# USING GLOBAL INDICATORS TO INFORM THE CONSERVATION OF HIGH NATURE VALUE AREAS

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*“The great challenge of the twenty-first century is to raise people everywhere to a decent standard of living while preserving as much of the rest of life as possible.”*

*— Edward O. Wilson*

# TABLE OF CONTENTS

# SUMMARY

In the era of the Anthropocene, humans are reshaping the world, impacting its ecosystems, climate regime and biodiversity. To improve our understanding about the new challenges that the Earth system is facing, macroscale analyses are now required. Macro-analyses allow us to identify global patterns and trends, as well as to locate altered regions subjected to important or accelerating deteriorations. The identification and monitoring of such regions is possible through the development and use of global indicators. This thesis explores three dimensions of global indicators' applications by answering three fundamental questions, respectively: (1) **What to protect?** This requires in the studied case **learning about the system**, (2) **How is protection effective?** This entails **auditing management actions** and (3) **How to improve monitoring?** This is possible through site-specific assessments which aim to provide results that **raise policy makers' awareness**, emphasising needed actions or efforts. I answer these questions through the study of forest and wetland ecosystems, highly impacted by anthropogenic factors. I then conclude this work by examining each indicator within an international policy context, such as their potential use within an Aichi Biodiversity Target framework.

**The first chapter** contributes to the development of a global indicator that quantifies forest habitat rarity levels. I used this indicator to test a hypothetical link with the occurrence of small range species. Through this study, I addressed to the following questions: (1) Where are the rarest forest habitats within each biogeographical realm? (2) Does rare forest habitat host rare species (i.e. restricted range-size) that would be adapted to it? (3) Is the relationship mainly explained by current ecological variables such as Habitat Rarity or historical ones? Available global species range data are still relatively coarse, which limits their relevance for conservation application. The identification of an indicator available at high resolution (i.e. rare forests habitat) to locate both rare species and habitats would be an interesting asset to explore for prioritisation of areas to protect. I used multivariate distances to build the Habitat Rarity index with a combination of climatic and forest related variables. Global data of forest bird specialists was used to compile a corrected weighted endemism index (E) as a response variable. We tested this index (E) against ecological and historical predictors (e.g. mean temperature, climate change velocity) across different biogeographical realms and islands. The results shown that (1) the rarest forests habitat are mainly located in mountainous areas, (2) rare forest habitat does not always explain the distribution of rare species (3) climate change velocity of the Quaternary period is the main factor explaining rare species distribution. The developed Habitat Rarity index allows us to **learn about the system** by investigating the distribution pattern of restricted range species for potential further application in conservation.

**The second chapter** tests the ability of protected areas to prevent forest loss according to their conservation requirements, using 'forest loss extent' as a global indicator to assess the percentage of forest loss within protected areas. The initial hypothesis was that areas with high protection levels should have less forest loss than areas where the sustainable use of resources is allowed, independently of the location. I used the International Union for Conservation of Nature (IUCN) protected areas categories to estimate protected areas' conservation objective. I considered three different spatial scales: per site, per IPBES (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services) subregion, and global. I found that globally, the expected pattern of having less loss in the highest protection level is confirmed. However, the IUCN categories that should benefit the best protection presented increasing trends of loss. Those results were not shared at the IPBES subregion level. The Caribbean, North-East Asia and West-Africa subregions presented issues in their conservation commitment, as their highest IUCN categories had more forest loss than the lower categories of protection. Finally, I highlighted the world regions where forest loss was higher outside protected areas, which include Eastern Europe, the Caribbean, Mesoamerica and North-Africa. By auditing protected areas' commitment, I aimed through this study to orient protection effort towards the sites that present difficulties in preserving their forests. IPBES subregions that present numerous sites defective in their protection abilities should reach policy consideration, to better study the underlying causes of forest loss and develop solutions. Therefore, the percentage of forest loss index is mainly framed in the context of both **auditing management actions** and **raising decision makers' awareness**.

**The third chapter** assesses natural wetlands evolution within the Mediterranean basin and their exposure to climatic and land-use change. This study provides a standardized and harmonised site-specific method by selecting different sets of indicators accounting for the state and dynamic of natural wetlands and related biodiversity. Those indicators were tested as potential wetlands Essential Variables. The results showed that within the 15 years analysed, the area of natural wetland habitats declined by 5% in the studied sites, mostly in the eastern part of the basin. Natural wetlands were directly impacted by land-cover change, mainly replaced by agricultural areas and artificial wetlands. Natural wetland loss was exacerbated in the less protected sites in the Near East where substantial warming occurred combined with a decrease in precipitation regime. I also identified gaps in species data coverage that can jeopardize analysis of the ability of protected areas to safeguard waterbird communities. Thus, this study aims to **raise awareness of decision makers** about Mediterranean wetlands evolution, threats to global changes and needs for further monitoring.

# INTRODUCTION

## 1. THE FOREST AND WETLAND SYSTEMS IN THE CONTEXT OF THE ECOLOGICAL CRISIS

The increasing human domination of nature is causing global biodiversity depletion at an unprecedented pace. Overexploitation of biological resources, habitat loss and fragmentation, pollution, species invasions, poaching, diseases and climate change have increased rates of global species extinctions to higher levels than those observed in fossil records (Barnosky et al., 2011; Ceballos et al., 2015; Pimm et al., 2014; Scheele et al., 2014). Global species decline is observable at local scale through an overall decrease in species abundance (Young et al., 2016) and an increase in species turnover, with local extinction of native species and replacement by competing ones (Dornelas et al., 2014). Endemic species with narrow distribution are thus the most vulnerable, as their local extinction may be irreversible (Purvis et al., 2000). Consequently, species decline leads to a spatial homogenization of Earth's biota (Haddad et al., 2015) combined with a gradual alteration of ecosystem services, affecting in the long run human well-being (Isbell et al., 2017).

The ecosystem that is the most affected by species loss on Earth is the freshwater ecosystem, with one third of its species threatened with extinction (Young et al., 2016; Collen et al., 2014). Many species are specialised or have a part of their life cycle that depends on freshwater ecosystems, which make those species especially vulnerable (Keddy et al., 2009). Despite their small global representativeness (<1% of terrestrial cover, Gleick, 1998), freshwater ecosystems, especially wetlands, provide particularly valuable services for people. These include water supply and quality, hydrological regulation, erosion control, food and recreation. Thus, wetlands are one of the most valuable ecosystems per unit area (Costanza et al., 2014). But wetlands are disappearing at a significant rate, with 64 to 71% of the area present in 1900 estimated to have been lost during the 20th century (Davidson, 2014). The causes of their decline are numerous and mostly anthropogenic: diversions and damming of river flows, contamination, global warming, invasions of exotics, and the practices of filling and draining (Brinson and Malvárez, 2002). Given the significance of wetlands for human health, water and food security, wetlands state has to be monitored, especially in politically instable areas where wetlands threats are hefty and which deterioration can imperil the local population such as in the Mediterranean basin (Cramer et al., 2018).

Unlike wetlands, forests cover one third of the world land surface (Keenan et al. 2015) with highly diverse ecological and environmental properties. They play a key role in climate regulation, $CO_2$ sequestration, protection from drought and erosion, food supply and numerous other services (Luyssaert et al., 2008; Malhi et al., 2008; Balmford et al., 2002). They also present the most biodiverse terrestrial habitat on the planet (Jenkins, Pimm, and Joppa 2013), being essential for the preservation of many endangered and endemic species (Gibson et al., 2011; Moura et al., 2013), especially in the tropics (Stevens, 1989). Primary forests are the most valuable, hosting specialised species that support irreplaceable ecosystem functions (Gibson et al., 2011). But they are threatened by increasing anthropogenic pressures that occurred over the last decades (Laurance et al., 2014a; Faria and Almeida, 2016; Schmitz et al., 2015), particularly within the tropical biome (Leblois et al., 2017). Consequently, the loss of intact forests is increasing, with a reduction of 7.2% of their global coverage between the years 2000 and 2013 (Potapov et al., 2017).

The fastest means to halt the pace of loss of natural habitats and their related biodiversity at global scale is to extend their protection coverage (Rodrigues et al., 2004; Bruner et al., 2001). However, effectively protecting global biodiversity presents substantial challenges, and requires global knowledge and agreements, achievable through the coupling of science and policy. To improve our understanding of the Earth system's functioning and facilitate dialogue between scientists and policy makers, the development of global indicators is necessary.

## 2. GLOBAL INDICATORS DEVELOPMENT

The global ecological crisis requires global solutions, and therefore the development of global tools to improve our understanding of the ecosystems and their dynamics. By definition, an indicator is a metric that provides information about the condition and trajectory of a system (Bell and Morse, 2008). As defined by the Convention on Biological Diversity, *"biodiversity indicators are a fundamental part of any monitoring system providing the mechanism for determining whether policies and actions are having the desired effect. They are also designed to communicate simple and clear messages to decision makers. Indicators use quantitative data to measure aspects of biodiversity, ecosystem condition, ecosystem services, and drivers of change, and aim to enhance understanding of how biodiversity is changing over time and space"* (Herkt et al., 2013). Biodiversity indicators are not only important at the global level, but also at the national and sub-national level (https://www.bipindicators.net). In this thesis, global indicators refer to metrics that benefit data coverage going beyond the national level and transferable to different places (e.g. a bioindicator common to all studied sites to assess ecosystem health) and that can be interpolated at global level.

Indicators can thus be used for several purposes: to learn about the system, to raise policy-maker and public awareness, to audit management actions, and to inform policy decisions (Joseph, 2008). Different indicators allow for collection of several dimensions of information on the same system. They can inform about the state of a system (e.g. nitrogen surplus), assess its pressures (e.g. Human Footprint Index), state its response to disturbance (e.g. resilience indicators) or policy response to its pressures (e.g. management effectiveness indicators), and inform about the benefits that people gain from it (e.g. ecosystem services, economic indicators) (Jones et al. 2013). They can be used to rank the importance of a system according to its function, services, species community, or rarity for prioritisation (e.g. the most biodiverse countries) (Mittermeier et al., 1997). However, there is considerable complexity to tackle when creating meaningful indicators. Indicators should be clearly interpretable, produced with affordable human and financial costs, and often are required to be informative at multiple spatial and temporal resolutions (Jones et al. 2010).

The idea to develop global biodiversity indicators emerged in the last decades and was emphasised by the international recognition of the need for halting biodiversity and natural habitat loss. In this context, the Convention on Biological Diversity (CBD, 1992) set up 20 biodiversity Aichi Targets to be achieved by 2020 (CBD, 2010). To date, a set of 147 indicators have been identified to audit the progress made in achieving those targets assessing the global pressures, states, benefits and policy responses applied to each target (https://www.bipindicators.net). Their number rapidly increased in the last years revealing a significant effort to cover gaps identified in some studies (Mcowen et al., 2016; Tittensor et al., 2014). Even though improvements have still to be done (Driscoll et al., 2018), the development of global indicators provides a baseline for other international biodiversity conventions such as the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) or the Sustainable Development Goals (SDGs).

This thesis provides a contribution in the development and use of large scale indicators related to conservation objectives addressing three roles of indicators: (1) to learn about the system, (2) to audit protection actions and (3) to raise awareness of decision makers. In this regard, this thesis gives some insights in answering the following questions:

(1) **What to protect?** In Chapter 1, I tested the performance of a potential new indicator of species rarity, focusing on rare forest habitat. Being able to locate areas where both rare habitats and species occur could facilitate protection prioritisation. That requires however testing a hypothetical link of spatial relationship between species and habitat rarity, and therefore, to **learn about the system**.

(2) **How is protection effective?** In Chapter 2, I assessed the reliability of different level of protection in preserving forest loss, using an indicator to **audit protection actions**. I also provided a spatial representation of the results at the site and region levels, to **raise decision makers' awareness** regarding areas where protection should be reinforced.

(3) **How to improve global monitoring?** In Chapter 3, I used multiple indicators to assess the state and dynamic of different natural wetlands sites and related biodiversity under land-cover and climate change. The produced results can be used to **raise decision makers' awareness** to localise for instance the wetland sites where actions to enforce climate change mitigation measures should be considered

## 3. WHAT TO PROTECT? LEARNING ABOUT THE SYSTEM

Given the limitation of conservation resources, prioritization of areas to protect is of prime importance regarding the wide human pressure on nature. The knowledge gathered by global indicators can help in identifying areas to protect that harbour higher ecological values, optimizing the conservation cost. Prioritization is challenging as it requires a good representation of biodiversity and ecosystem services, including an understanding of gaps in protection coverage, of connectivity between protected areas (Rodrigues et al., 2004) and of sufficient protection extent (Ferrier, 2002).

Several prioritisation schemes have been proposed based on global biodiversity hotspots, endemic birds' areas, centres of plant diversity, gap analysis, among others (Brooks et al., 2006; Rodrigues et al., 2004), as well as ecosystem services (Naidoo et al., 2008). Nevertheless, the valuations of those areas are essentially species based and rely on expert knowledge that generates low spatial accuracy, which rapidly limits their informative usefulness for conservation (Smith et al., 2009). Many terrestrial eukaryotes are still unknown, especially species with small range and low abundance, being small-sized (e.g. invertebrates), or present in areas difficult to access (e.g. hearts of tropical forests, underground, deep valleys, or ocean depths) (Costello et al., 2012). The estimated number of undiscovered species varies greatly across studies (Scheffers et al., 2012), with around 25% of terrestrial species according to Costello, Wilson, and Houlding (2012) and around 87% of terrestrial animals, mainly invertebrates according to Mora et al. (2011). Moreover, the coarse grain of species distribution data (recommended to be used at 100x100 km resolution, Hurlbert and Jetz, 2007) can be detrimental to locate restricted range species for conservation. Even though small range species are spatially aggregated worldwide (Pimm et al., 2014), their accurate spatial distribution is not assessed. The development of an indicator based on biophysical conditions that would allow identification of areas where small range species might occur at high resolution would be relevant for prioritisation (Bunce et al., 2013). However, species distribution does not solely depend on current ecological factors but on historical ones as well.

In Chapter 1, I developed a Habitat Rarity (HR) index designed to account for forest habitat rarity at high resolution. I tested the HR index as a predictor of species range-size across realms, that I compared to other ecological or historical factors. Therefore, Chapter 1 contributes to improving our understanding towards small species range-size distribution, for potential conservation use.

## 4. HOW IS PROTECTION EFFECTIVE? AUDITING PROTECTION ACTIONS

Auditing actions is needed to assess the progress made in achieving international objectives, identifying the success rate of contracting parties and potential sources of failure. It should stimulate the target achievement and also allow the adjustment of too ambitious goals (Butchart et al., 2016).

In conservation, auditing protection management is usually used in the context of managed sites such as protected areas. Large scale assessments can be achieved using indicators from monitoring via satellite imagery (e.g. Forest Loss, or the composite indicator Human Footprint, Allan et al., 2017; Jones et al., 2018; Nagendra et al., 2013), or based on surveys of protected areas or project staff (e.g. the Management Effectiveness Tracking Tool (Stolton et al., 2003), New South Wales State of Our Parks (Growcock et al., 2009), or the Rapid Assessments and Prioritization of Protected Area Management (Ervin, 2002)).

The main challenge of large-scale protected areas effectiveness assessment lies in the large diversity of management goals that can have various sub-national, national or international overlapping denominations and objectives. A global harmonisation of protection goals is conducted by the joint effort between the International Union for Conservation of Nature (IUCN) and the United Nations Environment Programme World Conservation Monitoring Centre (UNEP-WCMC) to build and update the World Database of Protected Areas (WDPA).

The development of the protected areas IUCN management categories allows estimation of protected areas commitments at an international scale (Dudley, 2013). By using the IUCN categories as reference to test protected areas abilities in following their commitment, several studies provided global assessment, raising concerns towards their protection efficiency or increasing exposure to anthropogenic pressures (Jones et al. 2018; Watson et al. 2014).

The expansion of the protected area network is essential to halt biodiversity loss (Barnes et al., 2016; Rodrigues et al., 2004). In this regards, the Aichi target 11 advocates 17% of terrestrial and 10% marine protected areas coverage by 2020. The rush in meeting the Aichi target 11 is weighted with the worry of establishing protected areas without appropriate resources allocated to meet their conservation objectives (Barnes et al., 2018; Rife et al., 2012).

In this regards, Chapter 2 explores the abilities of IUCN management categories in preventing forest loss.

## 5. HOW TO IMPROVE GLOBAL MONITORING? LARGE SCALE SITE-SPECIFIC MONITORING TO RAISE AWARENESS

To tackle the ecological crises challenge, there is a need to detect environmental and biodiversity changes at multiple spatial and temporal scales (Peters et al., 2014). Even though most observation programmes emerged from local initiatives, impairing data comparison (e.g. university research programmes), international coordination comes forth with the emergence of different scientific communities and facilities (e.g. NEON, GEO BON, ILTER, Kissling et al., 2018). Among them, the Group on Earth Observations and Biodiversity Observation Network (GEO BON) developed the framework of Essential Biodiversity Variables (EBVs), inspired by the Essential Climate Variables (ECVs). The EBVs framework aims to prioritize information needed for global monitoring and to mobilize, standardize and harmonize biodiversity data to document biodiversity change across spatial and temporal scales (Pereira et al., 2013). Pettorelli et al., 2016 defined EBVs as *"a variable or a group of linked variables that allows quantification of the rate and direction of change in one aspect of the state of biodiversity over time and across space. An EBV is critical for understanding and predicting changes in the most integrated and established global indicators of biodiversity".* Six classes of EBVs were identified: genetic composition, species population, species traits, community composition, ecosystem structure and ecosystem functions (Pereira et al., 2013). Among those classes, different EBVs were distinguished such as 'habitat extent' for the class 'ecosystem structure', that regroups different variables or indicators such as 'proportion of forest cover' or 'proportion of wetland cover' (i.e. ecosystem structure (EBV class) > Habitat Extent (EBV) > proportion of forest cover, wetland cover, and other variables or indicators).

Through the increasing number of international summits and associated reports, the production of global indicators was fostered during the last years as well as the number of policy implementations (Bark and Crabot, 2016), tightening the link between global indicators and decision making. However, global indicators designed to estimate current or future ecological status and audit international biodiversity targets to orient policy (Pereira et al., 2010) still lack spatial plasticity. Their recurrent inability in being down-scalable to national or sub-national levels - which are the main decision-making centres - make them hardly relevant in a practice setting. National or local policies have thus to rely on a different scale of knowledge when available. Framing local or national ecological issues into a regional or global context would allow assessment of the urgency of a situation, facilitating justification to take imperative actions. Therefore, the development of large-scale standardized site-specific studies can be seen as a means to introduce science as a guiding tool for policy. With the rise of high resolution satellites' remote-sensing data products (e.g. Hansen et al., 2013; Pekel et al., 2016), the above mentioned "scientific international coordination", as well as citizen science programmes, the feasibility of such studies is increasing and some even accounted for thousands of delineated sites (Haase et al., 2018; Jones et al., 2018; Leroux et al., 2010).

Further, global indicators play a non-negligible role in the general public awareness and concern towards conservation issues at an international level (Merry, 2011; Miller et al., 2017). Numbers and trends can be easily communicated through the use of some indicators such as forest loss (that can be extended to different forest types) or Human Footprint that are quite straightforward to understand. They can foster public interest by involving citizens in monitoring programmes, which are sometimes promoted via widespread media coverage (Nichols and Williams, 2006). Their international use can allow identification of sensitive areas and raise the issue in the political sphere supported by the public.

In this context, I conducted a site-specific analysis across the Mediterranean wetlands in Chapter 3. This study provides insights on areas where natural wetland loss occurred including their current protection coverage across the Mediterranean, and put them in perspective under the climate change threat. In this chapter, I applied an EBV framework to test the use of potential Essential Variables for wetland monitoring. In addition, Chapter 2 aimed to inform decision makers regarding the identification of ineffective IPBES subregions or sites in protecting forests under the highest protection.

## 6. OBJECTIVE OF THE THESIS

The main aim of this thesis is to improve our global understanding and raise awareness about the state and evolution of highly valuable natural areas through the use of global indicators. I explore their development and use, focusing on forests and natural wetland habitats. Each chapter is intended for publication and is conducted through the comparison of different world regions.

## REFERENCES

Allan, J.R., Venter, O., Maxwell, S., Bertzky, B., Jones, K., Shi, Y., and Watson, J.E.M. (2017). Recent increases in human pressure and forest loss threaten many Natural World Heritage Sites. Biological Conservation *206*, 47–55.

Balmford, A., Bruner, A., Cooper, P., Costanza, R., Farber, S., Green, R.E., Jenkins, M., Jefferiss, P., Jessamy, V., Madden, J., et al. (2002). Economic Reasons for Conserving Wild Nature. Science *297*, 950–953.

Bark, R., and Crabot, J. (2016). International benchmarking: policy responses to biodiversity and climate change in OECD countries. International Journal of Biodiversity Science, Ecosystem Services & Management *12*, 328–337.

Barnes, M.D., Craigie, I.D., Harrison, L.B., Geldmann, J., Collen, B., Whitmee, S., Balmford, A., Burgess, N.D., Brooks, T., Hockings, M., et al. (2016). Wildlife population trends in protected areas predicted by national socio-economic metrics and body size. Nature Communications *7*, 12747.

Barnes, M.D., Glew, L., Wyborn, C., and Craigie, I.D. (2018). Prevent perverse outcomes from global protected area policy. Nature Ecology & Evolution *2*, 759–762.

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., et al. (2011). Has the Earth's sixth mass extinction already arrived? Nature *471*, 51–57.

Bell, S., and Morse, S. (2008). Sustainability Indicators: Measuring the immeasurable (2nd ed) (London: Earthscan).

Brinson, M.M., and Malvárez, A.I. (2002). Temperate freshwater wetlands: types, status, and threats. Environmental Conservation *29*, 115–133.

Brooks, T.M., Mittermeier, R.A., Fonseca, G.A.B. da, Gerlach, J., Hoffmann, M., Lamoreux, J.F., Mittermeier, C.G., Pilgrim, J.D., and Rodrigues, A.S.L. (2006). Global Biodiversity Conservation Priorities. Science *313*, 58–61.

Bruner, A.G., Gullison, R.E., Rice, R.E., and Fonseca, G.A.B. da (2001). Effectiveness of Parks in Protecting Tropical Biodiversity. Science *291*, 125–128.

Bunce, R.G.H., Bogers, M.M.B., Evans, D., Halada, L., Jongman, R.H.G., Mucher, C.A., Bauch, B., de Blust, G., Parr, T.W., and Olsvig-Whittaker, L. (2013). The significance of habitats as indicators of biodiversity and their links to species. Ecological Indicators *33*, 19–25.

Butchart, S.H.M., Marco, M.D., and Watson, J.E.M. (2016). Formulating Smart Commitments on Biodiversity: Lessons from the Aichi Targets. Conservation Letters *9*, 457–468.

CBD (2010). Conference of the parties to the convention on biological diversity.

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., and Palmer, T.M. (2015). Accelerated modern human–induced species losses: Entering the sixth mass extinction. Science Advances *1*, e1400253.

Collen, B., Whitton, F., Dyer, E.E., Baillie, J.E.M., Cumberlidge, N., Darwall, W.R.T., Pollock, C., Richman, N.I., Soulsby, A.-M., and Böhm, M. (2014). Global patterns of freshwater species diversity, threat and endemism. Global Ecology and Biogeography *23*, 40–51.

Costanza, R., de Groot, R., Sutton, P., van der Ploeg, S., Anderson, S.J., Kubiszewski, I., Farber, S., and Turner, R.K. (2014). Changes in the global value of ecosystem services. Global Environmental Change *26*, 152–158.

Costello, M.J., Wilson, S., and Houlding, B. (2012). Predicting Total Global Species Richness Using Rates of Species Description and Estimates of Taxonomic Effort. Syst Biol *61*, 871–871.

Cramer, W., Guiot, J., Fader, M., Garrabou, J., Gattuso, J.-P., Iglesias, A., Lange, M.A., Lionello, P., Llasat, M.C., Paz, S., et al. (2018). Climate change and interconnected risks to sustainable development in the Mediterranean. Nature Climate Change 1.

Davidson, N.C. (2014). How much wetland has the world lost? Long-term and recent trends in global wetland area. Mar. Freshwater Res. *65*, 934–941.

Dornelas, M., Gotelli, N.J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., and Magurran, A.E. (2014). Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss. Science *344*, 296–299.

Driscoll, D.A., Bland, L.M., Bryan, B.A., Newsome, T.M., Nicholson, E., Ritchie, E.G., and Doherty, T.S. (2018). A biodiversity-crisis hierarchy to evaluate and refine conservation indicators. Nature Ecology & Evolution *2*, 775–781.

Dudley, N. (2013). Guidelines for applying protected area management categories.

Ervin, J. (2002). WWF: rapid assessment and 39. prioritization of protected area management (RAPPAM) methodology.

Faria, W.R., and Almeida, A.N. (2016). Relationship between openness to trade and deforestation: Empirical evidence from the Brazilian Amazon. Ecological Economics *121*, 85–97.

Ferrier, S. (2002). Mapping Spatial Pattern in Biodiversity for Regional Conservation Planning: Where to from Here? Syst Biol *51*, 331–363.

Gaston, K.J., and Fuller, R.A. (2009). The sizes of species' geographic ranges. Journal of Applied Ecology *46*, 1–9.

Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E., et al. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. Nature *478*, 378–381.

Gleick, P.H. (1998). The human right to water. Water Policy *1*, 487–503.

Growcock, A.J., Sutherland, E.F., and Stathis, P.T. (2009). Challenges and experiences in implementing a management effectiveness evaluation program in a protected area system. Australasian Journal of Environmental Management *16*, 218–226.

Haase, P., Tonkin, J.D., Stoll, S., Burkhard, B., Frenzel, M., Geijzendorffer, I.R., Häuser, C., Klotz, S., Kühn, I., McDowell, W.H., et al. (2018). The next generation of site-based long-term ecological monitoring: Linking essential biodiversity variables and ecosystem integrity. Science of The Total Environment *613–614*, 1376–1384.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., et al. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances *1*, e1500052.

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., et al. (2013). High-Resolution Global Maps of 21st-Century Forest Cover Change. Science *342*, 850–853.

Herkt, M., O&#39, B., Connor, Terrapon, H., and Milam, A. (2013). Review of the use of remotely-sensed data for monitoring biodiversity change and tracking progress towards the Aichi Biodiversity Targets.

Hurlbert, A.H., and Jetz, W. (2007). Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. PNAS *104*, 13384–13389.

Isbell, F., Gonzalez, A., Loreau, M., Cowles, J., Díaz, S., Hector, A., Mace, G.M., Wardle, D.A., O'Connor, M.I., Duffy, J.E., et al. (2017). Linking the influence and dependence of people on biodiversity across scales. Nature *546*, 65–72.

Jenkins, C.N., Pimm, S.L., and Joppa, L.N. (2013). Global patterns of terrestrial vertebrate diversity and conservation. PNAS *110*, E2602–E2610.

Jones, J.P.G., Collen, B., Atkinson, G., Baxter, P.W.J., Bubb, P., Illian, J.B., Katzner, T.E., Keane, A., Loh, J., Mcdonald-Madden, E., et al. (2010). The Why, What, and How of Global Biodiversity Indicators Beyond the 2010 Target. Conservation Biology *25*, 450–457.

Jones, J.P.G., Asner, G.P., Butchart, S.H.M., and Karanth, K.U. (2013). The 'why', 'what' and 'how' of monitoring for conservation. In Key Topics in Conservation Biology 2, (Wiley-Blackwell), pp. 327–343.

Jones, K.R., Venter, O., Fuller, R.A., Allan, J.R., Maxwell, S.L., Negret, P.J., and Watson, J.E.M. (2018). One-third of global protected land is under intense human pressure. Science *360*, 788–791.

Joseph, L.N. (2008). Theory to guide management of species for conservation.

Keddy, P.A., Fraser, L.H., Solomeshch, A.I., Junk, W.J., Campbell, D.R., Arroyo, M.T.K., and Alho, C.J.R. (2009). Wet and Wonderful: The World's Largest Wetlands Are Conservation Priorities. BioScience *59*, 39–51.

Keenan, R.J., Reams, G.A., Achard, F., de Freitas, J.V., Grainger, A., and Lindquist, E. (2015). Dynamics of global forest area: Results from the FAO Global Forest Resources Assessment 2015. Forest Ecology and Management *352*, 9–20.

Kissling, W.D., Ahumada, J.A., Bowser, A., Fernandez, M., Fernández, N., García, E.A., Guralnick, R.P., Isaac, N.J.B., Kelling, S., Los, W., et al. (2018). Building essential biodiversity variables (EBVs) of species distribution and abundance at a global scale. Biol Rev *93*, 600–625.

Laurance, W.F., Sayer, J., and Cassman, K.G. (2014). Agricultural expansion and its impacts on tropical nature. Trends in Ecology & Evolution *29*, 107–116.

Leblois, A., Damette, O., and Wolfersberger, J. (2017). What has Driven Deforestation in Developing Countries Since the 2000s? Evidence from New Remote-Sensing Data. World Development *92*, 82–102.

Leroux, S.J., Krawchuk, M.A., Schmiegelow, F., Cumming, S.G., Lisgo, K., Anderson, L.G., and Petkova, M. (2010). Global protected areas and IUCN designations: Do the categories match the conditions? Biological Conservation *143*, 609–616.

Luyssaert, S., Schulze, E.-D., Börner, A., Knohl, A., Hessenmöller, D., Law, B.E., Ciais, P., and Grace, J. (2008). Old-growth forests as global carbon sinks. Nature *455*, 213–215.

Malhi, Y., Roberts, J.T., Betts, R.A., Killeen, T.J., Li, W., and Nobre, C.A. (2008). Climate Change, Deforestation, and the Fate of the Amazon. Science *319*, 169–172.

Mcowen, C.J., Ivory, S., Dixon, M.J.R., Regan, E.C., Obrecht, A., Tittensor, D.P., Teller, A., and Chenery, A.M. (2016). Sufficiency and Suitability of Global Biodiversity Indicators for Monitoring Progress to 2020 Targets. Conservation Letters *9*, 489–494.

Merry, S.E. (2011). Measuring the World: Indicators, Human Rights, and Global Governance: with CA comment by John M. Conley. Current Anthropology *52*, S83–S95.

Miller, D.C., Rana, P., and Wahlén, C.B. (2017). A Crystal Ball for Forests?: Analyzing the Social-Ecological Impacts of Forest Conservation and Management over the Long Term. Environment and Society *8*, 40–62.

Mittermeier, R.A., Robles-Gil, P., and Mittermeier, C.G. (1997). Megadiversity. Earth's Biologically Wealthiest Nations.

Mora, C., Tittensor, D.P., Adl, S., Simpson, A.G.B., and Worm, B. (2011). How Many Species Are There on Earth and in the Ocean? PLOS Biology *9*, e1001127.

Moura, N.G., Lees, A.C., Andretti, C.B., Davis, B.J.W., Solar, R.R.C., Aleixo, A., Barlow, J., Ferreira, J., and Gardner, T.A. (2013). Avian biodiversity in multiple-use landscapes of the Brazilian Amazon. Biological Conservation *167*, 339–348.

Nagendra, H., Lucas, R., Honrado, J.P., Jongman, R.H.G., Tarantino, C., Adamo, M., and Mairota, P. (2013). Remote sensing for conservation monitoring: Assessing protected areas, habitat extent, habitat condition, species diversity, and threats. Ecological Indicators *33*, 45–59.

Naidoo, R., Balmford, A., Costanza, R., Fisher, B., Green, R.E., Lehner, B., Malcolm, T.R., and Ricketts, T.H. (2008). Global mapping of ecosystem services and conservation priorities. PNAS *105*, 9495–9500.

Nichols, J.D., and Williams, B.K. (2006). Monitoring for conservation. Trends in Ecology & Evolution *21*, 668–673.

Pekel, J.-F., Cottam, A., Gorelick, N., and Belward, A.S. (2016). High-resolution mapping of global surface water and its long-term changes. Nature *540*, 418–422.

Pereira, H.M., Leadley, P.W., Proença, V., Alkemade, R., Scharlemann, J.P.W., Fernandez-Manjarrés, J.F., Araújo, M.B., Balvanera, P., Biggs, R., Cheung, W.W.L., et al. (2010). Scenarios for Global Biodiversity in the 21st Century. Science *330*, 1496–1501.

Pereira, H.M., Ferrier, S., Walters, M., Geller, G.N., Jongman, R.H.G., Scholes, R.J., Bruford, M.W., Brummitt, N., Butchart, S.H.M., Cardoso, A.C., et al. (2013). Essential Biodiversity Variables. Science *339*, 277–278.

Peters, D.P.C., Loescher, H.W., SanClements, M.D., and Havstad, K.M. (2014). Taking the pulse of a continent: expanding site-based research infrastructure for regional- to continental-scale ecology. Ecosphere *5*, art29.

Pettorelli, N., Wegmann, M., Skidmore, A., Mücher, S., Dawson, T.P., Fernandez, M., Lucas, R., Schaepman, M.E., Wang, T., O'Connor, B., et al. (2016). Framing the concept of satellite remote sensing essential biodiversity variables: challenges and future directions. Remote Sens Ecol Conserv *2*, 122–131.

Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts, C.M., and Sexton, J.O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. Science *344*, 1246752.

Potapov, P., Hansen, M.C., Laestadius, L., Turubanova, S., Yaroshenko, A., Thies, C., Smith, W., Zhuravleva, I., Komarova, A., Minnemeyer, S., et al. (2017). The last frontiers of wilderness: Tracking loss of intact forest landscapes from 2000 to 2013. Science Advances *3*, e1600821.

Purvis, A., Gittleman, J.L., Cowlishaw, G., and Mace, G.M. (2000). Predicting extinction risk in declining species. Proceedings of the Royal Society of London B: Biological Sciences *267*, 1947–1952.

Rife, A.N., Erisman, B., Sanchez, A., and Aburto-Oropeza, O. (2012). When good intentions are not enough … Insights on networks of "paper park" marine protected areas. Conservation Letters *6*, 200–212.

Rodrigues, A.S.L., Akçakaya, H.R., Andelman, S.J., Bakarr, M.I., Boitani, L., Brooks, T.M., Chanson, J.S., Fishpool, L.D.C., Fonseca, D., B, G.A., et al. (2004). Global Gap Analysis: Priority Regions for Expanding the Global Protected-Area Network. BioScience *54*, 1092–1100.

Scheele, B.C., Hunter, D.A., Grogan, L.F., Berger, L., Kolby, J.E., Mcfadden, M.S., Marantelli, G., Skerratt, L.F., and Driscoll, D.A. (2014). Interventions for Reducing Extinction Risk in Chytridiomycosis-Threatened Amphibians. Conservation Biology *28*, 1195–1205.

Scheffers, B.R., Joppa, L.N., Pimm, S.L., and Laurance, W.F. (2012). What we know and don't know about Earth's missing biodiversity. Trends in Ecology & Evolution *27*, 501–510.

Schmitz, C., Kreidenweis, U., Lotze-Campen, H., Popp, A., Krause, M., Dietrich, J.P., and Müller, C. (2015). Agricultural trade and tropical deforestation: interactions and related policy options. Reg Environ Change *15*, 1757–1772.

Smith, R.J., Veríssimo, D., Leader-Williams, N., Cowling, R.M., and Knight, A.T. (2009). Let the locals lead.

Stolton, S., Hockings, M., Dudley, N., MacKinnon, K., and Whitten, T. (2003). Reporting progress in protected areas : a site-level management effectiveness tracking tool (The World Bank).

Tittensor, D.P., Walpole, M., Hill, S.L.L., Boyce, D.G., Britten, G.L., Burgess, N.D., Butchart, S.H.M., Leadley, P.W., Regan, E.C., Alkemade, R., et al. (2014). A mid-term analysis of progress toward international biodiversity targets. Science *346*, 241–244.

United Nation (1992). Convention on Biological Diversity.

Watson, J.E.M., Dudley, N., Segan, D.B., and Hockings, M. (2014). The performance and potential of protected areas. Nature *515*, 67–73.

Young, H.S., McCauley, D.J., Galetti, M., and Dirzo, R. (2016). Patterns, Causes, and Consequences of Anthropocene Defaunation. Annual Review of Ecology, Evolution, and Systematics *47*, 333–358.

# CHAPTER 1

## HABITAT RARITY AS A DETERMINANT OF FOREST BIRD RANGE SIZE

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*"Now when you cut a forest, an ancient forest in particular, you are not just removing a lot of big trees and a few birds fluttering around in the canopy. You are drastically imperilling a vast array of species within a few square miles of you. ... Many of them are still unknown to science, and science has not yet discovered the key role undoubtedly played in the maintenance of that ecosystem, as in the case of fungi, microorganisms, and many of the insects."*
*— Edward O. Wilson*

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## ABSTRACT

**Aim:** In view to improve prioritization in conservation strategies and help identify the most unique habitats and associated species, we analysed the geographical variability in the relationship between habitat rarity and forest bird range-size in each biogeographical realm and main islands. Several determinants of species range-size were already identified in the literature such as climate rarity or climate change velocity. Therefore, we compared the habitat rarity to other predictors, highlighting underlying processes in explaining rare species patterns.

**Location:** Forest ecosystems at global scale.

**Method:** We developed two Habitat Rarity (HR) indices to study the relationship between HR and forest bird range-size across realms and main islands. The HR indices computed the likelihood that any site has a similar environmental combination elsewhere in a realm, accounting for both ecological and climatic variables ($HR_{All}$), for climatic variables only ($HR_{Clim}$). Species rarity was computed as the average of the inverse of the species ranges within each cell (E). We tested the habitat-rarity-range-size relationship using linear regressions, which we compared to current and historical drivers of species rarity.

**Results:** We found that forests harbouring rare environmental features were globally mainly located in mountainous areas. The $HR_{All}$ index performed generally better to explain forest birds range size than $HR_{Clim}$. However, the direction of the relationship was not consistent across realms. $HR_{All}$ was a good predictor of bird range-size in the rare forests of Africa, Palearctic and South-America, but showed negative relationships in Indo-Pacific forests. No relationship was detected in North-America and Australia. Other variables such as climate change velocity, maximum temperature of the warmest month and precipitation seasonality were very good predictors to explain the distribution of rare species.

**Main conclusion:** The HR index can potentially be used as a species rarity surrogate in Africa, Palearctic and South America, but more studies are needed to support the habitat-rarity-range-size relationship across spatial scales.

**Keywords**: climate rarity, forest birds, global forests, habitat rarity, Mahalanobis distance, species range-size.

## INTRODUCTION

The main ecological and historical processes explaining the distribution of species range size remain an open question in ecological research (Li et al. 2016; Brown 2014; Pimm and Brown 2004). Species range sizes are not distributed evenly globally, with narrow range species mainly present in isolated places that favour speciation processes such as mountainous areas and islands (Steinbauer et al., 2016a; Gillespie and Roderick, 2014a; Orme et al., 2006), as well as in low latitudes, especially in the tropics (Stevens, 1989). This latitudinal gradient was mainly explained by climatic history, where unstable areas that presented high climate change velocity in the past would have led small range species to extinction because of their higher sensitivity of sudden changes (Harris et al. 2014). Stable climatic areas such as mountain ranges or the tropics were then considered as refuges for small range species, explaining their high diversity (Sandel et al. 2011).

Although past climatic events played an important role in the distribution of small range species (Araújo et al. 2008; Jansson 2003), previous studies have reported that the distribution of range-size can be also affected by current climate (Li et al. 2016; Sandel et al. 2011a; Ohlemüller et al. 2008; Pither 2003), land size (Morueta-Holme et al. 2013; Hawkins and Felizola Diniz-Filho 2006), topography (Li et al. 2016), species traits, as well as species interactions (Brooker et al., 2007; Calosi et al., 2008; Laube et al., 2013a). Contemporary factors related to isolation processes such as environmental, behavioural or physical isolation (physical barrier or distance) are shaping species range, fostering small range patterns emergence, and are generally combined with low dispersal abilities (Laube et al., 2013b). Indeed, isolation can narrow distribution widths and species ecological niche, encouraging adaptation and specialisation to the conditions of the occupied area (Reif et al. 2016; Slatyer, Hirst, and Sexton 2013; Devictor et al. 2010). Thus, a habitat having particular environmental conditions should host a specific species community adapted to it. Such a habitat would be then described as rare, as presenting uncommon features in comparison with its average properties. Habitat rarity can be quantified through the use of distance matrices to differentiate what is dissimilar (rare) and the selection of relevant variables that portray the habitat characteristics.

By computing cells presenting analogous climatic conditions, Ohlemüller et al. (2008) tested the relationship of climatic rarity with the richness of species range-size in South-America and Europe. They found high correlation with areas harbouring rare climates and the richness of small range species among the two continents studied, giving some hints about locations where small range species can be the most vulnerable to climate change. Since then, several studies used climatic rarity as a variable to explain species range-size distribution (Sandel et al. 2011a; Morueta-Holme et al. 2013; Irl et al. 2015). Even though different responses of species range-size to climate rarity emerged from those studies, to our knowledge, this relationship has never been assessed between different locations worldwide. To improve our understanding on the influence of historical and current environmental condition on species range-size given the heterogeneity of climate and habitats on earth, it is important to study the responses of species communities to different variables across space. Moreover, climate alone does not capture a full picture of the abiotic characteristics influencing species niche as land-cover, for instance, is also shaping current species distribution (e.g. Barbet-Massin, Thuiller, and Jiguet 2012; Jetz, Wilcove, and Dobson 2007; Hansen et al. 2001). Thus, the use of environmental parameters in addition to climate might strengthen the relationship with species range.

Forests represent about one third of the world land surface (Keenan et al., 2015) covering a wide range of areas with diverse ecological and environmental properties such as topography, hydrology, tree coverage and phenology. Forests also support the majority of terrestrial species, making them the most biodiverse habitat on the planet (Jenkins et al., 2013). The identification of rare ecosystems as well as a better understanding of their relationship with rare species can thus help setting priorities for conservation. Indeed, as forests ecosystems are highly sensitive to change and are affected by human disturbance (Holtmeier and Broll, 2005; Pan et al., 2013), the identification of areas which have rare environmental conditions should facilitate the identification of regions that might harbour unique species assemblages which could be at risk (Stuart L. Pimm and Jenkins 2005; Purvis et al. 2000).

Therefore, we explored whether the rarity of forest habitats can be used as a surrogate for species range-size through the development of a Habitat Rarity (HR) index. We characterized forests habitats HR through climate, topography, soil properties and vegetation cover (including primary production and phenology). We then assessed how different groups of variables contribute to explain the average of rare birds species within birds' communities by comparing a bird rarity index (E) with two HR indices taking into account: climate rarity alone ($HR_{Clim}$), and including both climate and other environmental variables ($HR_{All}$). We also investigated the contribution of each input variable used to compute the HR indices spatially (e.g. rare forests habitat in southern Europe harbour unusual aridity) and its potential weight in driving the relationship of species rarity.

To assess the relative importance of the HR in explaining species rarity, we added other competing variables in multi-predictor models such as climate extremes and seasonality (i.e. precipitation of the driest month, precipitation of the wettest month, maximum temperature of the warmest month, precipitation seasonality (Hijmans et al. 2005), climate change velocity of the late quaternary as historical climatic predictor (Sandel et al. 2011a), and net primary production (NPP) to account for productivity (Imhoff et al. 2004). It has been demonstrated that an increase of extreme climate tolerance would generate broader species range-size as the climatic ecological niche is bigger (Bozinovic, Calosi, and Spicer 2011). Similarly, an increase of precipitation seasonality, on which food availability depends, can promote extinction risk of local populations (Bozinovic, Calosi, and Spicer

2011; Pither 2003). Finally, areas with higher climate change velocity would select for larger range size, and favour dispersal ability (Morueta-Holme et al. 2013), and an increase of NPP that reflects forest productivity would lead to an increase of specialised species and so restricted range-size (Belmaker, Sekercioglu, and Jetz 2012).

Because birds are perhaps the class with the best information on species distribution, and because they have the highest dispersal abilities among vertebrates, they represent a good candidate to test the impact of current habitat features on their distribution. Moreover, the composition of forest bird communities can have a strong dependency on forest type and properties (Roll, Geffen, and Yom-Tov 2015; Jankowski et al. 2013; Pomara et al. 2012; Lee and Rotenberry 2005).

In this study, we (1) provide a first global map of rare forests habitat ($HR_{All}$) at 5×5 and 100×100 $km^2$ resolution and compute a climate rarity index ($HR_{Clim}$) to (2) test the hypothetical relationship of forest habitat or climatic rarity with species range-size among different locations, such as biogeographical realms and main islands, (3) compare the relevance of the relationship with alternative species rarity predictors, and (4) assess the weight of each input variable in the $HR_{All}$ index values and their influence on the habitat-rarity-range-size relationship. The spatial weight of each input variable was tested to know what variable increases the HR score and where.

## MATERIALS AND METHODS

### STUDY AREA AND REFERENCE DATA

Forested areas were delineated from the European Spatial Agency Climate Change land cover map Initiative (Defourny et al. 2016, ESA CCI: http://www.esa-landcover-cci.org/) using a broad definition of forests (areas with at least 15 percent of tree cover), covering a diverse set of forests types: 1) broadleaved evergreen, 2) broadleaved deciduous, 3) needle-leaved evergreen, 4) needle-leaved deciduous, 5) mixed leaf type, 6) flooded fresh water and 7) flooded saline water.

We considered six biogeographical realms based on the maps of Cox (2001) and Olson et al. (2001): Nearctic and Palearctic realms from Olson, and South American, African, Indo-Pacific and Australian realms from Cox. However, we slightly reshaped the Indo-Pacific realm delineation around the Himalayas as forests patches inflated the rarity index when associated with the Palearctic. We therefore joined a number of ecoregions defined by Olson originally attributed to the Palearctic realm to the Indo-Pacific one in order to generate a continuous forest cover (see Figure S1). As spatial isolation has a strong impact on species range-size, and because of the resolution considered, we excluded most of the islands from the analyses with the exception of Madagascar, Papua New Guinea and Borneo that have a continuous land area (e.g. unlike New Zealand) and considered large enough to have sparse forests hosting different species communities (Vences et al. 2009). Each one of these islands was analysed separately from the realms.

We selected the breeding range of forest bird specialist species using dataset differenciating birds habitat use from Birdlife international (BirdLife International and NatureServe, 2015), resulting in a total of 7,468 bird species available at 5×5 km resolution. To improve the accuracy of the 5×5 km data, we estimated the potential Extent of Suitable Habitat (ESH) that reduced the commission error given by the Extent of Occurrence (Beresford et al. 2010). The ESH of each forest-dependent species was produced taking into account their altitudinal limits by clipping their range according to the forest cover and altitude (BirdLife International and NatureServe 2015). Despite those corrections, even though fine-scale species range maps are relevant for conservation application, their accuracy is still insufficient (Hurlbert and Jetz 2007). Therefore, we modified the species data resolution to a 100×100 km grain.

To quantify species rarity, we searched for a metric that is continuous (higher sensitivity) and independent from species richness in a way that for the same amount of rare species, areas with higher species richness would have the same score as areas with lower richness. To discard most of the relationship with range-size and species richness, we used the corrected weighted endemism index of species within a grid cell (*E; Crisp et al. 2001)* at 100×100 km. This index was calculated as the inverse of the sum of the range areas of each species $A_i$, divided by the number of species occurring in each cell *n* as (equation 1):

$$(1) \qquad E=\frac{1}{n}\sum_{i=1}^{n}\frac{1}{A_i}$$

Therefore, a cell with a high E value is considered as hosting a high proportion of rare species. A slight correlation of $r^2$=-0.02 with species richness remained.

## FOREST HABITAT DEFINITION AND CHARACTERIZATION

We characterized forest habitat by different variables portraying the vegetation structure and topography (environmental variables), as well as climate types influencing forest composition. A set of 19 continuous variables was compiled from global datasets available at 1 km resolution (Table S1). Even though the analyses we performed to compute the Habitat Rarity index took into account correlation between variables, only the variables presenting pairwise correlations lower than 0.8 were selected out of the 19 to avoid biased weight in the rarity indicator (Figure S2, S3). This led to a final selection of 11 variables. Climatic conditions were characterised by five variables: (1) temperature seasonality, (2) maximum temperature of the warmest month, (3) mean annual precipitation obtained from interpolated maps from 1950 to 2000, (4) precipitation of the driest month (Hijmans et al. 2005), and (5) an aridity index (Trabucco et al. 2008). 'Forest-related' variables were characterized by six variables, computed as mean values over the period 2001 to 2010 of: the (6) Maximum and (7) Minimum annual Normalized Difference Vegetation index (NDVI maximum and NDVI minimum, Carroll et al. 2004), (8) tree height (Simard et al. 2011), (9) tree cover density (Crowther et al. 2015), (10) soil pH (Hengl et al. 2014), and (11) slope (Farr et al. 2007). All the forest-related variables have been previously used in the literature to explain species distribution patterns (Roll, Geffen, and Yom-Tov 2015; John et al. 2007; Irl et al. 2015b). We aggregated each selected variable from 1km to 5km resolution by averaging using a Mollweide projection. The 5 km spatial resolution was considered fine enough to highlight forests habitat features, and coarse enough to reduce interpolation bias from input variables and the effects of temporal changes since the data were collected across a long time period (Table S1). For the forest delineation, we used the ESA CCI map available originally at 300 m resolution that we lowered to 5km x 5km cell resolution to match the spatial scale of the variables. Additionally, to reduce the forest edge effect bias affecting the rarity values, we selected only 5km x 5km cells presenting more than 50% tree cover.

### Habitat Rarity index

We computed the Habitat Rarity (HR) for each cell in each realm at 5×5 km resolution. By comparing each forest cell to the entire realm, we aimed to reveal forests features that are not present elsewhere within the realm, making these areas unique niches. The multivariate distance of each cell $i$ to all the other cells in the environmental hyperspace was computed using the Mahalanobis distance ($D$) for each of the set of environmental and climate variables (De Maesschalck, Jouan-Rimbaud, and Massart 2000; Mahalanobis 1936) following equation 2:

$$(2)\, D_i^2 = [x\|i-\mu]^T [C]^{-1} [x\|i-\mu]$$

where $x_i$ is the vector of the values of the environmental variables for each cell $i$, $\mu$ is the mean of the environmental variables within a realm, and [C] is the covariance matrix of the eleven environmental variables in the realm. As $D_i^2$ follows a Chi-squared distribution, we used the probability density function to convert the resulting distances into the probability of a cell P(x,y) of having similar values to the mean of the 'area of interest' (here the biogeographical realms; Dubois et al. 2013). Habitat Rarity was then defined as HR(x,y)=1-P(x,y) ranging from 0 to 1, representing low to high dissimilarity respectively. The Mahalanobis distance has many advantages such as being computationally fast, producing better fits compared to other methods (Tsoar et al. 2007; Farber and Kadmon 2003), and its consideration of the correlation between variables by diminishing the effect of the highly correlated ones as well as being independent of scales or measurement units by the use of the inverse covariance matrix.

We calculated two Habitat Rarity indices: 1) using both the climate and the forest-related variables described above ($HR_{All}$), and 2) the climate rarity index ($HR_{Clim}$) using climate variables only (from 1 to 5 as previously labelled) (Figure 1). More details about the computation of the HR can be found in Dubois et al. (2013) and Skøien et al. (2013). The software implementation used Python 2.7 (Van Rossum and Drake 2016) and GRASS 7 (Neteler et al. 2012), and the processing time was optimized using parallel processing by Martínez-López (2014) (code freely available at https://github.com/RoxanneLeb/Habitat_Rarity).

To assess the importance of each of the variables in the HR index, we excluded each variable once and computed HR using the other ten variables ($HR_{10}$). We then calculated the absolute difference between $HR_{all}$ and $HR_{10}$ in order to obtain a map with the spatial importance of each variable in $HR_{all}$ (Figure S4). A score of importance of variables, $I_{var}$, was then computed as equation 3 with $n_{xy}$ the total number of *xy* cells:

$$\left(3\right) I_{var} = ¿$$

Radar plots presenting the results of $I_{var}$ were then produced to highlight which variables were most important in each realm (Figure 2.b). Finally, in order to compare the HR values to bird species data, the 5×5 km resolution HR map (Figure S5, raster file available for downloading) was subsequently lowered to 100×100 km, aggregated by the mean values.

### STATISTICAL ANALYSES

To test the $HR_{All}$ and $HR_{Clim}$ indices as predictors of bird range-size, we used ordinary least square (OLS) regression with forest bird range-size ($E$) as the response variable, log-transformed to follow a Gaussian distribution. To test the relevance of the HR as a predictor variable, we added other competing variables in the models to explain species range-size such as precipitation of the driest month, precipitation of the wettest month, precipitation seasonality, maximum temperature of the warmest month (Hijmans et al. 2005), climatic velocity (Sandel et al. 2011a), and net primary production (NPP, Imhoff et al. 2004) to account for productivity that we normalised to have comparable slopes.

To prevent collinearity issues among the predictors, we discarded the ones that presented a Variance Inflation Factor (VIF) value above 5 (O'brien 2007): temperature seasonality, mean annual precipitation, minimum temperature of the coldest month, and mean annual precipitation. To test if the removal of any of the input variables influenced the relationship, we applied the OLS model separately on each one of the eleven response variables $HR_{10}$. We tested for the presence of spatial autocorrelation in the residuals of each OLS model using Moran's I, taking the eight nearest neighbouring cells. As spatial autocorrelation was significant for all models, we applied a spatial autoregressive error ($SAR_{err}$) model with a row-standardization for the spatial weights matrix (F. Dormann et al. 2007; Kissling and Carl 2008). To assess the $SAR_{err}$ model fits to the data, we used the Nagelkerke's pseudo-r squared (Nagelkerke 1991) as correlation coefficient, calculated as the squared Pearson correlation between predicted and observed data (Kissling and Carl 2008). We then focused on the results from the SARerr model that outperformed the OLS model by diminishing autocorrelation effect at a negligible level and providing a better fit to explain species rarity (Table S2). All statistical analyses were performed using R (R Core Team 2015) and the package ‘spdep’ for the $SAR_{err}$ model (Bivand, 2016).

## RESULTS

### HABITAT RARITY INDEX PER REALM

The rarest forest habitats of the Western-Hemisphere (North and South American realms) were mainly located in mountainous areas (Andes and Rocky Mountains), in the southern part of South-America, and the northern part of Mexico (Figure 1.a and S2). African forest habitats were highly distinct around the west coast from Senegal to Gabon, with high HR values in central Congo where the driest months presented unusual rainfall (see preD maps, Figure S4), as well as the South African forest habitat and east Congo within the Virunga area. In the Palearctic, all the Mediterranean forest habitats, the Norwegian and Korean forested area, and some parts in Eastern Russia were very rare in comparison to the realm average. In the Indo-Pacific realm the most distinct forest habitats were in northern China and central India. The rarest Australian forest habitats were mainly in the Cape York Peninsula. Concerning the islands studied, the mountainous areas of Papua presented very different environmental features from the rest of this island.

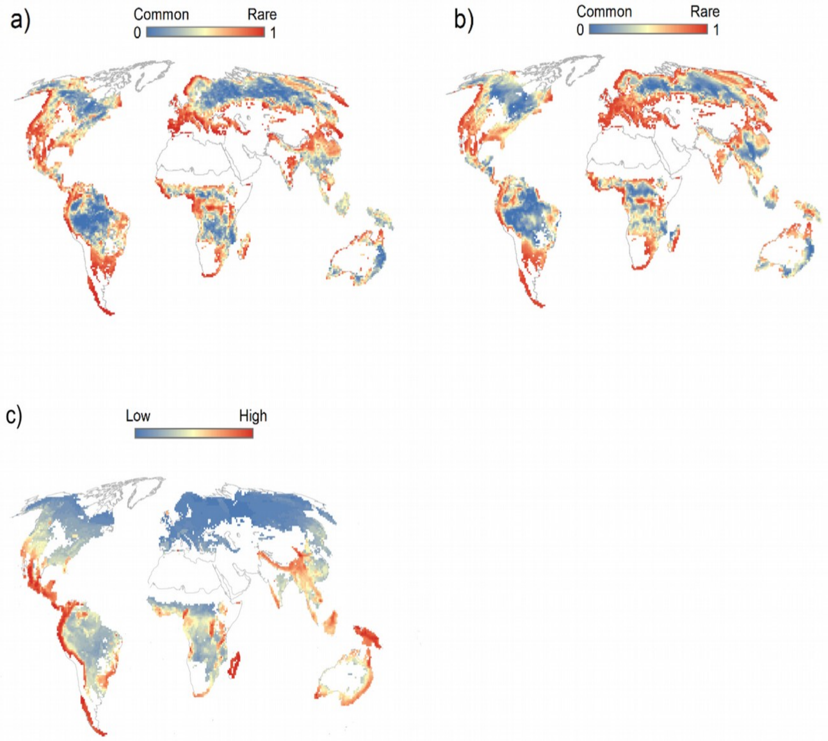

**Figure 1.** Habitat Rarity maps computed for each realm and islands at 100 km resolution with a) all variables ($HR_{all}$), b) climate variables ($HR_{clim}$), c) corrected weighted endemism index (E) map of forest bird at 100 km resolution, with high values in red revealing concentrations of restricted range species.

The highest importance score $I_{var}$ concerning the variable contribution to compute $HR_{All}$ was attributed to the soil pH reaching a maximum of 0.014 in Africa (Figure 2). The importance score excluding the soil pH also showed high values in Palearctic ($I_{var}$ = 0.010) and in Nearctic ($I_{var}$ = 0.011) close to the tree density $I_{var}$ in this realm. However, the importance of soil pH was outperformed in South-America by temperature seasonality, in Australia by the maximum NDVI and in Indo-Pacific, where rare forest habitats were mainly influenced by the maximum temperature of the warmest month. The precipitation of the driest month as well as the maximum temperature of the warmest month were also quite important in Africa ($I_{var}$ = 0.010; Figure S4). The correlation between the $HR_{All}$ and $HR_{Clim}$ indices was unsurprisingly strong among realms, ranging from 0.62 in Australia to 0.93 in Palearctic (Table S3).

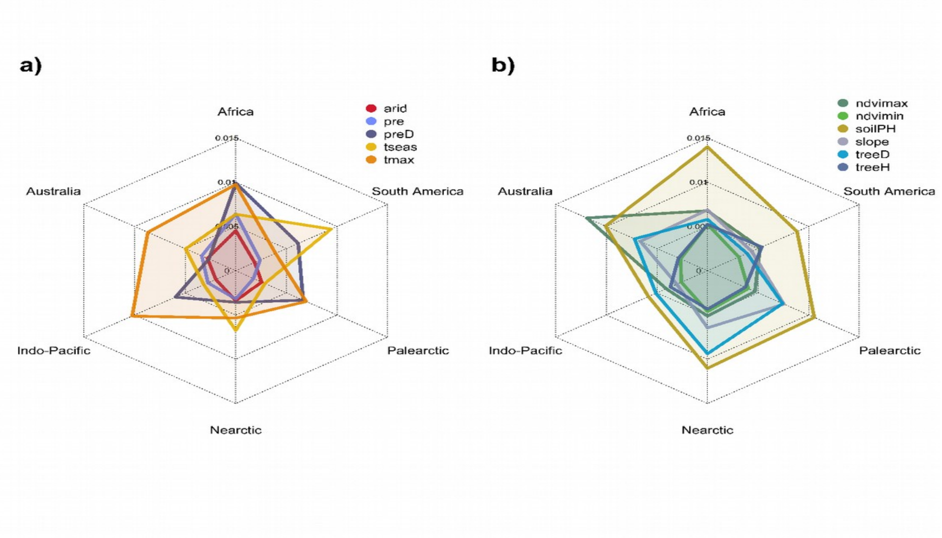

**Figure 2.** a) Importance of variables ($I_{var}$) for each realm (from 0 to 0.015) considering the climatic variables at 100 km resolution, b) importance of variables for each realm considering the variance of the absolute difference between $HR_{all}$ and $HR_{10}$ (from 0 to 0.015) considering the ecological variables at 100 km resolution. With arid = aridity index, pre = annual mean precipitation, preD = precipitation of the driest month, tseas = temperature seasonality, tmax = maximum temperature of the warmest month, ndvimax = maximum NDVI, ndvimin = minimum NDVI, soilPH = soil pH, slope, treeH = tree height, treeD = tree density.

## BIRD RANGE-SIZE AND HABITAT RARITY

The relationship between rare forest birds and habitat taking into account both environmental and climatic variables ($HR_{All}$) was significantly positive in Africa, Palearctic and South America under the single-predictor $SAR_{err}$ model (Table 1), which suggests that in those realms, forests with rare habitat host rarer species than common forests. In contrary, the relationship in Indo-Pacific was significantly negative. Both $HR_{All}$ and $HR_{Clim}$ indices always shared the same sign across realms but their significance can differ. For instance, $HR_{All}$ was significantly positive in Africa, while there was no relationship with $HR_{Clim}$ (Table 1). Inversly, $HR_{Clim}$ was significantly negative in Australia, while $HR_{All}$ showed no signal.

When we incorporated the HR indices into multi-predictor models, the slopes stayed constant when results were significant, unlike single-predictor models (Table 1). However, the significance of the HR indices changed in some realms, like in Africa where $HR_{All}$ was not significant anymore as well as in Indo-Pacific concerning $HR_{Clim}$, or in Palearctic where $HR_{Clim}$ became positively significant. Multi-predictor models were always better to explain species rarity with the lowest AIC, accounting for at best 93% of the variation in the North-American realm. Overall, the pseudo $R^2$ values were very high with a minimum value for the single-predictor model in Indo-Pacific of 72% and 73% for $HR_{All}$ and $HR_{Clim}$ respectively. Among all, the best predictors in explaining species rarity were climate change velocity of the Quartenary followed by maximum temperature of the warmest month, precipitation seasonality and NPP. All predictors had a constant pattern across realms when significant, with the exception of NPP that became significantly negative in the South-American realm. Thus, species rarity was usually higher in stable areas with low historical climate change velocity, low temperature extremes and precipitation seasonality and high productivity. Climate velocity had a constant negative relationship with species range size across realms and island – with the exception of Madagascar ($p$ = 0.067, Table 2) where none of the predictors were significant. Regarding the two other islands studied, a significant positive relationship appeared between rarity and bird range-size in Papua.

The removal of each one of the input variables from the HR index changed the nature or significance of the relationship in some cases, demonstrating the importance of some variables to hold the relationship (Table S4). For instance, in Africa, the removal of tree density from the HR index reversed the relationship with birds range-size. In that case, places with uncommon levels of tree density would host restricted range species. Inversely, the removal of the same variable reversed the negative relationship in Australia and Indo-Pacific, meaning that areas with average tree density in those realms would host restricted range species. In addition to tree density, temperature seasonality also inverted the negative relationship in North-America where the relationship became positively significant with the removal of the tree density variable. Tree density, maximum temperature of the warmest month, and aridity were the variables that led to the positive relationship in Palearctic where small range species occurred mostly around the Mediterranean.

## DISCUSSION

Our study showed that in Africa, Palearctic and South America, forests with rare habitat ($HR_{All}$) host more rare species than common ones, and that species rarity increased in South America with rare climate ($HR_{Clim}$). Nevertheless, both HR indices failed to predict the distribution of range-size in North America, and predicted an inverse pattern than the expected one for the Indo-Pacific and, for $HR_{Clim}$ only, the Australian forests. The multiple predictor models help in understanding those patterns highlighting the underlying drivers explaining species rarity. For instance, species rarity was strongly driven by a latitudinal gradient in North America as shown by an increasing productivity and decreasing precipitation seasonality as well as climate change velocity, in line with previous studies (Sandel et al. 2011a; Hawkins and Felizola Diniz-Filho 2006).

In Australia, productive forests with both low maximum extreme climate and precipitation seasonality also hosted rarer species. Moreover, the Australian forests showed spatial discontinuity between the few forests patches that are localised in distinct bioregions (Bloomfield, Knerr, and Encinas-Viso 2017). The size of species range can thus depend mostly on the forest area of each patch rather than its habitat property. Other drivers that were not taken into account in this study such as isolation by distance from the different forests patches could then improve the model in explaining Australian forest bird range-size. In the Indo-Pacific realm, the rarest forests were present in some parts of the Western China Himalayas, where a high level of small range birds has been observed (Lei et al. 2003), and lowland central China. The lowland areas of central China identified as rare according to the $HR_{All}$ index host a low proportion of small range birds. The mountainous physical barriers in Western China shaped by intense tectonic activities occurring in the late Pliocene (J. Li and Fang 1999) caused species isolation over millions of years (Päckert et al. 2012). This long term isolation combined with an exceptional climatic – and thus habitat – stability led to an intense diversification process within the south-western mountainous area (Qu et al. 2014). As Chinese forests are mostly present in mountains, those having the highest and lowest elevations present rarer features compared to the middle elevation forests where most rare birds species occur (Lei et al. 2003). Therefore, historical drivers of bird range-size in the Indo-Pacific are very strong (Lei et al. 2015) as testified by the climate velocity values, while the Habitat Rarity metric predicts an inverse pattern with small range species mostly present in common forest habitat.

Most of the forested mountain range habitat appeared unsurprisingly rare by their highly heterogeneous environmental condition and slope. Small range-size species in these areas are known to be explained by complex contributions of both historical and contemporary factors (Morueta-Holme et al. 2013; Fjeldså, Bowie, and Rahbek 2012). Therefore, adding predictor variables to the single SARerr model allowed revealing a HR effect masked by other factors. For instance, adding multiple predictors revealed a positive effect of HR on species range-size in Africa that might have been masked by significant negative correlates such as maximum temperature of the warmest month or climatic velocity within the single predictor model.

Our results concerning both $HR_{All}$ and $HR_{Clim}$ were consistent with previous findings by Ohlemüller et al. (2008), although we used a different approach. Indeed, they used neighbouring cells to compute climatic rarity at coarse resolution, and small range species richness as proxy for species rarity. Nevertheless, by comparing each cell to the realm's forests, we found similar rare zones to Ohlemüller et al. (2008), such as the Andes Mountains, the northern and western parts of the Iberian Peninsula, the Alps and Norway. By revealing rare climatic areas and focusing their analyses on South

America and Europe, Ohlemüller et al. (2008) suggested that climatic rarity constrained species range-size within these two continents. However, we showed through this study that this pattern is not consistent through all realms and that the inclusion of variables characterizing habitat features can improve the model performances, depending on the location. Our results strengthen the importance of historical factors to explain species distribution patterns, with small range species occurring mostly in low climate velocity areas as it was recently widely acknowledged (Morueta-Holme et al. 2013; Sandel et al. 2011).

The HR indices depend on the choice of the input variables, and the removal of one of them can induce changes in the nature of the relationship with bird range-size. For instance, the relationship with restricted range species became positively significant in North America as initially expected with the removal of the variable tree cover density within the Habitat Rarity computation. Despite the fact that tree density is representative of certain ecosystem types (Crowther et al. 2015), tree density displayed the rarest pattern in the southern Canadian forests, which was not connected with rare species patterns in the North American realm.

The various results obtained using habitat or climate rarity within the islands did not enable us to draw coherent conclusions about a relationship with species rarity. Moreover, Irl et al. (2015) found a minor importance of climate rarity as a potential factor of range-size in the Canary Islands (Spain) to explain birds range size. More studies are thus needed to assess a potential effect of rarity on range-size in island ecosystems.

We used a 100x100 km resolution matching that of the small range species data, but the relationship between HR and range-size can be affected by grain size. Indeed, it was shown that using finer resolution fostered the emergence of very narrow-range species (Rahbek 2005) specialized to their environment (Reif et al. 2016; Belmaker, Sekercioglu, and Jetz 2012). Moreover, the HR value depends on the reference area of comparison and the variables used, relative to the research question. Areas which are common at the realm level can be unique at a smaller spatial scale, revealing for instance localized niches for species with limited dispersal abilities. Therefore, when applying this metric to other species, even though global range-size patterns are correlated among vertebrates (Lamoreux et al. 2006), the rare or distinct areas highlighted at a realm scale may be less relevant for more dispersal limited species such as non-flying species. This suggests that future analyses with other grain sizes or reference areas may reveal further associations of habitat rarity and distribution of range-size. Thus, it would be interesting to compute HR metrics using neighbouring cells – which would better match species dispersal behaviour – using Mahalanobis distances. To do so, a moving window approach could be implemented in further studies to test the predictive power of the model in detecting small range species.

The absence of relationship observed in some realms between bird range-size and forest habitat rarity index can be attributed to different factors. First, we did not consider the different forests types (e.g. oak or beech forests) that can have a significant effect in the composition of birds' communities (Fleishman and Mac Nally 2006; Lee and Rotenberry 2005). By developing this rarity index, we aimed to allow the inclusion of other taxonomic groups (e.g. trees, amphibians or mammals) in further research, as well as the improvement of the HR index regarding the increasing high resolution data availability. A $HR_{All}$ raster file from the $25km^2$ map is thus made freely available as well as the computation code (Figure S5 available for downloading, and code url in method section). Second, forests can be prone to recent human-induced changes modifying their properties that can potentially affect their rarity captured by variables such as NDVI, tree height or density. For example, forest plantations within a primary forest could appear rarer due to smaller and sparse trees with different reflectance of the canopy. Reversely, former rare forest habitats can become more common by human intervention that artificially modify disturbance regimes through land management or abandonment (e.g. fire regime modification, grazing, etc.). Even though the scale analysed at 100×100 km might barely capture such practices, it is important for the interpretation of the 5×5 km map or future work to keep in mind that the $HR_{All}$ index integrating environmental data should be interpreted with care.

The conservation importance of a habitat cannot be assessed without considering its species community. Therefore, the integration of species – plants and animals – is essential for the conservation value of a site (Eken et al. 2004). However, as uncertainty concerning the distribution of restricted range species is still high (Pimm et al. 2014), habitat rarity can be an interesting proxy to consider in the identification of important areas to protect at finer scale when they are congruent with the presence of unique species assemblages. As highlighted by Asaad et al. (2017), the uniqueness of a habitat is one of the important criteria to consider in the identification of areas for biodiversity conservation, among three others: fragile and sensitive habitats, areas important for ecological integrity and habitat representativeness that encompasses the habitat attributes. The integration of all these criteria is thus needed to provide a complete and comprehensive assessment of places to protect. Working at a habitat level such as forest allows taking into consideration its different ecosystems for prioritisation. Nevertheless, it would be relevant to compare the rarest places within smaller connected ecological units (e.g. ecoregions or forests types) to identify which location should be prioritized within the entire ecological unit.

We demonstrated through this study that the habitat-rarity-range-size relationship is not congruent between realms and that the integration of both climatic and environmental variables can be important to consider. The Habitat Rarity index we developed allows the inclusion of as many continuous variables as desired and can be used to process fine grain data at high speed. It can be therefore easily improved in the near future by the emergence of new global data with finer resolution, that captures other habitat properties. We suggest that the use of the Habitat Rarity metric as an indicator of small range species could be applied in South America, Palearctic and Africa, especially with the support of additional studies regarding spatial uncertainty, metric sensitivity to different species order, to different spatial scales and to different computing approaches (neighbouring cells comparison).

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## REFERENCES

Asaad, I., Lundquist, C. J., Erdmann, M. V., Costello, M. J. (2017). Ecological Criteria to Identify Areas for Biodiversity Conservation. *Biological Conservation*. Accessed October 26. doi:10.1016/j.biocon.2016.10.007.

Barbet-Massin, M., Thuiller, W., and Jiguet, F. (2012). The Fate of European Breeding Birds under Climate, Land-Use and Dispersal Scenarios. *Global Change Biology* 18 (3): 881–90. doi:10.1111/j.1365-2486.2011.02552.x.

Barry Cox. 2001. "The Biogeographic Regions Reconsidered." *Journal of Biogeography* 28 (4): 511–23. https://doi.org/10.1046/j.1365-2699.2001.00566.x.

Belmaker, J., Sekercioglu, C.H., and Jetz W. (2012). Global Patterns of Specialization and Coexistence in Bird Assemblages. Journal of Biogeography 39 (1):193–203. https://doi.org/10.1111/j.1365-2699.2011.02591.x.

Beresford, A. E., G. M. Buchanan, P. F. Donald, S. H. M. Butchart, L. D. C. Fishpool, and C. Rondinini. 2010. Poor Overlap between the Distribution of Protected Areas and Globally Threatened Birds in Africa. *Animal Conservation* 14 (2): 99–107. https://doi.org/10.1111/j.1469-1795.2010.00398.x.

BirdLife International and NatureServe. (2015). Bird Species Distribution Maps of the World. BirdLife International, Cambridge, UK and NatureServe, Arlington, USA.

Bivand, R. and Piras, G. (2016). Comparing Implementations of Estimation Methods for Spatial Econometrics. Journal of Statistical Software.

Bloomfield, N. J. Knerr N., Encinas-Viso F. (2017). A comparison of network and clustering methods to detect biogeographical regions. *Ecography* 40. doi:10.1111/ecog.02596.

Bozinovic, F., Calosi P., and Spicer J. I. 2011. "Physiological Correlates of Geographic Range in Animals." *Annual Review of Ecology, Evolution, and Systematics* 42 (1): 155–79. https://doi.org/10.1146/annurev-ecolsys-102710-145055.

Brooker, R. W., Travis J. M. J., Clark E. J., and Dytham C. (2007). Modelling Species' Range Shifts in a Changing Climate: The Impacts of Biotic Interactions, Dispersal Distance and the Rate of Climate Change. *Journal of Theoretical Biology* 245 (1): 59–65. doi:10.1016/j.jtbi.2006.09.033.

Brown, J. H. (2014). Why Are There so Many Species in the Tropics? *Journal of Biogeography* 41 (1): 8–22. doi:10.1111/jbi.12228.

Calosi, P., Bilton, D.T., Spicer, J. I., and Atfield, A. (2008). Thermal Tolerance and Geographical Range Size in the Agabus Brunneus Group of European Diving Beetles (Coleoptera: Dytiscidae). *Journal of Biogeography* 35 (2): 295–305. doi:10.1111/j.1365-2699.2007.01787.x.

Carroll, M. L., DiMiceli, C.M., Sohlberg, R.A., and Townshend, J.R.G. (2004). 250 M MODIS Normalized Difference Vegetation Index. University of Maryland, College Park, Maryland. ISO 690.

Cox, B. (2001). The Biogeographic Regions Reconsidered. *Journal of Biogeography* 28 (4): 511–23. doi:10.1046/j.1365-2699.2001.00566.x.

Crisp, M. D., S. Laffan, H. P. Linder, and A. Monro. 2001. "Endemism in the Australian Flora." Journal of Biogeography 28 (2): 183–98. https://doi.org/10.1046/j.1365-2699.2001.00524.x.

Crowther, T. W., Glick, H. B., Covey, K. R., Bettigole, C., Maynard, D. S., … Bradford M. A. (2015). Mapping Tree Density at a Global Scale. *Nature* 525 (7568): 201–5. doi:10.1038/nature14967.

Defourny, P., Bontemps, S., Lamarche, C., Brockmann, C., Boettcher, M., Wevers, J., … Santoro, M. (2016). Land Cover CCI: Product User Guide Version.

De Maesschalck, R., Jouan-Rimbaud, D., and Massart, D. L. (2000). The Mahalanobis Distance. Chemometrics and Intelligent Laboratory Systems 50 (1):1–18. https://doi.org/10.1016/S0169-7439(99)00047-7.

Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W., Venail, P., Villéger, S., and Mouquet, N. (2010). “Defining and Measuring Ecological Specialization.” Journal of Applied Ecology 47 (1):15–25. https://doi.org/10.1111/j.1365-2664.2009.01744.x.

Dubois, G., Schulz, M., Skøien, J., Bastin, L., and Peedell, S. (2013). eHabitat, a Multi-Purpose Web Processing Service for Ecological Modeling. *Environmental Modelling & Software* 41 (March): 123–33. doi:10.1016/j.envsoft.2012.11.005.

Dormann, C. F, McPherson, J. M., Araújo, M. B., Bivand, R., Bolliger, J., … Wilson, R. (2007). Methods to Account for Spatial Autocorrelation in the Analysis of Species Distributional Data: A Review. *Ecography* 30 (5): 609–28. doi:10.1111/j.2007.0906-7590.05171.x.

Eken, G., Bennun, L., Brooks, T. M., Darwall, W., Lincoln, D. C. (2004). Key Biodiversity Areas as Site Conservation Targets. *BioScience* 54 (12): 1110–18. doi:10.1641/0006-3568(2004)054[1110:KBAASC]2.0.CO;2.

Farber, O., and Kadmon, R. (2003). Assessment of Alternative Approaches for Bioclimatic Modeling with Special Emphasis on the Mahalanobis Distance. Ecological Modelling 160 (1):115–30. https://doi.org/10.1016/S0304-3800(02)00327-7.

Farr, T. G., Rosen, P. A., Caro, E., Crippen, R., Duren, R., Hensley, S., … Alsdorf, D. (2007). The Shuttle Radar Topography Mission. *Reviews of Geophysics* 45 (2): RG2004. doi:10.1029/2005RG000183.

Fjeldså, J., Bowie, R. C. K., and Rahbek, C. (2012). The role of mountain ranges in the diversification of birds. *Annual Review of Ecology, Evolution, and Systematics* 43: 249-265.

Fleishman, E., and R. Mac Nally. 2006. “Patterns of Spatial Autocorrelation of Assemblages of Birds, Floristics, Physiognomy, and Primary Productivity in the Central Great Basin, USA.” Diversity and Distributions 12 (3): 236–43. https://doi.org/10.1111/j.1366-9516.2006.00240.x.

Gillespie, R. G., and Roderick, G. K. (2014). Evolution: geology and climate drive diversification. *Nature* 509 (7500): 297-298.

Hansen, A. J., Neilson, R. P., Dale, V. H., Flather, C. H., Iverson, L. R., Currie, D. J., Shafer, S., Cook, R., and Bartlein, P. J. (2001). Global Change in Forests: Responses of Species, Communities, and BiomesInteractions between Climate Change and Land Use Are Projected to Cause Large Shifts in Biodiversity. BioScience 51 (9):765–79. https://doi.org/10.1641/0006-3568(2001)051[0765:GCIFRO]2.0.CO;2.

Harris, J. B. C., Berton C., Putra, D. D., Gregory, S. D., Brook, B. W., Prawiradilaga, D. M., Sodhi, N. S., Wei, D., and Fordham, D. A. (2014). Rapid deforestation threatens mid-elevational small range birds but climate change is most important at higher elevations. *Diversity and distributions 20*(7): 773-785.

Hawkins, B. A. and Felizola Diniz-Filho, J. A. (2006). Beyond Rapoport’s Rule: Evaluating Range Size Patterns of New World Birds in a Two-Dimensional Framework. *Global Ecology and Biogeography* 15 (5): 461–69. doi:10.1111/j.1466-822X.2006.00243.x.

Hengl, T., Mendes de Jesus, J., MacMillan, R. A., Batjes, N. H., Heuvelink, G. B. M., Ribeiro, E., Samuel-Rosa, A. (2014). SoilGrids1km — Global Soil Information Based on Automated Mapping. *PLOS ONE* 9 (8): e105992. doi:10.1371/journal.pone.0105992.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., and Jarvis. A. (2005). Very High Resolution Interpolated Climate Surfaces for Global Land Areas. *International Journal of Climatology* 25 (15): 1965–78. doi:10.1002/joc.1276.

Holtmeier, F. and Broll, G. (2005). Sensitivity and Response of Northern Hemisphere Altitudinal and Polar Treelines to Environmental Change at Landscape and Local Scales. *Global Ecology and Biogeography* 14 (5): 395–410. doi:10.1111/j.1466-822X.2005.00168.x.

Hurlbert, A. H., and Jetz, W. (2007). Species Richness, Hotspots, and the Scale Dependence of Range Maps in Ecology and Conservation. *Proceedings of the National Academy of Sciences* 104 (33): 13384–89. doi:10.1073/pnas.0704469104.

Irl, S. D. H., Harter, D. E. V., Steinbauer, M. J., Gallego Puyol, D., Fernández-Palacios, J. M., Jentsch, A., and Beierkuhnlein, C. (2015). Climate vs. Topography – Spatial Patterns of Plant Species Diversity and Range-size on a High-Elevation Island. *Journal of Ecology* 103 (6): 1621–33. doi:10.1111/1365-2745.12463.

Jankowski, J. E., Merkord, C. L., Rios, W. F., Cabrera, K. G., Revilla, N. S., and Silman, M. R. (2013). The Relationship of Tropical Bird Communities to Tree Species Composition and Vegetation Structure along an Andean Elevational Gradient. *Journal of Biogeography* 40 (5): 950–62. doi:10.1111/jbi.12041.

Jansson, R. (2003). Global patterns in range-size explained by past climatic change. *Proceedings of the Royal Society of London B: Biological Sciences* 270(1515): 583-590.

Jenkins, C. N, Pimm, S. L., and Joppa, L. N. (2013). Global Patterns of Terrestrial Vertebrate Diversity and Conservation. *Proceedings of the National Academy of Sciences* 110 (28): E2602–10. doi:10.1073/pnas.1302251110.

Jetz, W., Wilcove, D. S., and Dobson, A. P. (2007). Projected Impacts of Climate and Land-Use Change on the Global Diversity of Birds. PLOS Biology 5 (6):e157. https://doi.org/10.1371/journal.pbio.0050157.

John, R., J. W. Dalling, K. E. Harms, J. B. Yavitt, R. F. Stallard, M. Mirabello, S. P. Hubbell, … Foster R. B. 2007. “Soil Nutrients Influence Spatial Distributions of Tropical Tree Species.” Proceedings of the National Academy of Sciences 104 (3): 864–69. https://doi.org/10.1073/pnas.0604666104.

Keenan, R. J., Reams, G. A., Achard, F., de Freitas, J.V., Grainger, A., and Lindquis, E. (2015). Dynamics of Global Forest Area: Results from the FAO Global Forest Resources Assessment 2015. *Forest Ecology and Management, Changes in Global Forest Resources from 1990 to 2015* 352 (September): 9–20. doi:10.1016/ j.foreco.2015.06.014.

Keil, P., Schweiger, O., Kühn, I., Kunin, W. E., Kuussaari, M., Settele, J., Henle, K. (2012). Patterns of Beta Diversity in Europe: The Role of Climate, Land Cover and Distance across Scales. *Journal of Biogeography* 39 (8): 1473–86. doi:10.1111/j.1365-2699.2012.02701.x.

Kier, G. H. Kreft, Lee, T. M., Jetz, W., Ibisch, P. L., Nowicki, C., Mutke, J. and Barthlott, W. (2009). A global assessment of range-size and species richness across island and mainland regions. *Proceedings of the National Academy of Sciences* 106(23): 9322-9327.

Kissling, W. D. and Gudrun C. (2008). Spatial Autocorrelation and the Selection of Simultaneous Autoregressive Models. *Global Ecology and Biogeography* 17 (1): 59–71. doi:10.1111/j.1466-8238.2007.00334.x.

Kozak, K. H., and Wiens, J. J. (2007). Climatic Zonation Drives Latitudinal Variation in Speciation Mechanisms. *Proceedings of the Royal Society of London B: Biological Sciences* 274 (1628): 2995–3003. doi:10.1098/rspb.2007.1106.

Kühn, I. (2007). Incorporating spatial autocorrelation may invert observed patterns. *Diversity and Distributions* 13(1): 66-69.

Lamoreux, J. F., Morrison, J. C., Ricketts, T. H., Olson, D. M., Dinerstein, E., McKnight, M. W., and Shugart, H. H. (2006). Global tests of biodiversity concordance and the importance of range-size. *Nature* 440(7081): 212-214.

Laube, I., Korntheuer, H., Schwager, M., Trautmann, S., Rahbek, C., and Böhning-Gaese, K. (2013). Towards a More Mechanistic Understanding of Traits and Range Sizes. *Global Ecology and Biogeography* 22 (2): 233–41. doi:10.1111/j.1466-8238.2012.00798.x.

Lee, P-Y., and Rotenberry, J. T. (2005). “Relationships between Bird Species and Tree Species Assemblages in Forested Habitats of Eastern North America.” Journal of Biogeography 32 (7):1139–50. https://doi.org/10.1111/j.1365-2699.2005.01254.x.

Lei, F. M., Qu, Y-H., Lu, J-L., Liu, Y., and Yin, Z-H. (2003a). Conservation on diversity and distribution patterns of small range birds in China. *Biodiversity and Conservation* 12(2): 239-254.

Lei, F. M., Qu, Y-H., Tang, Q-Q, An, S-C. (2003b). Priorities for the conservation of avian biodiversity in China based on the distribution patterns of small range bird genera. *Biodiversity and Conservation* 12(12): 2487-2501.

Lei, F., Qu, Y-H., Song, G., Alstrom, P., Fjeldså, J. (2015). The potential drivers in forming avian biodiversity hotspots in the East Himalaya Mountains of Southwest China. Integrative zoology 10(2): 171-181.

Li, J. and Fang, X. 1999. Uplift of the Tibetan Plateau and environmental changes. *Chinese Science Bulletin*, *44*(23), 2117-2124.

Li, Y., Li, X., Sandel, B., Blank, D., Liu, Z., Liu, X., and Yan, S. (2016). Climate and Topography Explain Range Sizes of Terrestrial Vertebrates. *Nature Climate Change* 6 (5): 498–502. doi:10.1038/nclimate2895.

Mahalanobis, P.C. (1936). On the Generalised Distance in Statistics. Proceedings of the National Institute of Science of India, no. 12:49–55.

Martinez-López, J. (2014). eHabitat Python and GRASS GIS Library. doi:10.5281/zenodo.10612.

Metzger, M. J., Bunce, R. G. H., Jongman, R. H. G., Sayre, R., Trabucco, A., and Zomer, R. (2013). A High-Resolution Bioclimate Map of the World: A Unifying Framework for Global Biodiversity Research and Monitoring. Global Ecology and Biogeography 22 (5):630–38. https://doi.org/10.1111/geb.12022.

Meyer, C., H. Kreft, R. Guralnick, and W. Jetz. 2015. “Global Priorities for an Effective Information Basis of Biodiversity Distributions.” Nature Communications 6 (September): 8221. https://doi.org/10.1038/ncomms9221.

Morueta-Holme, N., Enquist, B. J., McGill, B. J., Boyle, B., Jørgensen, P. M., Ott, J. E., Svenning, J-C. (2013). Habitat Area and Climate Stability Determine Geographical Variation in Plant Species Range Sizes. Ecology Letters 16 (12):1446–54. https://doi.org/10.1111/ele.12184.

Nagelkerke, N. J. D. (1991). A Note on a General Definition of the Coefficient of Determination. *Biometrika* 78 (3): 691–92. doi:10.2307/2337038.

Neteler, M., Bowman, M. H., Landa, M., and Metz., M. (2012). GRASS GIS: A multi-purpose open source GIS. *Environmental Modelling & Software* 31: 124-130.

O'brien, Robert M. 2007. "A Caution Regarding Rules of Thumb for Variance Inflation Factors." Quality & Quantity 41 (5): 673–90. https://doi.org/10.1007/s11135-006-9018-6.

Ohlemüller, R., Anderson, B. J., Araújo, M. B., Butchart, S. H. M., Kudrna, O., Ridgely, R. S., and Thomas, C. D. (2008). The Coincidence of Climatic and Species Rarity: High Risk to Small range Species from Climate Change. *Biology Letters* 4 (5): 568–72. doi:10.1098/rsbl.2008.0097.

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell. (2001), G. V. N. Terrestrial Ecoregions of the World: A New Map of Life on Earth A New Global Map of Terrestrial Ecoregions Provides an Innovative Tool for Conserving Biodiversity. *BioScience* 51 (11): 933–38. doi:10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2.

Orme, C. D. L, Davies, R. G., Olson, V. A., Thomas, G. H., Ding, T.-S., Gaston, K. J. (2006). Global Patterns of Geographic Range Size in Birds. *PLoS Biol* 4 (7): e208. doi:10.1371/journal.pbio.0040208.

Päckert M, Martens, J., Sun, Y.-H., Severinghaus, L. L., Nazarenko, A. A., Ting, J., Töpfer, T., and Tietze, D. T. (2012) Horizontal and elevational phylogeographic patterns of Himalayan and Southeast Asian forest passerines (Aves: Passeriformes). *Journal of Biogeography* 39: 556–573

Pan, Y., Birdsey, R. A., Phillips, O. L., and Jackson, R. B. (2013). The Structure, Distribution, and Biomass of the World's Forests. *Annual Review of Ecology, Evolution, and Systematics* 44 (1): 593–622. doi:10.1146/annurev-ecolsys-110512-135914.

Pey-Yi, L. and Rotenberry, J. T. (2005). Relationships between Bird Species and Tree Species Assemblages in Forested Habitats of Eastern North America. *Journal of Biogeography* 32 (7): 1139–50. doi:10.1111/j.1365-2699.2005.01254.x.

Pimm, S. L., and Brown J. H. (2004). Domains of Diversity. *Science* 304 (5672): 831–33. doi:10.1126/science.1095332.

Pimm, S. L. and Jenkins, C. (2005). Sustaining the variety of life. *Scientific American* 293 (3): 66-73.

Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N., Raven, P. H., Roberts, C. M. and Sexton, J. O. (2014). The Biodiversity of Species and Their Rates of Extinction, Distribution, and Protection. *Science* 344 (6187): 1246752. doi:10.1126/science.1246752.

Pither, J. (2003). Climate Tolerance and Interspecific Variation in Geographic Range Size. Proceedings of the Royal Society of London B: Biological Sciences 270 (1514):475–81. https://doi.org/10.1098/rspb.2002.2275.

Pomara, L. Y., Ruokolainen, K., Tuomisto, H., and Young, K. R. (2012). Avian Composition Co-Varies with Floristic Composition and Soil Nutrient Concentration in Amazonian Upland Forests. *Biotropica* 44 (4): 545–53. doi:10.1111/j.1744-7429.2011.00851.x.

Purvis, A., Gittleman, J.L., Cowlishaw, G., and Mace, G. M. (2000). Predicting Extinction Risk in Declining Species. Proceedings of the Royal Society of London B: Biological Sciences 267 (1456):1947–52. https://doi.org/10.1098/rspb.2000.1234.

Python Software Foundation. Python Language Reference, version 2.7. Available at http://www.python.org

Qu, Y., Ericson, P. G. P., Quan, Q., Song, G., Zhang, R., Gao, B. and Le, F. (2014). Long-term isolation and stability explain high genetic diversity in the Eastern Himalaya. *Molecular ecology*, 23(3): 705-720.

R Development Core Team. (2015). *R: A Language and Environment for Statistical Computing.* Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org/.

Rahbek, C. (2005). The Role of Spatial Scale and the Perception of Large-Scale Species-Richness Patterns. *Ecology Letters* 8 (2): 224–39. doi:10.1111/j.1461-0248.2004.00701.x.

Reif, J., Hořák, D., Krištín, A., Kopsová, L., and Devictor, V. (2015). Linking Habitat Specialization with Species' Traits in European Birds. *Oikos*, July, n/a-n/a. doi:10.1111/oik.02276.

Roll, U., E. Geffen, and Y. Yom-Tov. (2015). Linking Vertebrate Species Richness to Tree Canopy Height on a Global Scale. *Global Ecology and Biogeography* 24 (7): 814–25. doi:10.1111/geb.12325.

Sandel, B., Arge, L., Dalsgaard, B., Davies, R. G., Gaston, K. J., Sutherland, W. J. and Svenning, J.-C. (2011). The Influence of Late Quaternary Climate-Change Velocity on Species Range-size. *Science* 334 (6056): 660–64. doi:10.1126/science.1210173.

Simard, M., Pinto, N., Fisher, J. B., and Baccini, A. (2011). Mapping Forest Canopy Height Globally with Spaceborne Lidar. *Journal of Geophysical Research: Biogeosciences* 116 (G4): G04021. doi:10.1029/2011JG001708.

Skøien, J. O., Schulz, M., Dubois, G., Fisher, I., Balman, M., May, I. and Ó Tuama, É. (2013). A Model Web approach to modelling climate change in biomes of Important Bird Areas. *Ecological informatics* 14: 38-43.

Slatyer, R. A., Hirst, M., and Sexton, J. P. (2013). Niche breadth predicts geographical range size: a general ecological pattern. *Ecology letters* 16(8): 1104-1114.

Steinbauer, M. J., Field, R., Grytnes, J.-A., Trigas, P., Ah-Peng, C., Attorre, F., … Beierkuhnlein, C. (2016). Topography-driven isolation, speciation and a global increase of range-size with elevation. *Global Ecology and Biogeography* 25(9), 1097-1107.

Trabucco, A, Zomer, R. J., Bossio, D. A., van Straaten, O. and Verchot, L. V. (2008). Climate Change Mitigation through Afforestation / Reforestation: A Global Analysis of Hydrologic Impacts. *Agriculture, Ecosystems and Environment* 126. http://www.cifor.org/library/2538/climate-change-mitigation-through-afforestation-reforestation-a-global-analysis-of-hydrologic-impacts/.

## TABLES

**Table 1.** Single and multi-predictor simultaneous autoregressive error (SARerr) models to study the relationship of between small range birds and Habitat Rarity for each realm using eleven environmental variables ($HR_{all}$) or climatic variables only ($HR_{clim}$). Multi-predictor models include net primary production (NPP), precipitation of the driest month (Pdry), precipitation of the wettest month (Pwet), precipitation seasonality (Pseas), maximum temperature of the warmest month (Tmax), and logarithm of climate change velocity (Velocity). With SE = standard-error, **p* < 0.05, ***p* < 0.01, ****p* < 0.001.

| Mainland | Predictor | Slope | SE | $R^2$ | AIC | Predictor | Slope | SE | $R^2$ | AIC |
|---|---|---|---|---|---|---|---|---|---|---|
| Africa | Single | | | | | Single | | | | |
| | $HR_{All}$ | 0.09 * | 0.04 | 0.81 | -411.27 | $HR_{Clim}$ | 0.05 | 0.04 | 0.81 | -408.04 |
| | Multi | | | | | Multi | | | | |
| | Intercept | -6.22 *** | 0.20 | 0.83 | -501.49 | Intercept | -5.14 *** | 0.17 | 0.83 | -477.25 |
| | $HR_{all}$ | 0.07 | 0.04 | | | $HR_{clim}$ | 0.06 | 0.04 | | |
| | NPP | -0.05 | 0.11 | | | NPP | 0.00 | 0.11 | | |
| | Pdry | 0.04 | 0.36 | | | Pdry | -0.13 | 0.37 | | |
| | Pwet | 0.43 | 0.33 | | | Pwet | 0.44 | 0.34 | | |
| | Pseas | -1.07 | 0.93 | | | Pseas | -0.69 | 0.96 | | |
| | Tmax | -0.60 *** | 0.17 | | | Tmax | -0.79 *** | 0.16 | | |
| | Log(velocity) | -0.25 *** | 0.03 | | | Log(velocity) | -4.93 *** | 0.75 | | |
| Australia | Single | | | | | Single | | | | |
| | $HR_{All}$ | -0.08 | 0.05 | 0.86 | -323.56 | $HR_{Clim}$ | -0.16 *** | 0.06 | 0.86 | -327.29 |
| | Multi | | | | | Multi | | | | |
| | Intercept | -4.87 *** | 0.26 | 0.89 | -361.71 | Intercept | -4.84 *** | 0.21 | 0.89 | -367.89 |
| | $HR_{all}$ | -0.08 | 0.05 | | | $HR_{clim}$ | -0.17 ** | 0.06 | | |
| | NPP | 1.04 *** | 0.13 | | | NPP | 0.97 *** | 0.13 | | |
| | Pdry | 0.37 | 0.65 | | | Pdry | 0.44 | 0.64 | | |
| | Pwet | 0.26 | 0.45 | | | Pwet | 0.51 | 0.45 | | |
| | Pseas | -2.16 ** | 0.68 | | | Pseas | -2.06 ** | 0.68 | | |
| | Tmax | -0.86 ** | 0.32 | | | Tmax | -0.71 * | 0.31 | | |
| | Log(velocity) | 0.00 | 0.03 | | | Log(velocity) | -0.75 | 0.66 | | |
| Indo-Pacific | Single | | | | | Single | | | | |
| | $HR_{all}$ | -0.32 *** | 0.05 | 0.79 | -310.83 | $HR_{clim}$ | -0.20 *** | 0.05 | 0.78 | -288.26 |
| | Multi | | | | | Multi | | | | |
| | Intercept | -6.21 *** | 0.18 | 0.84 | -507.1 | Intercept | -5.41 *** | 0.14 | 0.84 | -502.92 |
| | $HR_{all}$ | -0.16 ** | 0.05 | | | $HR_{clim}$ | -0.04 | 0.05 | | |
| | NPP | 0.60 *** | 0.12 | | | NPP | 0.69 *** | 0.12 | | |
| | Pdry | 0.70 | 0.43 | | | Pdry | 0.63 | 0.44 | | |
| | Pwet | -0.05 | 0.09 | | | Pwet | -0.04 | 0.09 | | |
| | Pseas | -0.03 | 0.37 | | | Pseas | -0.03 | 0.37 | | |
| | Tmax | -0.42 *** | 0.10 | | | Tmax | -0.59 *** | 0.09 | | |
| | Log(velocity) | -0.13 *** | 0.02 | | | Log(velocity) | -4.01 *** | 0.53 | | |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| North-America | Single | | | | | Single | | | | |
| | $HR_{all}$ | 0.01 | 0.03 | 0.92 | -1261.6 | $HR_{clim}$ | 0.06 | 0.04 | 0.92 | -1264 |
| | Multi | | | | | Multi | | | | |
| | Intercept | -6.46 *** | 0.11 | 0.93 | -1303.8 | Intercept | -6.11 *** | 0.11 | 0.92 | -1282.5 |
| | $HR_{all}$ | -0.04 | 0.03 | | | $HR_{clim}$ | 0.01 | 0.04 | | |
| | NPP | 0.33 ** | 0.12 | | | NPP | 0.37 ** | 0.12 | | |
| | Pdry | 0.43 | 0.28 | | | Pdry | 0.46 | 0.28 | | |
| | Pwet | 0.09 | 0.29 | | | Pwet | 0.02 | 0.29 | | |
| | Pseas | -0.88 *** | 0.18 | | | Pseas | -1.03 *** | 0.18 | | |
| | Tmax | 0.12 | 0.09 | | | Tmax | 0.00 | 0.09 | | |
| | Log(velocity) | -0.07 *** | 0.01 | | | Log(velocity) | -0.24 ** | 0.01 | | |
| Palearctic | Single | | | | | Single | | | | |
| | $HR_{all}$ | 0.12 *** | 0.02 | 0.82 | -1733.6 | $HR_{clim}$ | 0.03 | 0.02 | 0.92 | -2001.7 |
| | Multi | | | | | Multi | | | | |
| | Intercept | -7.12 *** | 0.08 | 0.83 | -1830.6 | Intercept | -6.48 *** | 0.07 | 0.93 | -2042.8 |
| | $HR_{all}$ | 0.11 *** | 0.03 | | | $HR_{clim}$ | 0.07 ** | 0.02 | | |
| | NPP | 0.19 | 0.14 | | | NPP | 0.23 | 0.14 | | |
| | Pdry | -1.03 *** | 0.28 | | | Pdry | -0.20 | 0.27 | | |
| | Pwet | 1.85 *** | 0.36 | | | Pwet | 0.14 | 0.23 | | |
| | Pseas | -0.30 *** | 0.09 | | | Pseas | -0.39 *** | 0.11 | | |
| | Tmax | 0.07 | 0.08 | | | Tmax | -0.24 *** | 0.07 | | |
| | Log(velocity) | -0.09 *** | 0.01 | | | Log(velocity) | -0.96 *** | 0.01 | | |
| South-America | Single | | | | | Single | | | | |
| | $HR_{all}$ | 0.16 *** | 0.04 | 0.90 | -7.781 | $HR_{clim}$ | 0.26 *** | 0.04 | 0.90 | -27.28 |
| | Multi | | | | | Multi | | | | |
| | Intercept | -5.92 *** | 0.16 | 0.92 | -417.5 | Intercept | -6.00 *** | 0.12 | 0.92 | -424.1 |
| | $HR_{all}$ | 0.10 * | 0.04 | | | $HR_{clim}$ | 0.14 ** | 0.04 | | |
| | NPP | -0.23 ** | 0.08 | | | NPP | -0.28 *** | 0.07 | | |
| | Pdry | 0.30 * | 0.12 | | | Pdry | 0.17 | 0.12 | | |
| | Pwet | -0.20 | 0.27 | | | Pwet | -0.42 | 0.27 | | |
| | Pseas | 0.29 | 0.65 | | | Pseas | -0.29 | 0.65 | | |
| | Tmax | -0.56 *** | 0.11 | | | Tmax | -0.80 *** | 0.11 | | |
| | Log(velocity) | -0.27 *** | 0.02 | | | Log(velocity) | -8.27 *** | 0.61 | | |

**Table 2.** Single and multi-predictor simultaneous autoregressive error (SARerr) models to study the relationship of between small range birds and Habitat Rarity for each island using eleven environmental variables ($HR_{all}$) or climatic variables only ($HR_{clim}$). Multi-predictor models include net primary production (NPP), precipitation of the driest month (Pdry), precipitation of the wettest month (Pwet), precipitation seasonality (Pseas), maximum temperature of the warmest month (Tmax), and logarithm of climate change velocity (Velocity). With SE = standard-error. **p* < 0.05, ***p* < 0.01, ****p* < 0.001.

| | $SAR_{err}$ | | | | | $SAR_{err}$ | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Island | Predictor | Slope | SE | $R^2$ | AIC | Predictor | Slope | SE | $R^2$ | AIC |
| Borneo | Single | | | | | Single | | | | |
| | $HR_{all}$ | 0.05 | 0.18 | 0.59 | -36.36 | $HR_{clim}$ | 0.05 | 0.18 | 0.59 | -36.36 |
| | Multi | | | | | Multi | | | | |
| | Intercept | -5.71 *** | 0.63 | 0.82 | -87.00 | Intercept | -4.83 *** | 0.46 | 0.83 | -85.02 |
| | $HR_{all}$ | 0.32 * | 0.17 | | | $HR_{clim}$ | 0.38 * | 0.17 | | |
| | NPP | 0.26 * | 0.12 | | | NPP | 0.23 | 0.12 | | |
| | Pdry | 0.46 * | 0.22 | | | Pdry | 0.57 ** | 0.22 | | |
| | Pwet | -0.32 | 0.46 | | | Pwet | -0.21 | 0.47 | | |
| | Pseas | 35.04 *** | 7.38 | | | Pseas | 32.91 *** | 7.76 | | |
| | Tmax | -1.18 | 0.69 | | | Tmax | -1.84 ** | 0.58 | | |
| | Log(velocity) | -0.18 *** | 0.05 | | | Log(velocity) | -3.72 *** | 1.25 | | |
| Madagascar | Single | | | | | Single | | | | |
| | $HR_{all}$ | -0.27 * | 0.10 | 0.45 | -61.65 | $HR_{clim}$ | -0.26 * | 0.10 | 0.45 | -61.65 |
| | Multi | | | | | Multi | | | | |
| | Intercept | -4.02 *** | 0.53 | 0.61 | -59.90 | Intercept | -4.01 | 0.43 | 0.64 | -59.64 |
| | $HR_{all}$ | -0.16 | 0.12 | | | $HR_{clim}$ | -0.17 | 0.12 | | |
| | NPP | 0.47 * | 0.20 | | | NPP | 0.47 * | 0.20 | | |
| | Pdry | 0.64 | 0.38 | | | Pdry | 0.70 | 0.38 | | |
| | Pwet | -1.31 | 0.79 | | | Pwet | -1.28 | 0.78 | | |
| | Pseas | 1.32 | 2.60 | | | Pseas | 1.38 | 2.57 | | |
| | Tmax | -0.20 | 0.39 | | | Tmax | -0.18 | 0.38 | | |
| | Log(velocity) | 0.03 | 0.10 | | | Log(velocity) | 0.35 | 1.72 | | |
| Papua | Single | | | | | Single | | | | |
| | $HR_{all}$ | 0.90 *** | 0.17 | 0.64 | -26.74 | $HR_{clim}$ | 0.89 *** | 0.17 | 0.64 | -26.74 |
| | Multi | | | | | Multi | | | | |
| | Intercept | -4.59 *** | 0.37 | 0.79 | -40.7 | Intercept | -4.05 *** | 0.36 | 0.79 | -60.25 |
| | $HR_{all}$ | 0.29 | 0.26 | | | $HR_{clim}$ | 0.45 * | 0.23 | | |
| | NPP | 0.21 | 0.14 | | | NPP | 0.17 | 0.12 | | |
| | Pdry | 0.33 | 0.19 | | | Pdry | 0.17 | 0.17 | | |
| | Pwet | -0.82 | 0.79 | | | Pwet | -0.51 | 0.71 | | |
| | Pseas | 2.29 | 3.29 | | | Pseas | 6.71 * | 3.08 | | |
| | Tmax | -0.83 * | 0.40 | | | Tmax | -0.75 * | 0.36 | | |
| | Log(velocity) | -0.21 *** | 0.04 | | | Log(velocity) | -7.81 *** | 1.06 | | |

# SUPPLEMENTARY MATERIALS

**Table S1.** Presentation of the 19 variables considered for Habitat rarity computation.

| variables | year | references |
|---|---|---|
| BIO1 = Annual Mean Temperature | 1950-2000 | Hijmans, Robert J. et al. 2005. "Very High Resolution Interpolated Climate Surfaces for Global Land Areas." *International Journal of Climatology* 25 (15): 1965–78. doi:10.1002/joc.1276. |
| BIO4 = Temperature Seasonality | | |
| BIO5 = Max Temperature of Warmest Month | | |
| BIO6 = Min Temperature of Coldest Month | | |
| BIO7 = Temperature Annual Range (BIO5-BIO6) | | |
| BIO10 = Mean Temperature of Warmest Quarter | | |
| BIO11 = Mean Temperature of Coldest Quarter | | |
| BIO12 = Annual Precipitation | | |
| BIO14 = Precipitation of Driest Month | | |
| BIO17 = Precipitation of Driest Quarter | | |
| Growing degree-days on 0 degree base | 1950-2000 | Metzger, M. J. et al. 2013. A high-resolution bioclimate map of the world: a unifying framework for global biodiversity research and monitoring. *Global Ecology and Biogeography*, *22*(5), 630-638. |
| Potential evapotranspiration seasonality | | |
| Aridity index | 1950-2000 | Trabucco, A. et al. 2008. "Climate Change Mitigation through Afforestation / Reforestation: A Global Analysis of Hydrologic Impacts." *Agriculture, Ecosystems and Environment* 126. http://www.cifor.org/library/2538/climate-change-mitigation-through-afforestation-reforestation-a-global-analysis-of-hydrologic-impacts/. |
| NDVI min (annual mean) | 2001-2010 | Carroll, M. L. et al. "250 M MODIS Normalized Difference Vegetation Index." University of Maryland, College Park, Maryland. ISO 690. |
| NDVI max (annual mean) | | |
| Slope | - | Farr, Tom G. et al. 2007. "The Shuttle Radar Topography Mission." *Reviews of Geophysics* 45 (2): RG2004. doi:10.1029/2005RG000183. |
| Tree density (%) | 2014 | Crowther, T. W. et al. 2015. "Mapping Tree Density at a Global Scale." *Nature* 525 (7568): 201–5. doi:10.1038/nature14967. |
| Canopy height (m) | 2005 | Simard, M. 2011. "Mapping Forest Canopy Height Globally with Spaceborne Lidar." *Journal of Geophysical Research: Biogeosciences* 116 (G4): G04021. doi:10.1029/2011JG001708. |
| Soil pH for the topsoil - 0 to 5 cm | 2000-2011 | Hengl, T. et al. 2014. "SoilGridA1km - Global Soil Information Based on Automated Mapping." *PLOS ONE* 9 (8): e105992. doi:10.1371/journal.pone.0105992. |

**Table S2.** Multiple-predictor regressions that model the relationship between forests birds range-size of either Habitat Rarity using all variables ($HR_{all}$) or climatic variables only ($HR_{clim}$) in realms and main islands using ordinary least squared (OLS) and spatial autoregressive error (SARerr) models. The predictors are net primary production (NPP), precipitation of the driest month (Pdry), precipitation of the wettest month (Pwet), precipitation seasonality (Pseas), maximum temperature of the warmest month (Tmax), and logarithm of climate change velocity (Velocity). With SAm = South America, Ne = Nearctic, Pa = Palearctic, Af = Africa, IP = Indo-Pacific, Au = Australia and p < 0.05*, p<0.01** p<0.001 ***.

| | | OLS | | | | $SAR_{err}$ | | | |
|---|---|---|---|---|---|---|---|---|---|
| Mainland | Predictor | Slope | SE | Moran's I | AIC | Slope | SE | Moran's I | AIC |
| Africa | Intercept | -5.21 *** | 0.20 | 0.22 | 855.89 | -6.22 *** | 0.20 | 0.04 | -501.49 |
| | $HR_{all}$ | 0.15 ** | 0.05 | | | 0.07 | 0.04 | | |
| | NPP | -0.21 * | 0.10 | | | -0.05 | 0.11 | | |
| | Pdry | 2.04 *** | 0.29 | | | 0.04 | 0.36 | | |
| | Pwet | 0.84 *** | 0.17 | | | 0.43 | 0.33 | | |
| | Pseas | -0.82 * | 0.35 | | | -1.07 | 0.93 | | |
| | Tmax | -2.46 *** | 0.17 | | | -0.60 *** | 0.17 | | |
| | Log(velocity) | -0.33 *** | 0.02 | | | -0.25 *** | 0.03 | | |
| Australia | Intercept | -4.49 *** | 0.21 | 0.46 | -68.364 | -4.87 *** | 0.26 | 0.03 | -361.71 |
| | $HR_{all}$ | -0.02 | 0.05 | | | -0.08 | 0.05 | | |
| | NPP | 1.16 *** | 0.17 | | | 1.04 *** | 0.13 | | |
| | Pdry | -2.52 ** | 0.78 | | | 0.37 | 0.65 | | |
| | Pwet | 2.24 *** | 0.45 | | | 0.26 | 0.45 | | |
| | Pseas | 0.49 | 0.64 | | | -2.16 ** | 0.68 | | |
| | Tmax | -2.49 *** | 0.31 | | | -0.86 ** | 0.32 | | |
| | Log(velocity) | -0.11 *** | 0.03 | | | 0.00 | 0.03 | | |
| Indo-Pacific | Intercept | -5.32 *** | 0.16 | 0.13 | 181.5 | -6.21 *** | 0.18 | -0.00 | -507.1 |
| | $HR_{all}$ | 0.18 *** | 0.05 | | | -0.16 ** | 0.05 | | |
| | NPP | 0.17 | 0.11 | | | 0.60 *** | 0.12 | | |
| | Pdry | -0.17 | 0.23 | | | 0.70 | 0.43 | | |
| | Pwet | 0.49 *** | 0.10 | | | -0.05 | 0.09 | | |
| | Pseas | -0.75 *** | 0.15 | | | -0.03 | 0.37 | | |
| | Tmax | -1.38 *** | 0.10 | | | -0.42 *** | 0.10 | | |
| | Log(velocity) | -0.18 *** | 0.02 | | | -0.13 *** | 0.02 | | |
| North-America | Intercept | -6.05 *** | 0.09 | 0.17 | -11.3 | -6.46 *** | 0.11 | 0.00 | -1303.8 |
| | $HR_{all}$ | -0.05 | 0.03 | | | -0.04 | 0.03 | | |
| | NPP | 0.12 | 0.09 | | | 0.33 ** | 0.12 | | |
| | Pdry | -2.68 *** | 0.15 | | | 0.43 | 0.28 | | |
| | Pwet | 1.20 *** | 0.23 | | | 0.09 | 0.29 | | |
| | Pseas | -2.42 *** | 0.09 | | | -0.88 *** | 0.18 | | |
| | Tmax | 1.43 *** | 0.08 | | | 0.12 | 0.09 | | |
| | Log(velocity) | -0.02 *** | 0.01 | | | -0.07 *** | 0.01 | | |
| Palearctic | Intercept | -7.10 *** | 0.07 | 0.24 | 501.9 | -7.12 *** | 0.08 | -0.01 | -1830.6 |
| | $HR_{all}$ | 0.22 *** | 0.02 | | | 0.11 *** | 0.03 | | |
| | NPP | 0.70 *** | 0.12 | | | 0.19 | 0.14 | | |
| | Pdry | -4.73 *** | 0.25 | | | -1.03 *** | 0.28 | | |
| | Pwet | 4.99 *** | 0.23 | | | 1.85 *** | 0.36 | | |
| | Pseas | -0.41 *** | 0.05 | | | -0.30 *** | 0.09 | | |
| | Tmax | -0.04 | 0.08 | | | 0.07 | 0.08 | | |
| | Log(velocity) | -0.08 *** | 0.01 | | | -0.09 *** | 0.01 | | |
| South- | Intercept | -6.30 *** | 0.14 | 0.21 | 1622.3 | -5.92 *** | 0.16 | 0.01 | -417.5 |
| | $HR_{all}$ | 0.31 *** | 0.06 | | | 0.10 * | 0.04 | | |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| America | NPP | -0.86 *** | 0.09 | | | -0.23 ** | 0.08 | | |
| | Pdry | 0.71 *** | 0.10 | | | 0.30 * | 0.12 | | |
| | Pwet | 0.64 ** | 0.21 | | | -0.20 | 0.27 | | |
| | Pseas | 0.99 *** | 0.28 | | | 0.29 | 0.65 | | |
| | Tmax | -1.09 *** | 0.13 | | | -0.56 *** | 0.11 | | |
| | Log(velocity) | -0.57 *** | 0.02 | | | 0.27 *** | 0.02 | | |
| Island | Predictor | Slope | SE | Moran's I | AIC | Slope | SE | Moran's I | AIC |
| Borneo | Intercept | -3.96 *** | 0.44 | 0.15 | -74.7 | -5.71 *** | 0.63 | -0.01 | -87.0 |
| | $HR_{all}$ | 0.59 ** | 0.21 | | | 0.32 * | 0.17 | | |
| | NPP | 0.29 * | 0.12 | | | 0.26 * | 0.12 | | |
| | Pdry | 0.57 ** | 0.20 | | | 0.46 * | 0.22 | | |
| | Pwet | -0.23 | 0.38 | | | -0.32 | 0.46 | | |
| | Pseas | 38.49 *** | 4.78 | | | 35.04 *** | 7.38 | | |
| | Tmax | -2.59 *** | 0.67 | | | -1.18 | 0.69 | | |
| | Log(velocity) | -2.74 * | 1.17 | | | -0.18 *** | 0.05 | | |
| Madagascar | Intercept | -4.30 *** | 0.49 | 0.23 | -44.55 | -4.02 *** | 0.53 | -0.10 | -59.9 |
| | $HR_{all}$ | -0.20 | 0.15 | | | -0.16 | 0.12 | | |
| | NPP | 0.66 ** | 0.24 | | | 0.47 * | 0.20 | | |
| | Pdry | 1.23 ** | 0.41 | | | 0.64 | 0.38 | | |
| | Pwet | -1.27 | 0.77 | | | -1.31 | 0.79 | | |
| | Pseas | 1.31 | 2.15 | | | 1.32 | 2.60 | | |
| | Tmax | -0.07 | 0.43 | | | -0.20 | 0.39 | | |
| | Log(velocity) | -2.22 | 2.10 | | | 0.03 | 0.10 | | |
| Papua | Intercept | -3.40 *** | 0.25 | 0.25 | -35.7 | -4.59 *** | 0.37 | 0.18 | -40.7 |
| | $HR_{all}$ | 0.73 ** | 0.24 | | | 0.29 | 0.26 | | |
| | NPP | 0.16 | 0.12 | | | 0.21 | 0.14 | | |
| | Pdry | 0.33 * | 0.16 | | | 0.33 | 0.19 | | |
| | Pwet | -0.51 | 0.68 | | | -0.82 | 0.79 | | |
| | Pseas | 6.26 * | 2.48 | | | 2.29 | 3.29 | | |
| | Tmax | -0.88 * | 0.41 | | | -0.83 * | 0.40 | | |
| | Log(velocity) | -6.87 *** | 0.76 | | | -0.21 *** | 0.04 | | |

**Table S3.** Correlation analyses between the different Habitat Rarity indices $HR_{All}$ and $HR_{Clim}$ in each realm. Values higher than 0.7 are marked in bold.

| | $HR_{All}$ x $HR_{Clim}$ |
|---|---|
| Africa | 0.67 |
| Australia | **0.82** |
| Indo-Pacific | 0.62 |
| Nearctic | **0.84** |
| Palearctic | **0.93** |
| South-America | **0.86** |

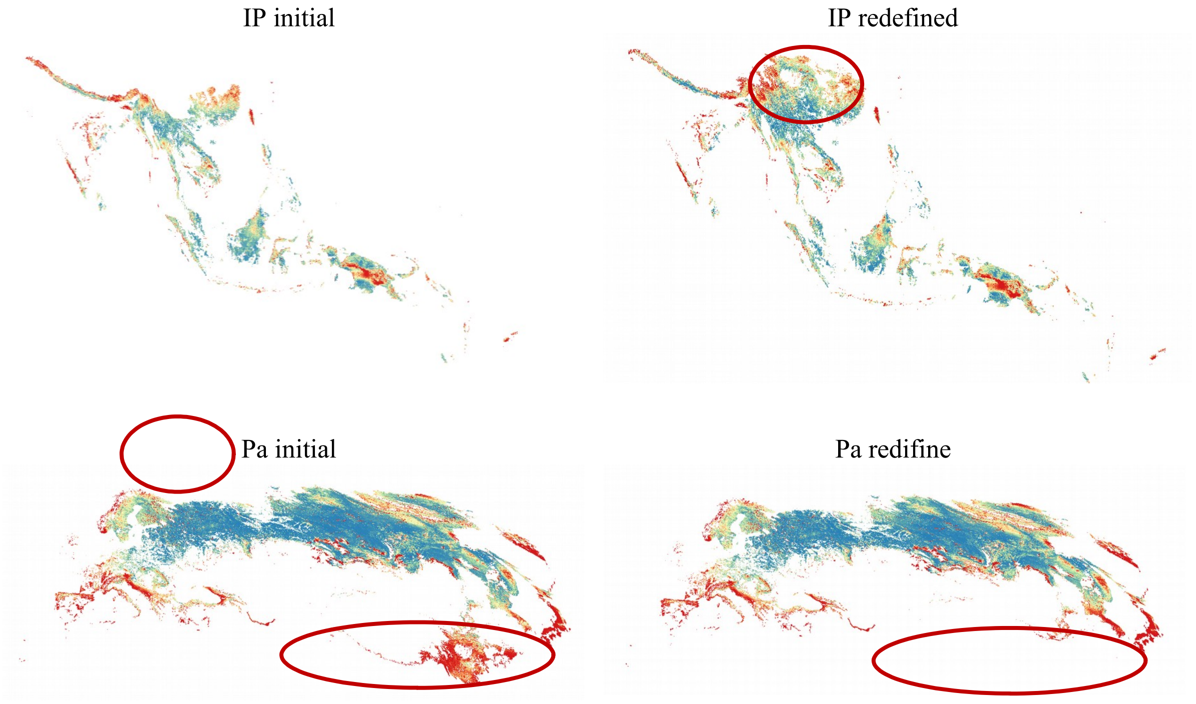
**Table S4.** Relationship between Habitat Rarity using ten factors $HR_{10}$ and forests birds range-size using OLS and $SAR_{err}$ models. Models are taking into account multiple predictors as Table 1 (NDVI maximum and minimum, precipitation of the driest month, precipitation of the wettest month, precipitation seasonality, temperature maximum of the warmest month, and climate change velocity) but only results concerning the $HR_{10}$ variable were displayed. With SAm = South America, Ne = Nearctic, Pa = Palearctic, Af = Africa, IP = Indo-Pacific, Au = Australia. With $p < 0.05$*, $p<0.01$** and $p<0.001$ ***.

| Mainlands | | OLS | | | | SARerr | | | |
|---|---|---|---|---|---|---|---|---|---|
| Realm | Variable | Slope | SE | AIC | Moran's I | Slope | SE | AIC | Moran's I |
| Af | $HR_{10,arid}$ | 0.39 *** | 0.05 | 833.34 | 0.26 | 0.13 * | 0.05 | -471.96 | 0.05 |
| | $HR_{10,pre}$ | 0.35 *** | 0.05 | 845.73 | | 0.09 * | 0.05 | -469.3 | |
| | $HR_{10,preD}$ | 0.50 *** | 0.04 | 778.07 | | 0.16 *** | 0.05 | -475.61 | |
| | $HR_{10,Tmax}$ | 0.39 *** | 0.05 | 826.63 | | 0.14 ** | 0.05 | -473.73 | |
| | $HR_{10,Tseas}$ | 0.38 *** | 0.05 | 835.34 | | 0.11 * | 0.05 | -470.38 | |
| | $HR_{10,NDVImin}$ | 0.40 *** | 0.05 | 829.9 | | 0.11 * | 0.05 | -470.64 | |
| | $HR_{10,NDVImax}$ | 0.41 *** | 0.05 | 816.14 | | 0.19 *** | 0.05 | -479.8 | |
| | $HR_{10,soilPH}$ | 0.51 *** | 0.05 | 782.13 | | 0.29 *** | 0.05 | -501.81 | |
| | $HR_{10,treeD}$ | -0.83*** | 0.22 | 881.62 | | -0.35 * | 0.16 | -470.38 | |
| | $HR_{10,treeH}$ | 0.43 *** | 0.05 | 821.24 | | 0.13 ** | 0.05 | -472.6 | |
| | $HR_{10,slope}$ | 0.37 *** | 0.05 | 840.24 | | 0.16 ** | 0.05 | -475.59 | |
| Au | $HR_{10,arid}$ | 0.07 | 0.06 | -76.35 | 0.41 | -0.13 | 0.07 | -305.82 | 0.03 |
| | $HR_{10,pre}$ | 0.07 | 0.06 | -76.37 | | -0.10 | 0.07 | -304.60 | |
| | $HR_{10,preD}$ | 0.08 | 0.06 | -76.71 | | -0.13 | 0.07 | -305.88 | |
| | $HR_{10,Tmax}$ | 0.13 * | 0.06 | -79.93 | | -0.09 | 0.07 | -304.15 | |
| | $HR_{10,Tseas}$ | 0.06 | 0.06 | -75.94 | | -0.10 | 0.07 | -304.63 | |
| | $HR_{10,NDVImin}$ | 0.06 | 0.06 | -76.02 | | -0.17 * | 0.08 | -307.41 | |
| | $HR_{10,NDVImax}$ | 0.07 | 0.06 | -76.16 | | -0.18 * | 0.08 | -308.49 | |
| | $HR_{10,soilPH}$ | -0.02 | 0.06 | -75.00 | | -0.11 | 0.07 | -304.86 | |
| | $HR_{10,treeD}$ | -0.42 * | 0.20 | -79.52 | | 0.17 | 0.23 | -303.26 | |
| | $HR_{10,treeH}$ | 0.10 | 0.06 | -77.92 | | -0.15 * | 0.07 | -307.08 | |
| | $HR_{10,slope}$ | -0.04 | 0.06 | -75.41 | | -0.13 | 0.07 | -306.01 | |
| IP | $HR_{10,arid}$ | 0.27 *** | 0.05 | 148.58 | 0.17 | -0.09 | 0.06 | -505.74 | 0.03 |
| | $HR_{10,pre}$ | 0.27 *** | 0.05 | 149.41 | | -0.10 | 0.06 | -505.92 | |
| | $HR_{10,preD}$ | 0.26 *** | 0.05 | 154.93 | | -0.07 | 0.06 | -504.95 | |
| | $HR_{10,Tmax}$ | 0.30 *** | 0.05 | 145.13 | | -0.03 | 0.05 | -503.7 | |
| | $HR_{10,Tseas}$ | 0.28 *** | 0.05 | 149.26 | | -0.19 | 0.06 | -505.55 | |
| | $HR_{10,NDVImin}$ | 0.27 *** | 0.05 | 145.16 | | -0.06 | 0.06 | -504.61 | |
| | $HR_{10,NDVImax}$ | 0.37 *** | 0.05 | 149.89 | | -0.07 | 0.06 | -504.89 | |
| | $HR_{10,soilPH}$ | 0.38 *** | 0.05 | 117.2 | | 0.01 | 0.06 | -503.47 | |
| | $HR_{10,treeD}$ | 0.10 | 0.22 | 179.34 | | 0.01 | 0.18 | -503.46 | |
| | $HR_{10,treeH}$ | 0.23 *** | 0.05 | 155.9 | | -0.06 | 0.06 | -504.43 | |
| | $HR_{10,slope}$ | 0.29 *** | 0.05 | 142.61 | | -0.06 | 0.06 | -504.41 | |
| NAm | $HR_{10,arid}$ | -0.02 | 0.04 | -2.29 | 0.17 | -0.02 | 0.04 | -1227.5 | 0.01 |
| | $HR_{10,pre}$ | -0.02 | 0.04 | -2.06 | | -0.04 | 0.04 | -1228.0 | |
| | $HR_{10,preD}$ | -0.05 | 0.03 | -4.60 | | -0.02 | 0.04 | -1227.5 | |
| | $HR_{10,Tmax}$ | -0.04 | 0.03 | -3.12 | | -0.01 | 0.04 | -1227.2 | |
| | $HR_{10,Tseas}$ | 0.03 | 0.03 | -2.70 | | 0.04 | 0.04 | -1228.3 | |
| | $HR_{10,NDVImin}$ | -0.03 | 0.03 | -2.82 | | -0.02 | 0.04 | -1227.5 | |
| | $HR_{10,NDVImax}$ | -0.04 | 0.04 | -3.01 | | -0.04 | 0.04 | -1228.2 | |
| | $HR_{10,soilPH}$ | 0.07 | 0.04 | -5.24 | | -0.01 | 0.04 | -1227.1 | |
| | $HR_{10,treeD}$ | 0.26 ** | 0.09 | -10.89 | | 0.22 * | 0.09 | -1233 | |
| | $HR_{10,treeH}$ | 0.00 | 0.03 | -1.93 | | -0.02 | 0.04 | -1227.5 | |
| | $HR_{10,slope}$ | 0.03 | 0.04 | -2.80 | | -0.03 | 0.04 | -1227.6 | |
| Pa | $HR_{10,arid}$ | 0.30 *** | 0.03 | 532.19 | 0.23 | 0.10 *** | 0.03 | -1748.8 | 0.00 |
| | $HR_{10,pre}$ | 0.30 *** | 0.03 | 540.03 | | 0.10 *** | 0.03 | -1748.7 | |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | $HR_{10,preD}$ | 0.21 *** | 0.03 | 602.26 | | 0.12 *** | 0.03 | -1754.3 | |
| | $HR_{10,Tmax}$ | 0.28 *** | 0.03 | 558.97 | | 0.07 * | 0.03 | -1743.4 | |
| | $HR_{10,Tseas}$ | 0.34 *** | 0.03 | 503.39 | | 0.15 *** | 0.03 | -1759.7 | |
| | $HR_{10,NDVImin}$ | 0.28 *** | 0.03 | 543.06 | | 0.12 *** | 0.03 | -1755 | |
| | $HR_{10,NDVImax}$ | 0.26 *** | 0.03 | 566.86 | | 0.07 * | 0.03 | -1743.5 | |
| | $HR_{10,soilPH}$ | 0.34 *** | 0.03 | 499.05 | | 0.17 *** | 0.03 | -1766.7 | |
| | $HR_{10,treeD}$ | 0.56 *** | 0.09 | 620.91 | | 0.09 | 0.08 | -1739.2 | |
| | $HR_{10,treeH}$ | 0.26 *** | 0.03 | 567.45 | | -0.02 | 0.03 | -1748.3 | |
| | $HR_{10,slope}$ | 0.33 *** | 0.03 | 499.16 | | 0.14 *** | 0.03 | -1760.4 | |
| SAm | $HR_{10,arid}$ | 0.53 *** | 0.06 | 1821.4 | 0.22 | 0.21 *** | 0.06 | -390.73 | -0.01 |
| | $HR_{10,pre}$ | 0.48 *** | 0.07 | 1835.4 | | 0.18 ** | 0.06 | -386.96 | |
| | $HR_{10,preD}$ | 0.54 *** | 0.07 | 1822.5 | | 0.22 *** | 0.06 | -390.78 | |
| | $HR_{10,Tmax}$ | 0.35 *** | 0.07 | 1853.1 | | 0.16 ** | 0.05 | -384.75 | |
| | $HR_{10,Tseas}$ | 0.46 *** | 0.07 | 1833.7 | | 0.13 * | 0.05 | -381.92 | |
| | $HR_{10,NDVImin}$ | 0.42 *** | 0.07 | 1843.0 | | 0.11* | 0.05 | -380.68 | |
| | $HR_{10,NDVImax}$ | 0.65 *** | 0.07 | 1790.4 | | 0.20 *** | 0.05 | -389.63 | |
| | $HR_{10,soilPH}$ | 0.63 *** | 0.07 | 1796 | | 0.36 *** | 0.05 | -418.95 | |
| | $HR_{10,treeD}$ | -1.45*** | 0.30 | 1854 | | -0.84 *** | 0.23 | -389.25 | |
| | $HR_{10,treeH}$ | 0.73 *** | 0.06 | 1763.7 | | 0.14 * | 0.06 | -382.35 | |
| | $HR_{10,slope}$ | 0.24 *** | 0.07 | 1865.8 | | 0.23 *** | 0.05 | -395.15 | |

**Figure S1.** Indo-Pacific (IP) and Palearctic (Pa) redefined. Inclusion in IP of the following ecoregions defined by Olson et al., 2001 (and exclusion in Pa)

Inclusion in IP of the following ecoregions (and exclusion from Pa):
Eco code: PA0509: Hengduan Shan Conifer Forests
Eco code: PA0102: Yunnan Plateau subtropical evergreen forests
Eco code: PA0101: Guizhou Plateau broadleaf and mixed forests
Eco code: PA 0437: Sichuan Basin evergreen broadleaf forests
Eco code: PA0415: Changjang Plain evergreen forests
Eco code: PA0417: Daba Mountains evergreen forests
Eco code: PA0434: Qin Ling Mountains deciduous forests
Eco code: PA1017: Southest Tibet shrublands and meadows
Eco code: PA1003 Eastern Himalayan alpine shrub and meadows
Eco code: PA1307 Baluchistan xeric woodlands
Eco code: PA1018 Sulaiman Range alpine meadows
Eco code: PA0514 Northeastern Himalayan subalpine conifer forests
Eco code: PA0516 Nujiang Langcang Gorge alpine conifer and mixed forests

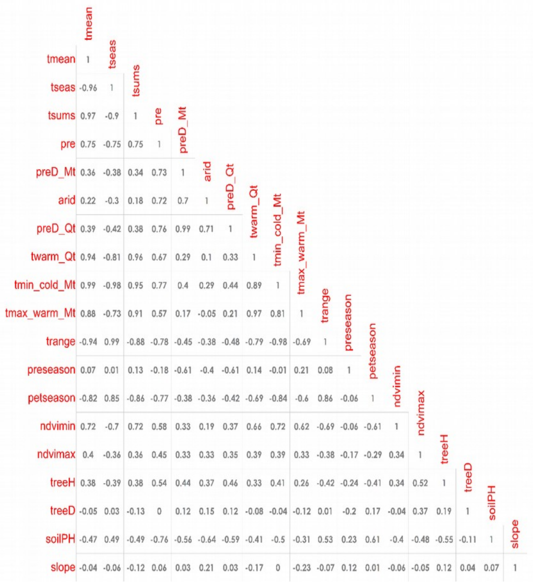

IP initial

IP redefined

Pa initial

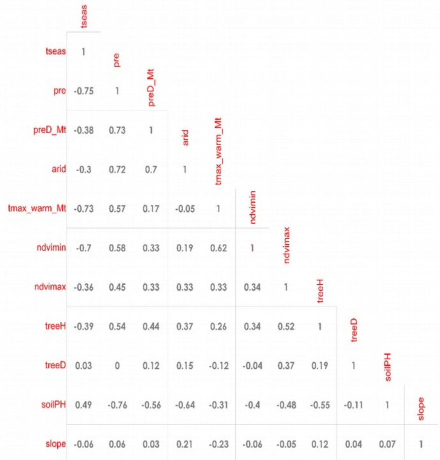
Pa redifine

**Figure S2.** Correlation among the 19 variables, with tmean = mean annual temperature, tseas = temperature seasonality, tsums = growing degree-days on 0°C from (Metzger et al. 2013), pre = precipitation, preD_Mt = precipitation of the driest month, arid =aridity, preD_Qt = precipitation of the driest quarter, twarm_Qt = temperature of the warmest quarter, tmin_cold_Mt = minimum temperature of the coldest month, tmax_warm_Mt = maximum temperature of the warmest month, trange = temperature annual range (max temperature of the warmest month - min temperature of coldest month), preseason = precipitation seasonality, petseason = potential evapotranspiration seasonality from (Metzger et al. 2013), ndvimin = minimum NDVI, ndvimax = maximum NDVI, treeH = tree height, treeD = tree density, soilPH = soil pH.



| | tmean | tseas | tsums | pre | preD_Mt | arid | preD_Qt | twarm_Qt | tmin_cold_Mt | tmax_warm_Mt | trange | preseason | petseason | ndvimin | ndvimax | treeH | treeD | soilPH | slope |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| tmean | 1 | | | | | | | | | | | | | | | | | | |
| tseas | -0.96 | 1 | | | | | | | | | | | | | | | | | |
| tsums | 0.97 | -0.9 | 1 | | | | | | | | | | | | | | | | |
| pre | 0.75 | -0.75 | 0.75 | 1 | | | | | | | | | | | | | | | |
| preD_Mt | 0.36 | -0.38 | 0.34 | 0.73 | 1 | | | | | | | | | | | | | | |
| arid | 0.22 | -0.3 | 0.18 | 0.72 | 0.7 | 1 | | | | | | | | | | | | | |
| preD_Qt | 0.39 | -0.42 | 0.38 | 0.76 | 0.99 | 0.71 | 1 | | | | | | | | | | | | |
| twarm_Qt | 0.94 | -0.81 | 0.96 | 0.67 | 0.29 | 0.1 | 0.33 | 1 | | | | | | | | | | | |
| tmin_cold_Mt | 0.99 | -0.98 | 0.95 | 0.77 | 0.4 | 0.29 | 0.44 | 0.89 | 1 | | | | | | | | | | |
| tmax_warm_Mt | 0.88 | -0.73 | 0.91 | 0.57 | 0.17 | -0.05 | 0.21 | 0.97 | 0.81 | 1 | | | | | | | | | |
| trange | -0.94 | 0.99 | -0.88 | -0.78 | -0.45 | -0.38 | -0.48 | -0.79 | -0.98 | -0.69 | 1 | | | | | | | | |
| preseason | 0.07 | 0.01 | 0.13 | -0.18 | -0.61 | -0.4 | -0.61 | 0.14 | -0.01 | 0.21 | 0.08 | 1 | | | | | | | |
| petseason | -0.82 | 0.85 | -0.86 | -0.77 | -0.38 | -0.36 | -0.42 | -0.69 | -0.84 | -0.6 | 0.86 | -0.06 | 1 | | | | | | |
| ndvimin | 0.72 | -0.7 | 0.72 | 0.58 | 0.33 | 0.19 | 0.37 | 0.66 | 0.72 | 0.62 | -0.69 | -0.06 | -0.61 | 1 | | | | | |
| ndvimax | 0.4 | -0.36 | 0.36 | 0.45 | 0.33 | 0.33 | 0.35 | 0.39 | 0.39 | 0.33 | -0.38 | -0.17 | -0.29 | 0.34 | 1 | | | | |
| treeH | 0.38 | -0.39 | 0.38 | 0.54 | 0.44 | 0.37 | 0.46 | 0.33 | 0.41 | 0.26 | -0.42 | -0.24 | -0.41 | 0.34 | 0.52 | 1 | | | |
| treeD | -0.05 | 0.03 | -0.13 | 0 | 0.12 | 0.15 | 0.12 | -0.08 | -0.04 | -0.12 | 0.01 | -0.2 | 0.17 | -0.04 | 0.37 | 0.19 | 1 | | |
| soilPH | -0.47 | 0.49 | -0.49 | -0.76 | -0.56 | -0.64 | -0.59 | -0.41 | -0.5 | -0.31 | 0.53 | 0.23 | 0.61 | -0.4 | -0.48 | -0.55 | -0.11 | 1 | |
| slope | -0.04 | -0.06 | -0.12 | 0.06 | 0.03 | 0.21 | 0.03 | -0.17 | 0 | -0.23 | -0.07 | 0.12 | 0.01 | -0.06 | -0.05 | 0.12 | 0.04 | 0.07 | 1 |

**Figure S3.** Correlation among the 11 selected variables, with *tseas* = temperature seasonality, *pre* = precipitation, *preD_Mt* = precipitation of the driest month, *arid* =aridity, *tmax_warm_Mt* = maximum temperature of the warmest month, *ndvimin* = minimum NDVI, *ndvimax* = maximum NDVI, *treeH* = tree height, *treeD* = tree density, *soilPH* = soil pH.



| | tseas | pre | preD_Mt | arid | tmax_warm_Mt | ndvimin | ndvimax | treeH | treeD | soilPH | slope |
|---|---|---|---|---|---|---|---|---|---|---|---|
| tseas | 1 | | | | | | | | | | |
| pre | -0.75 | 1 | | | | | | | | | |
| preD_Mt | -0.38 | 0.73 | 1 | | | | | | | | |
| arid | -0.3 | 0.72 | 0.7 | 1 | | | | | | | |
| tmax_warm_Mt | -0.73 | 0.57 | 0.17 | -0.05 | 1 | | | | | | |
| ndvimin | -0.7 | 0.58 | 0.33 | 0.19 | 0.62 | 1 | | | | | |
| ndvimax | -0.36 | 0.45 | 0.33 | 0.33 | 0.33 | 0.34 | 1 | | | | |
| treeH | -0.39 | 0.54 | 0.44 | 0.37 | 0.26 | 0.34 | 0.52 | 1 | | | |
| treeD | 0.03 | 0 | 0.12 | 0.15 | -0.12 | -0.04 | 0.37 | 0.19 | 1 | | |
| soilPH | 0.49 | -0.76 | -0.56 | -0.64 | -0.31 | -0.4 | -0.48 | -0.55 | -0.11 | 1 | |
| slope | -0.06 | 0.06 | 0.03 | 0.21 | -0.23 | -0.06 | -0.05 | 0.12 | 0.04 | 0.07 | 1 |

**Figure S4.** Maps of HR10 and of the absolute difference between HRall and HR10 computed for each input variable removed from HRall at 100 km resolution.

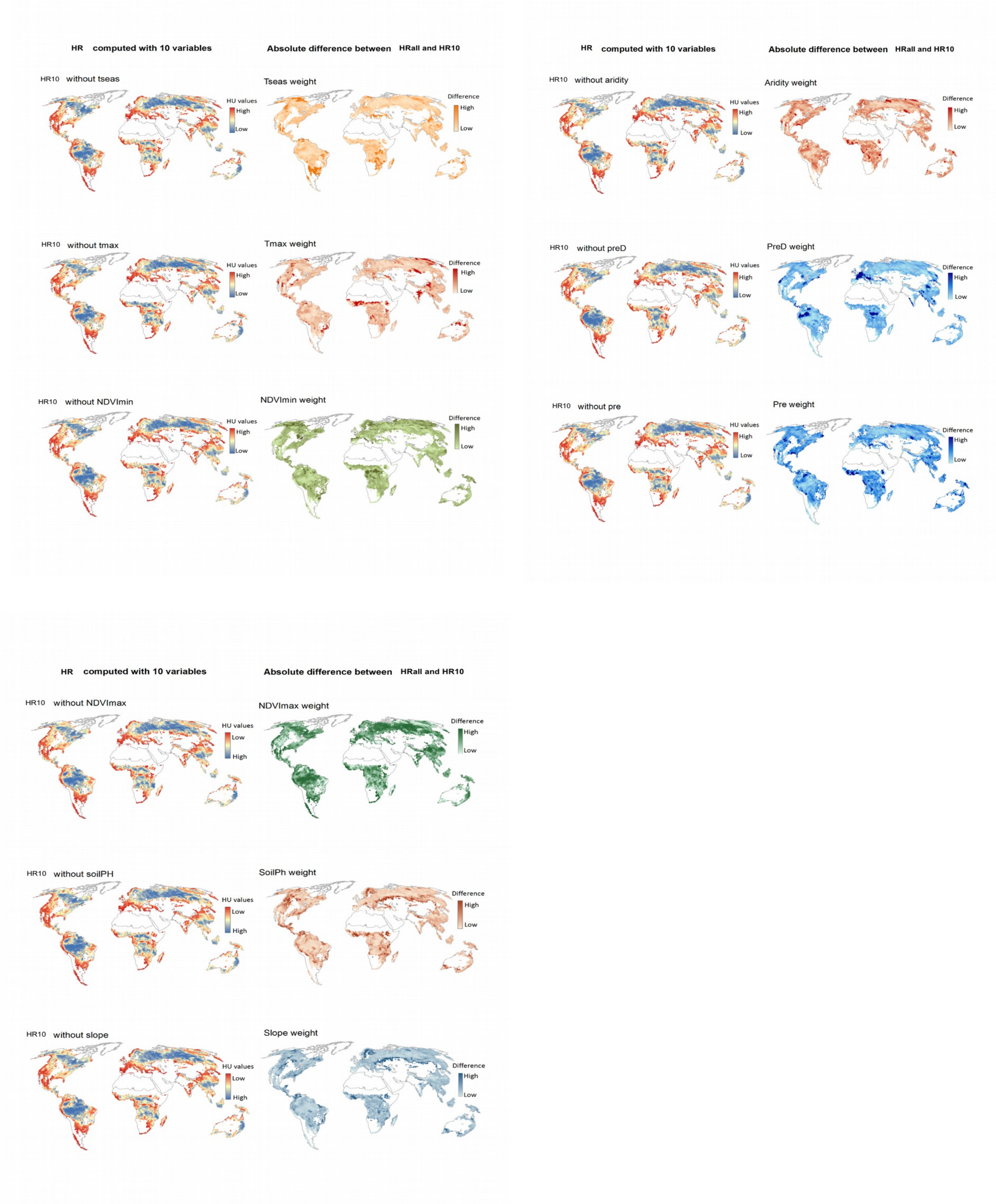


**Figure S5.** Habitat Rarity ($HR_{all}$) map computed for each realm and island at 5km resolution.

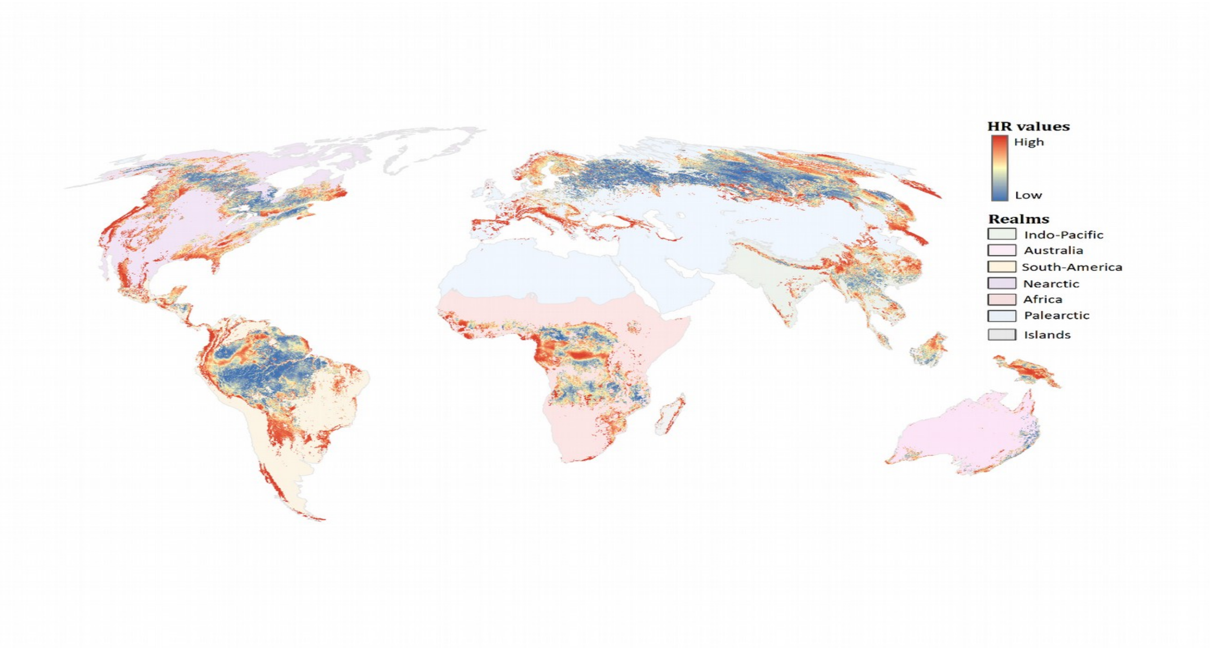
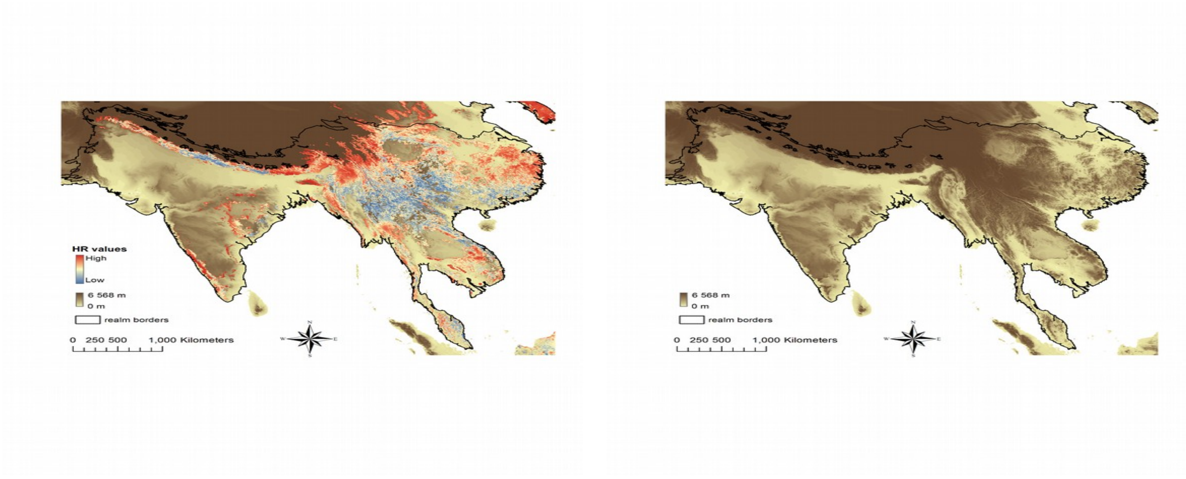


**Figure S6.** a) Habitat Rarity with all variables in Indo-Pacific and elevation maps at 5 km resolution, b) Elevation map in Indo-Pacific at 5 km resolution.

a) b)



# Chapter 2

## Global spatial and temporal patterns of forest loss across IUCN categories of protected areas

Roxanne Leberger [1,2], Isabel M. D. Rosa[1,2], Florian Wolf[1], Carlos A. Guerra[1,2], Henrique M. Pereira[1,2]

*"Destroying rain forest for economic gain is like burning a Renaissance painting to cook a meal."*
*— Edward O. Wilson*

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## ABSTRACT

Global forests are under increasing pressure and the establishment of protected areas has long been used as a conservation tool to preserve them. Seven categories of protected areas have been implemented by the International Union for Conservation of Nature (IUCN) with different management objectives and protection levels, ranging from Ia, where human presence is restricted, to VI allowing sustainable use of resources so that Ia = Ib > II = III > IV = VI > V. However, recent studies brought doubts over the conservation efficiency in preventing ecosystem degradation of the IUCN categories conceptual ranking. In this study, we analysed forest loss and trends between 2001 and 2014 within IUCN protected areas at global scale and per IPBES subregion. Our results showed that worldwide, the highest protection categories experienced less forest loss than those allowing human intervention (Ia-III < IV-VI), although this result was reversed in three IPBES subregions. Globally, the IUCN categories had the following ranking III < Ia = Ib = II < IV = V = VI, which varied across IPBES subregions, with four subregions having more loss within protected areas than outside. Further, we found significant increasing trends of forest loss in high protection areas compared to lower categories (Ia-III > IV-VI). Our findings suggest that although higher-protection IUCN categories have been more efficient in preventing forest loss, this loss might be accelerating in those sites. Therefore, subregions with poor protection performance should benefit from additional support and the post-2020 discussion should go beyond simple general aerial targets.

**Keywords:** Forest conservation, Forest loss, IUCN protected areas, IPBES subregion, protected areas audit

## INTRODUCTION

Forests provide diverse ecosystem services and play a key role for the preservation of endangered and endemic species (Gibson et al., 2011; Moura et al., 2013), covering one third of the terrestrial areas (Keenan et al., 2015), and are of prime importance for human well-being. Due to increasing social demand for agricultural and forest products coupled by a significant urban sprawl and infrastructure development (Faria and Almeida, 2016; Schmitz et al., 2015), forests worldwide have experienced increasing pressures over the last decades (Laurance et al., 2014a). The impact of forest loss can be substantial when affecting intact forests hosting irreplaceable biodiversity and ecosystem services (Gibson et al., 2011; Foley et al., 2005). Forest loss has been shown to be strongly linked to underlying drivers such as changes in population density, international trade and economic development (Leblois et al., 2017; Faria and Almeida, 2016). Even though it is widely recognised that active anthropogenic deforestation has a major impact on forest degradation (Margono et al., 2014), natural environmental factors such as diseases (Kurz et al., 2008), wildfires (Potapov et al., 2008), or drought events (Peng et al., 2011; Phillips et al., 2009) are also responsible for a significant amount of forest loss. The importance of these drivers, however, varies greatly across regions and so does the extension of forest loss (Sloan and Sayer, 2015), with tropical rainforests experiencing twice as much loss between 2000 and 2012 than temperate or boreal forests (Leblois et al., 2017). In this context, developing countries are particularly vulnerable to increasing trends in forest loss due to agricultural development, expansion of road infrastructures, and the reliance of people on forest resources (Laurance et al., 2014b, 2014a).

**Table 1.** Protected areas management categories definition from IUCN (https://www.iucn.org).

| IUCN category | | Description |
|---|---|---|
| Ia | Strict Nature Reserve | - Strictly protected: human visitation, use and impacts are strictly controlled and limited to ensure protection of the conservation values<br>- Protect biodiversity and geological/geomorphical features<br>- Can serve as reference areas for scientific research and monitoring |
| Ib | Wilderness Area | - Unmodified or slightly modified areas without permanent or significant human habitation<br>- Protected and managed so as to preserve their natural condition |
| II | National Park | - Large natural or near natural areas<br>- Protect large-scale ecological processes, along with the complement of species and ecosystems characteristic of the area<br>- Provide a foundation for environmentally and culturally compatible, spiritual, scientific, educational, recreational, and visitor opportunities |
| III | Natural Monument or Feature | - Protect a specific natural monument, which can be a landform, sea mount, submarine cavern, geological feature such as a cave or even a living feature such as an ancient grove<br>- Generally quite small protected areas and often have high visitor value |
| IV | Habitat Species Management Area | - Protect particular species or habitats and management reflects this priority<br>- Can need regular, active interventions to address the requirements of particular species or to maintain habitats |
| V | Protected Landscape / Seascape | - Interaction of people and nature over time has produced an area of distinct character with significant, ecological, biological, cultural and scenic value<br>- Safeguarding the integrity of this interaction is vital to protecting and sustaining the area and its associated nature conservation and other values |
| VI | Protected area with sustainable use of natural resources | - Conserve ecosystems and habitats together with associated cultural values and traditional natural resource management systems<br>- Most of the area in a natural condition, where a proportion is under sustainable natural resource management and where low-level non-industrial use of natural resources compatible with nature conservation |

Despite the persistent decrease of intact forest area during the 2000-2013 period, the contribution of protected areas (PAs) to control this loss was significant (Potapov et al., 2017). The establishment of PAs is indeed one of the most common conservation actions to prevent the degradation of forests, with the international goal to extend them to cover at least 17% (Aichi Target 11) of terrestrial and inland water (https://www.cbd.int/sp/targets/). To account for different conservation strategies and use of resources within these areas, different protection categories were defined. The six categories of PAs currently in use were described in the Guidelines for Protected Area Management Categories (IUCN/WCMC, 1994), and are related to their conservation goals, management objectives, and protection levels (Table 1). They were defined with distinct protection levels from category I, being described as access restricted areas, to category VI, allowing the 'sustainable use of natural ecosystems'. Nevertheless, the outcomes of the conservation management of some low-protection categories (e.g., IUCN categories IV to VI) has been a source of debate (e.g., Shafer, 2015; Locke and Dearden, 2005).

Although several studies have shown the important role of PAs in preventing forest loss in different parts of the world (e.g., Soares-Filho et al., 2010; Andam et al., 2008), there is growing concern on their efficiency in preventing forest loss and other forms of ecosystem degradation (Jones et al., 2018). Indeed, it has been shown that, in the field, the implementation of PAs does not always guarantee an improvement in conservation management (Watson et al., 2014). For instance, in several PAs located in Asia, vegetation loss within these areas was indistinguishable from unprotected lands (Clark et al., 2013), and in Tanzania, some of these PAs had higher rates of forest loss than unprotected lands (Rosa et al. in review). Similarly, oil and gas concessions can overlap park boundaries in the Amazon and in sub-Saharan Africa, including International Union for Conservation of Nature (IUCN) category I and II sites threatening indigenous lands (Lessmann et al., 2016; Osti et al., 2011; Finer and Orta-Martínez, 2010; Finer et al., 2008). As a result of the increasing global demand for agricultural and forest resources, PAs have been downgraded, downsized or degazetted, facilitating the exploitation of their resources (Mascia and Pailler, 2011; Pedlowski et al., 2005).

Several studies have compared forest loss inside and outside these areas (e.g., Allan et al., 2017; Laurance et al., 2012; Joppa and Pfaff, 2010). However, the incidence and persistence of forest loss over time inside PAs of different IUCN categories has yet to be assessed. Monitoring the temporal trend of loss is important to investigate which categories are under greater risk of future degradation. With the major advances in the field of remote sensing over the last couple of years, we are now able to monitor globally and at high-resolution tree cover change on an annual basis (Hansen et al., 2013) and inform about the world state of forests (http://www.globalforestwatch.org/). Temporally and spatially explicit forest monitoring has the potential to contribute to a more sustainable management and rapid assessment of governmental policy implementation. In this regard, the Intergovernmental Platform for Biodiversity and Ecosystem Services (IPBES) – that was set up to strengthen the link between science and policy - implemented environmental, regional and subregional assessments to investigate the status and trends of worldwide ecosystems. IPBES world regions and subregions were thus defined to help move towards a homogenisation of regional studies to facilitate the dialogue between scientists and policy makers, contributing to improve management of natural resources (Brooks et al., 2016).

Using a 15-year time series of annual tree cover loss (Hansen et al. 2013), this study aims to provide the first global assessment of incidence and persistence of forest loss inside the different IUCN categories across different spatial scales (individual PAs, IPBES subregions, globally). As the degree of forest intactness (no loss) can be associated to naturalness, we hypothesised that forest loss occurs mainly in the categories with lower protection status. Secondly, we assessed the significance of the temporal trend in this loss (i.e., which categories are in a trajectory of increasing/decreasing loss). In its essence, this study offers a framework to monitor forest loss inside PAs, tracking temporal and spatial variation, thus highlighting regions of the world and individual PAs where current practices are leading to forest destruction and new management strategies have to be implemented to mitigate and minimize this loss.

## METHODS

### DATASETS

To analyse global forest loss, we used the data produced by Hansen et al. (2013) version 1.2, available at 30 m resolution, and covering a 15-year period (from 2000 to 2014). In particular, we downloaded the overall loss dataset which shows the accumulated loss between 2000-2014 (i.e., pixels are classified as 1 where a forested area changed to non-forested and 0 where there was no change); the loss year dataset, which shows the year in which the loss occurred (i.e., pixels are classified from 1 to 14, corresponding to 2001 through 2014, respectively), and the initial tree cover dataset for the year 2000 used as reference in all our analyses. To convert from tree cover to forest (i.e., binary map, 1 – forest, 0 – non-forest) we assumed a conservative threshold of 20% tree cover based on the methodology adopted by Heino et al. (2015) covering more than 0.5 hectares (FAO definition of forest, Kenneth, 2012). In this study, we focused on analysing gross forest loss only. Forest gain was not included in the analyses as it was not available on an annual basis in this dataset (only gain over the entire time period is provided), and its interpretation is more subjective; e.g., might result from forest plantation (Tropek et al., 2014) as it is the case in many category V protected areas for instance (Dudley, 2008), or the occurrence of natural regeneration.

To investigate forest loss within PAs we downloaded the World Database on Protected Areas (WDPA), which contains their location and associated information, such as IUCN category and year of implementation (IUCN and UNEP-WCMC, 2017). The IUCN categories (Table 1) provide a gradient of naturalness ranging from the most natural (category I) to the least natural condition (category V) with equivalent naturalness levels for the categories Ia and Ib, II and III as well as IV and VI (Ia = Ib > II = III > IV = VI > V, Dudley, 2008). The WDPA database contains several PAs with missing information (e.g., unreported categories, unverified PAs), therefore, we adopted a conservative approach when selecting the PAs to be included in the analysis. We only considered in our analysis terrestrial PAs larger than 1 km$^2$ that contained forest area in 2000, were created before the year 2000 (thus avoiding confusion between year of loss and eventual newly created areas within our period of analysis), and had their IUCN category reported and verified. This resulted in the exclusion of a large proportion of the original number of PAs (initial n = 214,807, with 57% of PAs smaller than 1 km$^2$, 20% unreported, and 47% of areas more recent than the year 2000 or without year of implementation), resulting in a dataset of 15,282 PAs (Figure 1, Table S1).

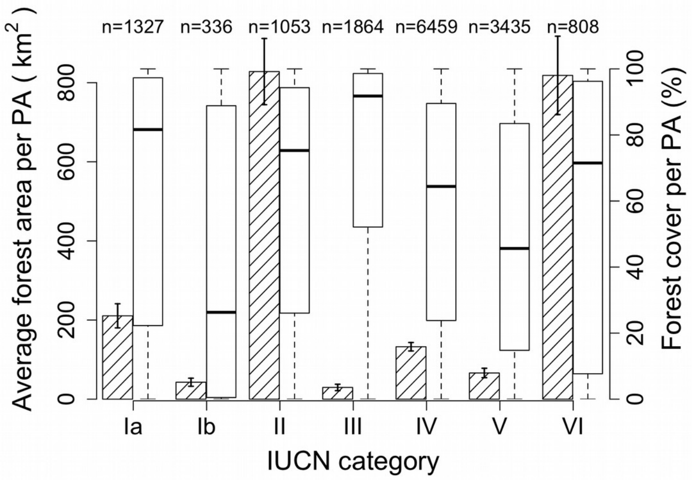

**Figure 1.** Forest area average (km$^2$, with standard error bar, shaded), and the distribution of the percentage of forest cover within the protected areas per IUCN category. The number of protected areas in each IUCN category is provided by *n*.

To assess how our results vary across the globe we performed our analysis for each IPBES subregion. Their delimitation was obtained from Brooks et al. (2016). Sixteen of the regions included the selected PAs: 1) Caribbean, 2) Central Africa, 3) Central and Western Europe, 4) Central Asia, 5) East Africa and adjacent islands, 6) Eastern Europe, 7) Mesoamerica, 8) North Africa, 9) North America, 10) North-East Asia, 11) Oceania, 12) South America, 13) South Asia, 14) South-East Asia, 15) Southern Africa, and 16) West Africa.

### DETERMINING FOREST LOSS

In our analysis, we used the percentage of forest loss per individual PA ($\%Loss_{PA}$) as well as the temporal trend of loss per protected area ($Trend_{PA}$). The percentage of loss per individual PA was calculated by dividing forest loss that occurred between 2001 and 2014 by its initial forest area in 2000. To investigate the significance of the temporal trends in percentage of loss, we calculated the annual loss of forest in each PA relative to the initial forest area in 2000. Then, we mapped the slope of a Generalized Least Squares (GLS) model using the nmle package fitted with the scaled annual deforestation values as response variable, and the year as the only explanatory variable. The GLS models accounted for temporal autocorrelation in the forest loss data considering the first lag between residuals.

To assess for significant differences in the percentage of forest loss between IUCN categories, we fitted a generalized linear model with logit link function under the binomial family accounting for the weight (number of forest cells in 2000 in each PA). The trend of loss across IUCN categories was assessed by implementing a linear model using the slopes of the trends produced by the GLS model for each PA. In both cases, predictor variables included the IUCN level, and the forest cover in 2000 for each PA. This last variable was used to account for the effect of forest size that can affect the proportion of forest loss per PA. Indeed, small forests would more likely have a higher proportion of loss compared to large ones. We used category Ia as a reference, having theoretically the least forest loss expected. We then performed the same analyses aggregating the categories Ia through III and IV though VI to test whether ‘exploitation categories’ had higher loss that ‘conservation categories’ (i.e., Ia-III < IV-VI), and to account for unbalanced PAs numbers when considering individual IUCN categories within IPBES subregion levels. Finally, we performed these analyses separately for each IPBES region. In addition, we calculated the ratio of forest loss inside PAs compared to the loss that occurred outside PAs (sum of forest loss in all PAs divided by the sum of forest loss outside all PAs in a subregion) globally and for each IPBES region. All the analyses were performed in R using the packages survey and nmle (R Core Team, 2016). All code and data (with information on specific protected sites) is available at https://github.com/RoxanneLeb/Forest_Loss_IUCN.

## RESULTS

The 15,282 protected areas (PAs) that matched the selection criteria included 3,216,925 km$^2$ of forests under protection in 2000 (Table S2). We found that globally, forest cover was unevenly distributed within the IUCN categories. For instance, category Ib had the smallest extent of forest cover within its PAs boundaries (26% of forest cover as median), in comparison with categories Ia and III where most of their PAs were covered by at least 80% of forest (Figure 1). Moreover, we found a strong spatial pattern with most of category V located in either Western Europe or North America (44% and 31% of category V PAs) (Figure 2). Similarly, category IV is mainly distributed across Central and Western Europe, Eastern Europe and North-East Asia (36%, 27%, 21% respectively), category Ia is mostly present in Central and Western Europe and Oceania (55%), and 50% of category Ib is in North-America.

Globally, areas covered by PAs exhibit less forest loss than areas outside their boundaries (ratio = 0.63, Table 2). However, this pattern was not consistent across all IPBES subregions, with more loss within the PAs than outside in Eastern Europe, the Caribbean, Mesoamerica and North Africa. Moreover, the rate of loss in all those subregions was higher than the global average (median of 1.12%, 1.41%, 1.76% and 14.20% of forest loss respectively, compared to a global median of 0.72%, Table 2).

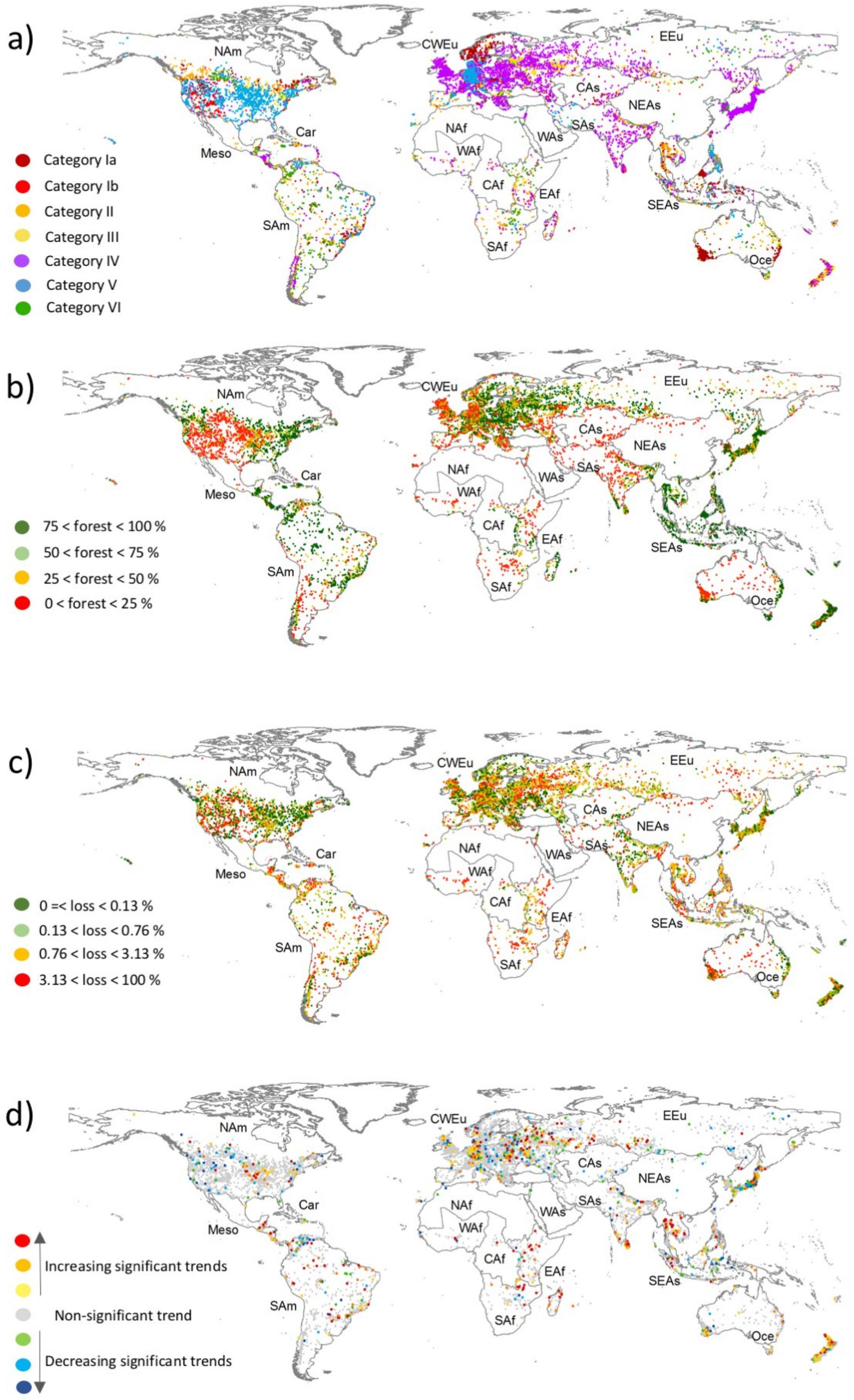

**Figure 2.** a) Spatial distribution of the different protected areas included in our analysis, coloured by IUCN category, b) Percentage of forest loss between 2000 and 2014 within individual protected areas ($\%\text{Loss}_{\text{PA}}$) with quantiles from green (low percentage of loss) to red (high percentage of loss, c) percentage of forest cover per protected area from green highly forested to red poorly forested, d) Significant trend (increase or decrease) of forest loss between 2000 and 2014 within individual protected areas ($\text{Trend}_{\text{PA}}$) coloured from yellow to red according to the slope steepness (highest increase in red) and from green to dark blue according to the slope steepness (highest decrease in blue).

From 2000 through 2014, as expected, the forest loss occurring in the PAs belonging to categories I through III was lower than in the categories IV to VI, globally and in most regions. Still, three IPBES subregions presented a reversed pattern: Caribbean, North-East Asia and West Africa, although the high percentage of loss might be inflated by the small forest fragments (Table 2).

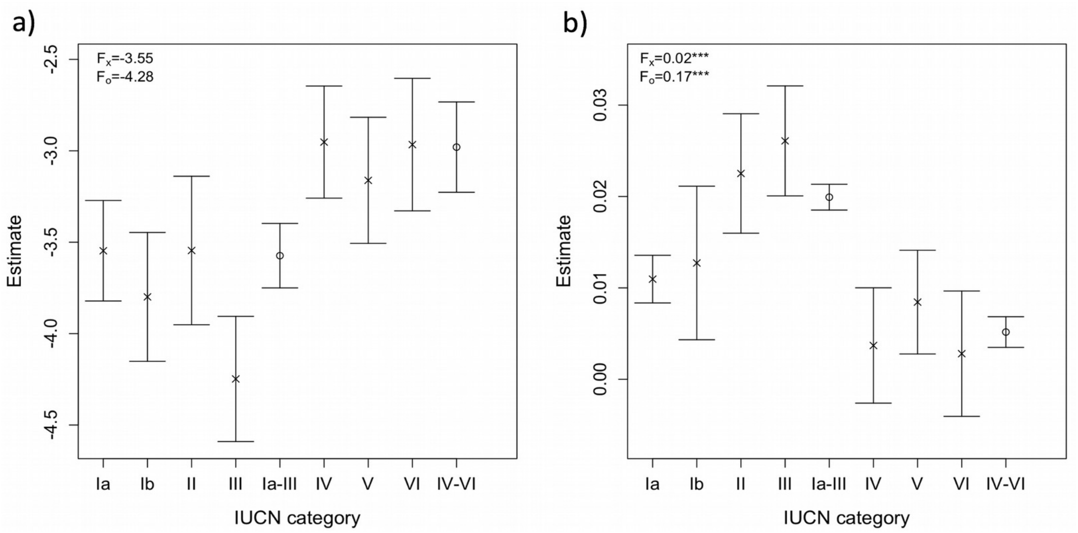

**Figure 3.** a) Estimate of the proportion of forest loss per protected area (PA) for each IUCN category between 2000 and 2014 (middle cross). We used a generalized linear model with binomial family (weighted with number of forest cells per PA in 2000) between IUCN management categories compared to Ia, taking into account the number of forest cells per PA in 2000 normalized by its maximum values (estimate = $F_{+}$), which provides the ranking III < Ia = Ib = II < IV = V = VI. The opened dots represent the estimate of the gerenalized linear model for the merged categories Ia-III and IV-VI, with the number of forest cells per PA in 2000 normalized by its maximum values (estimate = $F_o$). b) Trend of forest loss per PA for each IUCN category between 2000 and 2014 using linear model. Crosses represent the estimate of the linear model for each IUCN category. The dots represent the estimate of the linear model for the merged categories Ia-III and IV-VI. In both plots, the standard error is represented around each estimate.

The ranking of percentage of forest loss per PA between IUCN categories at global scale, from the least to the most impacted, was III < Ia = Ib = II < IV = V = VI (Figure 3a). However, this ranking was not consistent at the IPBES subregions scale (Figure 4, Table S3). Moreover, East Africa and North America did not present any differences with the forest loss that occurred in Ia. What suggest that either all protected areas experienced few forest loss, or that an important amount of loss was recorded in all PAs. East Africa presented a percentage of forest loss at least twice as high as North-America within its PAs (1.94, 0.38 % of forest loss, Table 2), which remains much higher than the global average (0.72%, Table 2). Oceania had the smallest percentage of forest loss (0.24%) between 2000 and 2014, even though category Ia was one of the most impacted. Central and Western Europe as well as Mesoamerica were the subregions that were the closest to the original IUCN category ranking, even though category Ib had un important variance in Europe and was underrepresented in Mesoamerica. Category Ib presented poor results in preventing forest loss in several subregions, with the highest rate of loss in North-America (169 PAs studied in this category, Figure 4), as well as in South-Asia (98 PAs), North-East Asia (14 PAs) and East-Africa (3 PAs).

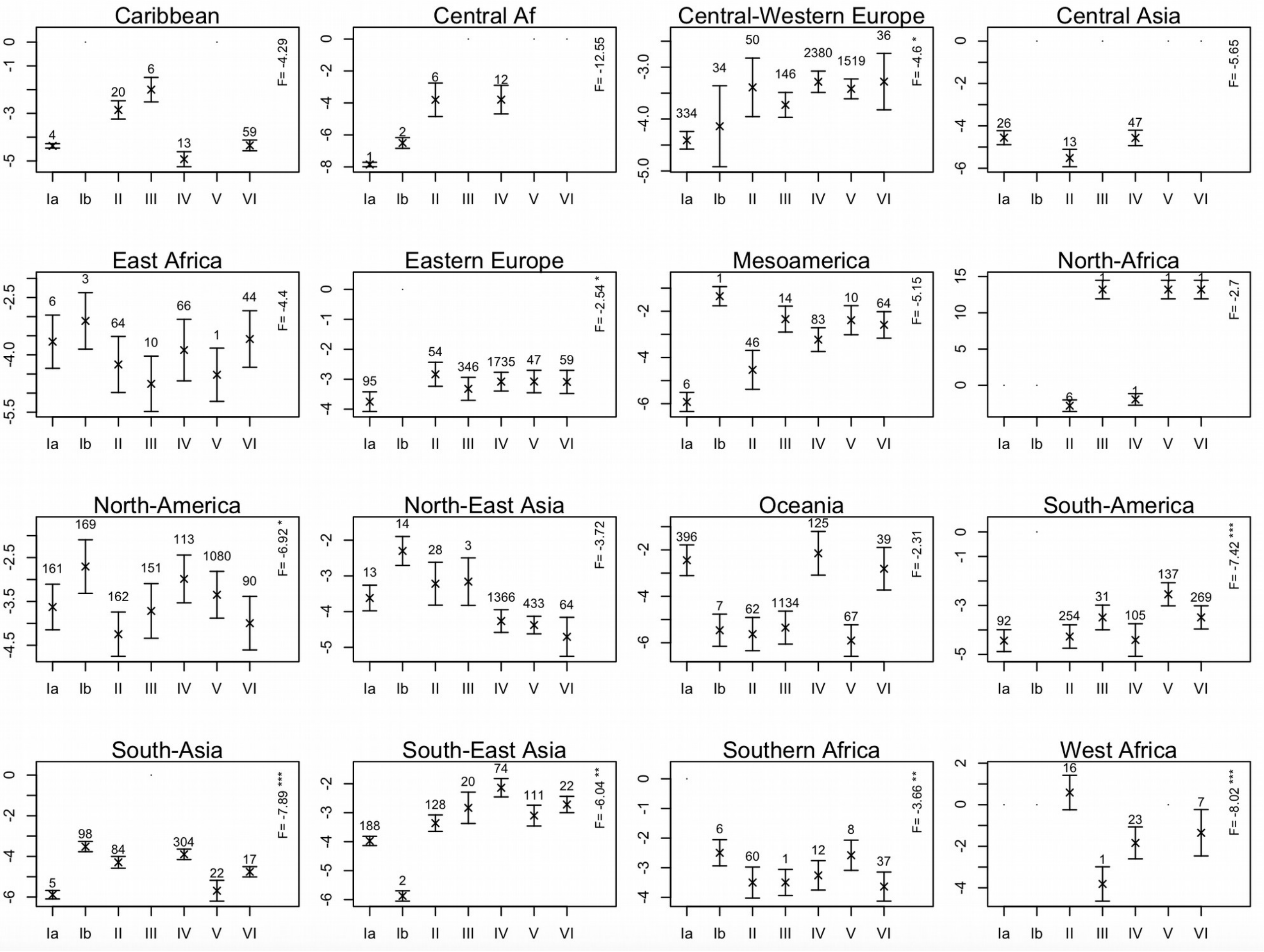

**Figure 4.** Generalised linear model (GLM) values of percentage of forest loss within each IUCN category, among the IPBES subregions. The value of each IUCN category corresponds to the model intercept (Ia) plus the estimate of each category, and is represented by the middle cross surrounded by the standard error. The number of protected areas is displayed above. The effect of forest size F as model parameter is indicated to the right with its significance level ($p < 0.05$*, $p<0.01$** and $p<0.001$ ***).

Regarding the 14-year global trend in forest loss, we found that PAs from the merged Ia-III categories had higher trends of loss than the lower ones, what resulted in I-III > IV-VI (Figure 2b). Forest loss was only significantly accelerating in most of the sites from IUCN categories II and III during the 14-year period while decelerating in IV and VI (Table S4). However, within the IPBES subregions, the trend of forest loss rarely differed significantly from Ia (Table S3). Still, South-East Asia experienced a persistent acceleration of forest loss in categories II and Ia. Also, IUCN categories II and III in East Africa presented a decrease in forest loss compared to category Ia, what might be related with an increase of loss in Ia.

**Table 2.** Generalised linear model (GLM) values of percentage of forest loss for each IUCN merged category (Ia-III and IV-VI). The values of the IUCN merged category Ia-III correspond to the model intercept, the values of the IV-VI category correspond to the intercept summed with the estimate of this category, with the standard error in parenthesis and *n* the number of protected areas. The forest size parameter estimate (Forest) is displayed with significance level ($p < 0.05$*, $p < 0.01$** and $p < 0.001$ ***). At global scale and for each IPBES subregion, the median of percentage of forest loss (Loss%) with quantiles in brackets is shown, as well as the ratio of the percentage of forest loss inside divided by the percentage of unprotected forest loss relative to the forest area in 2000 (values > 1 mean more loss within protected areas than outside, values close to 0 mean less forest loss within protected areas boundaries compared to outside).

| IPBES sub | Ia-III | IV-VI | Forest | Loss (%) | Ratio in/out |
|---|---|---|---|---|---|
| Global | -3.574<br>(0.176) n=4580 | -2.980<br>(0.247) n=10702 | -0.71 | 0.72<br>[0.12, 0.73] n=15282 | 0.63 |
| Caribbean | -2.853<br>(0.335) n= 30 | - 4.381<br>(0.339) n= 72 | 3.38 | 1.41<br>[0.26, 4.63] n=102 | 1.71 |
| Central Africa | -4.185<br>(0.870) n=9 | -3.872<br>(0.582) n=12 | -15.91 | 0.31<br>[0.31, 3.14] n=21 | 0.10 |
| Central and Western Europe | -3.975<br>(0.208) n=564 | -3.346<br>(0.223) n=3935 | -30.61 | 0.72<br>[0.08, 2.64] n=4499 | 0.35 |
| Central Asia | -4.812<br>(0.322) n=39 | -4.489<br>(0.371) n=47 | -65.29* | 0.41<br>[0.10, 1.80] n=86 | 0.41 |
| East Africa | -4.197<br>(0.211) n=83 | -3.673<br>(0.311) n=111 | -1.66 | 1.94<br>[1.74, 5.10] n=194 | 0.30 |
| Eastern Europe | -3.245<br>(0.263) n=495 | -3.085<br>(0.277) n=1841 | 2.31* | 1.12<br>[0.23, 3.54] n=2335 | 1.17 |
| Mesoamerica | -4.033<br>(0.577) n=67 | -2.715<br>(0.666) n=157 | 5.28 | 1.76<br>[0.45, 3.91] n=224 | 1.90 |
| North Africa | -2.817<br>(0.796) n=7 | 0.091<br>(1.400) n=3 | 10.41 | 14.20<br>[5.38, 87.58] n=10 | 2.04 |
| North America | -3.580<br>(0.263) n=643 | -3.324<br>(0.281) n=1283 | -107.95** | 0.38<br>[0.01, 2.78] n=1926 | 0.21 |
| North-East Asia | -3.191<br>(0.621) n=58 | -4.340<br>(0.524) n=1863 | -4.38 | 0.68<br>[0.15, 1.94] n=1921 | 0.57 |
| Oceania | -4.822<br>(0.290) n=1599 | -4.571<br>(0.571) n=231 | -4.89 | 0.24<br>[0.05, 1.94] n=1830 | 0.15 |
| South America | -4.247<br>(0.197) n=377 | -3.052<br>(0.214) n=511 | -3.17*** | 1.13<br>[0.27, 3.77] n=888 | 0.24 |
| South-Asia | -4.040<br>(0.171) n=187 | -3.931<br>(0.210) n=242 | -57.92*** | 0.60<br>[0.16, 2.36] n=530 | 0.65 |
| South-East Asia | -3.606<br>(0.194) n=338 | -2.341<br>(0.289) n=207 | -5.09*** | 1.58<br>[0.59, 3.87] n=545 | 0.36 |
| Southern Africa | -3.514<br>(0.282) n=67 | -3.556<br>(0.281) n=57 | -3.94*** | 3.53<br>[1.13, 2.36] n=124 | 0.31 |
| West Africa | 0.481<br>(0.769) n=17 | -1.725<br>(0.723) n=30 | -313.86*** | 95.72<br>[8.24, 100] n=47 | 0.29 |

## DISCUSSION

In order to respond to an emerging uncertainty regarding the forest conservation (Allan et al., 2017), we analysed the status and trends of global forest loss within protected areas (PAs), considering the difference between IUCN categories and IPBES subregions. Even though globally, forest loss was less

important within PAs boundaries, and higher protection level was more performant in preventing forest loss compared to the lower ones, we showed that results can vary greatly among subregions. Indeed, while the overall PAs incurred more loss within their boundaries than unprotected forests in Eastern Europe, the Caribbean, Mesoamerica and North Africa subregions, higher forest loss occurred within categories I-III compared to IV-VI in the Caribbean, North-East Asia and West Africa.

Countries within those regions should investigate the reasons why such loss took place to ensure the conservation of their forests, notably the ones under the highest protection level. Several studies already provided some insights. For instance, it has been reported that Eastern Europe PAs can lack efficiency in preventing forest disturbances such as fires or illegal logging (Wendland et al., 2015; Kuemmerle et al., 2009; Achard et al., 2006). Similarly, there have been reports of important forest loss in Jamaica (Caribbean), including in PAs of categories I and II (Chai and Tanner, 2010), due to the rise of yam farming, roads network extension and population density (Newman et al., 2014, 2018). Asia is known for its high rate of forest loss (Hansen et al., 2013) that also occurs within its PAs given the little or absence of protection to forest loss (Spracklen et al., 2015). Further, it has been reported that in North-East Asia, Mongolia (as representative country of the studied PAs from this region, Figure 2) suffers from inadequate protection (Tsogtbaatar, 2013; Dorjsuren, 2008). Finally, while forest loss remained quite low in Central Africa with rather efficient protection (Rudel, 2013), we found convergent results with Bowker et al. (2017) regarding a higher forest loss inside than outside PAs in West Africa.

When analysing per IUCN category, we found convergent patterns to Leroux et al. (2010) based on human footprint, as well as common threads with the IUCN ranking standard. Indeed, as they also showed, our ranking emphasised the performance of category III ('Natural monument or feature'), mainly present in Oceania, such as III < Ia = Ib = II < IV = V = VI. However, the performance of category Ib was worse than what they stated (Ib = III < Ia < II = VI < IV < V, Leroux et al., 2010). Besides, the ranking we found was following the IUCN logic (i.e. Ia = Ib > II = III > IV = VI > V), with highly protected areas showing less loss than the others. However, the IPBES subregions analysis showed high variation in forest loss among the different IUCN categories, with no consistent pattern. This result strengthens the importance of multi-scale analysis to locate world regions that would need conservation guidance, and no one-size-fits-all policy towards global forest protection. For instance, in North America and East Africa, the percentage of forest loss between

IUCN categories was undistinguishable, questioning the efficiency of category characterisation at this scale in those areas.

Between 2000 and 2014, the trend of forest loss was increasing in most of the PAs in categories II and III at a global scale that resulted in Ia-III > IV-VI ranking of trend of loss with merged categories, raising concerns on the future ability of these areas to sustain their status and preserve their ecological value for which they were protected in the first place. Further, we found that the PAs within category II and III reported increasing forest loss, questioning their ability to preserve intact forests (Potapov et al., 2017). These results are not in accordance with Geldmann et al. (2014) that found a decrease of human pressure in the categories Ib and III between 1990 and 2010. This can be explained by an increase of loss in the 2010-2014 period observed in the category Ib for instance (Figure S1). Our results bring, in any case, an increasing concern regarding the trend in the numerous studied PAs Ia and II of South-East Asia. Although we did not explore the potential causes of forest loss between the different IUCN categories, it has been shown that the efficiency of PAs to prevent this loss is related to different factors like management planning, spatial isolation, size, seniority, accounting for the distance to human activity and their accessibility (Joppa and Pfaff, 2009).

We are aware that our analysis does not differentiate human-induced forest loss from environmentally-induced due to data limitations (Hansen et al., 2013), and the damage caused by pest or fire for instance was not assessed. Therefore, our results should be taken with care and with special consideration by practitioners. IUCN categories are established worldwide, but their implementation within the countries varies quite widely, i.e. while Ia and Ib are established to have no human interference, in practice that is not the case in many parts of the world. Thus, despite natural events that might happen, we would expect a stable forest cover, as it is unlikely that such events would occur persistently over time within a PA to explain the significant trend found in many of these areas. Also, activities such as forest clearing can be needed to maintain the presence of open areas for conservation management in other IUCN categories (Hansson and Fogelfors, 2000). We considered these events to remain local, occurring on a regular basis on targeted sites without being massively extended and should, therefore, have a negligible impact on our results.

Studying forest loss by comparing different IUCN categories is challenging, since the same IUCN category (Dudley, 2008) can be managed differently between countries. By studying relatively large and ancient protected sites, we would expect that they already fulfil their protection goals and match the condition of their categorisation. Moreover, the IUCN categories do not reflect management effectiveness, as they all have their own objectives. However, we would not expect all categories to have the same level of forest loss, as they still reflect a relative importance of protection, related here to the degree of naturalness (categories Ia and Ib being the most protected areas). Nonetheless, we demonstrated that the highest levels of IUCN categories experienced a linear increase of forest loss worldwide.

The fact that long term established PAs (pre-2000) with high protection levels experienced forest loss can be explained by several factors. For instance, the attribution of IUCN categories became more selective with time, the exposure to pressures increased with human activities that get closer to old protected sites, while newer PAs were implemented in more isolated places (Butchart et al., 2012; Geldmann et al., 2014). The management of some of the studied sites should be rethought or reinforced, in particular in the IPBES subregions that encountered noticeable loss in high categories levels, and investigate the areas where no distinction in forest loss occurred between categories. Overall, the sites that presented a forest loss increase should be considered with assiduity as they can potentially require an improvement of their forest protection. We thus call for monitoring assessment integrating all PAs to quantify their level of forest loss and changes, with results displayed on online platforms such as web-services, which could be relevant for practitioners. We believe that this effort can be done in the near future by projects already in place (e.g., Digital Observatory of Protected Areas (Joint Research Centre of the European Commission, 2018), Global Forest Watch). Due to the importance of safeguarding pristine forest ecosystems from increasing pressures they are subjected to, we should ensure that the highest IUCN protected areas categories are efficient in their protection commitment by focusing on the ones presenting deficiencies.

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## REFERENCES

Achard, F., Mollicone, D., Stibig, H.-J., Aksenov, D., Laestadius, L., Li, Z., Popatov, P., and Yaroshenko, A. (2006). Areas of rapid forest-cover change in boreal Eurasia. Forest Ecology and Management *237*, 322–334.

Allan, J.R., Venter, O., Maxwell, S., Bertzky, B., Jones, K., Shi, Y., and Watson, J.E.M. (2017). Recent increases in human pressure and forest loss threaten many Natural World Heritage Sites. Biological Conservation *206*, 47–55.

Andam, K.S., Ferraro, P.J., Pfaff, A., Sanchez-Azofeifa, G.A., and Robalino, J.A. (2008). Measuring the effectiveness of protected area networks in reducing deforestation. PNAS *105*, 16089–16094.

Bowker, J.N., De Vos, A., Ament, J.M., and Cumming, G.S. (2017). Effectiveness of Africa's tropical protected areas for maintaining forest cover. Conservation Biology *31*, 559–569.

Brooks, T.M., Akçakaya, H.R., Burgess, N.D., Butchart, S.H.M., Hilton-Taylor, C., Hoffmann, M., Juffe-Bignoli, D., Kingston, N., MacSharry, B., Parr, M., et al. (2016). Analysing biodiversity and conservation knowledge products to support regional environmental assessments. Scientific Data *3*, sdata20167.

Butchart, S.H.M., Scharlemann, J.P.W., Evans, M.I., Quader, S., Aricò, S., Arinaitwe, J., Balman, M., Bennun, L.A., Bertzky, B., Besançon, C., et al. (2012). Protecting Important Sites for Biodiversity Contributes to Meeting Global Conservation Targets. PLOS ONE *7*, e32529.

Chai, S.-L., and Tanner, E. (2010). Are We Losing the Best Parts of Our Protected Areas in Tropical Mountains? Biotropica *42*, 739–747.

Clark, N.E., Boakes, E.H., McGowan, P.J.K., Mace, G.M., and Fuller, R.A. (2013). Protected Areas in South Asia Have Not Prevented Habitat Loss: A Study Using Historical Models of Land-Use Change. PLOS ONE *8*, e65298.

Dorjsuren, C. (2008). Global Forest Resources Assessment 2010 - Mongolia -. Country progress report: recommendation of harmonization and standardization of MAR terms. Forest Water Reseach Centre (FRC), Ministry of Nature and the Environment of Mongolia (MNE).

Dudley, N. (2008). Guidelines for Applying Protected Area Management Categories (IUCN).

Faria, W.R., and Almeida, A.N. (2016). Relationship between openness to trade and deforestation: Empirical evidence from the Brazilian Amazon. Ecological Economics *121*, 85–97.

Finer, M., and Orta-Martínez, M. (2010). A second hydrocarbon boom threatens the Peruvian Amazon: trends, projections, and policy implications. Environ. Res. Lett. *5*, 014012.

Finer, M., Jenkins, C.N., Pimm, S.L., Keane, B., and Ross, C. (2008). Oil and Gas Projects in the Western Amazon: Threats to Wilderness, Biodiversity, and Indigenous Peoples. PLOS ONE *3*, e2932.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., et al. (2005). Global Consequences of Land Use. Science *309*, 570–574.

Geldmann, J., Joppa, L.N., and Burgess, N.D. (2014). Mapping change in human pressure globally on land and within protected areas. Conserv. Biol. *28*, 1604–1616.

Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E., et al. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. Nature *478*, 378–381.

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., et al. (2013a). High-Resolution Global Maps of 21st-Century Forest Cover Change. Science *342*, 850–853.

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., et al. (2013b). High-resolution global maps of 21st-century forest cover change. Science *342*, 850–853.

Hansson, M., and Fogelfors, H. (2000). Management of a semi-natural grassland; results from a 15-year-old experiment in southern Sweden. Journal of Vegetation Science *11*, 31–38.

Heino, M., Kummu, M., Makkonen, M., Mulligan, M., Verburg, P.H., Jalava, M., and Räsänen, T.A. (2015). Forest Loss in Protected Areas and Intact Forest Landscapes: A Global Analysis. PLOS ONE *10*, e0138918.

IUCN/WCMC (1994). Guidelines for Protected Area Management Categories.

Joint Research Centre of the European Commission (2018). The Digital Observatory for Protected Areas (DOPA) Explorer 2.0. Accessed 05/2018, Ispra, Italy. Available at: http://dopa-explorer.jrc.ec.europa.eu.

Jones, K.R., Venter, O., Fuller, R.A., Allan, J.R., Maxwell, S.L., Negret, P.J., and Watson, J.E.M. (2018). One-third of global protected land is under intense human pressure. Science *360*, 788–791.

Joppa, L.N., and Pfaff, A. (2009). High and Far: Biases in the Location of Protected Areas. PLOS ONE *4*, e8273.

Joppa, L.N., and Pfaff, A. (2010). Global protected area impacts. Proceedings of the Royal Society of London B: Biological Sciences rspb20101713.

Keenan, R.J., Reams, G.A., Achard, F., de Freitas, J.V., Grainger, A., and Lindquist, E. (2015). Dynamics of global forest area: Results from the FAO Global Forest Resources Assessment 2015. Forest Ecology and Management *352*, 9–20.

Kenneth, M. (2012). FRA 2015 Tems and Definitions.

Kuemmerle, T., Chaskovskyy, O., Knorn, J., Radeloff, V.C., Kruhlov, I., Keeton, W.S., and Hostert, P. (2009). Forest cover change and illegal logging in the Ukrainian Carpathians in the transition period from 1988 to 2007. Remote Sensing of Environment *113*, 1194–1207.

Kurz, W.A., Dymond, C.C., Stinson, G., Rampley, G.J., Neilson, E.T., Carroll, A.L., Ebata, T., and Safranyik, L. (2008). Mountain pine beetle and forest carbon feedback to climate change. Nature *452*, 987–990.

Laurance, W.F., Carolina Useche, D., Rendeiro, J., Kalka, M., Bradshaw, C.J.A., Sloan, S.P., Laurance, S.G., Campbell, M., Abernethy, K., Alvarez, P., et al. (2012). Averting biodiversity collapse in tropical forest protected areas. Nature *489*, 290–294.

Laurance, W.F., Sayer, J., and Cassman, K.G. (2014a). Agricultural expansion and its impacts on tropical nature. Trends in Ecology & Evolution *29*, 107–116.

Laurance, W.F., Clements, G.R., Sloan, S., O'Connell, C.S., Mueller, N.D., Goosem, M., Venter, O., Edwards, D.P., Phalan, B., Balmford, A., et al. (2014b). A global strategy for road building. Nature *513*, 229–232.

Leblois, A., Damette, O., and Wolfersberger, J. (2017). What has Driven Deforestation in Developing Countries Since the 2000s? Evidence from New Remote-Sensing Data. World Development *92*, 82–102.

Leroux, S.J., Krawchuk, M.A., Schmiegelow, F., Cumming, S.G., Lisgo, K., Anderson, L.G., and Petkova, M. (2010). Global protected areas and IUCN designations: Do the categories match the conditions? Biological Conservation *143*, 609–616.

Lessmann, J., Fajardo, J., Muñoz, J., and Bonaccorso, E. (2016). Large expansion of oil industry in the Ecuadorian Amazon: biodiversity vulnerability and conservation alternatives. Ecol Evol *6*, 4997–5012.

Locke, H., and Dearden, P. (2005). Rethinking protected area categories and the new paradigm. Environmental Conservation *32*, 1–10.

Margono, B.A., Potapov, P.V., Turubanova, S., Stolle, F., and Hansen, M.C. (2014). Primary forest cover loss in Indonesia over 2000-2012. Nature Clim. Change *4*, 730–735.

Mascia, M.B., and Pailler, S. (2011). Protected area downgrading, downsizing, and degazettement (PADDD) and its conservation implications. Conservation Letters *4*, 9–20.

Moura, N.G., Lees, A.C., Andretti, C.B., Davis, B.J.W., Solar, R.R.C., Aleixo, A., Barlow, J., Ferreira, J., and Gardner, T.A. (2013). Avian biodiversity in multiple-use landscapes of the Brazilian Amazon. Biological Conservation *167*, 339–348.

Newman, M.E., McLaren, K.P., and Wilson, B.S. (2014). Long-term socio-economic and spatial pattern drivers of land cover change in a Caribbean tropical moist forest, the Cockpit Country, Jamaica. Agriculture, Ecosystems & Environment *186*, 185–200.

Newman, M.E., McLaren, K.P., and Wilson, B.S. (2018). Using the forest-transition model and a proximate cause of deforestation to explain long-term forest cover trends in a Caribbean forest. Land Use Policy *71*, 395–408.

Osti, M., Coad, L., Fisher, J.B., Bomhard, B., and Hutton, J.M. (2011). Oil and gas development in the World Heritage and wider protected area network in sub-Saharan Africa. Biodivers Conserv *20*, 1863–1877.

Pedlowski, M.A., Matricardi, E. a. T., Skole, D., Cameron, S.R., Chomentowski, W., Fernandes, C., and Lisboa, A. (2005). Conservation units: a new deforestation frontier in the Amazonian state of Rondônia, Brazil. Environmental Conservation *32*, 149–155.

Peng, C., Ma, Z., Lei, X., Zhu, Q., Chen, H., Wang, W., Liu, S., Li, W., Fang, X., and Zhou, X. (2011). A drought-induced pervasive increase in tree mortality across Canada’s boreal forests. Nature Clim. Change *1*, 467–471.

Phillips, O.L., Aragão, L.E.O.C., Lewis, S.L., Fisher, J.B., Lloyd, J., López-González, G., Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C.A., et al. (2009). Drought Sensitivity of the Amazon Rainforest. Science *323*, 1344–1347.

Potapov, P., Hansen, M.C., Stehman, S.V., Loveland, T.R., and Pittman, K. (2008). Combining MODIS and Landsat imagery to estimate and map boreal forest cover loss. Remote Sensing of Environment *112*, 3708–3719.

Potapov, P., Hansen, M.C., Laestadius, L., Turubanova, S., Yaroshenko, A., Thies, C., Smith, W., Zhuravleva, I., Komarova, A., Minnemeyer, S., et al. (2017). The last frontiers of wilderness: Tracking loss of intact forest landscapes from 2000 to 2013. Science Advances *3*, e1600821.

Rudel, T.K. (2013). The national determinants of deforestation in sub-Saharan Africa. Phil. Trans. R. Soc. B *368*, 20120405.

Schmitz, C., Kreidenweis, U., Lotze-Campen, H., Popp, A., Krause, M., Dietrich, J.P., and Müller, C. (2015). Agricultural trade and tropical deforestation: interactions and related policy options. Reg Environ Change *15*, 1757–1772.

Shafer, C.L. (2015). Cautionary thoughts on IUCN protected area management categories V–VI. Global Ecology and Conservation *3*, 331–348.

Sloan, S., and Sayer, J.A. (2015). Forest Resources Assessment of 2015 shows positive global trends but forest loss and degradation persist in poor tropical countries. Forest Ecology and Management *352*, 134–145.

Soares-Filho, B., Moutinho, P., Nepstad, D., Anderson, A., Rodrigues, H., Garcia, R., Dietzsch, L., Merry, F., Bowman, M., Hissa, L., et al. (2010). Role of Brazilian Amazon protected areas in climate change mitigation. Proc Natl Acad Sci U S A *107*, 10821–10826.

Spracklen, B.D., Kalamandeen, M., Galbraith, D., Gloor, E., and Spracklen, D.V. (2015). A Global Analysis of Deforestation in Moist Tropical Forest Protected Areas. PLOS ONE *10*, e0143886.

Tropek, R., Sedláček, O., Beck, J., Keil, P., Musilová, Z., Šímová, I., and Storch, D. (2014). Comment on “High-resolution global maps of 21st-century forest cover change.” Science *344*, 981–981.

Tsogtbaatar, J. (2013). Deforestation and Reforestation of Degraded Forestland in Mongolia. In The Mongolian Ecosystem Network, (Springer, Tokyo), pp. 83–98.

Watson, J.E.M., Dudley, N., Segan, D.B., and Hockings, M. (2014). The performance and potential of protected areas. Nature *515*, 67–73.

Wendland, K.J., Baumann, M., Lewis, D.J., Sieber, A., and Radeloff, V.C. (2015). Protected Area Effectiveness in European Russia: A Postmatching Panel Data Analysis. Land Economics *91*, 149–168.

# SUPPLEMENTARY MATERIALS

**Table S1.** Representativeness of the study.

| IUCN | Nb of PAs studied | Total nb of forested PAs from WDPA before 2000 | % of forested PAs studied compared with forested PAs from WDPA before 2000 |
|---|---|---|---|
| Ia | 1327 | 7050 | 19% |
| Ib | 336 | 2036 | 17% |
| II | 1053 | 3296 | 32% |
| III | 1864 | 12701 | 15% |
| IV | 6459 | 34451 | 19% |
| V | 3435 | 32519 | 11% |
| VI | 808 | 3008 | 27% |
| All | 15282 | 95061 | 16% |

**Table S2.** Forest cover in 2000 (km$^2$) for each IUCN management category and per IPBES.

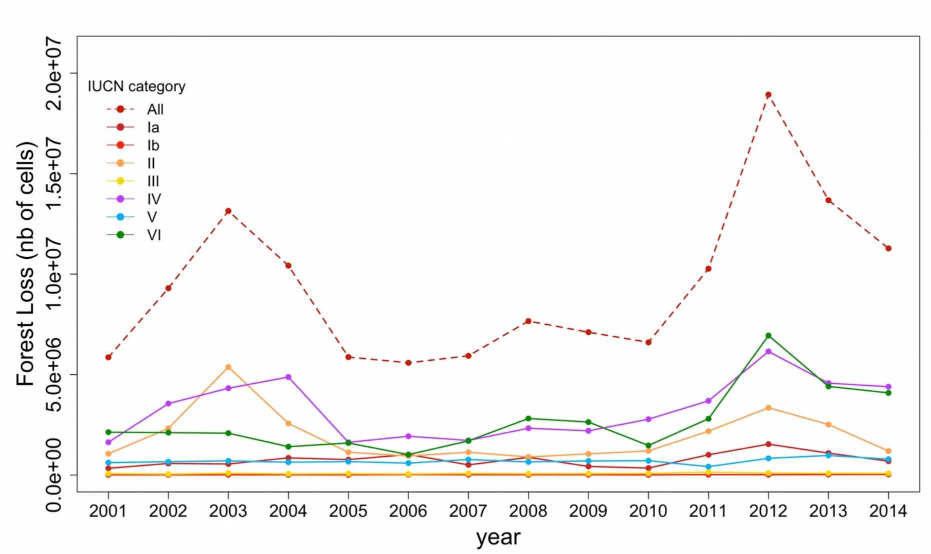
| IPBES sub | Ia | Ib | II | III | IV | V | VI | All |
|---|---|---|---|---|---|---|---|---|
| Global | 302742 | 15578 | 944350 | 59858 | 931970 | 246259 | 716167 | 3216925 |
| Caribbean | 84 | - | 3342 | 84 | 113 | - | 740 | 4363 |
| Central Africa | 530 | 7 | 18081 | - | 26680 | - | - | 45298 |
| Central and Western Europe | 1528 | 600 | 2061 | 603 | 12043 | 12443 | 286 | 29559 |
| Central Asia | 4905 | - | 6423 | - | 15618 | - | - | 26936 |
| East Africa | 1992 | 303 | 64615 | 3015 | 64002 | 977 | 46388 | 181293 |
| Eastern Europe | 174293 | - | 180705 | 10563 | 643772 | 4858 | 299220 | 1313412 |
| Mesoamerica | 398 | 13 | 9978 | 1960 | 6137 | 45 | 25842 | 44373 |
| North Africa | - | - | 1162 | 1 | 2 | 1 | 3 | 1169 |
| North America | 2212 | 4573 | 5614 | 558 | 1370 | 5238 | 1469 | 21034 |
| North-East Asia | 1635 | 766 | 25335 | 101 | 14883 | 24101 | 2092 | 68913 |
| Oceania | 181 | 390 | 3011 | 3176 | 121 | 1863 | 6 | 71920 |
| South America | 63037 | - | 388317 | 16994 | 23104 | 175456 | 281773 | 948680 |
| South-Asia | 688 | 2576 | 27834 | - | 43302 | 1024 | 7172 | 82696 |
| South-East Asia | 48431 | 32 | 99406 | 485 | 68225 | 8293 | 6682 | 231544 |
| Southern Africa | - | 3473 | 81419 | 11 | 10199 | 409 | 43669 | 139180 |
| West Africa | - | - | 4501 | 3 | 1449 | - | 603 | 6555 |

**Table S3.** For each IPBES subregion, model that considers the percentage of forest loss per protected area (PA) using a generalized linear model with binomial distribution between IUCN management categories, and model of the trend of loss per PA using linear model compared to Ia taking into account the amount of original forest. To facilitate the lecture of the table, we just kept the intercept, the original forest and the significant values.

| | | **Percentage of loss per PA** | | | | **Trend of loss per PA** | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Parameter | Estimate | SE | t | p | Estimate | SE | t | p |
| Caribbean | Intercept $_{\text{category Ia}}$ | -4.37 | 0.09 | -47.23 | 2.91e-68 | -0.05 | 0.04 | -1.37 | 0.37 |
| | IUCN category II | 1.51 | 0.39 | 3.92 | 1.67e-04 | - | | | |
| | IUCN category III | 2.37 | 0.51 | 4.60 | 1.29e-05 | - | | | |
| | IUCN category IV | - | | | | 0.10 | 0.05 | 2.21 | 0.03 |
| | Original forest | 3.52 | 0.36 | 0.21 | 0.831 | 2.43 | 0.04 | 1.01 | 0.95 |
| Central Africa | Intercept $_{\text{category Ia}}$ | -7.85 | 0.14 | -56.28 | 8.01e-20 | 0.13 | 0.10 | 1.43 | 0.36 |
| | IUCN category Ib | 1.35 | 0.34 | 4.00 | <0.001 | - | | | |
| | IUCN category II | 4.05 | 1.05 | 3.87 | <0.001 | - | | | |
| | IUCN category IV | 4.05 | 0.89 | 4.54 | 3.37e-04 | - | | | |
| | Original forest | -17.65 | 2.99 | -1.57 | 0.135 | 0.11 | 0.03 | 0.38 | 0.29 |
| Central and Western EU | Intercept $_{\text{category Ia}}$ | -4.41 | 0.17 | -25.98 | 1.02e-138 | -0.00 | 0.00 | 1.88 | 0.54 |
| | IUCN category III | 0.68 | 0.24 | 2.84 | <0.01 | - | | | |
| | IUCN category IV | 1.12 | 0.21 | 5.48 | 4.43e-08 | - | | | |
| | IUCN category V | 0.99 | 0.19 | 5.19 | 2.14e-07 | - | | | |
| | IUCN category VI | 1.13 | 0.54 | 2.08 | 0.04 | - | | | |
| | Original forest | -34.85 | 0.36 | -0.54 | 0.59 | -0.80 | 9.71 | -0.08 | <0.001 |
| Central Asia | Intercept $_{\text{category Ia}}$ | -4.55 | 0.33 | -13.78 | 4.77e-23 | -0.01 | 0.02 | -0.32 | 0.71 |
| | IUCN category II | -0.96 | 0.41 | -2.34 | 0.02 | - | | | |
| | Original forest | -53.86 | 0.65 | -1.68 | 0.09 | -1.12 | 2.41 | -0.46 | |
| East Africa | Intercept $_{\text{category Ia}}$ | -3.65 | 0.70 | -5.25 | 4.04e-07 | 0.15 | 0.05 | 3.33 | <0.01 |
| | IUCN category II | - | | | | -0.10 | 0.05 | -2.14 | 0.03 |
| | IUCN category III | - | | | | -0.12 | 0.06 | -2.04 | 0.04 |
| | Original forest | -1.32 | 0.59 | -1.27 | 0.21 | -0.09 | 0.16 | -0.54 | 0.99 |
| Eastern EU | Intercept $_{\text{category Ia}}$ | -3.75 | 0.33 | -11.42 | 2.05e-29 | -0.02 | 0.01 | -3.14 | <0.01 |
| | IUCN category II | 0.91 | 0.40 | 2.28 | 0.02 | - | | | |
| | IUCN category IV | 0.67 | 0.31 | 2.13 | 0.03 | - | | | |
| | Original forest | 2.30 | 0.51 | 2.35 | 0.22 | 0.16 | 0.06 | 5.29 | <0.001 |
| Mesoamerica | Intercept $_{\text{category Ia}}$ | -5.92 | 0.41 | -14.32 | 3.93e-33 | 0.02 | 0.04 | 0.54 | 0.76 |
| | IUCN category Ib | 4.57 | 0.41 | 11.05 | 8.57e-23 | - | | | |
| | IUCN category III | 3.58 | 0.56 | 6.37 | 1.11e-09 | - | | | |
| | IUCN category IV | 2.69 | 0.52 | 5.23 | 4.01e-07 | - | | | |
| | IUCN category V | 3.54 | 0.63 | 5.62 | 5.82e-08 | - | | | |
| | IUCN category VI | 3.33 | 0.57 | 5.82 | 2.09e-08 | - | | | |
| | Original forest | 4.62 | 0.62 | 1.24 | 0.22 | -0.04 | 0.33 | 1.66 | 0.76 |
| North Africa | Intercept $_{\text{category II}}$ | -2.82 | 0.80 | -3.54 | 0.02 | -0.04 | 0.06 | -0.74 | 0.84 |
| | IUCN category III | 16.02 | 1.28 | 12.53 | 2.33e-04 | - | | | |
| | IUCN category IV | 0.87 | 0.80 | 1.09 | 2.33e-04 | - | | | |
| | IUCN category V | 16.02 | 1.28 | 12.53 | 2.33e-04 | - | | | |
| | Original forest | 10.50 | 0.80 | 0.15 | 0.89 | 0.11 | 12.05 | 1.22 | 0.84 |
| North America | Intercept $_{\text{category Ia}}$ | -3.63 | 0.52 | -6.99 | 3.82e-12 | 0.01 | 0.01 | 1.43 | 0.48 |
| | IUCN category Ib | - | | | | -0.02 | 0.01 | -2.11 | 0.03 |
| | IUCN category IV | | | | | -0.03 | 0.01 | - 2.28 | 0.02 |
| | IUCN category VI | - | | | | -0.04 | 0.01 | -2.78 | 0.01 |
| | Original forest | -79.20 | 1.61 | -2.05 | 0.04 | -0.35 | 1.78 | 0.94 | 0.32 |
| North-East Asia | Intercept $_{\text{category Ia}}$ | -3.62 | 0.36 | -10.07 | 2.74e-23 | 0.01 | 0.02 | 0.56 | 0.77 |
| | IUCN category Ib | 1.32 | 0.41 | 3.25 | <0.01 | - | | | |
| | IUCN category IV | -0.65 | 0.32 | -2.03 | 0.04 | - | | | |
| | IUCN category V | -0.76 | 0.25 | -3.09 | <0.01 | - | | | |
| | IUCN category VI | -1.09 | 0.61 | -1.99 | 0.04 | - | | | |
| | Original forest | -2.74 | 1.61 | -0.07 | 0.95 | -0.35 | 1.19 | -0.30 | 0.33 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Oceania | Intercept $_{\text{category Ia}}$ | -2.45 | 0.66 | -3.70 | 2.26e-04 | 0.01 | 0.04 | 1.84 | 0.06 |
| | IUCN category Ib | -3.01 | 0.69 | -4.36 | 1.39e-05 | - | | | |
| | IUCN category II | -3.18 | 0.72 | -4.44 | 9.57e-06 | - | | | |
| | IUCN category III | -2.90 | 0.71 | -4.09 | 4.55e-05 | 0.03 | 0.01 | 5.02 | 0.46 |
| | IUCN category V | -3.46 | 0.68 | -5.10 | 3.81e-07 | 0.06 | 0.01 | 4.71 | <0.001 |
| | Original forest | 0.60 | 0.30 | 0.46 | 0.65 | 0.64 | 0.38 | 1.68 | <0.001 |
| South America | Intercept $_{\text{category Ia}}$ | -4.44 | 0.45 | -9.94 | 3.97e-22 | 0.03 | 0.01 | 3.68 | 0.01 |
| | IUCN category II | - | | | | -0.03 | 0.01 | -2.05 | 0.04 |
| | IUCN category III | | | | | -0.05 | 0.02 | -2.37 | 0.02 |
| | IUCN category V | 1.89 | 0.48 | 4.02 | 6.32e-05 | -0.04 | 0.01 | -3.18 | <0.01 |
| | IUCN category VI | 0.95 | 0.67 | 2.00 | 0.04 | - | | | |
| | Original forest | -2.98 | 0.63 | -4.72 | 2.81e-06 | 0.11 | 0.04 | 2.82 | 0.45 |
| South Asia | Intercept $_{\text{category Ia}}$ | -5.88 | 0.21 | -28.16 | 6.86e-107 | 0.02 | 0.04 | 0.10 | 0.92 |
| | IUCN category Ib | 2.37 | 0.25 | 9.36 | 2.29e-19 | - | | | |
| | IUCN category II | 1.59 | 0.29 | 5.52 | 5.32e-08 | - | | | |
| | IUCN category IV | 1.99 | 0.26 | 7.72 | 5.82e-14 | - | | | |
| | IUCN category VI | 1.13 | 0.25 | 4.45 | 1.05e-05 | - | | | |
| | Original forest | -47.47 | 0.44 | -4.57 | 6.16e-06 | 0.84 | 0.81 | 1.82 | 0.07 |
| South-East Asia | Intercept $_{\text{category Ia}}$ | -3.97 | 0.16 | -24.89 | 1.62e-91 | 0.01 | 0.01 | 1.74 | <0.01 |
| | IUCN category Ib | -1.90 | 0.18 | -10.68 | 2.78e-24 | - | | | |
| | IUCN category II | 0.61 | 0.28 | 2.16 | 0.03 | 0.04 | 0.01 | 2.85 | <0.01 |
| | IUCN category III | 1.14 | 0.54 | 2.11 | 0.04 | -0.00 | 0.03 | -0.28 | 0.06 |
| | IUCN category IV | 1.84 | 0.32 | 5.78 | 1.24e-08 | - | | | |
| | IUCN category V | 0.87 | 0.36 | 2.43 | 0.02 | - | | | |
| | IUCN category VI | 1.26 | 0.28 | 4.46 | 9.89e-06 | - | | | |
| | Original forest | -6.04 | 0.66 | -3.11 | 1.96e-03 | 0.40 | 0.17 | 2.44 | 0.01 |
| Southern Africa | Intercept $_{\text{category Ib}}$ | -2.50 | 0.44 | -5.65 | 1.12e-07 | 0.00 | 0.05 | 0.16 | 0.84 |
| | IUCN category III | -1.00 | 0.44 | -2.27 | 0.03 | - | | | |
| | IUCN category VI | -1.14 | 0.49 | -2.33 | 0.02 | - | | | |
| | Original forest | -4.25 | 0.39 | -2.99 | <0.01 | 0.42 | 0.29 | 1.45 | <0.001 |
| West Africa | Intercept $_{\text{category II}}$ | 0.59 | 0.83 | 0.71 | 0.48 | 0.03 | 0.03 | 0.79 | 0.32 |
| | IUCN category III | -4.40 | 0.83 | -5.32 | 3.69e-06 | - | | | |
| | IUCN category IV | -2.43 | 1.12 | -3.16 | <0.01 | - | | | |
| | Original forest | -319.64 | 1.57 | -5.50 | 2.07e-06 | -0.31 | 4.27 | -0.07 | 0.35 |

**Figure S1.** Total of forest loss (cell number) from 2001 to 2014 globally and per IUCN category.



# CHAPTER 3

# MEDITERRANEAN WETLAND CONSERVATION IN THE CONTEXT OF CLIMATE AND LAND COVER CHANGE

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*"No water, no life. No blue, no green."*
*– Sylvia Earle*

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## ABSTRACT

Wetlands are known to support diverse and unique species assemblages. Globally, but particularly in the Mediterranean basin, they are threatened by climate change and natural habitat loss. Despite an alarming decline of wetlands over the last century, standardized and systematic site assessments at large scale do not exist. In this context, the identification and use of essential variables (EVs) to monitor pressures and biodiversity can become a critical asset for increasing our understanding and informing decision makers. Here, we identified EVs associated with wetlands to assess the exposure of Mediterranean wetlands and biodiversity to climate and land cover change under different protection covers. Wetlands sites in the southeast of the Mediterranean basin combined low or no protection cover with the highest increases in temperature and losses in natural habitats. Unprotected sites were less well covered by bird observation data. To allow for trend assessments, biodiversity data coverage needs to be ensured across sites regardless of their protection level. Field observations can be complemented with remote-sensing variables identified here as EVs, and should be both regularly updated and extended to further wetland areas.

## MAIN STUDY

Mediterranean wetlands are of major concern, experiencing an estimated 50% loss over the last century[1,2]. At the same time, the Mediterranean basin is recognized as both a biodiversity and a climate change hotspot[3,4]. Although currently still hosting a wide variety of endangered species, the basin is expected to experience dramatic changes in the coming decades[5–7]. Climate change has already increased mean temperatures by 1.3°C in the region since the preindustrial period[5], and has also led to a rise in the frequency of severe drought events[8]. In addition, the increase in land cover change and land use intensity over the last 50 years is further deteriorating wetlands[9], with future projections predicting a rise in population density and a further loss of natural areas[10]. These dynamics have severe implications for wetlands, among which a significant decline in avian species as well as consequences for human well-being at both local and regional scales[11–13].

In the last decades, policymakers have reacted by implementing policy instruments (e.g., National conservation strategies, European Directives, Bern or Ramsar conventions), and increasing the extent of protected areas at national and international level. The evaluation and enforcement of these instruments at the national and, particularly, international level relies on large-scale assessments[14]. Regular reporting on the state and trends of ecosystems, biodiversity, and their drivers not only improves the understanding of the underlying processes but also facilitates informed decision making[15].

Protected areas are one of the main sources of in situ biodiversity and ecosystem function information[16]. Like elsewhere in the world, in the Mediterranean data are mostly scattered and without regional coherence across borders[15]. Although Mediterranean wetlands assessment is done at a regional and national scale[2], site-based approaches (e.g. habitat delineation or protected areas) for reporting wetlands states are lacking. The recent development of essential variables[17] - defined as variables that allow quantification of the rate and direction of change over time and across space[18] - allows for large scale assessments in different contexts such as informing about the ocean biodiversity and ecosystem changes[19], analysing policy objectives[20], as well as reporting and developing species monitoring programs[21]. Essential variables can also be used to identify large-scale indicators available at high resolution allowing for site-specific assessment. Their identification can allow the harmonisation of monitoring efforts across sites, coordination facilitation and data collection prioritisation, which in turn benefits decision making [22].

Here, we tested an essential variables approach to assess the effects of climate and land cover change on waterbird species diversity and natural wetland habitats between 1990 and 2005 in the Mediterranean basin. These variables were selected according to the availability of data for matching periods. We selected 236 Mediterranean wetland sites in coastal watersheds that drain into the Mediterranean sea from the Mediterranean Wetlands Observatory database[2] used for LULC (Land Use/Land Cover) (Figure 1). We used two climatic essential variables, i.e., temperature and precipitation, to represent climatic extremes and variability, including the mean, maximum, minimum, and seasonality[23] averaged from 1986 to 1995, and from 2001 to 2010. We tested the use of the essential biodiversity variables "habitat extent" to assess the land cover change (i.e. agricultural land, artificial wetlands, natural wetlands, urban and sea areas), and waterbird "species abundance" to assess wetland related biodiversity. From the species abundance on each site, we calculated community composition (alpha diversity) and temporal variation (beta diversity) averaged from 1991 to 1995 and from 2006 to 2010 for 158 waterbird species[24], representing the years 1990 and 2005 respectively. As all 236 sites did not benefit from a regular monitoring of waterbirds, only a subset could be used in the analyses of biodiversity change (n=111). Most of the sites with missing biodiversity information (55%) correspond to non-protected wetlands (for further details on site and variable selection see Table S1 and Methods).

We used a Partial Triadic Analysis[25] to perform a site-specific assessment taking into account changes in climate and land cover. This multivariate method allows the temporal and spatial characterization of the variation of different variables (e.g., mean temperature, habitat extent) as well as the temporal change of each site. To account for changes, we extracted Euclidean distances between 1990 and 2005 to obtain a "vector of change" (VoC) for each variable and each site across the first three axes of the dimensional space. Climate and land cover change were assessed with VoCs using either the eight climatic variables or the four land cover variables related to pressure, excluding the extent of

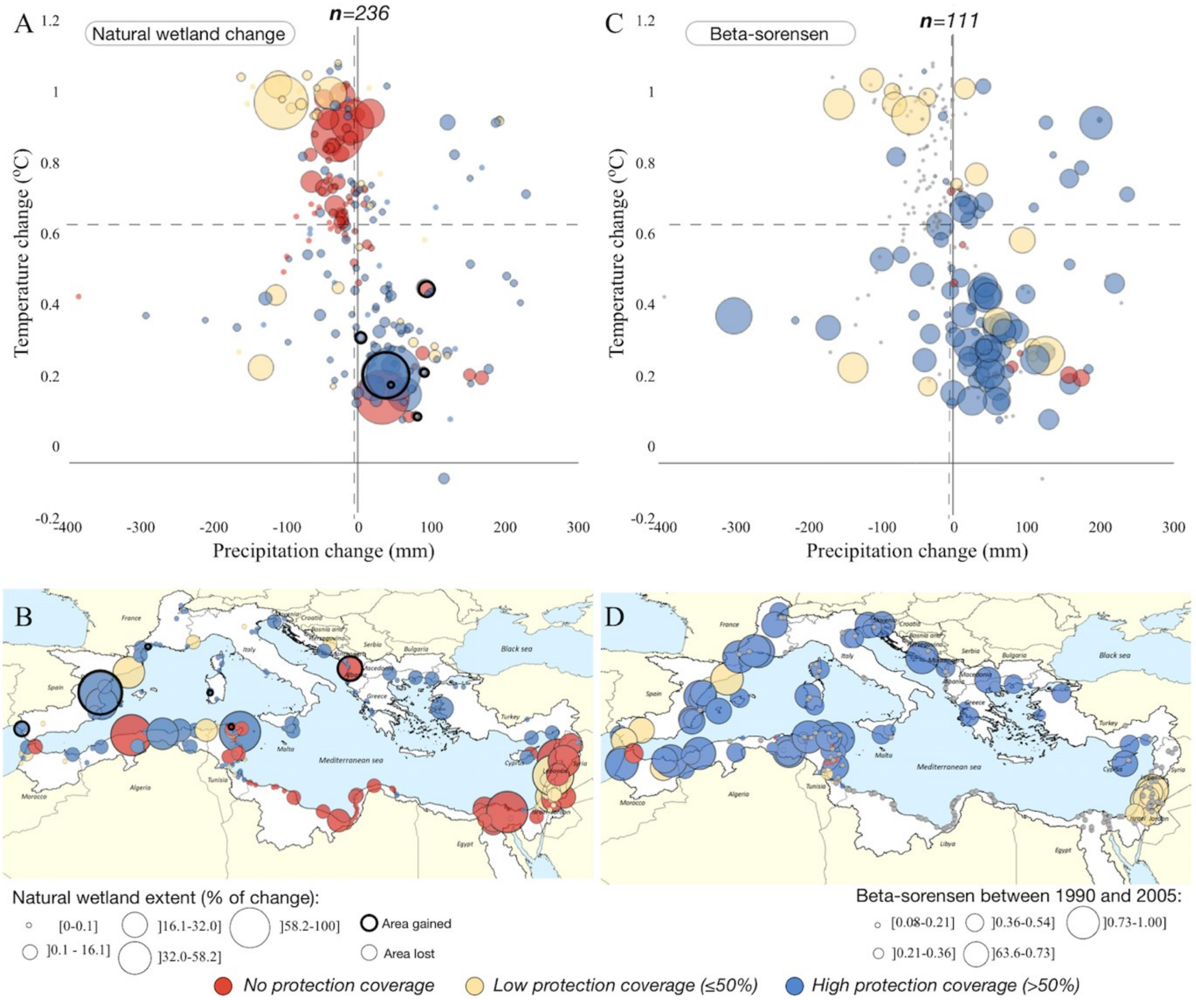

**Figure 1**. A) Proportion of natural wetland habitats change per site in 2005 compared with 1990 along the mean temperature and mean precipitation change gradients. The bubble size represents the percentage of change (PoC) of the natural wetland habitats within each wetland site. The outlines represent the direction of change of the natural wetland habitats extent: bold outlines show a positive change (gain), light outlines a negative change (loss), and the smallest bubbles with no outlines indicate no change, B) geographical layout of natural wetland change, C) Beta-Sorensen values per site between 1990 and 2005 along the mean temperature and mean precipitation change gradients. The bubble size represents the beta-Sorensen values (from 0 to 1) within each wetland site, D) geographical layout of the beta-Sorensen values. The colors represent the protection status of the sites such as red = no protection status ([0] in barplot), yellow = low protection coverage (]0-50] in barplot), blue = high protection coverage (]50-100] in barplot), and grey = sites without species data available, and the associated number of sites on the barplots that are present within medians delimitations (dashed lines).

natural wetland habitats considered here as a dependent variable. We identified the factors that can affect natural wetland habitats loss or water birds diversity by the use of generalised linear modelsand beta-regression. We finally assessed if most of the changes occurred predominantly in unprotected or protected sites using a Kruskal-Wallis test combined with Conover post-hoc test.

We classified each wetland site according to the protection coverage, relative to the surface area of a site considered under a protection programme or convention such as Natura 2000, National

Park or Ramsar (i.e., "high protection coverage" [>50% of the total surface area of a site], "low protection coverage" [≤50%], and "no protection coverage" [0%]; for further details see Methods). Of the 236 studied sites, 119 (50%) have a relatively high area with a protection status while for 78 (33%) no protection of a surface area was reported. Most of the wetlands with high protection coverage are located in Southern Europe, while sites in the Maghreb or Near East regions of the Mediterranean predominantly have low or no protection coverage (Figure 1).

Within the 15 years analysed, the area of natural wetland habitats declined by 5% in the studied sites (Figure 1B). Wetlands sites were directly impacted by the overall increase of land-cover change (VoC) mainly driven by agriculture and urbanisation (Figure 2A), while natural wetland habitats were mostly replaced by agricultural areas (2.6%), artificial wetlands (2.1%) and urban areas (0.3%) (Table S2). Wetland sites with high protection coverage were significantly less affected by natural wetland habitats loss than sites with low or no protection coverage (Kruskal-Wallis, $X^2$=11.76, df=2, $p < 0.01$, Table S5). In a few sites, an increase in natural wetland habitats was detected mainly due to restoration actions (e.g., Caracoles Estate in Doñana[26]).

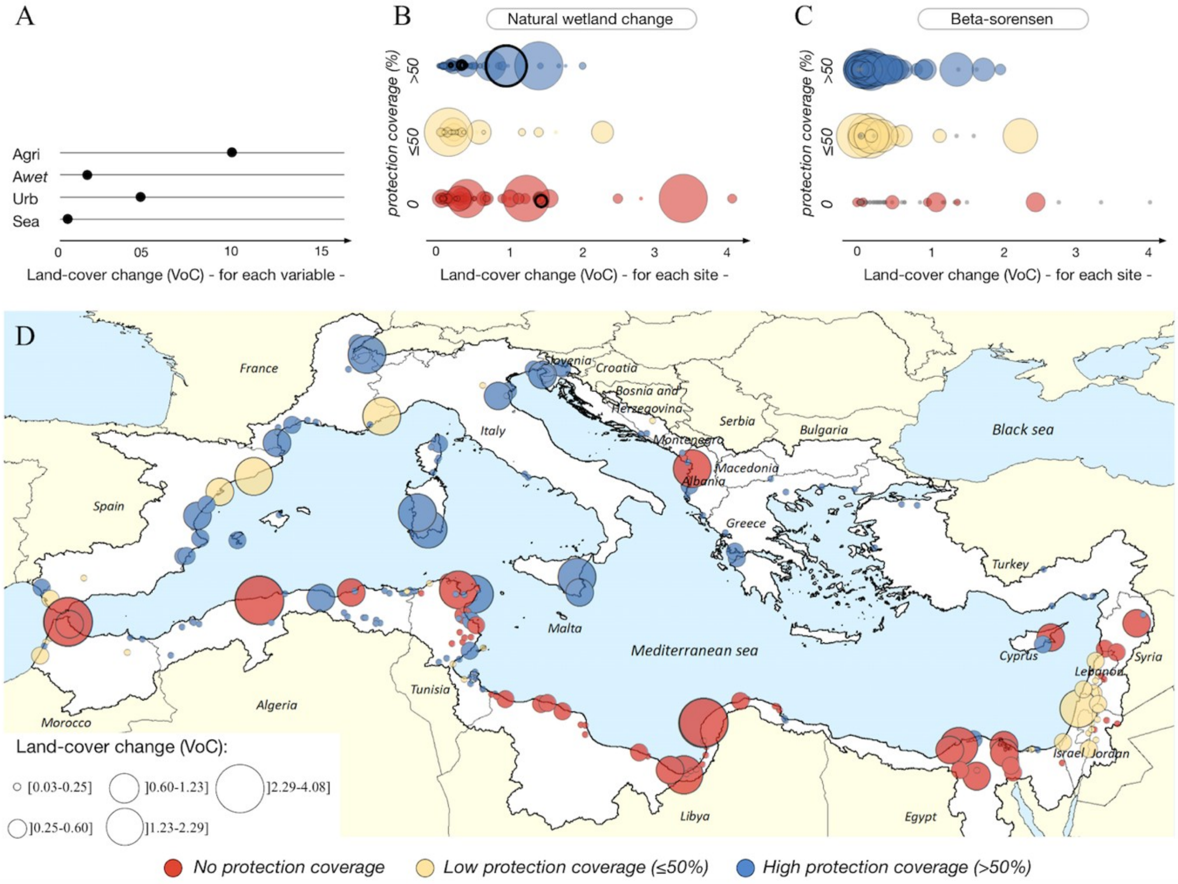

**Figure 2**. Partial Triadic Analysis to assess the change occurring among land cover variables in 1990 and 2005. As land cover variables, we considered agricultural, artificial wetland habitats, urban and sea areas. The

importance order of the vector of change (VoC, with high value for high land cover change) of each variable between 1990 and 2005 is represented in (a). The other top panels represent each site along the land cover VoC gradient with bubble size accounting for (b) natural wetland percentage of change (PoC) and (c) beta-Sorensen metric. The lower panel d) shows the spatial distribution of wetland sites experiencing a greater or lesser degree of land cover change as represented by the bubble size (climate VoC). The protection coverage is represented by a color code.

When comparing patterns in changes in mean temperature and precipitation between 1990 and 2005 (Figure 1), our results showed that 50% of the studied wetlands experienced a temperature increase above 0.6°C reaching a maximum of 1.1°C, and 70.6% of the sites experienced a decrease in precipitation (Figure 1A). Warming occurred mainly in the southeast of the Mediterranean where simultaneously most of the unprotected sites are located (Figure 1 and S1). Our results also indicate a decrease in precipitation in the southeast through the years (Figure 1) which is consistent with an increase in drought events and reduction of water availability in this area, as detected by other studies [8]. Even though mean temperature and precipitation are commonly used as reference variables to establish climate targets in policy conventions, these only cover part of the climatic complexity and variance (e.g., variabilities in climatic extremes). However, small changes in some climate variables can have significant impacts, depending on the sensitivity of the ecosystem. For instance, a small increase in the number of sea intrusions can severely alter the long-term salinity of coastal wetland systems[27]. Our analysis shows that among a larger set of climate variables, the overall impact of climate change (VoC) on the selected wetlands was mostly determined by changes in the different dimensions of temperature (i.e., minimum, maximum, and seasonality; Figure 3A).

Regarding the waterbirds species, neither Sorensen beta-diversity nor Simpson diversity showed a significant response to the climate or land-cover change at site level (Figure 3B, Table S4), with the exception of a significant decrease in species turnover with increasing maximum temperatures. Even though the spatial pattern of species diversity and turnover was relatively homogeneous (Figure 3D, Figure S2), species turn-over was higher for sites benefitting from protection coverage (Kruskal-Wallis, $\chi^2$=10.88, *d.f.*=2, *p*=0.00, two-tailed, Table S5). This could be linked to the recovery of depleted populations[14] that could also mask the impact of climate and land-cover change. The low number of significant impact can be partially explained by the fact that there is a substantial geographical bias in the distribution of waterbird monitoring programmes towards areas with higher protection coverage, with none of them located in the Near East where a signal for high species turnover occurred (Figure 1D and S4). Furthermore, a reduction of natural wetland habitats does not imply a reduction of available water surface, because the construction of dams and reservoirs can result in an increase of artificial wetland habitats, as was the case in the Mediterranean basin between 1984 and 2015[2,27]. Artificial water bodies can partly replace natural water bodies in the total available habitat for waterbirds, dampening the noticeable impact of natural habitat loss on these species. These data constraints limited our analysis in comparison with previous studies that found an accelerating loss of the Eastern Mediterranean birds population[11].

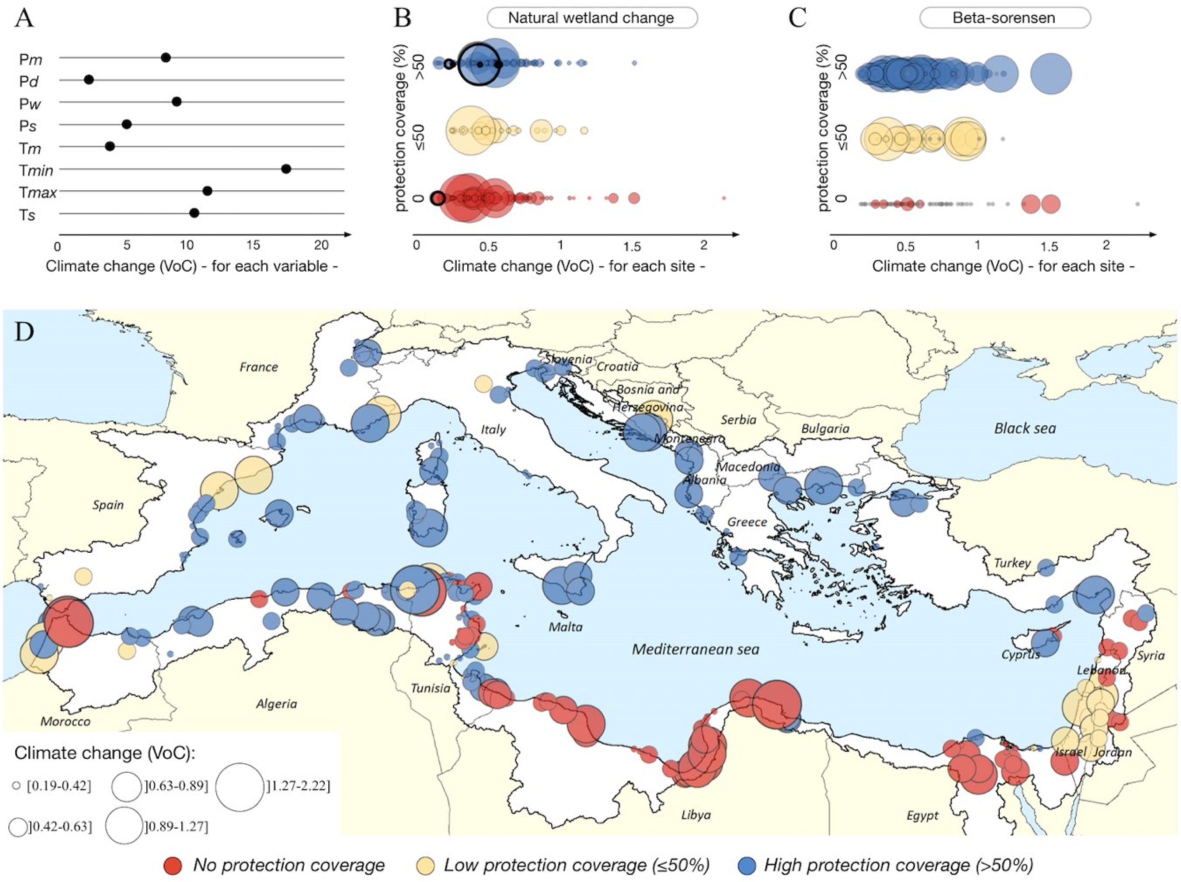

**Figure 3**. Partial Triadic Analysis to assess the change occurring among climate variables in 1990 and 2005. As climate variables, we considered annual temperature and precipitation mean, temperature and precipitation seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, precipitation of the driest and of the wettest month. A) The importance order of the vector of change (VoC, with high value for high climate change) of each variable between 1990 and 2005. The other top panels represent each site along the climate VoC gradient with bubble size accounting for (B) natural wetland percentage of change (PoC) and (C) beta-Sorensen metric. The lower panel d) shows the spatial distribution of wetland sites experiencing a greater or lesser extent of climate change as represented by the bubble size (climate VoC). The protection coverage is represented by a color code.

Waterbird counts are unevenly distributed in the basin and with regards to protected and unprotected sites. Found results could be further improved by a better repartitioning of protected and unprotected sites. The Mediterranean Waterbird Network, which assists in the implementation of the Ramsar Convention and the African-Eurasian Waterbird Agreement in the Mediterranean region, has already taken this to heart, and is currently strengthening waterbird monitoring in North Africa[29]. Also, integrating data on other species groups (e.g., endemic amphibians and fishes) that are more vulnerable to the degradation of wetland habitats than waterbirds, or use of distinct habitat features (e.g. temporary ponds or water courses), would add relevant information on wetlands' ecosystems states[9]. Moreover, at a local level, wetlands depend on complex hydrological cycles that go beyond site boundaries, partly determined by underground water and stream networks. Therefore, a site-based approach can reach limitations without the consideration of a buffer zone that integrates areas of major importance for the studied system (e.g. watersheds). Some specific variables outside the wetland sites should be monitored for their potential impact on the water system (e.g. distance to settlements, number of dams, population density, agricultural areas...).

Here, the use of an essential variables approach in a regional assessment of wetlands demonstrated the mismatch between hotspots of climate change, land-use change and habitat protection coverage within the Mediterranean basin. This approach, coupled with multivariate techniques, provides a framework for identifying biases in monitoring efforts and can inform strategic decision-making. The use of the essential biodiversity variables “habitat extent” with specific surface areas as indicators and climate variables “precipitation” and “temperature” with specific related variables (Table S6), allowed us to assess the exposure of sites to land cover and climate change. The essential variables approach did not allow us to establish real causality of the changes perceived, as the studied drivers are only part of a wide range of aspects of global change. Facilitating better decision-making for the conservation of wetlands relies on evidence of exposure to pressure as well as understanding the associated causality links. Therefore, the essential variables approach proves a valuable tool to provide the first parts of the puzzle, but it lacks information for concrete recommendations.

Nevertheless, these variables do provide a starting point to put all sites into a regional context that can inform local decision-makers on their state and trends, emphasising the sites where actions for climate change mitigation[29,30] or potential protection are required. Wetland sites with important conservation values face a number of barriers that hamper their ability to achieve their conservation goals, such as limited means, capacity and political priority[31,32]. The use of globally widely available data such as remote sensing data, could be part of the solution to at least provide information of some relevant variables at play for wetland conservation.

## METHODS

We considered 236 wetland sites located within a region defined by the limits of coastal watersheds that drain into the Mediterranean Sea. The wetland sites compilation involved the collection of data through different channels, such as the Mediterranean Wetland Outlook (MWO) that identified wetland sites from the north of the Mediterranean Sea, mainly based on national, European and global databases on protected areas, as well as the national Ramsar authorities that referenced the Maghreb and the Near-East sites. All land-cover and climate data were clipped from those site’s delimitation.

**Essential Variables definition and approach**. An Essential Variable (EV) is a variable or a group of linked variables that either (in the case of Essential Biodiversity Variable, EBV) (1) allows quantification of the rate and direction of change in one aspect of the state of biodiversity[17,33], or (for Essential Climatic Variable, ECV) that (2) critically contributes to the characterization of Earth's climate [33]. EVs can be used to frame the variables in a global context, setting global monitoring prioritisation, harmonisation and standardisation to avoid methodological dispersion[34].

Following an Essential Biodiversity Variable framework (EBV), Turak et al, (2017)[22] identified 22 priority activities for freshwater biodiversity conservation to be tackled by 2020 to allow its global mapping. In our study, we put those recommendations into practice by testing different variables as potential essential variables for wetland monitoring. We used harmonised and standardised site-based data (species, climatic and habitat-extent) at high spatial resolution across the Mediterranean.

We identified 15 primary variables that describe climatic, land cover, and bird species patterns closely related to wetlands ecosystem structure. Those variables were partitioned into four EV classes (i.e. Population abundance, ecosystem structure, temperature, precipitation[33,34], Table S7), and used to produce secondary variables (e.g. percentage of wetland change, or percentage of wetland converted in another land-cover type). The primary variables were selected according to their availability and their accordance with common criteria: i) cover the wetlands sites uniformly, ii) overlap in time – all variables were representative of two periods (1990 and 2005), and iii) have high spatial resolution capable of describing local processes.

The climate variables were downloaded from CHELSA (Karger et al. 2017) such as monthly mean, maximum and minimum temperature (°C) from which four variables were derived: 1) annual temperature mean (Tmean), 2) temperature seasonality (Tseas), 3) maximum temperature of the warmest month (Tmax), 4) minimum temperature of the coldest month (Tmin), and monthly precipitation (mm) data from which another four variables were processed: 1) annual precipitation (Pmean), 2) precipitation of the wettest month (Pwet), 3) precipitation of the driest month (Pdry), and 4) precipitation seasonality (Pseas). We computed yearly climatic variables using monthly data from 1986 to 1995 as a representation of 1990's climate, and from 2001 to 2010 to represent 2005's climate. We also transformed each climatic and land cover variable to produce secondary variables that account for changes. Concerning the climate variables, we performed a simple subtraction of their values at 2005 and 1990 such as: *variable diff = data2005 - data1990*. We then obtained the difference in mean temperature (Tmean diff) and precipitation (Pmean diff), in temperature and precipitation seasonality (Tseas diff and Pseas diff), in maximum and minimum temperature of the hottest and coldest month (Tmax diff and Tmin diff) as well as in precipitation of the driest and wettest month (Pdry diff and Pwet diff).

In this study, we interpreted the Essential Biodiversity Variable (EBV) "habitat extent" as the surface area of six different land cover types within each wetland site: natural wetlands, artificial wetlands, urban areas, agricultural lands, natural wetlands and sea (Land-Use Land-Cover data LULC, as defined by the Ramsar Convention, Table S1). We then transformed the initial km$^2$ unit of the land cover categories in percentage of cover per site (further used for the Partial Triadic Analysis), and in percentage of change (PoC) per site via the following equation: *variable PoC = (data2005 - data1990)/data1990*. We considered the percentage of change of natural wetlands representative of the wetland state.

For the bird species data (wintering waterbirds only), two variables were produced for each site: Simpson diversity (alpha diversity) and Sorensen beta diversity. Both fit the population abundance EBV[35]. The population abundance was obtained from regular surveys occurring between 1991 and 2010. We represented the 1990 period by averaging the data from 1991 to 1995, and the 2005 period by averaging from 2006 to 2010. Each period (represented from 1990 and 2005) has a slightly different number of sites surveyed (130 and 178 respectively). Therefore, we used only the sites where both dates were sampled resulting in 111 sites. In this study, we presented the results from beta-Sorensen to measure the change in community species composition (beta diversity) and Simpson diversity to measure the change in populations (alpha diversity) to explain the species response to changes. We assumed both climate and land cover changes increase beta diversity, by inducing a species turnover and favoured the incoming of new species, respectively. By evaluating the trend in alpha diversity, we measured if the change in beta diversity is related to an increase or a decrease in waterbird populations.

**Data processing.** The wetlands sites considered as ‘protected’ presented the following labels: Biotope Protection Order, Forest Reserve, Hunting Reserve, Land acquired by a regional conservatory of natural areas, land acquired by Natural Seaside and Lakeside Conservatory, Marine Protected Areas, Natura 2000, National Park, Nature Monument, Nature Park, Nature Reserve, protected area of Mediterranean Importance, Protected Landscape, Ramsar, Regional Park, Special Reserve, Waterfowl Hunting Bloc, Wildlife Refuge, World Heritage Site. International labels like Important Birds Areas (IBA) that are not part of a convention and do not impose any legal constraint were not considered as a form of protection per se if no any other kind of protection overlapped. As labels often overlapped within a site without any clear management objective defined, we considered the total percentage of protection cover per site to implement a protection grade. We considered the percentage of protection covered per site above and below 50 percent and without protection as three protection levels: highly protected, low protection level and not protected. The protected areas were designated from 1934 to 2016. Not all protected areas had information about their year of designation (n= 103, 44% of sites).

For LULC derived variables, we used data from 236 wetlands sites monitored in 1990 and 2005 at 30 meters of spatial resolution and with a Minimum Mapping Unit (MMU) = 1ha (see the “Essential Variables selection” section for more details). The used LULC database for the southern and eastern countries of the Mediterranean basin was developed in the framework of the GlobWetland-II project (GW-II 2010-2014, funded by the European Space Agency) and completed by the Mediterranean Wetlands Observatory (Tour du Valat) for the northern shore. All LULC (for 1990 and 2005) were derived from Landsat time series (see [36] for methods). The LULC classes were defined using a hybrid nomenclature that combines both CORINE Land Cover (CLC) and Ramsar definitions (see S1).

Out of the 305 sites covered by the GW-II/MWO database, 164 were also monitored for mid-winter waterbird populations between 1991 and 2010 following a specific guideline [24].

Concerning climate data, all following calculations were done following Karger et al., 2017 methodology[23]. To process the annual mean temperature (Tmean) we used the monthly average of the mean temperature across the studied period (from 1986 to 1995, and from 2001 to 2010). We extracted the monthly mean value of each cell using ArcGIS (spatial analyst tool, Cell Statistic by Mean). To get the maximum or minimum temperature of the warmest or coldest month (Tmax and Tmin), we processed the monthly average of the mean, maximum or minimum temperature across the studied period (from 1986 to 1995, and from 2001 to 2010). Like previously, we used the Spatial Analyst tool on ArcGIS (Cell Statistic by Maximum or Minimum) to extract the monthly maximum or minimum value of each cell. Regarding the temperature seasonality (Tseas), we used monthly temperature mean available from CHELSA by applying the standard deviation: sd(monthly temperature)*100 (see available code). The annual precipitation (Pmean) was obtained by calculating the sum of the monthly averages of the precipitation across the studied period (from 1986 to 1995, and from 2001 to 2010) using the Spatial Analyst tool on ArcGIS (Cell Statistic by Sum). The precipitation of the driest or wettest months (Pdry and Pwet) was determined using the monthly average of the minimum precipitation across the studied period (from 1986 to 1995, and from 2001 to 2010). To extract the monthly maximum (wettest month) or minimum (driest month) value of each cell, we used the Spatial Analyst tool on ArcGIS (Cell Statistic by Maximum or Minimum). Finally, the precipitation seasonality (Pseas) was obtained by computing the coefficient of variation [sd(monthly precipitation, e.g. from 1986 to 1995) / (1 + mean(monthly precipitation, e.g. from 1986 to 1995))] *100 (see available code).

**Statistical analysis.** To quantify the importance of changes for the studied variables and wetland sites between 1990 and 2005, we used a Partial Triadic Analysis (PTA)[25] considering the first three axes. PTA is a multivariate technique similar to a Principal Component Analysis (PCA) that integrates three dimensions such as variables, sites (as PCA), and time. It is thus possible to extract the changes that occurred between 1990 and 2005 within each site using Euclidean distances to take into account the simultaneous effects of several variables – what we define here as the ‘vector of change’ (VoC), but also to obtain the changes that occurred for each variable alone between these two dates.

This last point allows us to assess which variables are changing the most within the Mediterranean basin in comparison to the overall variables. We also made a site characterisation of the wetlands using the compromise between 1990 and 2005 (Figure S2). We implemented the PTA analysis on the climatic and the land-cover variables. We used the four temperature (Tmean, Tmax, Tmin, Tseas) and the four precipitation variables (Pmean, Pdry, Pwet, Pseas) in 1990 and 2005 to assess the overall climate change, as well as the four land cover variables that can affect natural wetlands change (percentage of agricultural land, artificial wetland, urban area, and sea covering each site in 1990 and 2005) to report the overall land cover change. We also assessed the conversion of the land-cover extent between the two years by using the Remote Sensing Software "GEOclassifier" (see https://www.swos-service.eu/documents_mapping-software/) to produce a conversion matrix (Table S2).

To account for the difference between the different protection coverage levels (no, low and high coverage) among all climate variables change, land cover variables PoC, climate and land cover VoC, natural wetland loss, beta-Sorensen as well as Simpson diversity, we performed a Kruskal-Wallis test followed by a Conover post-hoc test[37]. Different models were used to report the effect of every climate variable's change (e.g. Tmean diff), land cover variables PoC (e.g. Tmean PoC), and climate and land cover VoC on natural wetland loss, beta-Sorensen or Simpson diversity. Considering natural wetland habitats loss only, we selected all negative values of the initial natural wetland habitats percentage of change (discarding 36 sites out of the 236, among which 31 did not experience any change) divided by minus a hundred to produce normalised values between 0 and 1. We fitted a generalised linear model with binomial distribution to the data. The residuals from the beta-Sorensen metric followed a negative beta-distribution with ]0;1[ values that we fitted with a beta-regression model (logit link), while the ones from the Simpson diversity metric followed a Gaussian distribution, and were then fitted using a linear model.

Multivariate and statistical analyses were performed using R[38] with ade4 and betareg packages. The developed methodology can be applied to any ecosystems to assess the overall changes at diverse scales, regions and cases of study. In this regards all code is freely available at: https://github.com/RoxanneLeb/Mediterranean_wetland .

**Study limitations.** The low number of unprotected sites within the Europeans countries compared to the southern Mediterranean is due to different data providers. Indeed, the MWO reports mainly European protected sites while Ramsar authorities report many unprotected ones, including well-known wetlands (the number of protected areas is relatively low in many of the southern Mediterranean countries). In addition, we did not distinguish between types of protection label since we did not have sufficient information about the different management restrictions at the regional level (Table S7), nor enough human resources available to make strong statements about management types. To provide a complete assessment on the effectiveness of management actions, the definition, resources and goals of each protection status should be sharpened for future studies.

Concerning the use of EBVs at the Mediterranean scale, only wintering waterbirds data was available in a standardized monitoring framework whereas other species, notably endemic amphibians and fishes that might be even more impacted by climate and land cover changes in wetlands were not assessed[9]. Nevertheless, birds are one of the most studied groups, often used as ecological indicators. However, despite waterbirds being spread across a wide range of trophic levels and habitat characteristics, they are mainly migratory species, breeding outside the Mediterranean. Thus, the impact of climate and land use change can be relative as birds are not here all the year. Moreover, waterbirds are probably not reflecting all the consequences of the environmental changes on fish, reptiles or invertebrate species. For example, dam creation could increase deep water bird populations, but could also collapse migratory fish and shallow water invertebrate populations.

Wetland areas are affected by a wide range of pressures and data requirements that go beyond any given essential variable group (e.g. biodiversity, climate, ocean, etc.). Data availability or resolution did not allow us to include data on specific pressures that go beyond the current study (i.e. water availability, water use, water quality, infrastructure construction (dams), population density). In this sense, much of the information mentioned by Turak et al, (2017)[22] is still needed to achieve a most comprehensive assessment. This also includes information not only about the wetland sites themselves, but about the upstream system that regulates many of the local ecological functions and interactions. Their identification could be used to launch or orient systematic monitoring programs to identify wetlands degradation and their conservation threats.

## ACKNOWLEDGMENTS

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Forêts (Algeria), AAO/BirdLife Tunisia, Libyan Society for Birds and the Egyptian Environmental Affairs agency, as well as Anne Mimet for her valuable advice for the statistical analysis.

## REFERENCES

1. Perennou, C., Beltrame, C., Guelmami, A., Tomas Vives, P. & Caessteker, P. Existing areas and past changes of wetland extent in the Mediterranean region: an overview. *ecologia mediterranea* 38, (2012).
2. Geijzendorffer, I. R. *et al.* Mediterranean Wetland Outlook 2: Solutions for sustainable Mediterranean Wetlands. (2018).
3. Giorgi, F. Climate change hot-spots. *Geophys. Res. Lett.* 33, L08707 (2006).
4. Myers, N., Mittermeier, R. A., Mittermeier, C. G., Fonseca, G. A. B. da & Kent, J. Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858 (2000).
5. Guiot, J. & Cramer, W. Climate change: The 2015 Paris Agreement thresholds and Mediterranean basin ecosystems. *Science* 354, 465–468 (2016).
6. García-Ruiz, J. M., López-Moreno, J. I., Vicente-Serrano, S. M., Lasanta–Martínez, T. & Beguería, S. Mediterranean water resources in a global change scenario. *Earth-Science Reviews* 105, 121–139 (2011).
7. Klausmeyer, K. R. & Shaw, M. R. Climate Change, Habitat Loss, Protected Areas and the Climate Adaptation Potential of Species in Mediterranean Ecosystems Worldwide. *PLOS ONE* 4, e6392 (2009).
8. Mariotti, A. *et al.* Mediterranean water cycle changes: transition to drier 21st century conditions in observations and CMIP3 simulations. *Environ. Res. Lett.* 3, 044001 (2008).
9. Cuttelod, A., Garcia, N., Malak, D. A., Temple, H. J. & Katariya, V. *The Mediterranean: a biodiversity hotspot under threat*. 89–101 (J.-C. Vié, C. Hilton-Taylor, S.N. Stuart (Eds.), Wildlife in a Changing World: An Analysis of the 2008 IUCN Red List of Threatened Species, IUCN, 2009).
10. Bradshaw, C. J. A. & Brook, B. W. Human population reduction is not a quick fix for environmental problems. *PNAS* 111, 16610–16615 (2014).
11. Galewski, T. *et al.* Long-term trends in the abundance of Mediterranean wetland vertebrates: From global recovery to localized declines. *Biological Conservation* 144, 1392–1399 (2011).
12. Amano, T. *et al.* Successful conservation of global waterbird populations depends on effective governance. *Nature* 553, 199–202 (2018).
13. Schröter, D. *et al.* Ecosystem Service Supply and Vulnerability to Global Change in Europe. *Science* (2005). doi:10.1126/science.1115233
14. Gardner, R. C. *et al. State of the World's Wetlands and Their Services to People: A Compilation of Recent Analyses*. (Social Science Research Network, 2015).
15. Kark, S., Levin, N., Grantham, H. S. & Possingham, H. P. Between-country collaboration and consideration of costs increase conservation planning efficiency in the Mediterranean Basin. *PNAS* 106, 15368–15373 (2009).
16. Martin, L. J., Blossey, B. & Ellis, E. Mapping where ecologists work: biases in the global distribution of terrestrial ecological observations. *Frontiers in Ecology and the Environment* 10, 195–201 (2012).
17. Pereira, H. M. *et al.* Essential Biodiversity Variables. *Science* 339, 277–278 (2013).
18. Bojinski, S. *et al.* The Concept of Essential Climate Variables in Support of Climate Research, Applications, and Policy. *Bull. Amer. Meteor. Soc.* 95, 1431–1443 (2014).
19. Miloslavich, P. *et al.* Essential ocean variables for global sustained observations of biodiversity and ecosystem changes. *Global Change Biology* 24, 2416–2433 (2018).
20. Geijzendorffer, I. R. *et al.* Bridging the gap between biodiversity data and policy reporting needs: An Essential Biodiversity Variables perspective. *Journal of Applied Ecology* 53, 1341–1350 (2016).
21. Schmeller, D. S. *et al.* Towards a global terrestrial species monitoring program. *Journal for Nature Conservation* 25, 51–57 (2015).
22. Turak, E. *et al.* Essential Biodiversity Variables for measuring change in global freshwater biodiversity. *Biological Conservation* 213, 272–279 (2017).
23. Karger, D. N. *et al.* Climatologies at high resolution for the earth's land surface areas. *Scientific Data* 4, sdata2017122 (2017).
24. Delany, S. Guidelines for Participants in the International Waterbird Census (IWC). (2005).
25. Thioulouse, J., Simier, M. & Chessel, D. Simultaneous Analysis of a Sequence of Paired Ecological Tables. *Ecology* 85, 272–283 (2004).
26. Santamaria, L. *et al.* A new laboratory for science and wetland restoration. In Doñana, Water and Biosphere. ; *Confederación Hidrográfica del Guadalquivir. Ministerio de Medio Ambiente: Madrid, España* 313–315 (2006).
27. Herbert, E. R. *et al.* A global perspective on wetland salinization: ecological consequences of a growing threat to freshwater wetlands. *Ecosphere* 6, 1–43 (2015).

28. Pekel, J.-F., Cottam, A., Gorelick, N. & Belward, A. S. High-resolution mapping of global surface water and its long-term changes. *Nature* 540, 418–422 (2016).
29. Sayoud, M. S. *et al.* The first coordinated trans-North African mid-winter waterbird census: The contribution of the International Waterbird Census to the conservation of waterbirds and wetlands at a biogeographical level. *Biological Conservation* 206, 11–20 (2017).
30. Downard, R., Endter-Wada, J. & Kettenring, K. Adaptive wetland management in an uncertain and changing arid environment. *Ecology and Society* 19, (2014).
31. Jones, H. P., Hole, D. G. & Zavaleta, E. S. Harnessing nature to help people adapt to climate change. *Nature Climate Change* 2, 504–509 (2012).
32. Geijzendorffer , I.R., Beltrame, C., Chazee, L., Gaget, E., Galewski, T., Guelmami A., Perennou, C., Popoff, N., Guerra, C., Leberger, R., Jalbert, J., Grillas, P. *Increasing the impact of the Ramsar convention on the conservation of Mediterranean wetlands. Frontiers*. Under review.
33. Gill, D. A. *et al.* Capacity shortfalls hinder the performance of marine protected areas globally. *Nature* 543, 665–669 (2017).
34. Pettorelli, N. *et al.* Framing the concept of satellite remote sensing essential biodiversity variables: challenges and future directions. *Remote Sens Ecol Conserv* 2, 122–131 (2016).
35. Kissling, W. D. *et al.* Building essential biodiversity variables (EBVs) of species distribution and abundance at a global scale. *Biol Rev* 93, 600–625 (2018).
36. Perennou, C. *et al.* Chapter Six - Mapping Mediterranean Wetlands With Remote Sensing: A Good-Looking Map Is Not Always a Good Map. in *Advances in Ecological Research* (eds. Bohan, D. A., Dumbrell, A. J., Woodward, G. & Jackson, M.) 58, 243–277 (Academic Press, 2018).
37. Conover, W. J. & Iman, R. L. On multiple-comparison procedures. *Technical report, Los Alamos Scientific Laboratory* (1979).
38. R Development Core Team. *R: A Language and Environment for Statistical Computing*. (Fondation for Statistical Computing, 2016).

# SUPPLEMENTARY MATERIALS

**Table S1.** Land-cover classes composition.

| Land-cover | Class composition |
|---|---|
| Agricultural lands | Arable land, permanent crops, pastures (except wet), heterogeneous agricultural areas. |
| Artificial wetlands | Mines, dump and construction sites (excavations : gravel, bricks, clay pits, borrow pits, mining pools), coastal wetlands (salines), inland waters (canals and drainage channels), inland water bodies (aquaculture ponds ; ponds: farm, stock ponds ; water storage areas: barrage, dams, impoundments ; wastewater treatment areas: sewage farms, settling ponds, oxidation basins). |
| Natural wetlands | Wet pastures, wet forests including riparian, shrub-dominated wetlands (shrub swamp, shrub dominated freshwater marshes, shrub carr, alder thicket on inorganic soils), sand (shingle or pebble shores island bars, spites and sandy ilsets, dune systems and humid dune slacks), inland wetlands, coastal wetlands (except salines), inland waters (inland delta, courses, rivers, etc), marine waters (lagoon, estuaries etc.). |
| Urban areas | Urban fabric, industrial commercial and transport unit, mine (mineral extraction), dump and construction sites, artificial non-agricultural vegetated areas (green urban area, sport and leisure facilities). |
| Sea | Sea |

**Table S2.** Transition matrix of the surface in km$^2$ between 1990 and 2005 across land-cover classes taking into account the 236 wetland sites. With urban = urban area, agri = agricultural area, nat_dry = natural dryland area, nat_wet = natural wetland area, art_wet = artificial wetland area, sea = sea area, PoC (in %) = percentage of change (variable$_{2005}$-variable$_{1990}$/variable$_{1990}$)x100.

| | urban 1990 | agri 1990 | nat_dry 1990 | nat_wet 1990 | art_wet 1990 | sea 1990 | total | PoC |
|---|---|---|---|---|---|---|---|---|
| urban 2005 | 539.73 | 276.30 | 164.13 | 41.62 | 6.23 | 1.32 | 1,029.34 | 42.23 |
| agri 2005 | 0.37 | 8,342.55 | 1,069.77 | 311.04 | 85.58 | 0.04 | 9,809.35 | -31.59 |
| nat dry 2005 | 0.30 | 0.36 | 6,695.79 | 8.57 | 0.06 | 7.80 | 6,712.89 | -14.53 |
| nat wet 2005 | 0.98 | 6.66 | 0.21 | 11,384.90 | 1.55 | 9.28 | 11,403.59 | 187.53 |
| art wet 2005 | 0.49 | 126.48 | 43.55 | 255.45 | 1,497.67 | 0.16 | 1,923.79 | 6.73 |
| sea 2005 | 0.03 | 0.00 | 22.34 | 6.71 | 0.00 | 1,091.08 | 1,120.17 | 348.69 |
| total | 541.90 | 8,752.36 | 7,995.79 | 12,008.28 | 1,591.10 | 1,109.69 | 1,029.34 | |

**Table S3.** Values from the Partial Triadic Analysis on 3 axes by order of importance given the 'vector of change' considering all variables, climate variables only and land cover variables only. With as land-cover variables agri=agricultural area, art_wet=artificial wetland area, urb=urban area, sea=sea area, and as climate variables pdry=precipitation of the driest month, pmean=mean precipitation, pwet=precipitation of the wettest month, tmax= maximum temperature of the warmest month, tmean=mean temperature, tmin= minimum temperature of the coldest month, tseas=temperature seasonality.

| All variables | urb | tmax | tmin | agri | tseas | pwet | pmean | pseas | art_wet | tmean | pdry | sea |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Vector of change | 14.7 | 11.8 | 11.8 | 10.4 | 8.8 | 7.0 | 5.9 | 4.6 | 4.2 | 3.7 | 2.0 | 1.9 |
| Climatic variables | tmin | tmax | tseas | pmean | pseas | tmean | pdry | - | - | - | - | - |
| Vector of change | 17.0 | 11.6 | 10.8 | 8.8 | 5.04 | 4.1 | 2.8 | - | - | - | - | - |
| Land-use variables | agri | urb | art_wet | sea | - | - | - | - | - | - | - | - |
| Vector of change | 10.2 | 5.1 | 3.3 | 0.2 | - | - | - | - | - | - | - | - |

**Table S4.** Natural wetland loss, Sorensen beta-diversity and Simpson diversity according to the change in eight climatic variables, four land-cover variables, as well as the climatic and land-cover vector of change (VoC). The change in climate variables (diff) was accounted by the subtraction of the variable values between 2005 and 1990, while a percentage of change relative to 1990 (PoC = [$data_{2005}$ - $data_{1900}$]/ $data_{1990}$) was used to assess the land-cover change. A generalised linear model fitted with a quasibinomial distribution was applied to account for the natural wetland loss, while a beta-regression was applied concerning Sorensen beta-diversity, and a linear model was used for the Simpson diversity according to their respective distribution.

| Response variable | Explanatory variable | Coefficient | Standard error | p-value | QAIC |
|---|---|---|---|---|---|
| Natural wetland loss | Tmean diff | 0.551 | 0.918 | 0.559 | 48.8 |
| | Pmean diff | -0.003 | 0.002 | 0.142 | 48.4 |
| | Tmax diff | -0.277 | 0.165 | 0.094 | 48.2 |
| | Tmin diff | 0.043 | 0.093 | 0.642 | 49.1 |
| | Tseas diff | -2.043 | 0.797 | 0.011 | 46.8 |
| | Pdry diff | 0.011 | 0.052 | 0.834 | 49.1 |
| | Pwet diff | -0.005 | 0.009 | 0.591 | 49.0 |
| | Pseas diff | 0.004 | 0.018 | 0.810 | 49.1 |
| | Log(Agri PoC) | -0.838 | 0.564 | 0.139 | 48.3 |
| | Log(Artificial Wetland PoC) | 0.929 | 0.174 | 2.67e-07 | 41.7 |
| | Log(Urb PoC) | 0.240 | 0.214 | 0.263 | 48.7 |
| | Log(Sea PoC) | 0.543 | 0.740 | 0.464 | 49.0 |
| | Climate VoC | -0.434 | 0.627 | 0.490 | 49.0 |
| | Land-cover VoC | 0.857 | 0.324 | 0.008 | 42.5 |
| | PA decreasing cover | 0.468 | 0.159 | 0.004 | 46.2 |
| **Response variable** | **Explanatory variable** | **Coefficient** | **Standard error** | **p-value** | **Log-likelihood** |
| Beta Sorensen | Tmean diff | -0.41 | 0.34 | 0.22 | 10.78 |
| | Pmean diff | -0.00 | 0.00 | 0.32 | 10.55 |
| | Tmax diff | -0.34 | 0.11 | <0.01 | 14.62 |
| | Tmin diff | 0.03 | 0.06 | 0.60 | 10.18 |
| | Tseas diff | 0.13 | 0.52 | 0.81 | 10.07 |
| | Pdry diff | 0.01 | 0.03 | 0.67 | 10.14 |
| | Pwet diff | -0.00 | 0.01 | 0.69 | 10.12 |
| | Pseas diff | 0.02 | 0.01 | 0.17 | 10.98 |
| | Log(Agri PoC) | -0.35 | 0.33 | 0.29 | 10.59 |
| | Log(Artificial wet PoC) | 0.06 | 0.28 | 0.82 | 10.07 |
| | Log(Natural wet loss) | 0.06 | 0.11 | 0.56 | 06.28 |
| | Log(Urb PoC) | -0.00 | 0.14 | 0.95 | 10.05 |

| | | | | | |
|---|---|---|---|---|---|
| | Log(Sea PoC) | -0.59 | 0.68 | 0.39 | 10.43 |
| | Climate VoC | 0.57 | 0.33 | 0.08 | 11.57 |
| | Land-cover VoC | 0.00 | 0.19 | 0.99 | 10.04 |
| | PA decreasing cover | -0.13 | 0.42 | 0.37 | 10.47 |

| Response variable | Explanatory variable | Coefficient | Standard error | p-value | AIC |
|---|---|---|---|---|---|
| Simpson diversity | Tmean diff | 0.05 | 0.11 | 0.47 | 48.35 |
| | Pmean diff | 0.00 | 0.00 | 0.41 | 47.87 |
| | Tmax diff | 0.03 | 0.04 | 0.36 | 47.71 |
| | Tmin diff | 0.02 | 0.02 | 0.39 | 47.83 |
| | Tseas diff | -0.07 | 0.17 | 0.68 | 48.40 |
| | Pdry diff | 0.00 | 0.01 | 0.88 | 48.55 |
| | Pwet diff | 0.00 | 0.00 | 0.07 | 45.09 |
| | Pseas diff | 0.00 | 0.00 | 0.29 | 47.44 |
| | Log(Agri PoC) | 0.12 | 0.11 | 0.25 | 47.23 |
| | Log(Artificial Wetland PoC) | -0.12 | 0.09 | 0.16 | 46.56 |
| | Log(Natural wet loss) | 0.04 | 0.03 | 0.20 | 10.63 |
| | Log(Urb PoC) | -0.03 | 0.05 | 0.56 | 48.23 |
| | Log(Sea PoC) | 0.11 | 0.22 | 0.50 | 48.32 |
| | Climate VoC | -0.09 | 0.11 | 0.43 | 47.94 |
| | Land-cover VoC | -0.05 | 0.07 | 0.52 | 48.15 |
| | PA decreasing cover | 0.004 | 0.047 | 0.925 | 48.57 |

As variables we used 1) mean temperature (Tmean diff), 2) mean precipitation change (Pmean diff) and their interaction, 3) maximum temperature of the warmest month (Tmax diff), 4) minimum temperature of the coldest month (Tmin diff), 5) temperature seasonality (Tseas diff), 6) precipitation of the driest month (Pdry diff), 7) precipitation of the wettest month (Pwet diff), 8) precipitation seasonality (Pseas diff), 9) agricultural lands (Agri PoC), 10) artificial wetlands (Artificial Wetland PoC), 11) urban areas (Urb PoC), 12) sea (Sea PoC), 13) vector of change regarding the climate variables (Climate VoC), 14) vector of change regarding the land-cover variables (land-cover VoC), 15) protected area coverage classes from 100% to 0% cover (PA decreasing cover).

**Table S5.** Difference between the three classes of protected area (PA) coverage (no, low, and high coverage) (Kruskal-Wallis test, followed by a Conover post-hoc test when significant). The median of the variable value (e.g. mean temperature change between 1990 and 2005 (Tmean diff)) was reported for each protected coverage class only when the Kruskal-Wallis test was significant.

| Variable | Test | PA coverage | $X^2$ | df | p | median |
|---|---|---|---|---|---|---|
| Tmean diff | Kruskal-Wallis | All | 51.18 | 2 | <0.001 *** | - |
| | Conover | No - Low | | | 0.08 | 0.70 – 0.96 |
| | | No - High | | | <0.001 *** | 0.70 – 0.42 |
| | | Low - High | | | <0.001 *** | 0.96 – 0.42 |
| Tmax diff | Kruskal-Wallis | All | 15.96 | 2 | <0.001 *** | - |
| | Conover | No - Low | | | <0.05 * | 0.26 – 0.90 |
| | | No - High | | | <0.001 *** | 0.26 – 1.20 |
| | | Low - High | | | 0.44 | 0.90 – 1.20 |
| Tmin diff | Kruskal-Wallis | All | 17.13 | 2 | <0.001 *** | - |
| | Conover | No - Low | | | <0.05 * | 1.90 – 3.34 |
| | | No - High | | | <0.05 * | 1.90 – 1.45 |
| | | Low - High | | | <0.001 *** | 3.34 – 1.45 |
| Tseas diff | Kruskal-Wallis | All | 46.84 | 2 | <0.001 *** | - |
| | Conover | No - Low | | | 0.60 | -0.09 - -0.13 |
| | | No - High | | | <0.001 *** | -0.09 – 0.15 |
| | | Low - High | | | <0.001 *** | -0.13 – 0.15 |
| Pmean diff | Kruskal-Wallis | All | 7.82 | 2 | <0.05 * | - |
| | Conover | No - Low | | | 0.65 | 0.65 – 0.95 |
| | | No - High | | | <0.01 ** | 0.65 - -1.89 |
| | | Low - High | | | 0.10 | 0.95 - -1.89 |
| Pdry diff | Kruskal-Wallis | All | 11.24 | 2 | <0.001 *** | - |
| | Conover | No - Low | | | <0.01 ** | -0.07 - -0.35 |
| | | No - High | | | <0.01 ** | -0.07 - -0.57 |
| | | Low - High | | | 0.47 | -0.35 - -0.57 |
| Pwet diff | Kruskal-Wallis | All | 8.48 | 2 | <0.01 ** | - |
| | Conover | No - Low | | | 0.39 | -3.39 – -6.68 |
| | | No - High | | | <0.05 * | -3.39 – 0.96 |
| | | Low - High | | | <0.001 *** | -6.68 – 0.96 |
| Pseas diff | Kruskal-Wallis | All | 7.82 | 2 | <0.05 * | - |
| | Conover | No - Low | | | 0.65 | 0.65 – 0.95 |
| | | No - High | | | <0.01 *** | 0.65 – -1.89 |
| | | Low - High | | | 0.10 | 0.95 – -1.89 |
| Agri PoC | Kruskal-Wallis | All | 0.55 | 2 | 0.76 | - |
| | Conover | No - Low<br>No - High<br>Low - High | | | - | - |
| Art Wet PoC | Kruskal-Wallis | All | 3.00 | 2 | 0.22 | - |
| | Conover | No - Low<br>No - High<br>Low - High | | | - | - |
| Urb PoC | Kruskal-Wallis | All | 10.02 | 2 | <0.01 ** | - |
| | Conover | No - Low | | | <0.01 ** | 0.44 – 1.07 |
| | | No - High | | | 0.91 | 0.44 – 0.35 |
| | | Low - High | | | <0.01 ** | 1.07 - 0.35 |
| Sea PoC | Kruskal-Wallis | All | 1.42 | 2 | 0.49 | - |
| | Conover | No - Low<br>No - High<br>Low - High | | | - | - |
| Climate VoC | Kruskal-Wallis | All | 2.09 | 2 | 0.35 | - |
| | | No - High<br>No - Low<br>Low - High | | | - | - |
| Land-cover VoC | Kruskal-Wallis | All | 2.01 | 2 | 0.37 | - |
| | | No - High<br>No - Low<br>Low - High | | | - | - |
| Natural wetland loss | Kruskal-Wallis | All | 11.76 | 2 | <0.01 ** | - |
| | Conover | No - High | | | <0.05 * | -0.02 - -0.01 |
| | | No - Low | | | 0.56 | -0.02 - -0.02 |
| | | Low - High | | | <0.03 * | -0.02 - -0.01 |
| Beta Sorensen | Kruskal-Wallis | All | 10.88 | 2 | <0.05 * | - |
| | Conover | No - High | | | <0.05 * | 0.19 – 0.47 |
| | | No - Low | | | <0.01 ** | 0.19 – 0.54 |
| | | Low - High | | | 0.32 | 0.54 – 0.47 |
| Simpson diversity | Kruskal-Wallis | All | 1.90 | 2 | 0.39 | - |
| | Conover | No - High<br>No - Low<br>Low - High | | | - | - |

| EV type | EV Class | EV | Variable | Unit per site | Unit per time | Reference |
|---|---|---|---|---|---|---|
| EBV | Population abundance | | Simpson diversity | total | 1990 = mean (1991-1995)<br>2005 = mean (2006 - 2010) | Regular surveys following the method of Delany (2005) |
| | | | | | T1= mean (1991-1995)<br>T2 = mean (1996 – 2000)<br>T3 = mean (2001 - 2005)<br>T4 = mean (2006 - 2010)<br>Beta(1990) = species turnover between T1 and T2<br>Beta(2005) = species turnover between T3 and T4 | |
| | | | Sorensen beta-diversity | | | |
| | Ecosystem structure | Habitat Extent | Urban area | % | 1990<br>2005 | GW-II/MWO database derived from Landsat time series (Perennou et al, 2018) |
| | | | Agricultural land area | | | |
| | | | Sea area | | | |
| | | | Artificial wetland area | | | |
| | | | Natural wetland area | | | |
| ECV | Temperature | | Annual mean temperature | mean | 1990 = mean (1986-1995)<br>2005 = mean (2001-2010) | Krager et al. (2017) |
| | | | Temperature seasonality | | | |
| | | | Maximum temperature of warmest month | | | |
| | | | Minimum temperature of the coldest month | | | |
| | Precipitation | | Annual precipitation | | | |
| | | | Precipitation of wettest month | | | |
| | | | Precipitation of driest month | | | |
| | | | Precipitation seasonality | | | |

**Table S6.** Variables studied and their Essential Variable (EV) attribution. With EBV = Essential Biodiversity Variables, ECV = Essential Climate Variables, GW-II = GlobWetland-II project 2010-2014 and MWO = Mediterranean Wetland Outlook. All variables with * relate to recommended use as indicator.

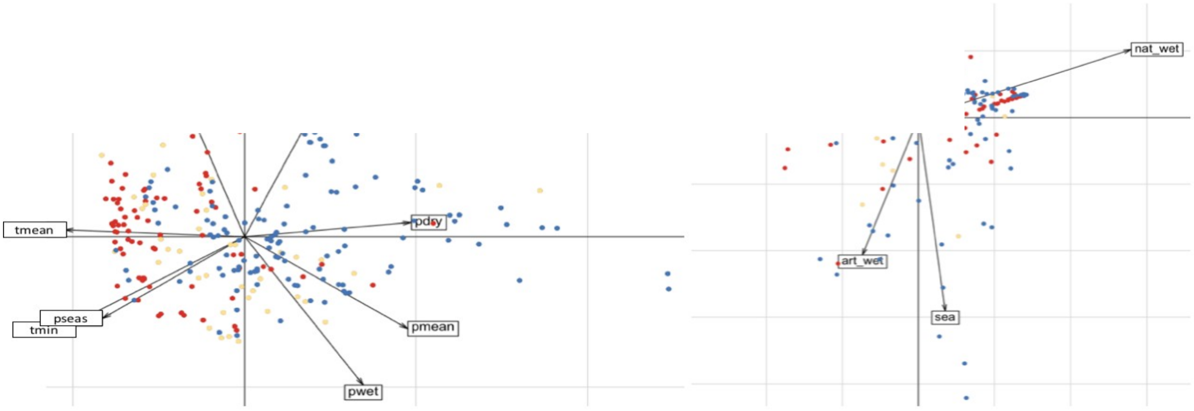


**Figure S1.** Partial Triadic Analysis compromise between 1990 and 2005 concerning a) climatic variables, and b) land cover variables with the sites as dots such as red = no protection coverage, orange = low protection coverage, blue = high protection coverage. With as land-cover variables agri=agricultural area, art_wet=artificial wetland area, urb=urban area, sea=sea area, and as climate variables pdry=precipitation of the driest month, pmean=mean precipitation, pwet=precipitation of the wettest month, tmax= maximum temperature of the warmest month, tmean=mean temperature, tmin= minimum temperature of the coldest month, tseas=temperature seasonality.

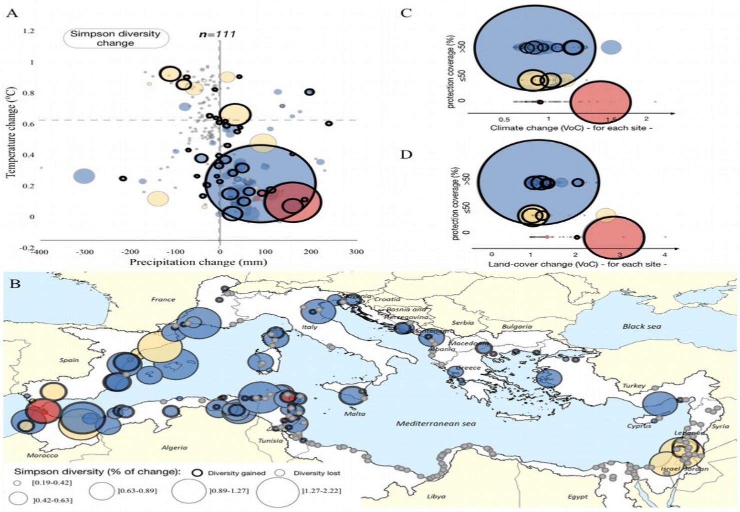
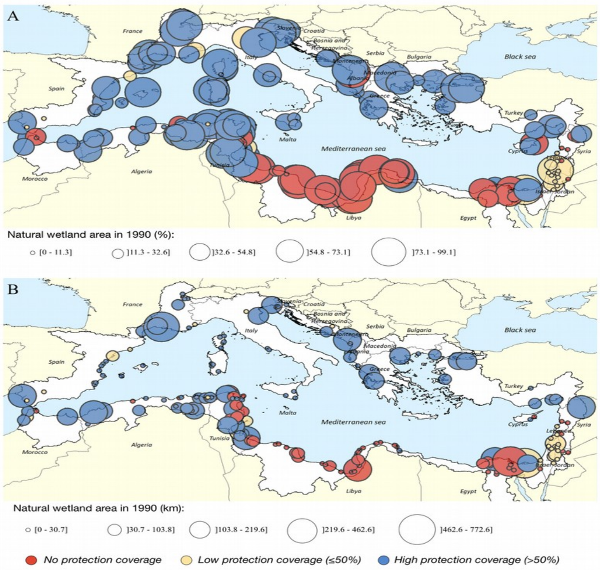


**Figure S2.** a) Simpson diversity values per site between 1990 and 2005 along the mean temperature and mean precipitation change gradients. The bubble size represents the Simpson diversity values within each wetland site, b) Simpson diversity values along the vector of change of climate variable gradient (VoC, with high value for high climate change), c) Simpson diversity values along the land-cover change gradient (VoC, with high value for high land-cover change). The colors represent the protection status of the sites such as red = no protection status, orange = low protection coverage, green = high protection coverage, and grey = sites without species data available. Bold circle = diversity gained, thin circle = diversity lost.

**Figure S4.** A) Percentage of natural wetland area per site in 1990, and B) Natural wetland area (km) in 1990. In red = no protection status, orange = low protection coverage, green = high protection coverage.



# SYNTHESIS

This thesis brings a contribution to the use of global indicators to support international conservation policy by focusing on two threatened ecosystems – forests and wetlands – essential to biodiversity and human well-being.

## 1. LEARN ABOUT THE SYSTEM

Assessing an indicator's performance in capturing patterns or processes is needed as a first step before its systematic use. A relevant indicator brings two dimensions of knowledge: it helps in improving our understanding of the studied system as well as providing a simple way of representing it. Analysing species distribution patterns allows us to test hypotheses about the mechanisms through which species diversity evolves or is maintained in ecosystems.

### 1.1. MAIN RESULTS

In Chapter 1, I assessed the relevance of the Habitat Rarity index as an indicator of species rarity across locations. The found pattern was not consistent between realms, and other factors such as climate change velocity from the late quaternary glacial-interglacial period, maximum temperature of the warmest month or precipitation seasonality demonstrated quite strong signals in explaining birds' rarity. Indeed, in most of the realms, areas that harbour high maximum temperatures, high precipitation variability during the year or historically instable climate favoured the establishment of species with large range-sizes which have a broader ecological niche and a higher tolerance to extremes (Bozinovic et al., 2011). Nevertheless, rare forest habitats were more prone to hosting small range-size birds in Africa, Palearctic and South-America, as well as in Papua New-Guinea.

These results are in line with other studies, confirming the importance of climate change velocity to explain species range-size (Burrows et al., 2014; Li et al., 2016; Sandel et al., 2011). In Chapter 1, I went further by comparing the contribution of several predictors in explaining species range-size, assessing their heterogeneity across nine different spatial locations. Even though climate change velocity was predominant in most realms to explain species rarity, precipitation seasonality in North America and precipitation of the wettest month in Palearctic were the strongest predictors in those realms.

### 1.2. LIMITATIONS AND STRENGTHS

This study presents two main conceptual limitations. First, a quantification of the links between habitat rarity, climate change velocity, specialisation of species and species range-size would improve this study by strengthening its conceptual dimension. Indeed, this study was based on the assumption that narrow-range species should have a restricted ecological niche with a higher degree of specialisation towards their environment. However, the link between species niche and range-size breadth is not systematic, as range-size is primarily linked to the commonness of species niche in the environment (e.g. a forest bird specialist should have a broad range-size if the forest is abundant). Thus, specialisation level is not clearly connected with species range-size, but rather with the degree of isolation that fosters selection processes that are taking place over an evolutionary time scale (Devictor et al., 2010). Thus, quantifying how part of the specialisation level or species range-size can be explained by either current or historical climate would add relevant information. The use of methods such as path-analysis could be considered (Grace and Pugesek, 1998).

Second, it is possible that a Habitat Rarity index (HR) computed by comparing each cell to neighbouring ones instead of an entire realm would give more conclusive results in explaining species rarity. Indeed, this approach could highlight local habitat anomalies allowing for more sensitive description of the distribution of bird communities, and particularly of other taxa with more limited spatial dispersion abilities. Also, it would allow the comparison of the HR index between the different realms. The neighbouring approach has already been explored by (Ohlemüller et al., 2008) but only at coarse spatial resolution. The development of similar methods at fine spatial grain using multivariate Mahalanobis distances would require more research, but could be achieved by the use of moving windows.

The ability of the HR index in predicting birds' rarity might rely on the choice of its input variables. Sensitivity analysis that used consecutive removal of one of the input variables demonstrated that changes can be inferred in the relationship. The habitat-species-rarity relationship could be further tested with different variables to select the combination to which birds might be most sensitive.

The link between habitat and species rarity was not as strong as expected, and the results indicate that one should perhaps rather discard this variable as an effective indicator for predicting species range. However, the above limitations prevent drawing any definitive conclusion on the ability of a habitat rarity indicator to predict species range-size. Rather, they encourage further research to reinforce the robustness of the results.

The main strength of the developed method of quantifying HR is its plasticity in incorporating different types of abiotic variables. Thus, it can be applied to different ecosystem types or properties (e.g. mapping rarity of ecological functions) and remains open to several ecological questions (e.g. can community turnover vary along an environmental rarity gradient, (Keil et al., 2012). It can open research areas that are still to explore, maybe leading to the emergence of new global indicators.

## 2. INFORM POLICY DECISION AND RAISE AWARENESS

In Chapters 2 and 3, I used variables derived from high resolution data for site-based assessment, with the aim to provide meaningful information for conservation. Therefore, the indicators used in those chapters can be applied as meaningful tools to raise decision makers' awareness.

### 2.1. FOREST AND WETLAND LOSS – MAIN RESULTS

In Chapter 2, I explored the ability of protected areas status to preserve forests at different scales: global, regional and per site. As previous studies framed their analysis in a global context (Allan et al., 2017; Jones et al., 2018; Leroux et al., 2010), the results allow pointing out world subregions where protection should be reinforced. For instance, the main policy-relevant messages this study can provide are that the Eastern European, Caribbean and Mesoamerican subregions do not provide efficient protection as more forest loss occurs within their protected areas than outside. In addition, IUCN categories are not respected in the Caribbean, North East Asia and West Africa, where most of the forest loss occurred within the highest levels of protection Ia-III compared to the lower ones IV-VI. The main limitation of this study is that the number of protected areas analysed represents just 16% of all forested protected areas. Even though the study's representativeness is quite low, it still includes many areas that do not benefit from having enough resources to protect what they are aiming for.

Chapter 3 provides monitoring solutions for natural wetlands around the Mediterranean basin, demonstrating a decrease of natural wetland areas by 5% in the studied sites between 1990 and 2005. I identified 15 variables that could be used to monitor wetlands habitat and biodiversity state and threats. The sites that encountered the most loss, which were also largely unprotected, were located in the Eastern Mediterranean where an unusually high level of warming occurred. Wetland restoration or protection in this area should be considered in order to mitigate climate change effects and water depletion, which were already the root of substantial social instabilities (Châtel, 2014). Variables used to account for biodiversity change in this study did not provide any conclusive results regarding the effect of climate or land-cover change on waterbirds species. Even though a turnover within a community or diversity loss can be a signal of local extinction, other drivers might be responsible for waterbirds community diversity change (Amano et al., 2018). Also, the spatial combination of species data with protected sites allowed the identification of data coverage gaps. Those gaps need to be addressed to improve assessment quality. Indeed, the results concerning species response to pressures are suspected to be biased, with data sampled mainly in protected wetlands.

## 2.2. WAYS FORWARD

In the introduction, I pointed out that so far, even though efforts are being made to preserve a certain level of downscaling (e.g. the Wetland Extent Index can be disaggregated from global scale to six regions), global indicators generated by georeferenced data remain scarce (Tittensor et al., 2014). One relevant exception is the Living Planet Index database that hold times-series species data over 1,736 protected areas around the world (Collen et al., 2009; Geldmann et al., 2014). At this stage of technological advance, Georeferenced Information System techniques provide sufficiently high resolution data to support the production of efficient global indicators. Those indicators should encompass the following criteria: relevance, sensitivity to change, generalisability, scalability and data collection feasibility (Schmeller et al., 2018). To avoid methodological dispersion, site-based studies should follow a coherent framework within the global context (e.g. under essential variable labels, (Haase et al., 2018). The monitoring of relevant site-based variables would allow the production of cross-scale information: per site, country, region and global scale. The studied variable could be then treated as a "scalable (site-based) global indicator".

Regarding Chapter 2, the use of forest data monitoring to quantify the 'forest loss extent' within each protected area should be systemised (using for instance the Hansen dataset, (Hansen et al., 2013). In the context of assessing forest loss, the use of time series of a 'forest loss extent' indicator instead of 'forest extent' would discard all re-grown forests. Indeed, re-grown forests can have different ecosystem properties, with different ecosystem dynamics and functioning (e.g. forest succession), not always appropriate for the remaining long-term established species community (Gibson et al., 2011). Moreover, it gives a direct insight on the pressures exerted on the forest system. The variable 'forest loss extent' could be then treated as a "scalable global indicator" and framed as an EBV as part of the 'habitat extent' variables, under the 'ecosystem structure' EBV class (Table 1). To mitigate the site sampling issue that will recurrently arise from site-based studies, the use of a Forest Extent Trends index inspired by Dixon et al. (2016) could estimate broad trends from incomplete data. Such an index could be extended to all "scalable site-based global indicators" of the EBV class 'habitat extent' (Table 1).

In Chapter 3, I framed monitoring indicators into an essential variables context in accordance with a global standard. To account for the effect of land-cover change, our results suggest to monitor the variable 'natural wetland extent' for each wetland site. As wetland recovery is not as dynamic as forest recovery, the use of 'wetland extent' and not 'extent of loss' would allow for highlighting highly beneficial ecosystem restoration. The variable 'natural wetland extent' could be then treated as a "scalable (site-based) global indicator", that can be used to feed the Wetland Extent Trends index (Dixon et al., 2016) which is subdivisable into six regions (Tittensor et al., 2014). The variable 'natural wetland extent' can be framed as an EBV as part of the 'habitat extent' variables, under the 'ecosystem structure' class (Table 1). Of course, the main challenge lies in the delimitation of wetland sites, but this effort can be done following published procedures (Perennou et al., 2018). The use of essential variables allowed us to assess natural wetland exposure to climate and land-use change. In this regard, I would also propose the use of the studied variables as potential "scalable (site-based) global indicators" (some examples in Table 1).

To increase information efficiency and accessibility towards decision makers, reported results should be integrated into web-services (e.g. DOPA explorer, Living Planet Index). This would facilitate the identification of studied sites (e.g. zoom in-out), emphasising the need to improve management policies in ineffectively protected sites, or to assess the need to protect areas that harbour valuable ecosystems threatened by global changes. The extension of such practices to other natural land-cover classes (e.g. natural grassland) would be valuable.

**Table 1.** Proposition of a "scalable site-based global indicator" classification of some of the studied variables. With EBV = Essential Biodiversity Variable. The EBV categorisation follow the one as proposed by the GEO BON community (https://geobon.org).

| EBV class | EBV | Scalable site-based global indicator | Extend Trends index |
|---|---|---|---|
| Ecosystem structure | Habitat extent | Forest loss extent | Forest Extent Trends index |
| | | Natural wetland extent | Natural Wetland Extent Trends index (Dixon et al., 2016) |
| | | Artificial wetland extent | Artificial Wetland Extent Trends index (Dixon et al., 2016) |
| | | Agriculture area | Agriculture Extent Trends index |
| Species abundance | Species population | Waterbirds abundance | Living Planet Index (Collen et al., 2009) |

## 3. AUDIT MANAGEMENT ACTIONS

Even though we are on the way to achieving the Aichi Target 11 by 2020 that requires protection coverage of 17 per cent of terrestrial and inland water areas and 10 per cent of coastal and marine areas, many protected areas are under intense human pressure (Jones et al. 2018). Reporting only the extent of protected land without considering the effectiveness of the protection coverage in reaching conservation goals might lead to incorrect expectations about the capabilities of protection coverage in protecting biodiversity. In Chapter 2, the results roughly confirm the IUCN categorisation ranking of protected areas, making clear the separation between the IUCN categories that require protected areas to remain untouched and the ones allowing sustainable use of resources. Nonetheless, the ability of high IUCN categories in preventing forest loss varies substantially among regions.

Auditing management activities can be tricky as management is often guided by overlapping international and national policies which brings a high level of complexity for auditing. Therefore, a substantial effort in collecting, identifying and classifying different management plans and integrating their current state and objectives within an open database for each protected site would foster auditing performance as well as international policy implementation.

Earth observation data are not enough to assess conservation effort. Although remote sensing is an efficient and direct way to measure land-cover, most taxa are invisible to satellites and assessment of complex processes supporting ecosystem services through remote-sensed proxies can have poor outcomes (Eigenbrod et al., 2010). It is then relevant to integrate other data-sources to take into account a larger portion of biodiversity and ecosystem services connecting Earth observation to biodiversity and ecosystems as suggested by (Bush et al., 2017). The coming implementation of such approaches has significant potential to boost auditing capabilities and management efficiency.

## 4. THE STUDIED INDICATORS IN THE CONTEXT OF THE AICHI BIODIVERSITY TARGET

Since the Convention on Biological Diversity (CBD) parties committed in 2011 to reach the 20 Aichi Biodiversity Targets by 2020, the rate of global indicators development increased to improve quantification of the fulfilment (Tittensor et al., 2014). In the preparation of setting up post 2020 objectives, if future research is more conclusive, a Habitat Rarity index could be used to define and prioritize uncommon habitats and associated biodiversity to help qualitatively assess the utility of the protected areas expansion goal, going beyond a simple and criticised quantitative aerial target (Aichi Target 11) (Jones et al. 2018; Butchart et al. 2012). This could lead for instance to the creation of a "Habitat Rarity protection extent trend" indicator to assess the proportion of rare habitat under protection. To quantify the reduction of at least half of the rate of natural habitat loss including forests and wetlands (Target 5), a 'Wetland Extent Trends Index' and a 'forest area defined as a percentage of total land area' are currently used as global indicators (Dixon et al., 2016). As previously mentioned, even though the Wetland Extent Trends index is necessary to assess global wetland trends and evaluate progress in international conventions (https://www.bipindicators.net/), site-based quantification of wetlands extent evolution is required to identify regions or sites that encounter anomalies, i.e. affected by climatic or anthropogenic pressures. Similarly, the percentage of forest loss within protected areas can be integrated to pursue the Aichi Target 11 in a qualitative manner as a protected areas well-being measurement that can also contribute in halting natural habitat loss within a constraining legal context. This can be applied to diverse habitat types within protected areas.

Research has never been so internationally connected and engaged with policy making. Although the biggest challenges have still to be addressed (Driscoll et al., 2018), the emergence and reinforcement of international will and agreements are shaping new pathways towards the increase of ecosystem resilience, in preparation for forthcoming environmental changes.

## REFERENCES

Allan, J.R., Venter, O., Maxwell, S., Bertzky, B., Jones, K., Shi, Y., and Watson, J.E.M. (2017). Recent increases in human pressure and forest loss threaten many Natural World Heritage Sites. Biological Conservation *206*, 47–55.

Amano, T., Székely, T., Sandel, B., Nagy, S., Mundkur, T., Langendoen, T., Blanco, D., Soykan, C.U., and Sutherland, W.J. (2018). Successful conservation of global waterbird populations depends on effective governance. Nature *553*, 199–202.

Bozinovic, F., Calosi, P., and Spicer, J.I. (2011). Physiological Correlates of Geographic Range in Animals. Annual Review of Ecology, Evolution, and Systematics *42*, 155–179.

Burrows, M.T., Schoeman, D.S., Richardson, A.J., Molinos, J.G., Hoffmann, A., Buckley, L.B., Moore, P.J., Brown, C.J., Bruno, J.F., Duarte, C.M., et al. (2014). Geographical limits to species-range shifts are suggested by climate velocity. Nature *507*, 492–495.

Bush, A., Sollmann, R., Wilting, A., Bohmann, K., Cole, B., Balzter, H., Martius, C., Zlinszky, A., Calvignac-Spencer, S., Cobbold, C.A., et al. (2017). Connecting Earth observation to high-throughput biodiversity data. Nature Ecology & Evolution *1*, 0176.

Butchart, S.H.M., Scharlemann, J.P.W., Evans, M.I., Quader, S., Aricò, S., Arinaitwe, J., Balman, M., Bennun, L.A., Bertzky, B., Besançon, C., et al. (2012). Protecting Important Sites for Biodiversity Contributes to Meeting Global Conservation Targets. PLOS ONE *7*, e32529.

Châtel, F.D. (2014). The Role of Drought and Climate Change in the Syrian Uprising: Untangling the Triggers of the Revolution. Middle Eastern Studies *50*, 521–535.

Collen, B., Loh, J., Whitmee, S., McRAE, L., Amin, R., and Baillie, J.E.M. (2009). Monitoring Change in Vertebrate Abundance: the Living Planet Index. Conservation Biology *23*, 317–327.

Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W., Venail, P., Villéger, S., and Mouquet, N. (2010). Defining and measuring ecological specialization. Journal of Applied Ecology *47*, 15–25.

Dixon, M.J.R., Loh, J., Davidson, N.C., Beltrame, C., Freeman, R., and Walpole, M. (2016). Tracking global change in ecosystem area: The Wetland Extent Trends index. Biological Conservation *193*, 27–35.

Driscoll, D.A., Bland, L.M., Bryan, B.A., Newsome, T.M., Nicholson, E., Ritchie, E.G., and Doherty, T.S. (2018). A biodiversity-crisis hierarchy to evaluate and refine conservation indicators. Nature Ecology & Evolution *2*, 775–781.

Eigenbrod, F., Armsworth, P.R., Anderson, B.J., Heinemeyer, A., Gillings, S., Roy, D.B., Thomas, C.D., and Gaston, K.J. (2010). The impact of proxy-based methods on mapping the distribution of ecosystem services. Journal of Applied Ecology *47*, 377–385.

Geldmann, J., Joppa, L.N., and Burgess, N.D. (2014). Mapping change in human pressure globally on land and within protected areas. Conserv. Biol. *28*, 1604–1616.

Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E., et al. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. Nature *478*, 378–381.

Grace, J.B., and Pugesek, B.H. (1998). On the Use of Path Analysis and Related Procedures for the Investigation of Ecological Problems. The American Naturalist *152*, 151–159.

Haase, P., Tonkin, J.D., Stoll, S., Burkhard, B., Frenzel, M., Geijzendorffer, I.R., Häuser, C., Klotz, S., Kühn, I., McDowell, W.H., et al. (2018). The next generation of site-based long-term ecological monitoring: Linking essential biodiversity variables and ecosystem integrity. Science of The Total Environment *613–614*, 1376–1384.

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., et al. (2013). High-Resolution Global Maps of 21st-Century Forest Cover Change. Science *342*, 850–853.

Jones, K.R., Venter, O., Fuller, R.A., Allan, J.R., Maxwell, S.L., Negret, P.J., and Watson, J.E.M. (2018). One-third of global protected land is under intense human pressure. Science *360*, 788–791.

Keil, P., Schweiger, O., Kühn, I., Kunin, W.E., Kuussaari, M., Settele, J., Henle, K., Brotons, L., Pe'er, G., Lengyel, S., et al. (2012). Patterns of beta diversity in Europe: the role of climate, land cover and distance across scales. Journal of Biogeography *39*, 1473–1486.

Leroux, S.J., Krawchuk, M.A., Schmiegelow, F., Cumming, S.G., Lisgo, K., Anderson, L.G., and Petkova, M. (2010). Global protected areas and IUCN designations: Do the categories match the conditions? Biological Conservation *143*, 609–616.

Li, Y., Li, X., Sandel, B., Blank, D., Liu, Z., Liu, X., and Yan, S. (2016). Climate and topography explain range sizes of terrestrial vertebrates. Nature Climate Change *6*, 498.

Ohlemüller, R., Anderson, B.J., Araújo, M.B., Butchart, S.H.M., Kudrna, O., Ridgely, R.S., and Thomas, C.D. (2008). The coincidence of climatic and species rarity: high risk to small range species from climate change. Biology Letters *4*, 568–572.

Perennou, C., Guelmami, A., Paganini, M., Philipson, P., Poulin, B., Strauch, A., Tottrup, C., Truckenbrodt, J., and Geijzendorffer, I.R. (2018). Chapter Six - Mapping Mediterranean Wetlands With Remote Sensing: A Good-Looking Map Is Not Always a Good Map. In Advances in Ecological Research, D.A. Bohan, A.J. Dumbrell, G. Woodward, and M. Jackson, eds. (Academic Press), pp. 243–277.

Sandel, B., Arge, L., Dalsgaard, B., Davies, R.G., Gaston, K.J., Sutherland, W.J., and Svenning, J.-C. (2011). The Influence of Late Quaternary Climate-Change Velocity on Species Endemism. Science *334*, 660–664.

Schmeller, D.S., Weatherdon, L.V., Loyau, A., Bondeau, A., Brotons, L., Brummitt, N., Geijzendorffer, I.R., Haase, P., Kuemmerlen, M., Martin, C.S., et al. (2018). A suite of essential biodiversity variables for detecting critical biodiversity change. Biological Reviews *93*, 55–71.

Tittensor, D.P., Walpole, M., Hill, S.L.L., Boyce, D.G., Britten, G.L., Burgess, N.D., Butchart, S.H.M., Leadley, P.W., Regan, E.C., Alkemade, R., et al. (2014). A mid-term analysis of progress toward international biodiversity targets. Science *346*, 241–244.

# APPENDIX

## CURRICULUM VITAE

### PERSONAL INFORMATION

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**Current position**

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| 2014 – present | Doctoral student (supervisors: Henrique M. Pereira and Gregoire Dubois)<br>*German Centre for Integrative Biodiversity Research (iDiv)*<br>*Martin Luther University Halle-Wittenberg (MLU), Germany*<br>Transferred in 2017 from<br>*Joint Research Centre of the European Commission (JRC, Ispra), Italy* |

**Previous positions**

| | |
|---|---|
| 2011-2013 | M.Sc in Ecological System Modelling<br>*Paul Sabatier University, France* |
| 2008-2010 | B.Sc. in Ecology<br>*Paul Sabatier University, France* |

### FELLOWSHIPS AND GRANTS

| | |
|---|---|
| 2017-2018 | Research contract under the Ecopotential project (iDiv). |
| 2014-2017 | Grantholder 20, Joint Research Centre of the European Commission. |

### PREVIOUS PUBLICATIONS

Legal, L., Dorado, O., Machkour-M'Rabet, S., **Leberger, R.,** Albre, J., Mariano, N. A., Gers C., and Winterton. P. 2014. *Ecological constraints and distribution of the primitive and enigmatic endemic Mexican butterfly: Baronia brevicornis.* The Canadian Entomologist.

Machkour-M'Rabet. S., **Leberger, R.,** León-Cortés, J. L., Gers, C., Legal, L. 2014. *Genetic characterization and population status of the only extant Baroninae swallowtail butterfly, Baronia brevicornis.* Journal of insect conservation.

Halle (Saale), den 09.11.2018

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## LIST OF PUBLICATIONS AND CONFERENCE PARTICIPATIONS

### PUBLICATIONS OF THE DISSERTATION:

**Leberger, R.,** Martinez-Lopez, J., Dubois, G., Achard, F., Buchanan, G.M., Pereira, H.M. *Habitat Rarity as a determinant of forest-birds range-size.* In prep.

**Leberger, R.,** Rosa, I.M., Wolf, F., Guerra, A.C., Pereira, H.M. 2019. *Global spatial and temporal patterns of forest loss across IUCN categories of protected areas. Biological Conservation, vol 241.*

**Leberger R.,** Geijzendorffer, I., Guelmami, A., Gaget, E., Galewski, T., Pereira, H. M., Guerra, C. *Mediterranean wetland conservation in the context of climate and land cover change. Regional Environmental Change.* In review.

### PUBLICATION CONTRIBUTION:

Geijzendorffer, I.R., Beltrame, C., Chazee, L., Gaget, E., Galewski, T., Guelmami A., Perennou, C., Popoff, N., Guerra, C., **Leberger, R.,** Jalbert, J., Grillas, P. 2019. *Increasing the impact of the Ramsar convention on the conservation of Mediterranean wetlands. Frontiers in Ecology and Evolution* 7, 1–6.

Kelly, R., Kim, H., **Leberger, R**., Wohlwend M. R., Pereira H. M. 2017. *Do publish*. eLetter. Science.

Review:

IPBES global assessment of biodiversity and ecosystem services, Chapter 3.4.3. *The Ramsar Convention on Wetlands.*

### TALKS AND POSTERS IN INTERNATIONAL CONFERENCES:

| | |
|---|---|
| 02-2018 | **Invited speaker**, La Tour du Valat, France. Using Essential Variables to monitor and inform wetland conservation in the Mediterranean basin. (talk) |
| 01-2017 | **Invited speaker**, Basque Centre for Climate Change (BC3), Bilbao, Spain. Habitat Rarity as a determinant of forest bird range-size. (talk) |
| 12-2016 | **iDiv annual conference**, Leipzig, Germany. Spatial and temporal pattern of forest loss across the IUCN protected areas categories. (poster) |
| 06-2016 | **Macroecology conference of the British Ecological Society (BES)**, Oxford, UK. Where are the most environmentally unique forested areas to protect? (talk) |
| 03-2016 | **Macroecology conference of the ecological society of Germany, Austria and Switzerland (Gfö)**, ‘when macroecology meets biogeography’, Trier, Germany. Where are the most unique forested area to preserve? – A cross-scale study – (talk) |
| 11-2015 | **iDiv annual conference**, Leipzig, Germany. Where are the most unique forested areas in the world? Relation with forest bird endemism and species richness. (talk) |
| 06-2015 | **European conference of macroecology**, Copenhagen, Denmark. Mapping forested areas with most unique features. Are they hosting most endemic forest bird species? (talk) |

## AUTHOR'S CONTRIBUTIONS

### CHAPTER 1

**Leberger, R.,** Martinez-Lopez, J., Dubois, G., Achard, F., Buchanan, G.M., Pereira, H.M. *Habitat Rarity as a determinant of forest-birds range-size.* In prep.

Study design: Leberger, R. (75%), Martinez-Lopez, J. (10%), Dubois, G. (5%), Buchanan, G.M. (5%), Pereira, H.M. (5%).
Data collection: Buchanan, G.M. (50%), Leberger, R. (30%), Martinez-Lopez, J. (20%).
Analysis: Leberger, R. (50%), Martinez-Lopez, J. (40%), Pereira, H.M. (10%).
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### CHAPTER 2

**Leberger, R.,** Rosa, I.M., Wolf, F., Guerra, A.C., Pereira, H.M. *Global spatial and temporal patterns of forest loss across IUCN categories of protected areas. Biological Conservation.* In prep.

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### CHAPTER 3

**Leberger R.,** Geijzendorffer, I., Guelmami, A., Gaget, E., Galewski, T., Pereira, H. M., Guerra, C. *Mediterranean wetland conservation in the context of climate and land cover change.* In prep.

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Roxanne Leberger

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# EIGENSTÄNDIGKEITSERKLÄRUNG

Hiermit erkläre ich, dass die Arbeit mit dem Titel "Using global indicators to inform the conservation of high nature value areas" bisher weder bei der Naturwissenschaftlichen Fakultät I Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt wurde.

Ferner erkläre ich, dass ich die vorliegende Arbeit selbstständig und ohne fremde Hilfe verfasst sowie keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe. Die den Werken wörtlich oder inhaltlich entnommenen Stellen wurden als solche von mir kenntlich gemacht.Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Halle (Saale), den 09.11.2018

Roxanne Leberger