximized unless habitat modification occurs (Newbold et al., 2015; Usubiaga-Liaño et al., 2019). Payment for ecosystem services (PES) has widely been advocated as a solution to this trade-off (Engel et al., 2008). Because monetary value is the most well understood unit among the general public, the promotion of biodiversity conservation through monetary compensation relating to the expansion of agricultural land would, at first glance, appear to be a reasonable approach (Salzman et al., 2018). However, because PES does not lead to any changes in human demand, halting the expansion of agricultural land is likely to encourage the expansion of agriculture into other areas, especially in economically disadvantaged countries (Marques et al., 2019). In light of the goal of achieving equitable global biodiversity conservation prescribed in Aichi Biodiversity Target 14, careful consideration should be given to the PES and relevant compensation schemes, such as biodiversity offsetting (zu Ermgassen et al., 2019).

The post-2020 targets should be directed toward the adoption of biodiversity-friendly approaches to agriculture that ensure the protection of biodiversity as well as global-private ecosystem services (i.e., it should keep Aichi Biodiversity Target 7), including retention forestry (Lindenmayer et al., 2012), shade-grown coffee cultivation (Perfecto et al., 2005; Jezeer et al., 2017), and organic farming (Feber et al., 2015; Garibaldi et al, 2017). Further, the new target should be aimed at encouraging aftercare of unused or unmanaged agricultural lands. According to a projection made by United Nations, Department of Economic and Social Affairs, Population Division (2019), the proportion of the global population living in urban areas will increase from 55% to 68% by 2050. If this trend continues, many agricultural plots will be abandoned, and opportunities for restoration, reintroduction, and rewilding will consequently arise (Corlett, 2016). However, currently no specific methods exist with ecological evidence and economic incentives for farmers or foresters; rather it may lead to unwanted outcomes. For instance, my own family, like many others, owns abandoned cultivated lands in Yamanashi, Japan. Although such land should be returned to forests in the context of biodiversity and ecosystem services conservations, reluctance to do so persists. One of the reasons for this reluctance is that the nesting/breeding of wild animals may cause damage to other areas of farmland (i.e., ecosystem disservices). The practical implications of these concerns could not, however be explored in this thesis. Therefore, as a follow-up phase to this study, I am working on establishing a practical method of forest restoration using a forest landscape model (iLand; http://iland.boku.ac.at/startpage).

Outro

Biodiversity is a yardstick that is indicative of variations of genes, species, and ecosystems (Primack, 2014). In the context of species diversity, even if all of the indexes reported so far were to applied (e.g., α, β, γ, Shannon and functional and phylogenetic diversity; Faith, 1992; Petchey and Gaston, 2006), it would not be possible to evaluate all aspects of an ecosystem (e.g., biomass, coverage, and density). Moreover, unqualified praise or trust of biodiversity should be avoided. For example, my previous study showed that the model's ability to predict the severity of shallow landslides (i.e., landslide volume) increased with richness of

tree species. However, I did not find any indications of a correspondence between the richness and a reduction in the severity (Kobayashi and Mori, 2017).

Nevertheless, biodiversity does enable an ideal state of an ecosystem to be visualized and conveyed on the same axis. As discussed in Chapter 3, this positively affects consensus building through the resolution of ethical/practical conflicts such as that between anthropocentrism and non-anthropocentrism. It also leads to biodiversity-friendly measures, considered as optimal solutions for achieving sustainable development in addition to economic incentives. For example, if dam construction to prevent droughts or floods is the desired goal, then the discussion should begin with consideration given to the restoration of degraded forests or the development of a green dam rather than to the pros and cons of concrete dam construction.

I would ask my readers to imagine a world in the distant future in which technology has advanced dramatically, all of the principles of natural science are thoroughly understood, and ecosystems are entirely controlled. Information on the genes and traits of all individuals would be recorded, and all seeds would be available anytime and anywhere. In such a world, would human beings still envision the significance of protecting biodiversity? Fortunately, that is not going to happen because organisms evolve. The emergence of new species has unlimited possibilities for humanity in addition their intrinsic values. Therefore, countless living organisms must live and propagate with adequate time with humanity. Protecting biodiversity is one of the simplest, most effective, and rational approaches for safeguarding the rights of both nature and humans, and ensuring the preservation of biodiversity is the task and the duty of the present generation.

6

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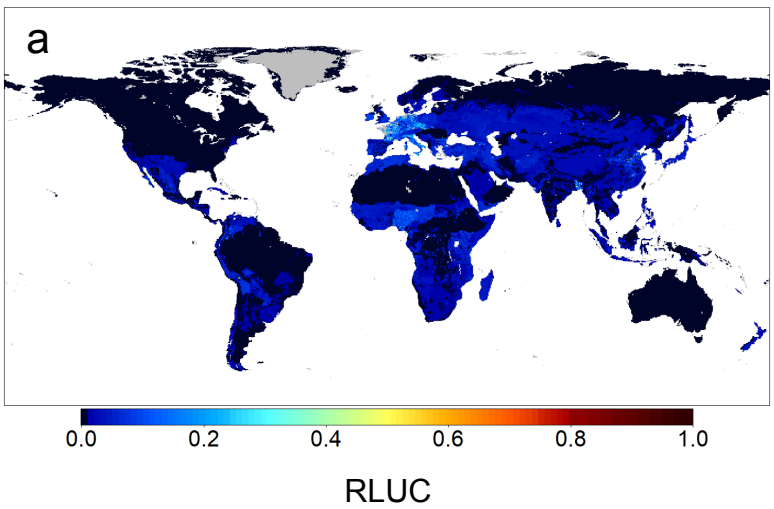
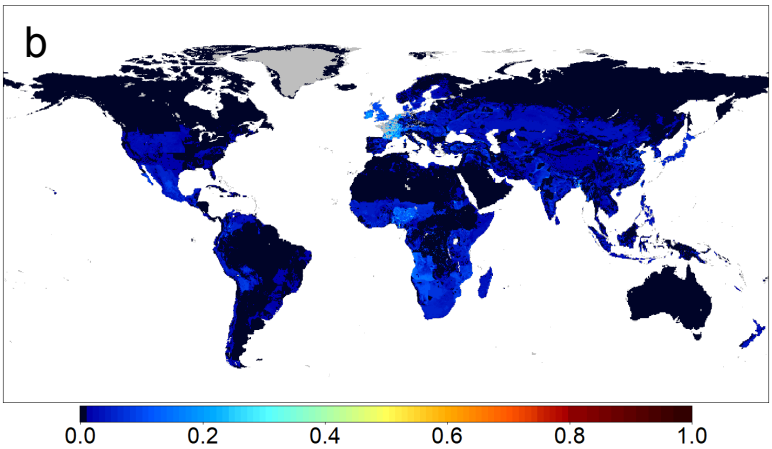
7

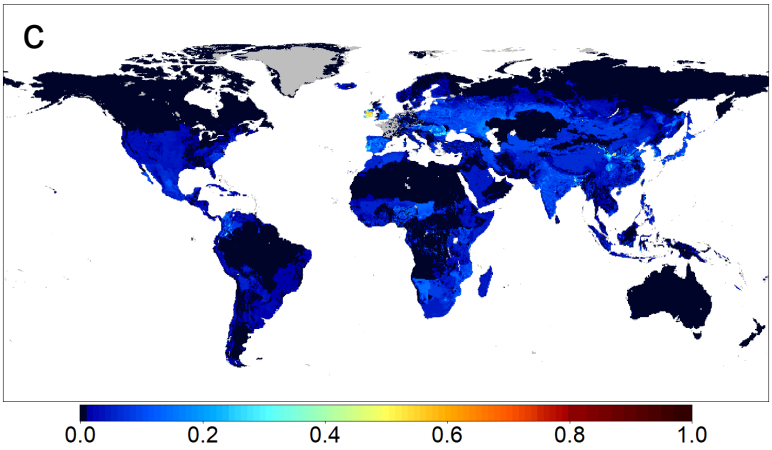
Appendix

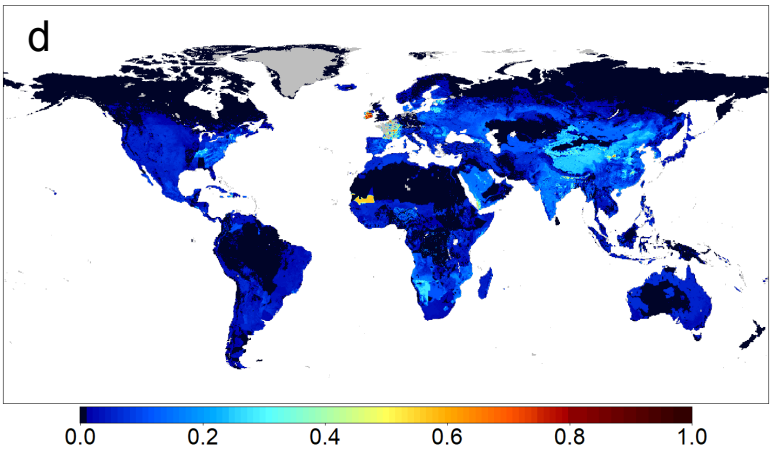
Appendix 1

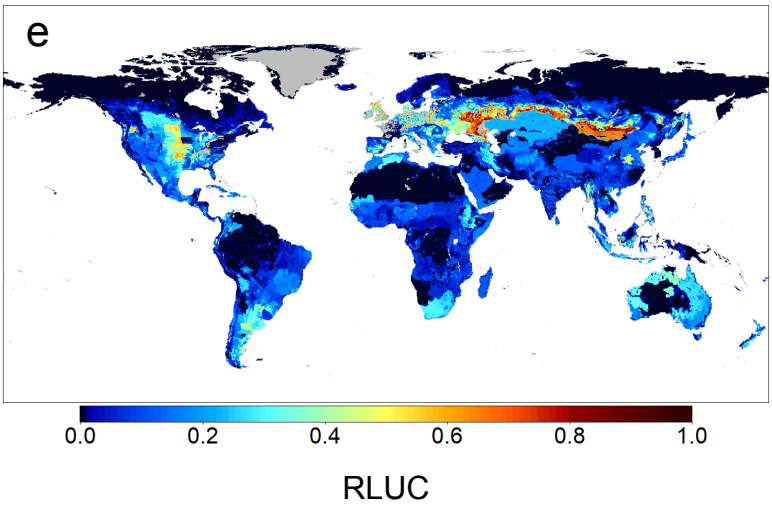
Figure: RLUC maps at a grid scale of 0.25° × 0.25° for the (a) 1500s, (b) 1600s, (c) 1700s, (d) 1800s, (e) 1900s, and (f) 2000s. The color gradient and gray coloration denote the RLUC and the cells in which the fraction of primary and secondary vegetation is less than 5%, respectively. Source: Kobayashi et al. (2019).

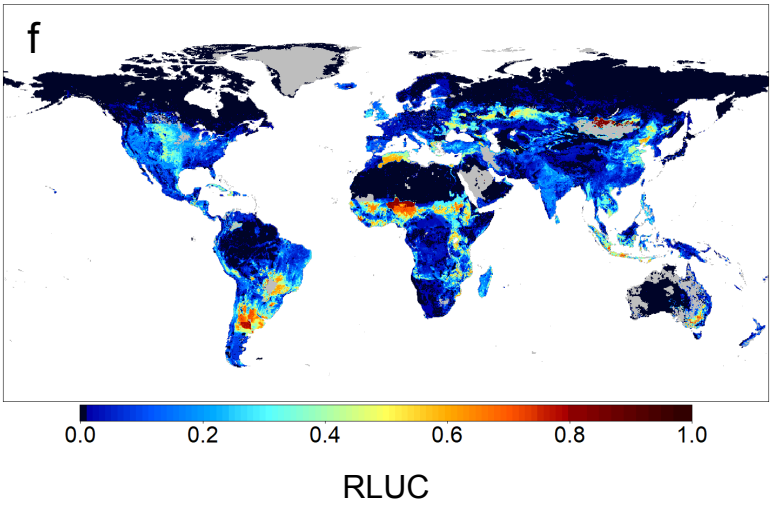



b
0.0
0.2
0.4
0.6
0.8
1.0
RLUC


c
0.0
0.2
0.4
0.6
0.8
1.0
RLUC

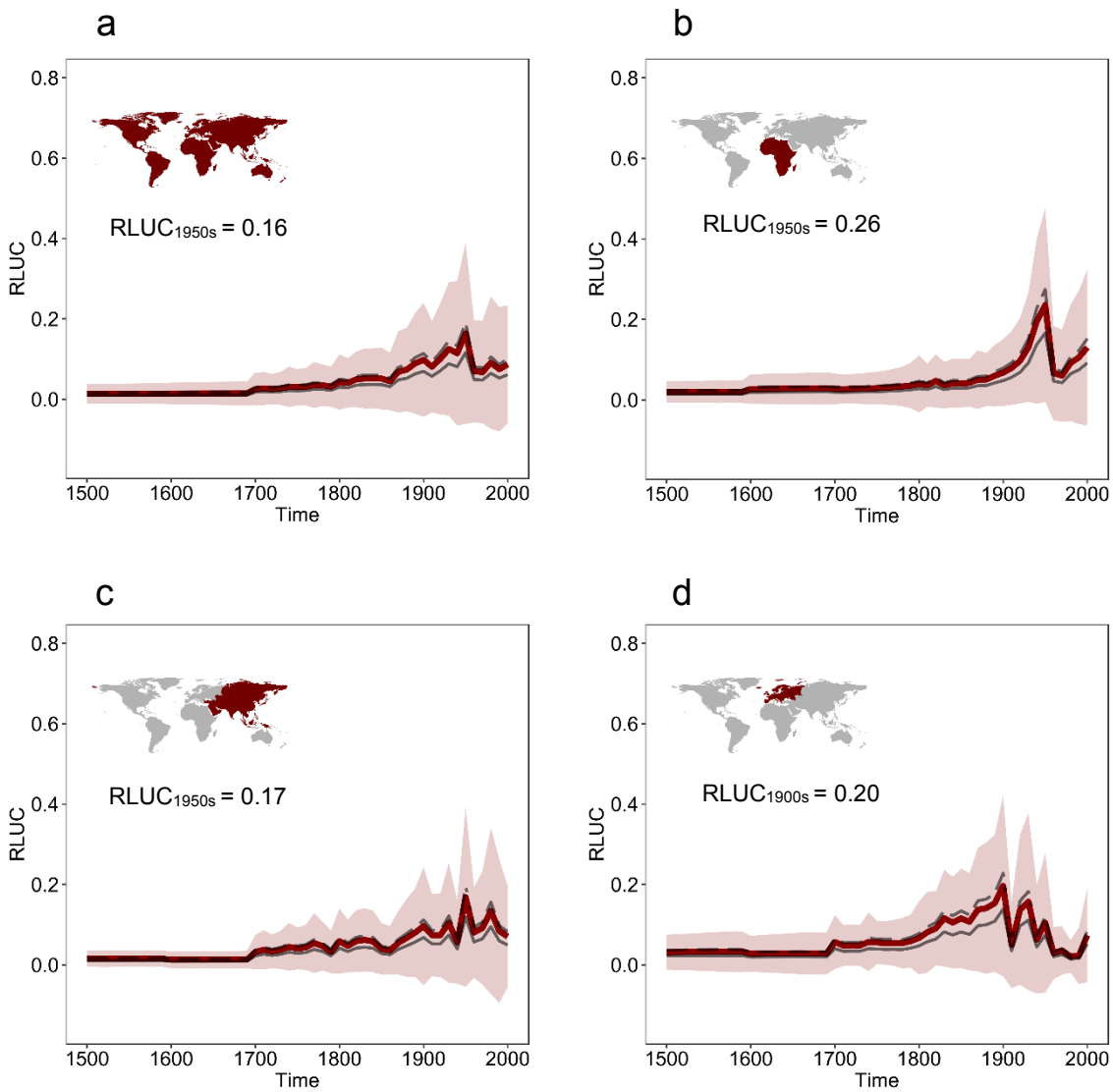

d
0.0
0.2
0.4
0.6
0.8
1.0
RLUC

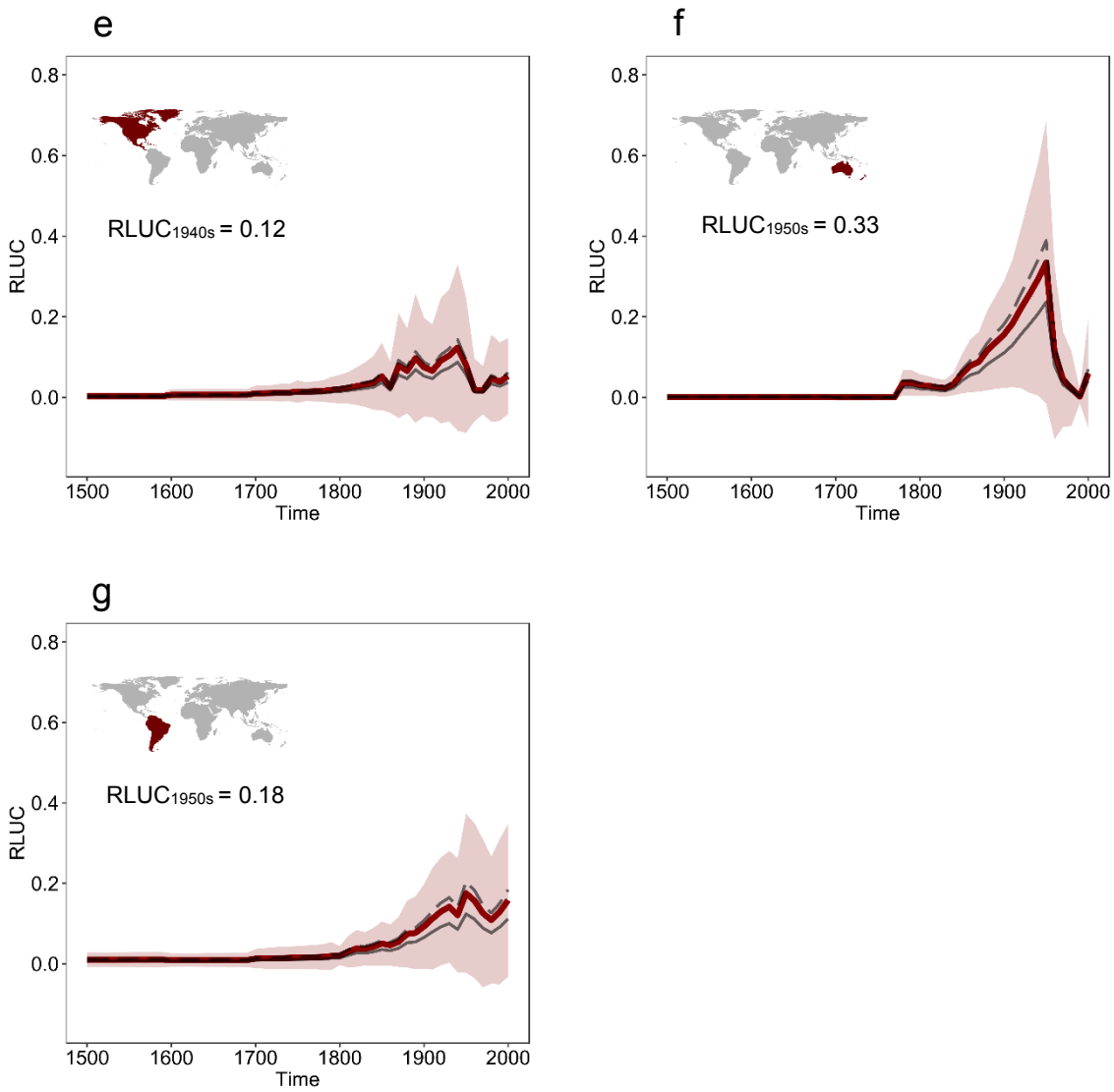

e
0.0
0.2
0.4
0.6
0.8
1.0
RLUC


f
0.0
0.2
0.4
0.6
0.8
1.0
RLUC

Appendix 2

Figure: Time series of the RLUC from 1500 to 2010. a, Global average, b-g, continental average for Africa (b), Asia (c), Europe (d), North America (e), Oceania (f), and South America (g). Red lines and shaded polygons denote changes in the average and standard deviation of the RLUC, respectively. The maximum RLUC is shown in each panel. Gray lines denote the changes in the average of the additional RLUCs when the σ values were changed to lower (solid; σ_s=0.13, σ_u=0.5, σ_c=0.34, σ_p=0.34) and higher values (dashed; σ_s=0.38, σ_u=1, σ_c=0.92, σ_p=0.92). Source: Kobayashi et al. (2019).

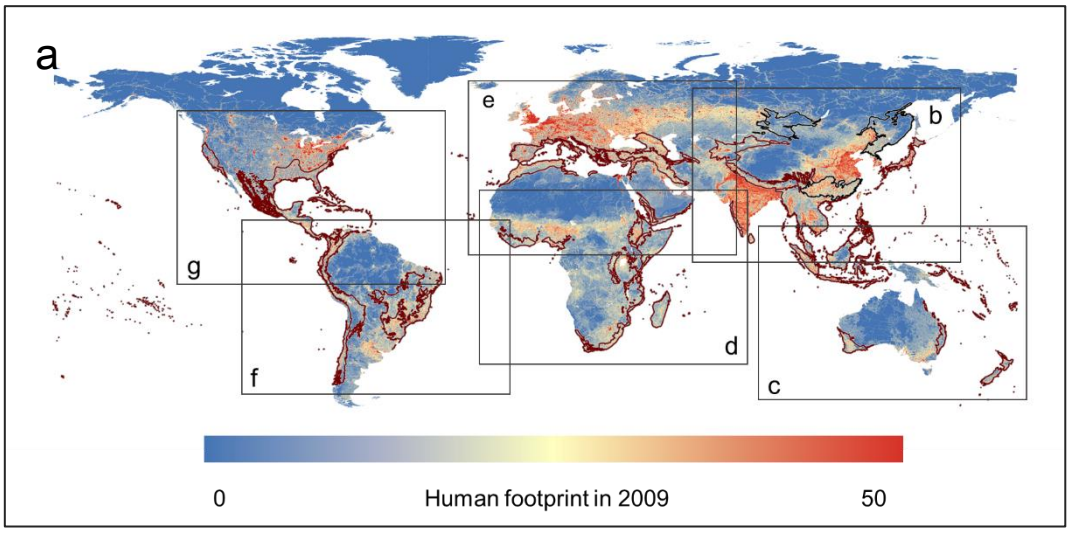


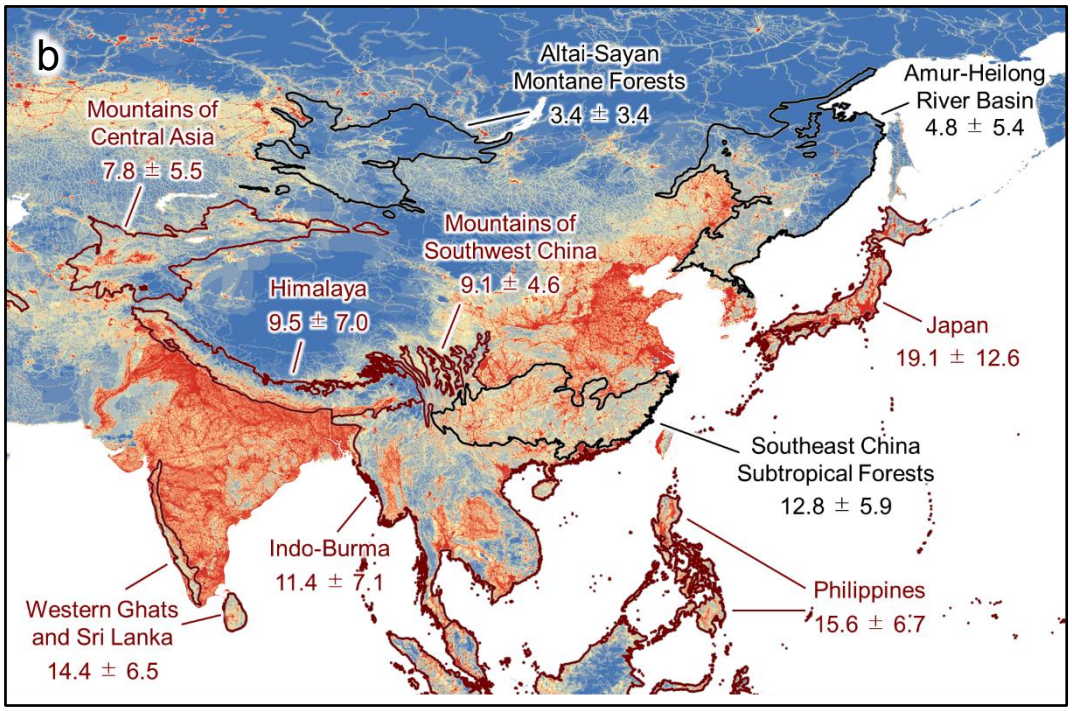

e
RLUC1940s = 0.12
RLUC
Time
f
RLUC1950s = 0.33
RLUC
Time
g
RLUC1950s = 0.18
RLUC
Time

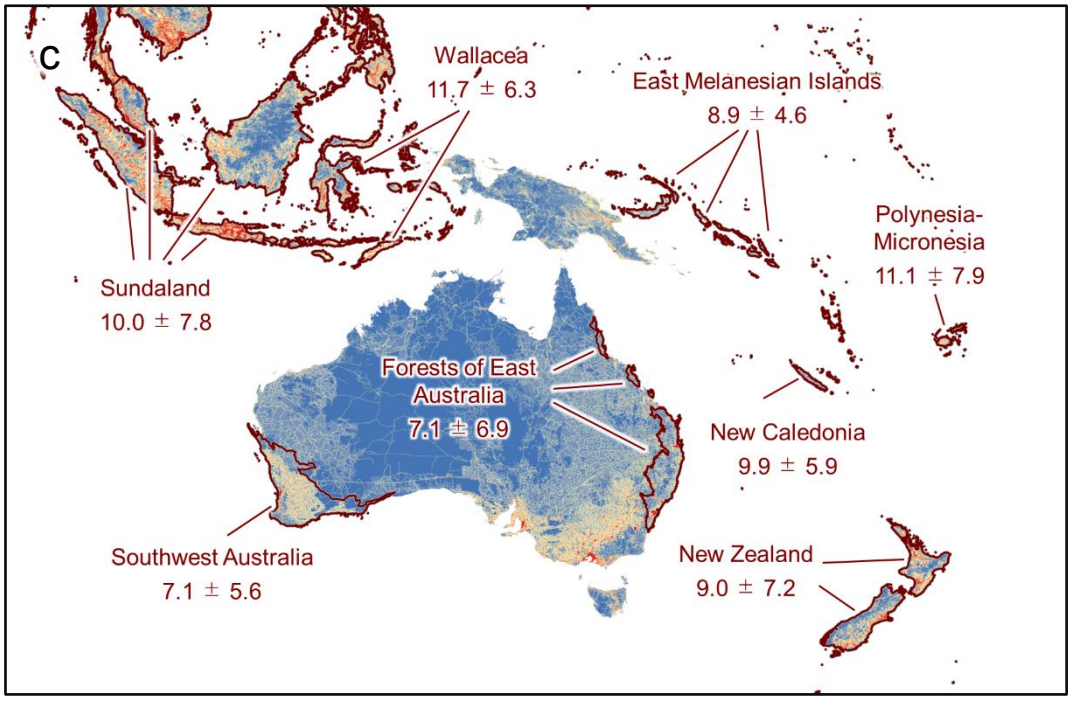
Appendix 3

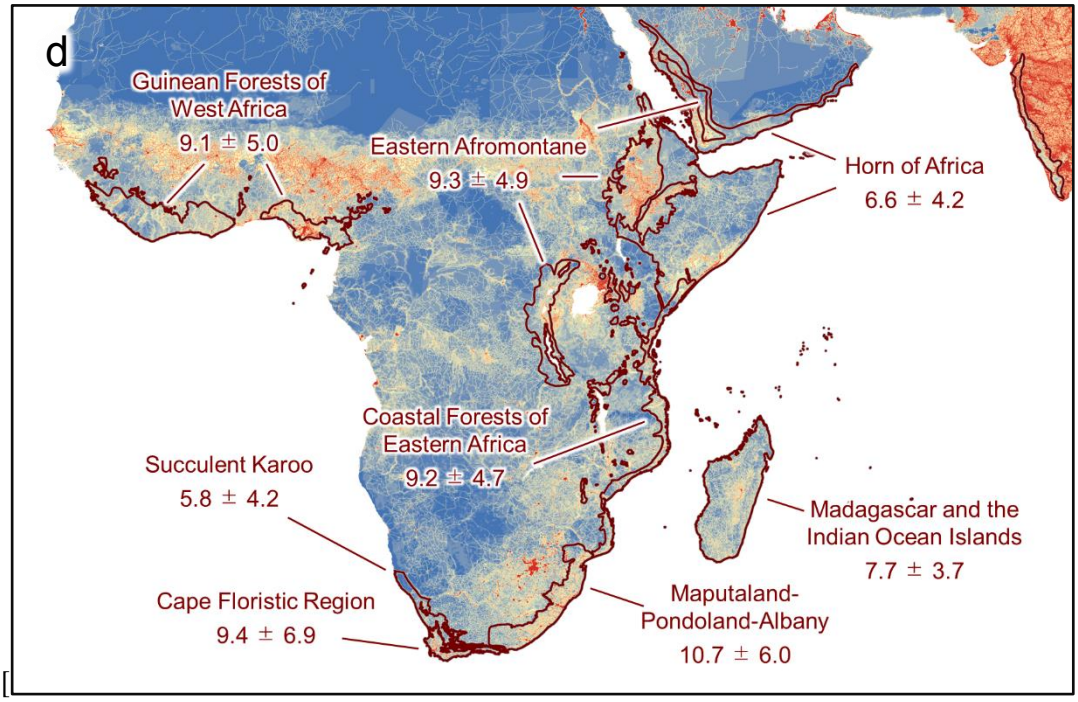
Supplementary methods: We assessed the level of land degradation in the three candidate regions (the Altai-Sayan Montane Forests, Amur-Heilong River Basin, and Southeast China Subtropical Forests) and existing biodiversity hotspots using the human footprint map for 2009 at a grid scale of 1 × 1 km^2 (Venter et al., 2016). The human footprint is the index of eight cumulative human pressures on the environment (0-50). Each human pressure was placed on a 0-10 scale according to the relative levels of pressure on the environment: built environments (10), cropland (0-7), pasture (0-4), population density (3.3-10), night lights (0-10), railways (0-8), major roadways (0-8), and navigable waterways (0-4). The map of the human footprint was downloaded from the Dryad Digital Repository (http://dx.doi.org/10.5061/dryad.052q5).

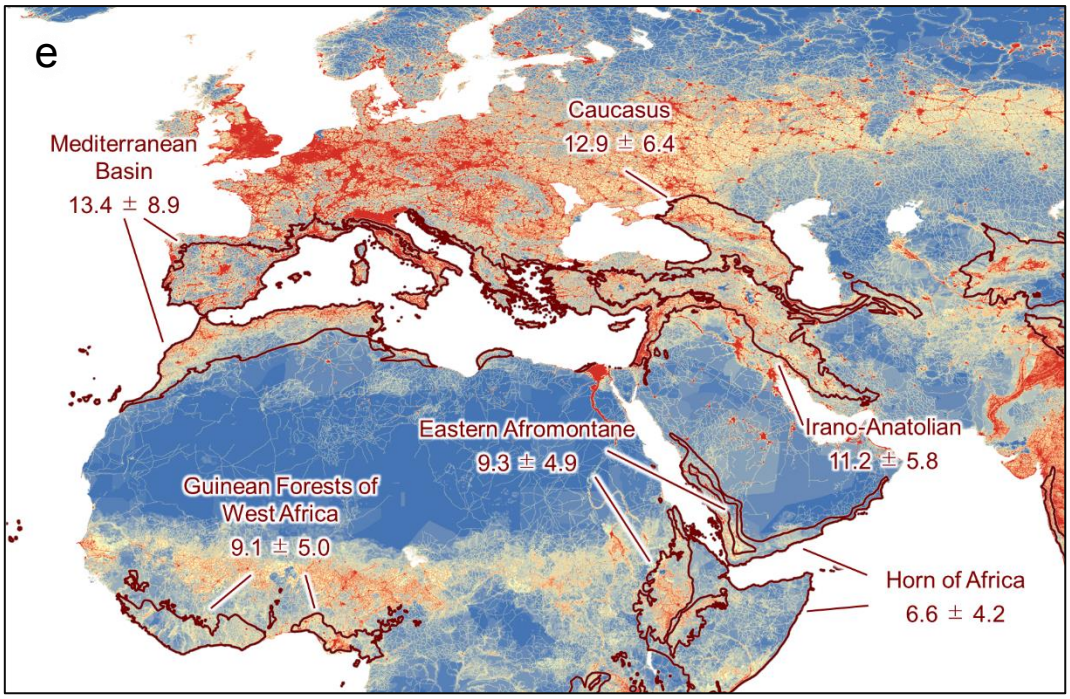
Figure: The global map of the human footprint in 2009. Color gradient, red line, and black line denote the human footprint (0-50), boundaries of biodiversity hotspots, and boundaries of the candidate regions, respectively. The mean and standard deviation of the human footprint are shown in each panel. Source: Kobayashi et al. (2019).

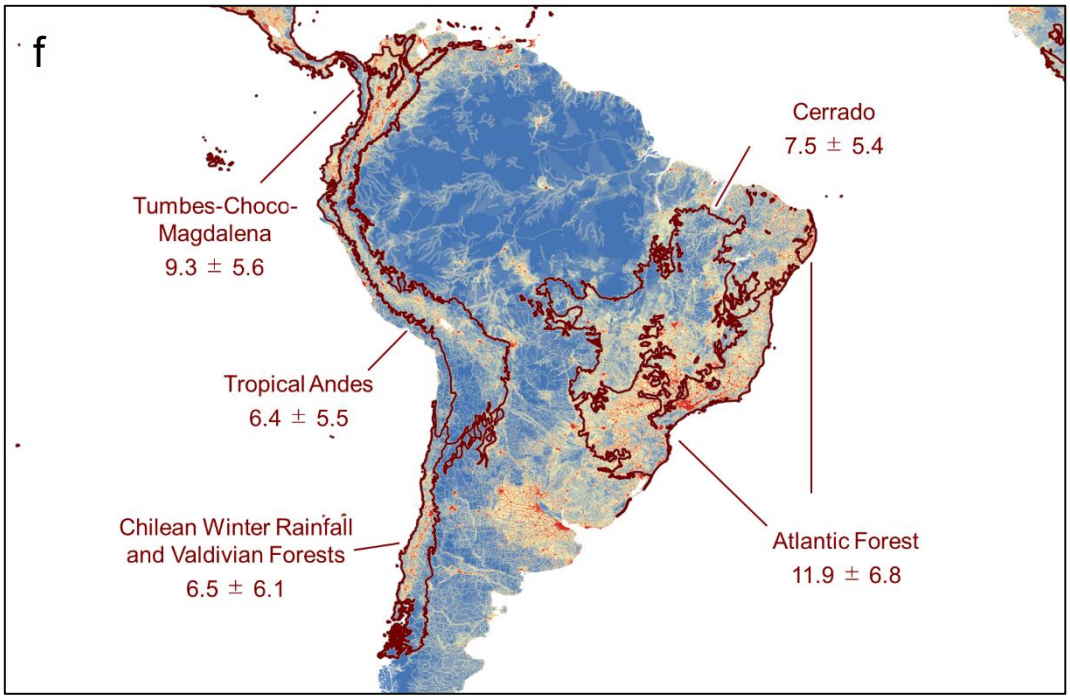


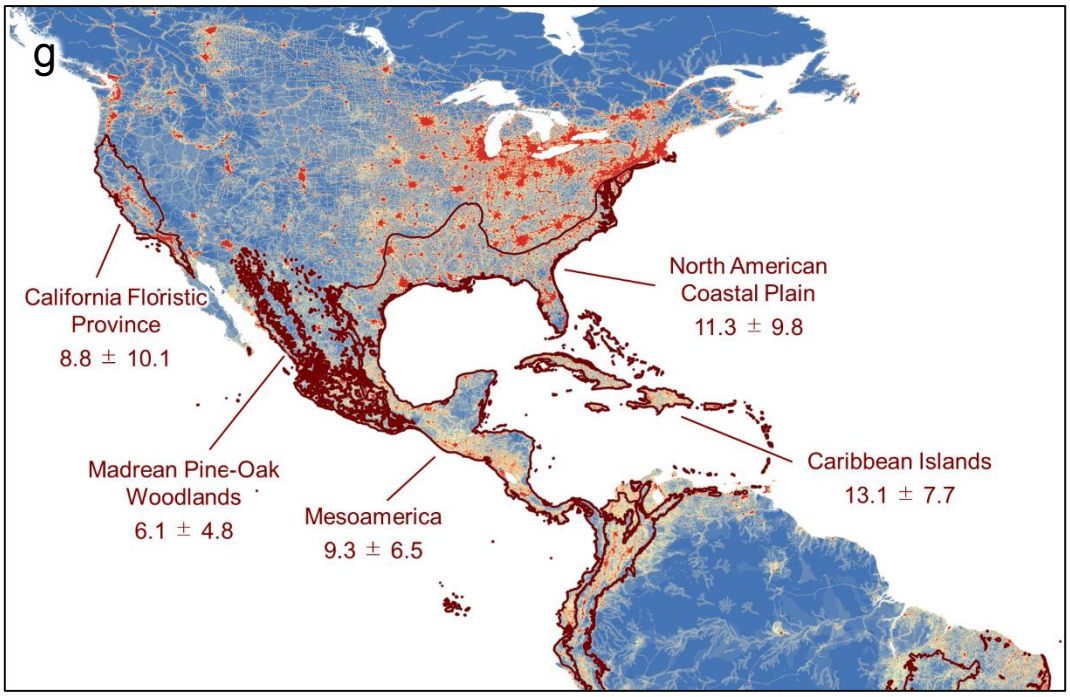

b
Altai-Sayan
Montane Forests
3.4 ± 3.4
Amur-Heilong
River Basin
4.8 ± 5.4
Mountains of
Central Asia
7.8 ± 5.5
Mountains of
Southwest China
9.1 ± 4.6
Himalaya
9.5 ± 7.0
Japan
19.1 ± 12.6
Southeast China
Subtropical Forests
12.8 ± 5.9
Indo-Burma
11.4 ± 7.1
Philippines
15.6 ± 6.7
Western Ghats
and Sri Lanka
14.4 ± 6.5


c
Wallacea
11.7 ± 6.3
East Melanesian Islands
8.9 ± 4.6
Polynesia-
Micronesia
11.1 ± 7.9
Sundaland
10.0 ± 7.8
Forests of East
Australia
7.1 ± 6.9
New Caledonia
9.9 ± 5.9
Southwest Australia
7.1 ± 5.6
New Zealand
9.0 ± 7.2


d
Guinean Forests of
West Africa
9.1 ± 5.0
Eastern Afromontane
9.3 ± 4.9
Horn of Africa
6.6 ± 4.2
Coastal Forests of
Eastern Africa
9.2 ± 4.7
Succulent Karoo
5.8 ± 4.2
Madagascar and the
Indian Ocean Islands
7.7 ± 3.7
Cape Floristic Region
9.4 ± 6.9
Maputaland-
Pondoland-Albany
10.7 ± 6.0


e
Caucasus
12.9 ± 6.4
Mediterranean
Basin
13.4 ± 8.9
Eastern Afromontane
9.3 ± 4.9
Irano-Anatolian
11.2 ± 5.8
Guinean Forests of
West Africa
9.1 ± 5.0
Horn of Africa
6.6 ± 4.2

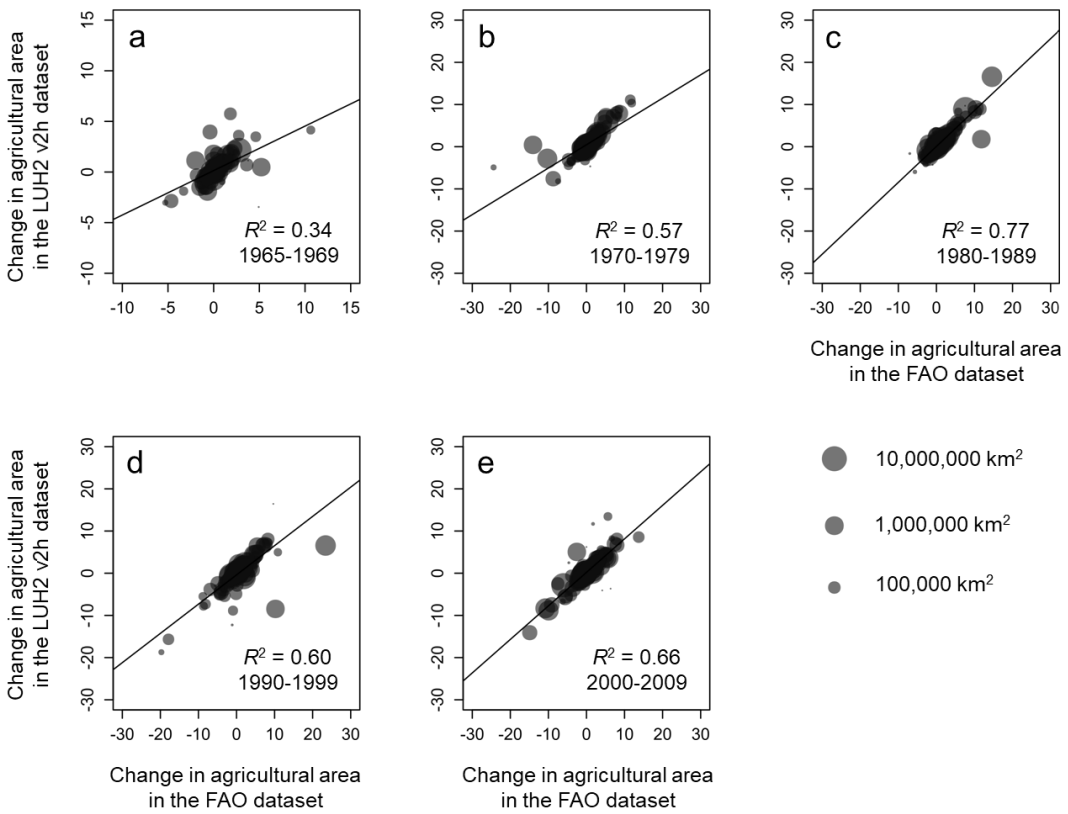

f
Cerrado
7.5 ± 5.4
Tumbes-Choco-
Magdalena
9.3 ± 5.6
Tropical Andes
6.4 ± 5.5
Chilean Winter Rainfall
and Valdivian Forests
6.5 ± 6.1
Atlantic Forest
11.9 ± 6.8


g
California Floristic
Province
8.8 ± 10.1
North American
Coastal Plain
11.3 ± 9.8
Madrean Pine-Oak
Woodlands
6.1 ± 4.8
Mesoamerica
9.3 ± 6.5
Caribbean Islands
13.1 ± 7.7

Appendix 4

Supplementary methods: Most global land-use change has been caused by the expansion of agricultural land (i.e., cropland and pasture; Hurtt et al., 2011). To assess the predictability of the LUH2 v2h dataset, we compared the timing and the magnitude of the change in agricultural land with national statistical data for 1965-2010. The statistical data were downloaded from the website of the Food and Agriculture Organization of the United Nations (FAO; http://www.fao.org/faostat/en/#home, accessed 18 January 2019). We calculated the percentage change in agricultural area in 154 countries for 1965-1970, 1970-1980, 1980-1990, 1990-2000, and 2000-2010 from the FAO statistical data and the LUH2 v2h dataset.

Figure: Comparison of the change in agricultural area between the FAO statistical data and the LUH2 v2h dataset for (a) 1965-1970, (b) 1970-1980, (c) 1980-1990, (d) 1990-2000, and (e) 2000-2010. The solid line and the size of the circle show the fit of the ordinary least-squares regression and the area of the country, respectively. The R^2 values were not high in any of the time windows. Source: Kobayashi et al. (2019).



Appendix 5

Table: Summary of the predicted vascular plant species richness (mean and standard deviation), the percentage of endemics or endemic level, and the percentages of forested and nonforested primary land in 850 in biodiversity hotspots and identified ecoregions. The number of biodiversity hotspots follows Mittermeier et al. (2011), but the North American Coastal Plain was identified as the 36th biodiversity hotspot in 2016 (see Fig. 4a). Source: Kobayashi et al. (2019).

Name	Predicted vascular plant species richness, mean ± s.d.	Forested primary land in 850 (%)	Nonforested primary land in 850 (%)	Percentage of endemics (%)	Endemic level*	Reference ID	Note
Biodiversity hotspots							
Atlantic Forest	2281 ± 576	70.1	29.9	40.0	-	23	
California Floristic Province	1069 ± 194	37.9	61.7	60.9	-	23	
Cape Floristic Region	2617 ± 742	0.0	100.0	69.0	-	23	
Caribbean Islands	2013 ± 345	37.1	62.8	50.4	-	23	
Caucasus	1603 ± 576	20.5	71.2	25.0	-	23	
Cerrado	1671 ± 258	65.6	34.3	44.0	-	23	
Chilean Winter Rainfall and Valdivian Forests	955 ± 309	53.6	45.5	50.3	-	23	
Coastal Forests of Eastern Africa	1740 ± 385	2.5	92.9	43.8	-	23	
East Melanesian Islands	-	73.8	25.7	37.5	-	23	
Eastern Afromontane	1546 ± 657	31.4	58.1	31.0	-	23	

Forests of East Australia	1142 ± 106	22.6	77.4	26.0	-	23
Guinean Forests of West Africa	2042 ± 405	57.9	34.2	20.0	-	23
Himalaya	1921 ± 695	78.6	17.2	31.6	-	23
Horn of Africa	733 ± 231	0.8	88.5	55.0	-	23
Indo-Burma	2133 ± 407	77.5	20.7	51.9	-	23
Irano-Anatolian region	1430 ± 380	3.7	80.2	41.7	-	23
Japan	2218 ± 347	88.9	5.8	34.8	-	23
Madagascar and the Indian Ocean Islands	1857 ± 589	49.6	47.8	89.2	-	23
Madrean Pine-Oak Woodlands	1581 ± 518	6.0	92.5	75.0	-	23
Maputaland-Pondoland-Albany	1264 ± 342	1.5	98.4	23.5	-	23
Mediterranean Basin	1436 ± 424	9.0	74.9	52.0	-	23
Mesoamerica	2561 ± 788	55.5	41.0	17.3	-	23
Mountains of Central Asia	1132 ± 282	14.0	75.9	27.3	-	23
Mountains of Southwest China	2522 ± 677	88.8	10.0	29.2	-	23
New Caledonia	-	78.8	19.4	74.4	-	23
New Zealand	973 ± 221	92.5	7.5	81.1	-	23
Philippines	2404 ± 244	89.2	10.6	65.8	-	23
Polynesia-Micronesia	-	71.2	28.4	57.7	-	23
Southwest Australia	965 ± 129	0.0	100.0	52.9	-	23

Succulent Karoo	1238 ± 693	0.0	100.0	38.4	-	23	
Sundaland	2518 ± 429	95.1	4.0	60.0	-	23	
Tropical Andes	2431 ± 1252	40.4	58.6	50.0	-	23	
Tumbes-Choco-Magdalena	3013 ± 1200	54.1	40.2	25.0	-	23	
Wallacea	2736 ± 490	80.6	18.5	15.0	-	23	
Western Ghats and Sri Lanka	1733 ± 343	51.1	42.1	51.5	-	23	
Identified ecoregions							
Afghan Mountains semidesert	771 ± 276	0.0	85.6	20.0	-	1	The percentage of endemics in Afghanistan was adopted.
Altai alpine meadow and tundra	935 ± 165	76.5	16.3	16.2	-	3	The percentage of endemics in the Altai-Sayan Montane Forests was adopted.
Altai montane forest and forest steppe	877 ± 255	57.2	28.7	16.2	-	3	The percentage of endemics in the Altai-Sayan Montane Forests was adopted.
Altai steppe and semidesert	897 ± 116	14.2	81.0	14.0	-	7	The percentage of endemics in Kazakhstan was adopted.
Amur meadow steppe	736 ± 118	96.6	0.0	15.9	-	18	The percentage of the endemic seed plant species richness in the humid and semihumid regions and temperate zone in Northeast China was adopted.
Angolan scarp savanna and woodlands	926 ± 106	0.0	98.0	-	H	9	
Appenine deciduous montane forests	1938 ± 275	34.8	57.0	10-20	-	4	
Atlantic coastal pine barrens	1184 ± 67	98.2	1.8	29.3	-	26	The percentage of endemics on the Geological Coastal Plain was adopted.

Bohai Sea saline meadow	1065 ± 186	0.0	94.5	10.1	-	18	The percentage of the endemic seed plant species richness in the humid and semihumid regions and warm temperate zone in Northern China was adopted.
Brigalow tropical savanna	815 ± 121	2.5	97.5	>33.33	-	25	The percentage of endemics in Queensland was adopted.
Cantabrian mixed forests	1597 ± 221	70.4	24.0	20.0	-	10	
Cape York Peninsula tropical savanna	904 ± 168	49.0	51.0	>33.33	-	25	The percentage of endemics in Queensland was adopted.
Central China loess plateau mixed forests	1193 ± 205	0.0	93.7	10.1	-	18	The percentage of the endemic seed plant species richness in the humid and semihumid regions and warm temperate zone in Northern China was adopted.
Central Mexican matorral	1102 ± 368	1.1	93.7	35.2	-	39	The percentage of endemics in Aguascalientes (Mexican political state) was adopted.
Changjiang Plain evergreen forests	1674 ± 184	54.5	34.7	38.8	-	18	The percentage of the endemic seed plant species richness in the humid and subtropical zones in Central and Southern China was adopted.
Dinaric Mountains mixed forests	1785 ± 332	80.3	10.8	>10	-	13	
Drakensberg alti-montane grasslands and woodlands	1157 ± 168	29.4	70.5	-	VH	9	
East Afghan montane conifer forests	954 ± 259	3.0	84.7	20.0	-	1	The percentage of endemics in Afghanistan was adopted.
East Central Texas forests	1200 ± 137	1.3	98.7	29.3	-	26	The percentage of endemics on the Geological Coastal Plain was adopted.

Einasleigh upland savanna	866 ± 113	15.9	84.1	>33.33	-	25	The percentage of endemics in Queensland was adopted.
Emin Valley steppe	796 ± 133	0.0	94.8	13.4	-	18	The percentage of the endemic seed plant species richness in the temperate and warm temperate desert in Northwest China was adopted.
Espinal	866 ± 167	3.9	96.0	11.7	-	5	The percentage of endemics in Argentina was adopted.
Florida sand pine scrub	1469 ± 80	61.2	38.5	29.3	-	26	The percentage of endemics on the Geological Coastal Plain was adopted.
Guajira-Barranquilla xeric scrub	1797 ± 576	13.4	82.8	30.0	-	17	
Guinean forest-savanna mosaic	1272 ± 281	24.2	65.0	-	H	9	
Guizhou Plateau broadleaf and mixed forests	2018 ± 223	89.1	9.3	38.8	-	18	The percentage of the endemic seed plant species richness in the humid and subtropical zone in Central and Southern China was adopted.
Helanshan montane conifer forests	782 ± 161	0.0	96.0	13.4	-	18	The percentage of the endemic seed plant species richness in the temperate and warm temperate desert in Northwest China was adopted.
Hindu Kush alpine meadow	1273 ± 226	42.4	41.5	20.0	-	1	The percentage of endemics in Afghanistan was adopted.
Huang He Plain mixed forests	1192 ± 230	0.0	86.1	10.1	-	18	The percentage of the endemic seed plant species richness in the humid and semihumid regions and warm temperate zone in Northern China was adopted.

Humid Pampas	1002 ± 114	0.2	99.8	11.7	-	5	The percentage of endemics in Argentina was adopted.
Jian Nan subtropical evergreen forests	2051 ± 215	96.5	1.0	38.8	-	18	The percentage of the endemic seed plant species richness in the humid and subtropical zone in Central and Southern China was adopted.
Kazakh steppe	746 ± 80	0.0	95.3	14.0	-	7	The percentage of endemics in Kazakhstan was adopted.
Kimberly tropical savanna	755 ± 89	0.2	99.8	14.3	-	6	The percentage of endemics in the Northern Province was adopted.
Manchurian mixed forests	1002 ± 241	91.2	7.8	15.9	-	18	The percentage of the endemic seed plant species richness in the humid and semihumid regions and temperate zone in Northeast China was adopted.
Meseta Central matorral	795 ± 372	1.1	96.8	43.2	-	39	The percentage of endemics in Zacatecas (Mexican political state) was adopted.
Middle Atlantic coastal forests	1238 ± 136	96.3	3.5	29.3	-	26	The percentage of endemics on the Geological Coastal Plain was adopted.
Mississippi lowland forests	1572 ± 132	99.7	0.0	29.3	-	26	The percentage of endemics on the Geological Coastal Plain was adopted.
Nama Karoo	892 ± 326	0.0	99.9	-	H	9	
Northeast China Plain deciduous forests	947 ± 165	20.8	77.0	15.9	-	18	The percentage of the endemic seed plant species richness in the humid and semihumid regions and temperate zone in Northeast China was adopted.
Okhotsk-Manchurian taiga	824 ± 158	92.9	6.3	10.8	-	40	The percentage of endemics in the Russian Far East was adopted.

Piney woods forests	1256 ± 110	87.8	11.9	29.3	-	26	The percentage of endemics on the Geological Coastal Plain was adopted.
Po Basin mixed forests	1687 ± 359	58.9	10.0	12.7	-	21	The percentage of endemics in Italy was adopted.
Qilian Mountains conifer forests	1276 ± 387	0.0	96.7	32.4	-	18	The percentage of the endemic seed plant species richness in the Qinghai-Tibet alpine and cold region was adopted.
Qilian Mountains subalpine meadows	750 ± 172	5.4	90.8	32.4	-	18	The percentage of the endemic seed plant species richness in the Qinghai-Tibet alpine and cold region was adopted.
Sayan alpine meadows and tundra	871 ± 181	97.0	0.0	16.2	-	3	The percentage of endemics in the Altai-Sayan Montane Forests was adopted.
Sayan intermontane steppe	793 ± 88	98.4	0.0	16.2	-	3	The percentage of endemics in the Altai-Sayan Montane Forests was adopted.
Sayan montane conifer forests	879 ± 124	97.2	1.5	16.2	-	3	The percentage of endemics in the Altai-Sayan Montane Forests was adopted.
Sichuan Basin evergreen broadleaf forests	1815 ± 366	9.1	87.2	38.8	-	18	The percentage of the endemic seed plant species richness in the humid and subtropical zone in Central and Southern China was adopted.
Sinú Valley dry forests	2070 ± 768	37.5	53.0	29.3	-	11	The percentage of endemics in Colombia was adopted.
Sonoran-Sinaloan transition subtropical dry forest	1048 ± 235	0.0	97.2	26.3	-	39	The percentage of endemics in Sonora (Mexican political state) was adopted.

Southeast Tibet shrublands and meadows	1452 ± 585	67.9	28.7	32.4	-	18	The percentage of the endemic seed plant species richness in the Qinghai-Tibet alpine and cold region was adopted.
Southeastern conifer forests	1304 ± 141	82.3	17.5	29.3	-	26	The percentage of endemics on the Geological Coastal Plain was adopted.
Southeastern mixed forests	1232 ± 116	99.7	0.0	29.3	-	26	The percentage of endemics on the Geological Coastal Plain was adopted.
Southern Africa bushveld	873 ± 113	0.0	99.9	-	H	9	
Southern Cone Mesopotamian savanna	1251 ± 239	99.9	0.0	11.7	-	5	The percentage of endemics in Argentina was adopted.
Suiphun-Khanka meadows and forest meadows	857 ± 142	85.6	12.1	10.8	-	40	The percentage of endemics in the Russian Far East was adopted.
Tamaulipan matorral	1051 ± 324	0.0	98.6	36.1	-	39	The percentage of endemics in Nuevo Leon (Mexican political state) was adopted.
Tehuacán Valley matorral	2042 ± 481	7.5	84.9	35.6	-	39	The percentage of endemics in Morelos (Mexican political state) was adopted.
Texas blackland prairies	1123 ± 108	5.2	94.8	29.3	-	26	The percentage of endemics on the Geological Coastal Plain was adopted.
Tibetan Plateau alpine shrublands and meadows	834 ± 139	56.0	39.5	32.4	-	18	The percentage of the endemic seed plant species richness in the Qinghai-Tibet alpine and cold region was adopted.
Ussuri broadleaf and mixed forests	1064 ± 147	98.1	0.2	10.8	-	40	The percentage of endemics in the Russian Far East was adopted.
West Sudanian savanna	943 ± 156	0.8	90.1	>47	-	9	

Western Gulf coastal grasslands	1265 ± 180	38.8	61.1	29.3	-	26	The percentage of endemics on the Geological Coastal Plain was adopted.
Yarlung Tsangpo arid steppe	1101 ± 231	96.0	0.0	32.4	-	18	The percentage of the endemic seed plant species richness in the Qinghai-Tibet alpine and cold region was adopted.
Yellow Sea saline meadow	1546 ± 157	11.4	80.4	38.8	-	18	The percentage of the endemic seed plant species richness in the humid and subtropical zone in Central and Southern China was adopted.
Yunnan Plateau subtropical evergreen forests	2313 ± 308	78.0	19.4	38.8	-	18	The percentage of the endemic seed plant species richness in the humid and subtropical zone in Central and Southern China was adopted.

* VH: very high, H: high, M: medium, L: low

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Appendix 6

Table: RLUC anomalies in 1500-2010 and related biodiversity hotspots and identified ecoregions. Source: Kobayashi et al. (2019).

Country	Time period	Description	Biodiversity hotspots	Identified ecoregions
China	1770s-1800s 1990s	abrupt decrease and increase	Indo-Burma Mountains of Central Asia Mountains of Southwest China	Amur meadow steppe Bohai Sea saline meadow Central China loess plateau mixed forests Changjiang plain evergreen forests Emin Valley steppe Guizhou Plateau broadleaf and mixed forests Helanshan montane conifer forests Huang He Plain mixed forests Jian Nan subtropical evergreen forests Manchurian mixed forests Northeast China Plain deciduous forests Qilian Mountains conifer forests Qilian Mountains subalpine meadows Sichuan Basin evergreen broadleaf forests Southeast Tibet shrublands and meadows Tibetan Plateau alpine shrublands and meadows Yarlung Tsangpo arid steppe Yellow Sea saline meadow Yunnan Plateau subtropical evergreen forests

Kazakhstan	1940s	abrupt decrease	Mountains of Central Asia	Altai steppe and semidesert Kazakh steppe
Mozambique	1940s	abrupt decrease	Coastal Forests on Eastern Africa	-
Namibia	1890s-1950s	abrupt decrease	Succulent Karoo	-
Saudi Arabia	1950s-2000s	abrupt decrease and increase	Eastern Afromontane Horn of Africa	-
Spain	1500s-2000s	data gap on the border with France	Mediterranean Basin	Cantabrian mixed forests
Ukraine	1920s	abrupt decrease	-	-
United States	1870s 1960s-1970s	abrupt decrease	California Floristic Province	Atlantic coastal pine barrens East central Texas forests Florida sand pine scrub Middle Atlantic coastal forests Mississippi lowland forests Piney woods forests Southeastern conifer forests Southeastern mixed forests Texas blackland prairies Western Gulf coastal grasslands

Appendix 7

Table: List of identified ecoregions in which the maximum and accumulated RLUC were lower than those in biodiversity hotspots (Low RLUC = TRUE). The identified and non-identified ecoregions included in the new candidate biodiversity hotspots (the Altai-Sayan Montane Forests, the Amur-Heilong River Basin, and the Southeast China Subtropical Forests) are also listed. Source: Kobayashi et al. (2019).

Name	Identified ecoregion	Low RLUC	Predicted vascular plant species richness, mean ± s.d.	Maximum RLUC	Accumulated RLUC
Appenine deciduous montane forests	TRUE	TRUE	1938 ± 275	0.25	2.96
Atlantic coastal pine barrens	TRUE	TRUE	1184 ± 67	0.29	3.12
Cantabrian mixed forests	TRUE	TRUE	1597 ± 221	0.14	2.47
Dinaric Mountains mixed forests	TRUE	TRUE	1785 ± 332	0.24	2.48
Florida sand pine scrub	TRUE	TRUE	1469 ± 80	0.23	1.90
Middle Atlantic coastal forests	TRUE	TRUE	1238 ± 136	0.24	3.27
Piney woods forests	TRUE	TRUE	1256 ± 110	0.17	1.91
Southeastern conifer forests	TRUE	TRUE	1304 ± 141	0.15	1.96
Southeastern mixed forests	TRUE	TRUE	1232 ± 116	0.25	2.90
Altai-Sayan Montane Forests					
Altai alpine meadow and tundra	TRUE	FALSE	935 ± 165	0.32	4.35
Altai montane forest and forest steppe	TRUE	FALSE	877 ± 255	0.49	5.14
Great Lakes Basin desert steppe	FALSE	-	541 ± 129	-	-
Sayan alpine meadows and tundra	TRUE	TRUE	871 ± 181	0.15	1.90

Sayan intermontane steppe	TRUE	TRUE	793 ± 88	0.24	2.59
Sayan montane conifer forests	TRUE	TRUE	879 ± 124	0.11	1.33
Amur-Heilong River Basin					
Amur meadow steppe	TRUE	FALSE	736 ± 118	0.29	4.94
Changbai Mountains mixed forests	FALSE	-	1407 ± 166	-	-
Manchurian mixed forests	TRUE	TRUE	1002 ± 241	0.12	2.12
Okhotsk-Manchurian taiga	TRUE	TRUE	824 ± 158	0.11	1.23
Suiphun-Khanka meadows and forest meadows	TRUE	FALSE	857 ± 142	0.29	4.50
Ussuri broadleaf and mixed forests	TRUE	TRUE	1064 ± 147	0.19	2.34
Southeast China Subtropical Forests					
Guizhou Plateau broadleaf and mixed forests	TRUE	TRUE	2018 ± 223	0.27	2.83
Jian Nan subtropical evergreen forests	TRUE	TRUE	2051 ± 215	0.22	2.31
Yunnan Plateau subtropical evergreen forests	TRUE	TRUE	2313 ± 308	0.22	2.29

Appendix 8

Supplementary information: Empirical and theoretical studies have shown that maintaining species diversity has the potential to enhance the quality and the quantity of ecosystem functions and thus of ecosystem services (Cardinale et al., 2012). This phenomenon has been attributed to two effects: complementarity and selection (Tilman 1999; Loreau and Hector 2001). The former effect arises from resource partitioning (niche differentiation) and positive interactions among species (facilitation). For the former effect, suitable environmental conditions vary for different species. For example, some plants are drought resistant, whereas others prefer high humidity levels (Figure 1a). If only one plant species grows within a particular location with a gradient of soil water content, then the total productivity will be determined by the response of this species (Figure 1b). However, if multiple species coexist within a specific location, they can grow in a favorable environment and become dominant, leading to an increase of total productivity (Figure 1c). For the latter effect, the total productivity increase by the presence of species such as legumes that fix atmospheric nitrogen and facilitate the growth of other plant species (Figure 1d).

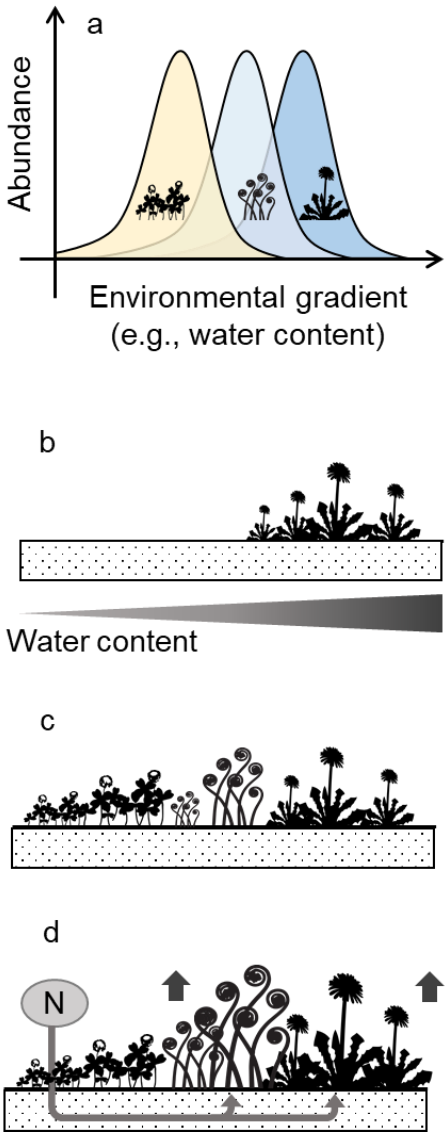

Figure 1

Biodiversity stabilizes primary productivity over time in the face of natural and anthropogenic environmental fluctuations and disturbance (Isbell et al., 2017). For example, as shown in Figure 2a, in a context of temperature fluctuations, only plant species that react positively to temperature rises will

thrive and their productivity will be synchronized with the temperature (Figure 2b). However, if two plant species that respectively react positively and negatively to temperature coexist (Figure 2c; red and blue lines, respectively), then their fluctuations are offset, and the total productivity is stabilized (Figure 2c; black line). This decrease in temporal variability based on interspecific competition and environmental changes is known as the negative covariance effect. Even if species do not demonstrate asynchrony in relation to environmental changes, statistical averaging leads to an increase in stability with diversity (the portfolio effect; Tilman, 1999).

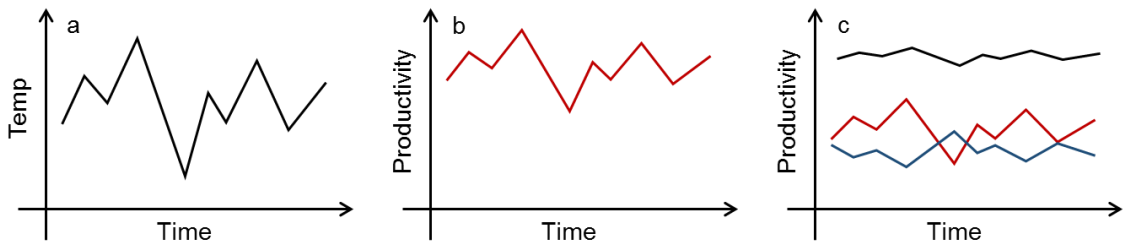

Figure 2

Appendix 9

Figure 1: Slope gradient map in Japan. The gray gradient and red respectively show slopes less than and greater than 30 degrees.

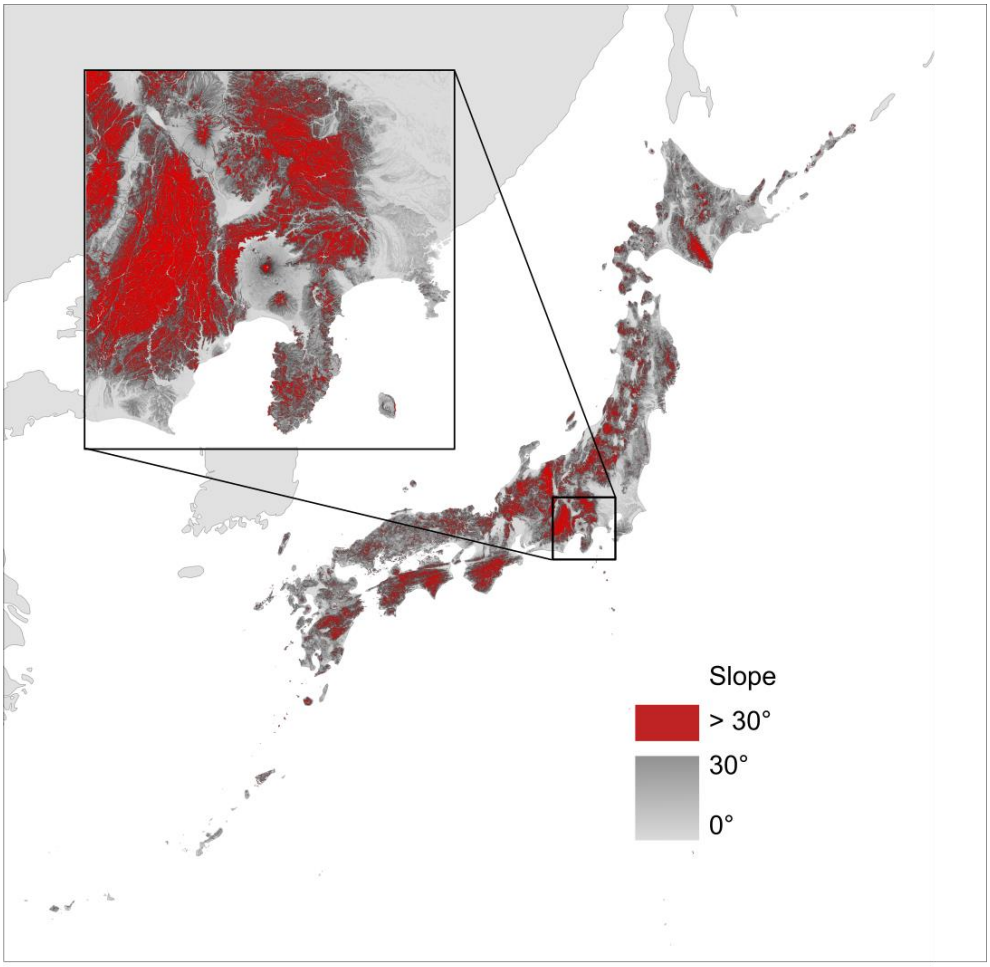

Figure 2: Distribution of roads (dark gray) and areas separated by 3 km or more from a road (red).

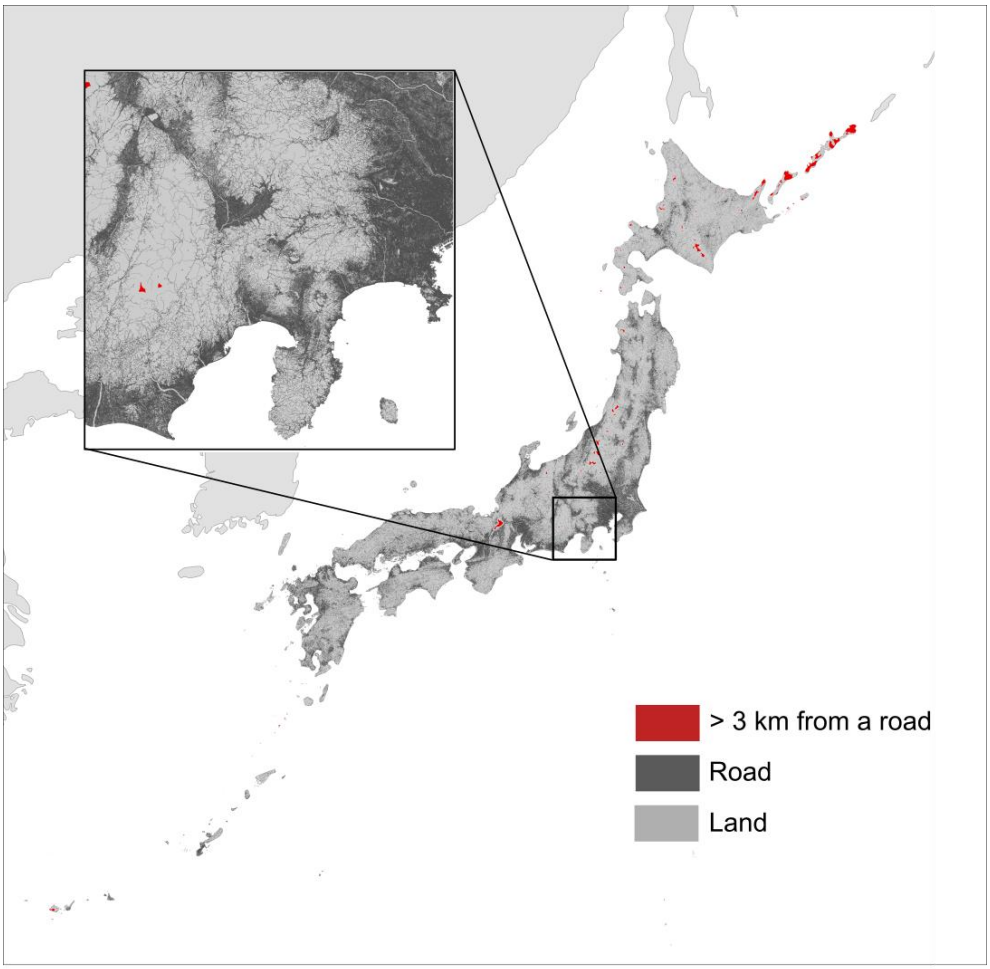

Figure 3: Distribution of Japanese forests (dark gray) and spatially limited areas for wild plants (red).

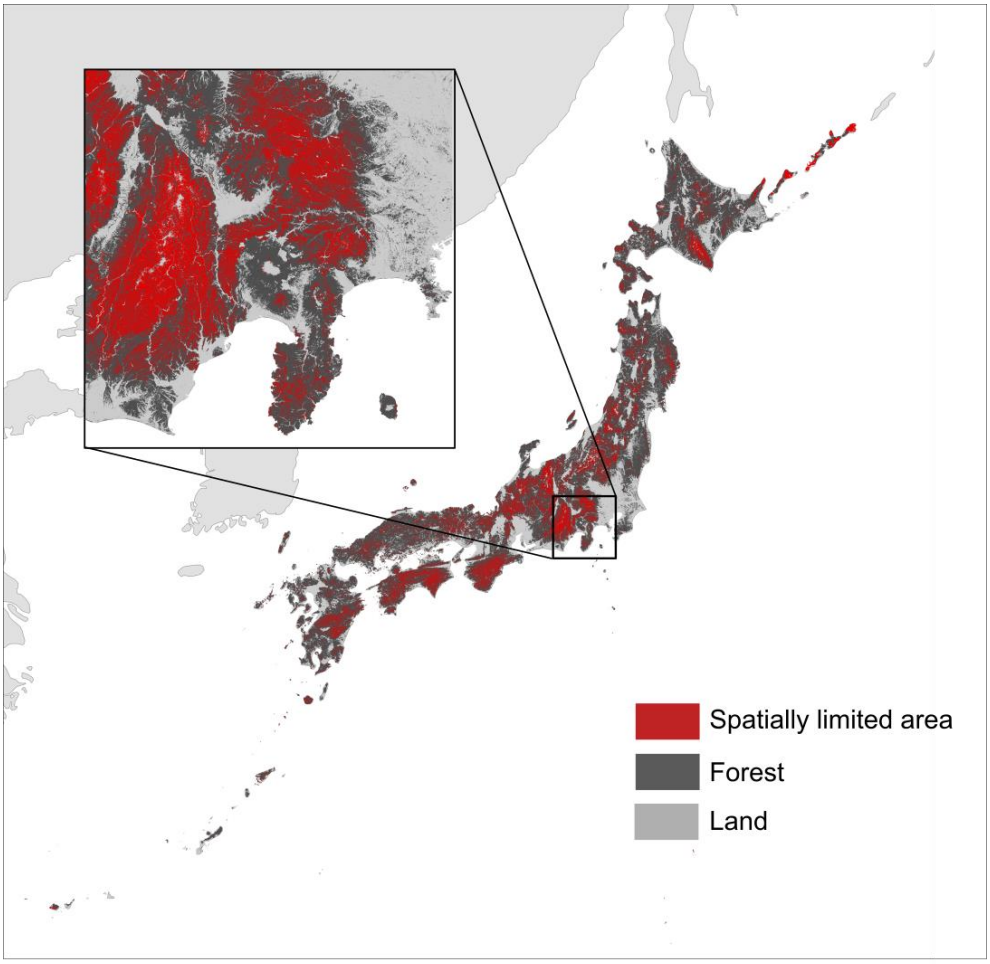

Figure 4: Distribution of croplands (dark gray) and areas 2 km or more distant from a cropland (orange).

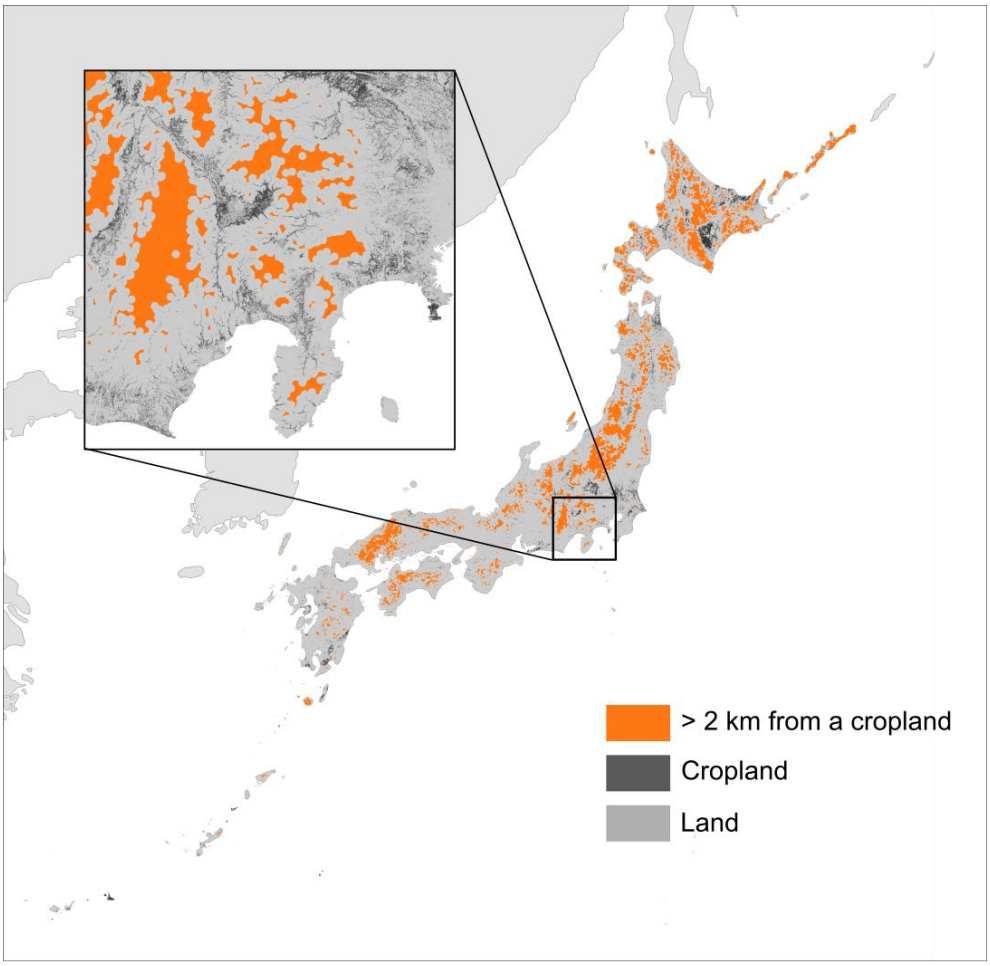

Figure 5: Distribution of Japanese forests (dark gray) and spatially limited areas for crop pollination (orange).

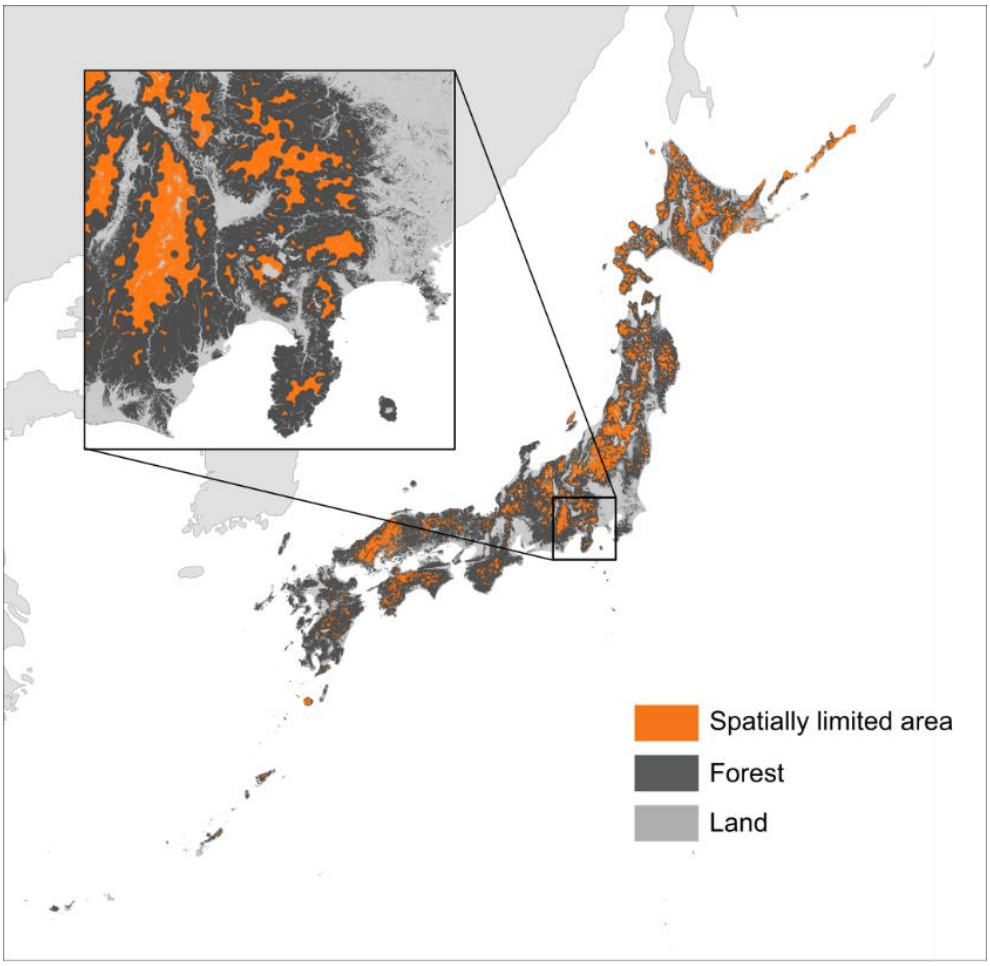

Figure 6: Watersheds upstream from intake points of Japanese waterworks that provide potable water for more than 5000 people (transparent blue).

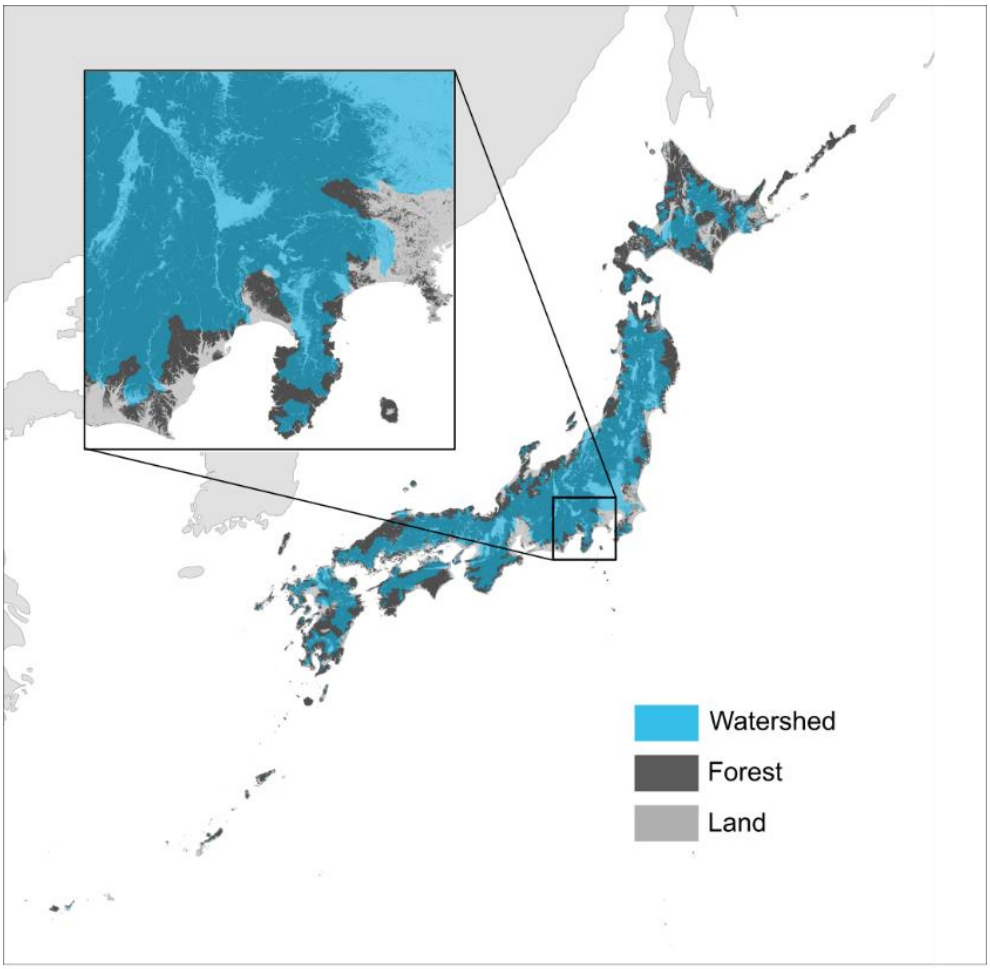

Figure 7: Distribution of forests (dark gray) and spatially limited areas for water purification (blue).

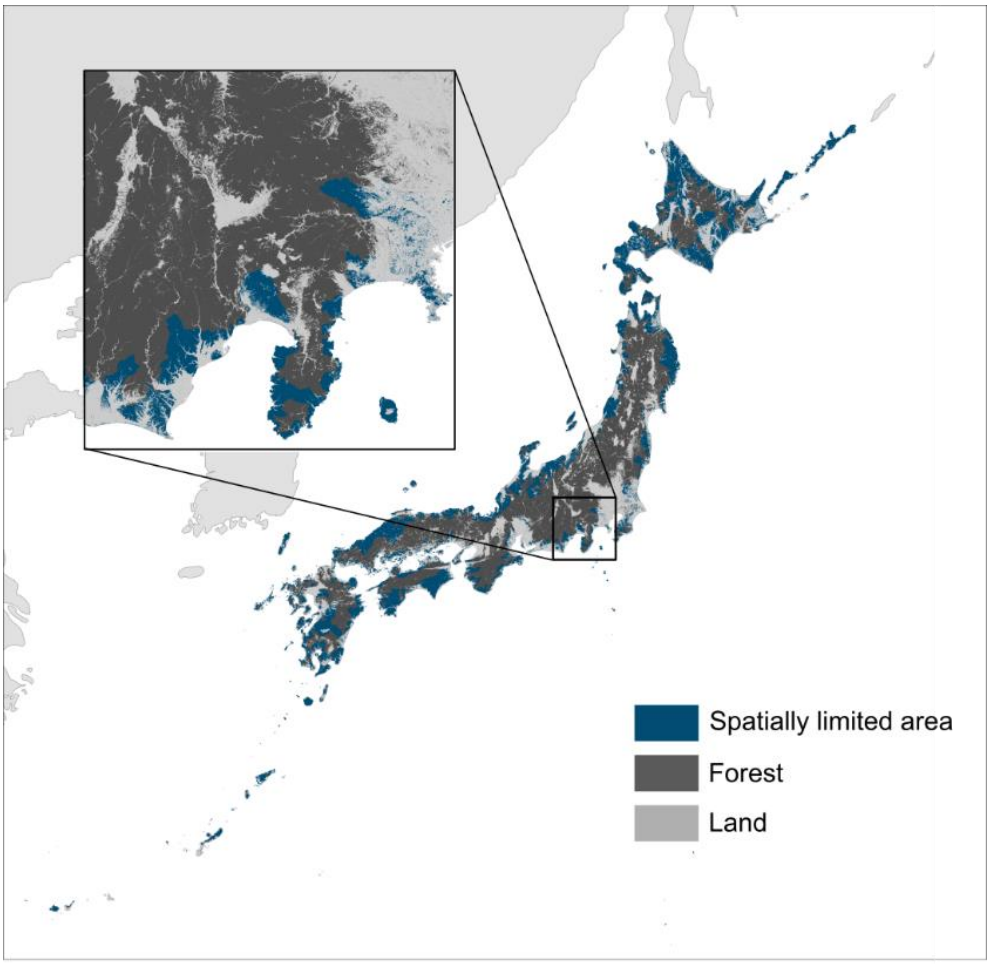

Figure 8: Buffers from roads (100 m), industrial areas (316 m), railways (1000 m), and airports (3162 m).

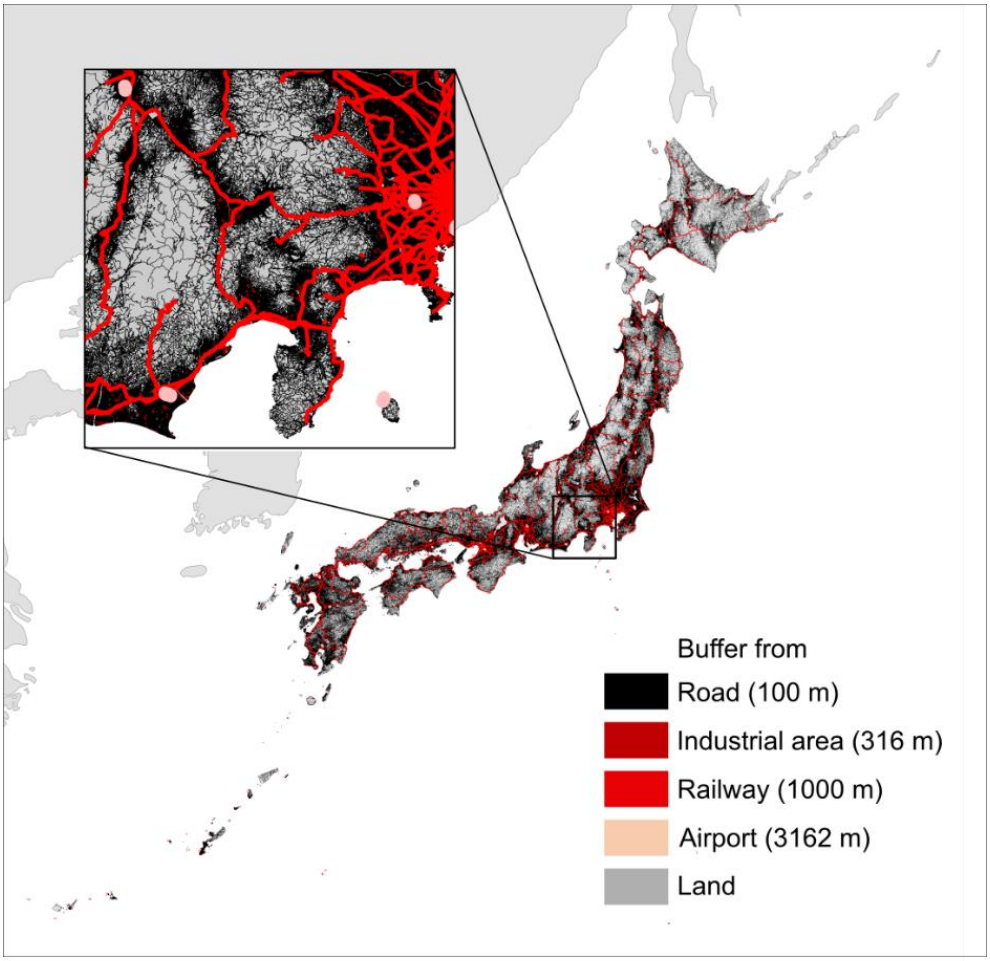

Figure 9: Buffers from urban areas (100, 316, 1000, 3162 m).

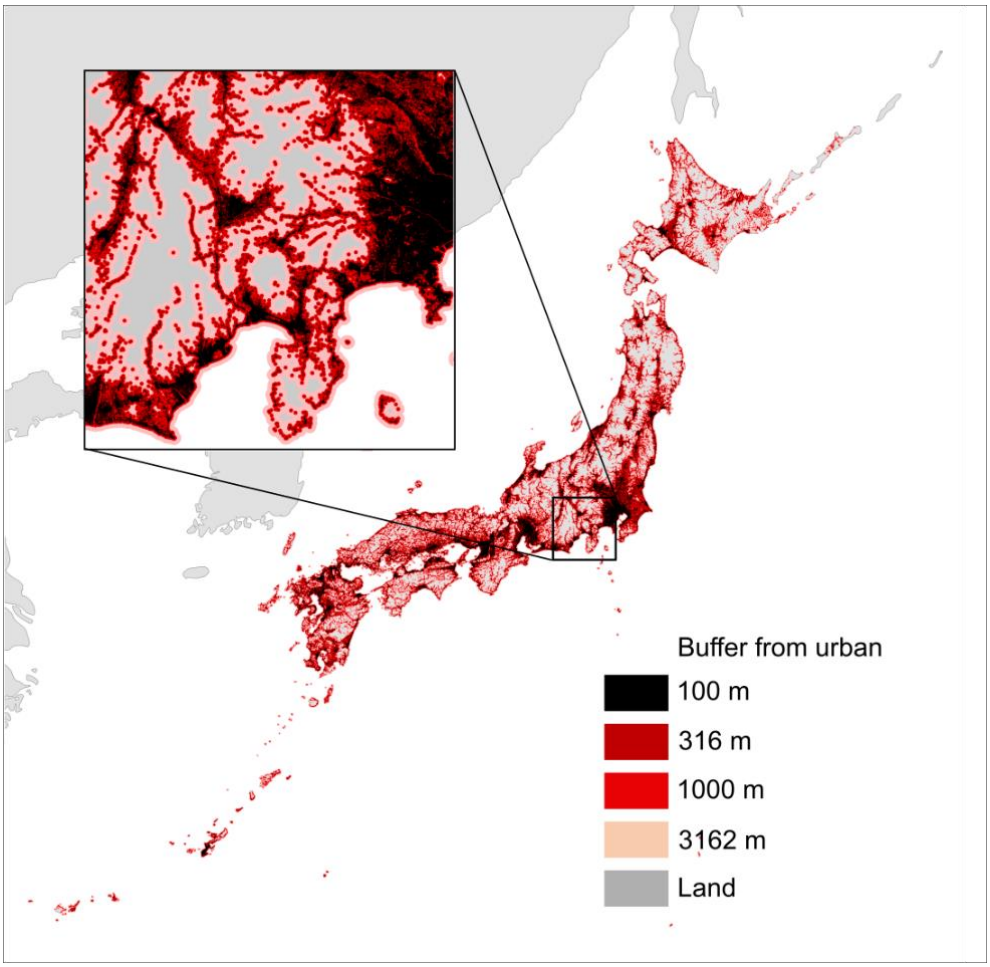

Figure 10: Distribution of forests (dark gray) and spatially limited areas for noise attenuation (green).

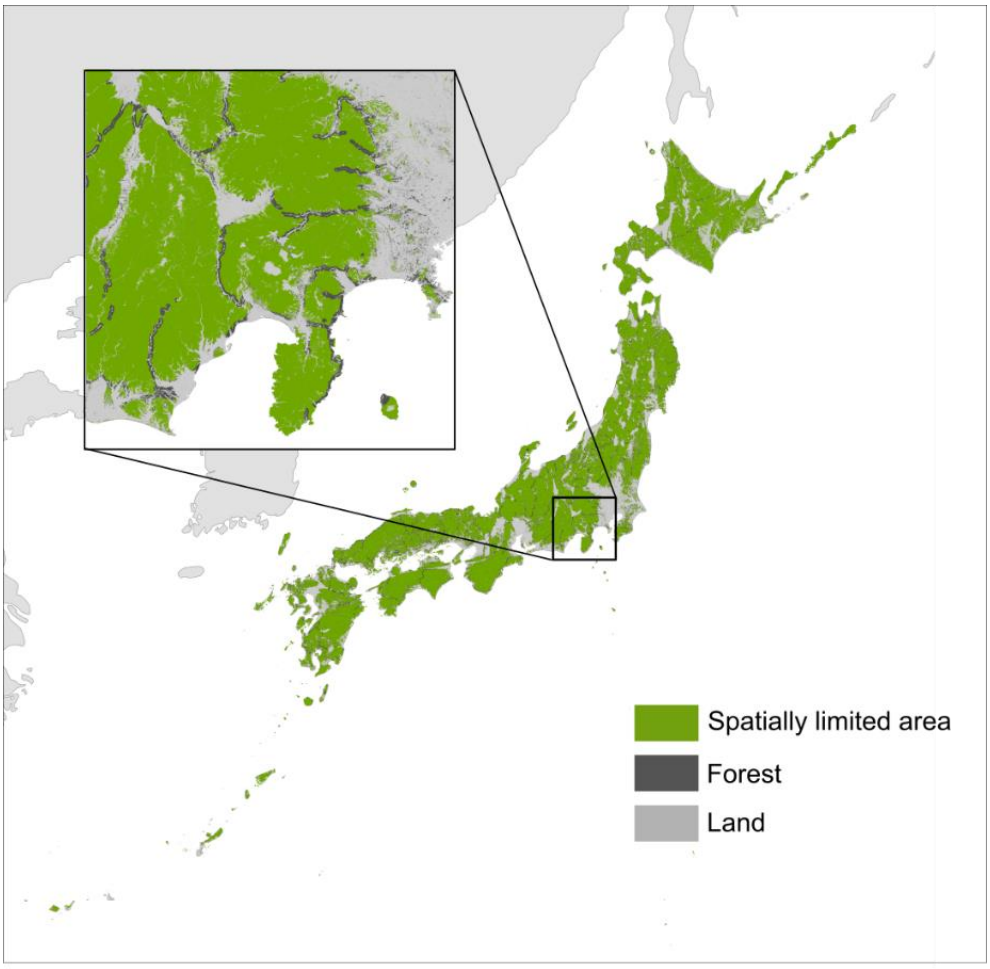

Figure 11: Watersheds upstream from artificial landscapes (urban, cropland, and rice paddy) (transparent purple).

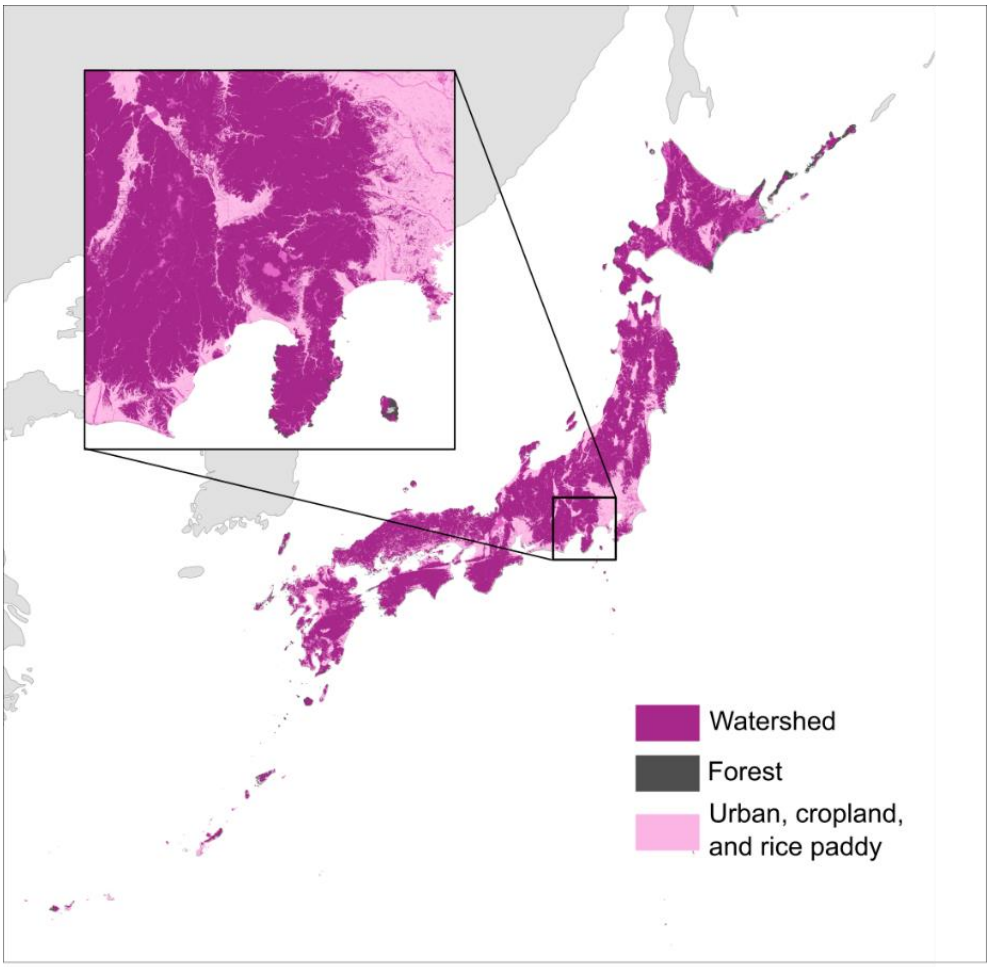

Figure 12: Distribution of forests (dark gray) and spatially limited areas for flood control (purple).