



DOCTORAL THESIS

Quantifying the impacts of land change on biodiversity

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School of Life Sciences

Author:

Martin Jung

Supervisors:

Jörn P. W. Scharlemann

Pedram Rowhani

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*Brighton,
17th March 2019*

Martin Jung

This thesis is the product of my own work, unless specifically mentioned. Chapter 2 has been published as [Jung et al. \(2018\)](#) in the Journal *Ecography* and has benefited from comments by Dr. Andy Purvis and Dr. Tim Newbold as well as from data supplied by Laura Bentley. Chapter 3 is currently in revision at the Journal *Nature Communications*, while chapter 4 and 5 are in preparation for submission. All chapters have been commented on by my supervisors Dr. Jörn P. W. Scharlemann and Dr. Pedram Rowhani.

University of Sussex
School of Life Sciences
Division of Evolution, Behaviour and Environment

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Quantifying the impacts of land change on biodiversity

by Martin Jung

ABSTRACT

Land is constantly changing because of natural and anthropogenic factors. One of the grand challenges facing humanity is the loss of biodiversity, caused by land change, which may affect ecosystem functioning. Attributes of land change, e.g. magnitude, time span, sequence or frequency, can be quantified reliably from remotely-sensed satellite data. Up to now, it was not clear how attributes of past land changes, e.g. those preceding biodiversity sampling, continue to influence local biodiversity across geographic regions and taxonomic groups. This thesis investigates the varying impacts of multiple attributes of land change on biodiversity globally by analysing links between broad-scale data on local biodiversity measures – calculated from the global PREDICTS database – and time series of different remotely-sensed satellite data from the period of 1984 to 2015. Overall past land changes were found to impact local biodiversity more than present differences on land, however with considerable variability among taxonomic groups. Abrupt land changes of greater magnitude, that occurred more recently, reduced local biodiversity measures more, although biodiversity recovered as time passed. Furthermore, impacts of past land change varied depending on trajectories of land-cover types, affecting national and global biodiversity projections. While biodiversity change, quantified from time series of North

American breeding bird surveys was correlated with, but not explained by, landscape-wide land changes, the frequency and magnitude of past, instead of concomitant, land changes was more important in explaining biodiversity change. These results indicate that global indicators of the impacts of land change on local biodiversity need to consider lasting influences of the past as ignoring them would result in incomplete assessments of biodiversity change. Remote sensing can assist in quantifying biologically-relevant attributes of land change in space and time, and such attributes should be incorporated into global assessments and projections of biodiversity change.

ACKNOWLEDGEMENTS

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CHAPTER **1**

General introduction

History, as well as life itself, is complicated; neither life nor history is an enterprise for those who seek simplicity and consistency

Jared Diamond

1.1 Introduction

The loss of biodiversity is of increasing concern worldwide because of its value to humankind. Biodiversity, the variability of organisms and the ecological complexes they are part of ([CBD and Secretariat of the Convention on Biological Diversity, 2014](#)), is constantly changing, with the number of extant species in many taxonomic groups – such as birds ([Jetz et al., 2012](#)) or mammals ([Upham et al., 2019](#)) – varying in space and time. However current global extinction rates have been estimated to be 100 to 1000 times higher than natural background rates ([Pimm et al., 2014](#); [Mace, 2014](#)), resulting in the Earth loosing most of its megafauna and many other species ([Sandom et al., 2014](#); [Ceballos et al., 2017](#); [Hallmann et al., 2017](#)), including those endemic to islands ([Blackburn et al., 2004](#)) or with certain ecological traits ([Fritz et al., 2009](#)). Increasingly humankind realizes that further losses of biodiversity would be detrimental, either because of its intrinsic value or because of the realization that ecosystem functions and services are essential for human and economic wellbeing ([Cardinale et al., 2012](#); [Mace, 2014](#)). For instance it has been shown that the loss of biodiversity – particularly at local scales –

may be correlated with a loss of ecosystem services (Albrecht et al., 2014) and functions (Hautier et al., 2015; Isbell et al., 2015). There are multiple pressures on biodiversity globally (Butchart et al., 2010; Steffen et al., 2015) and establishing robust links between biodiversity loss and pressures is often challenging (Cardinale et al., 2018; De Palma et al., 2018).

Box 1.1 Definitions

This thesis follows the definitions by Lambin and Geist (2006), who define **land cover** as the **conditions** of the Earth's land surface including abiotic and biotic structures. In contrast **land use** has been defined as the purposes to which humans exploit and manipulate land cover (Lambin and Geist, 2006). Satellite-based remote sensing is capable (see 1.1.1) of monitoring land-surface conditions, i. e. land cover, but is usually unable to identify land use *per se*. Land cover and land use often form a coupled human-environmental **land system** (Lambin and Geist, 2006; Turner et al., 2007) and in a unifying framework the term **land change** recognizes that natural and anthropogenic drivers as well as land-use and/or land-cover change can often not be separated (Turner et al., 2007; Lambin and Geist, 2006).

Land change – defined as change in land use and/or land cover caused by natural or anthropogenic factors (Box 1.1, Lambin et al., 2003; Turner et al., 2007; Song et al., 2018) – is among the main drivers of biodiversity loss across scales. Among 8,688 species listed in the International Union for Conservation of Nature (IUCN) Red List, 62.2% of species globally are threatened with extinction because of agricultural activities and 34.7% by urban development (Maxwell et al., 2016). Across biomes, vertebrate richness (Brum et al., 2013; Kehoe et al., 2017b) and distribution (Di Marco and Santini, 2015) can best be explained by the occurrence of anthropogenically altered land. Broad-scale syntheses found differences in land use and/or land cover to impact local biodiversity globally (Gibson et al., 2011; Murphy and Romanuk, 2014; Newbold et al., 2014, 2015; Alroy, 2017) with local species richness estimated to be reduced by 13% globally relative to undisturbed primary vegetation (Newbold et al., 2015), increasingly exceeding planetary boundaries (Newbold et al., 2016a). Impacts of land change are furthermore dependent on functional traits of species (Newbold et al., 2013; Jung et al., 2017) with species with large body size (Newbold et al., 2013, 2015) or narrow range (Newbold et al., 2018) being especially

affected. However, these broad-scale syntheses primarily investigated the impacts of spatial differences in land-use/land-cover at the time of biodiversity sampling (Gibson et al., 2011; Murphy and Romanuk, 2014; Newbold et al., 2015; Alroy, 2017). Land changes that occurred before biodiversity sampling are often ignored, despite published evidence of their impact on local biodiversity.

Past land changes continue to influence local biodiversity (Foster et al., 2003). These influences are detectable in altered soil biodiversity (Jakovac et al., 2016; Wood et al., 2017), vegetation growth (Fraterrigo et al., 2006) or species composition (Bellemare et al., 2002; Ewers et al., 2013; Jakovac et al., 2016). After a land change, biodiversity can recover (Chazdon, 2003) depending on key attributes (see 1.1.3 for further detail) such as magnitude or time passed since land change (Martin et al., 2013; Fu et al., 2017; Jones et al., 2018). However previous evidence on lasting impacts of past land change is not consistent, reporting either losses (Moreno-Mateos et al., 2017; Jones et al., 2018), mixed changes (Svensson et al., 2012; Thom and Seidl, 2016) or increases (Fu et al., 2017) in local biodiversity measures [predominantly species richness]. Furthermore, these studies investigated only a single attribute of land change, e. g. time passed, while those that assessed multiple attributes (Shackelford et al., 2017) across case studies surprisingly found most attributes to be not important in explaining differences in biodiversity.

Overall there remain several gaps in our knowledge of how land change affects local biodiversity: Importantly (i) most previous broad-scale studies only coarsely considered land changes in the past (Alkemade et al., 2009; Murphy and Romanuk, 2014; Newbold et al., 2015) and corresponding lasting effects (see 1.1.3) on local biodiversity (Dullinger et al., 2013; Hylander and Ehrlén, 2013); (ii) past land change has often been inferred from anecdotal, non-replicable information – i. e. encoded as “secondary vegetation” (Hudson et al., 2014) or “abandoned agriculture” (Gibson et al., 2011) – or land use/land-cover data from extrapolated estimates (Hurtt et al., 2011), impeding external validation and quantification of land change attributes; and (iii) many previous studies investigating impacts of past land change on biodiversity focussed on specific geographic regions (Bellemare et al., 2002; Ewers et al., 2013; Cousins et al., 2015), taxonomic groups (Hermy and Verheyen, 2007; Perring et al., 2018) or single biodiversity measures such as species richness (Martin et al., 2013; Fu et al., 2017), which have been shown to provide only a partial picture of biodiversity change (Su et al., 2004; Hillebrand et al., 2018), rather than

providing a comparative and comprehensive assessment globally. Here I will address these gaps by investigating if and how local biodiversity differs because of past land changes – quantified by satellite-based remote sensing (Figure 1.1) – and what attributes might drive these differences in biodiversity measures .

1.1.1 Land change in the Anthropocene

Land is always changing. Change can happen because of a variety of factors that vary across spatial and temporal scales (Lambin et al., 2003; Kennedy et al., 2014). Some natural events such as flooding, storms or plant diseases alter land cover infrequently (Turner et al., 1998), while others – such as repeated droughts or frequent wildfires – can define and shape entire ecoregions. Such is the case for the North American Midwest or South African Fynbos ecoregions which are characterized by frequent wildfires (Westerling et al., 2006; Kelly and Brotons, 2017). In rare instances natural factors can change entire biomes. The Sahara desert, covered by forests and savanna grasslands until 18,000 years B.P., has lost most of its natural vegetation because of changes in precipitation cycles (Hamilton, 1981). Yet, those extensive natural land changes are dwarfed by the pervasive impacts humans have on the Earth's surface and there is an increasing realization that any characterization of terrestrial biomes is incomplete without acknowledging the influence of humans (Ellis and Ramankutty, 2008; Kehoe et al., 2017b).

Humankind continues to shape the land (Ellis, 2011; Ellis et al., 2013b) with human-driven land changes occurring since 10,000 years B.P (Ellis et al., 2013b). Evidence of agricultural activities from ancient civilizations are noticeable even in the most remote places such as the Amazon basin (McMichael et al., 2017). Europe, once predominantly covered by forests, has lost most natural vegetation in the Middle Ages and early Renaissance (Kaplan et al., 2009), resulting in the human-dominated landscapes of the present. Land changes in those landscapes occur frequently (Kleyer et al., 2007), with the dominant land cover alternating between grass-, crop- and shrub-covered land (Kleyer et al., 2007; Manning et al., 2009). The temporal acceleration of anthropogenic factors impacting land (Steffen et al., 2015) have led researchers to declare a new geological epoch, the “Anthropocene”, varyingly dated to have started as early as 3000 years B.P. or as late as the 20th century (Ellis et al., 2013a).

Most of the knowledge of pre-20th century land change is derived from soil cores, historic texts, archaeological evidence or photographs and drawings (Klein Goldewijk et al., 2011, 2016). While these sources remain the best and often only data available, reconstructions of past land change rely on multiple assumptions (Klein Goldewijk and Verburg, 2013) and, when projected in space and time, can often be very different from independent soil-core based land cover reconstructions (Kaplan et al., 2017). For more recent time periods and as an alternative to reconstructed land change, satellite-based remote sensing directly measures conditions of the land surface of the Earth (Box 1).

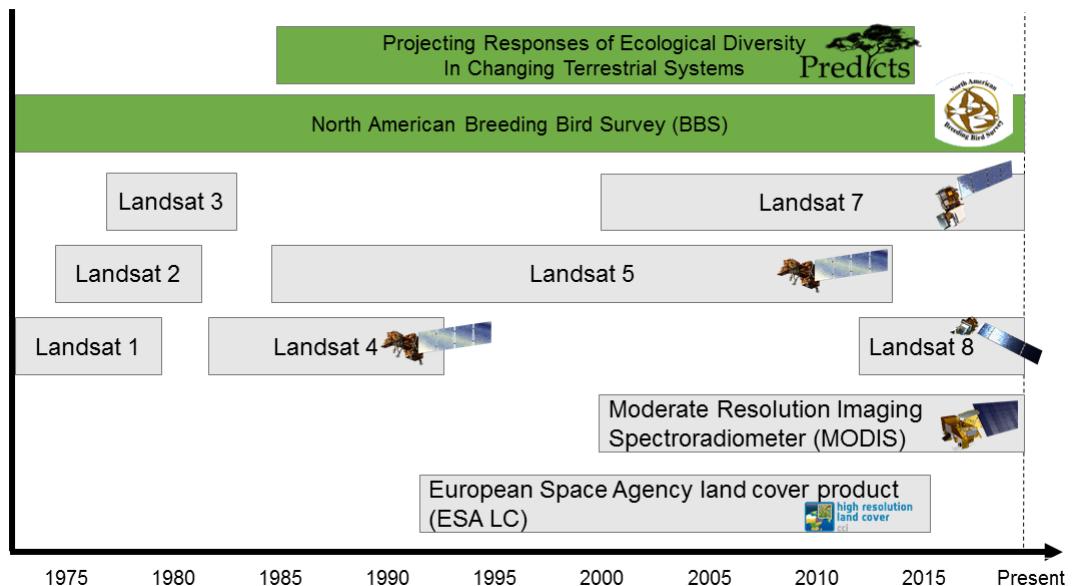


Figure 1.1: Temporal coverage of biodiversity (green) and remote sensing (grey) datasets used in this thesis. Legacy Landsat missions (1-3) are shown for completeness only.

Through technological advances humans have created a global spaceborne Earth observation system. The first satellite missions were used exclusively for military intelligence or weather observations. Since the mid-1970s satellite missions (Figure 1.1), such as Landsat or later the Terra & Aqua satellites with the Moderate Resolution Imaging Spectroradiometer (MODIS), were specifically designed to repeatedly photograph the Earth on a global scale (Schaaf et al., 2002; Zhang et al., 2006; Kennedy et al., 2014). These satellites carry highly sensitive sensors that measure the spectral reflectance from solar insolation. The near-infrared spectrum (Figure 1.2a) has been recognized to be particularly useful for monitoring the photosynthetic activity of vegetation and can be quantified through “vegetation indices” (Tucker, 1979; Tucker et al., 1981; Pettorelli et al., 2005; Jiang et al., 2008). Differences in the dynamics of vegetation indices (Figure 1.2b-c)

can be used to identify land change globally.

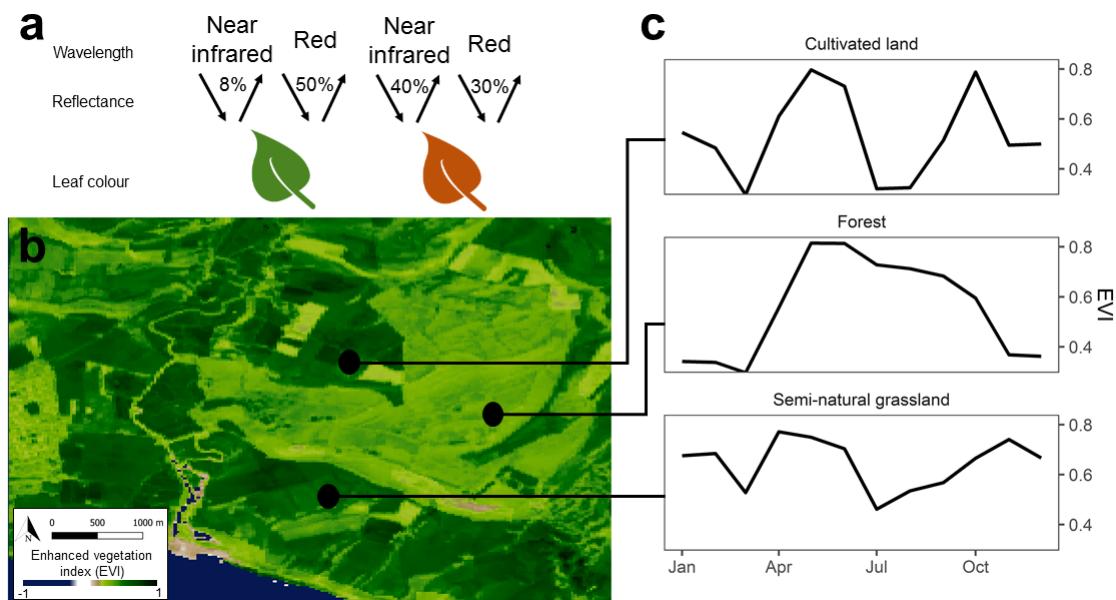


Figure 1.2: (a) Schematic of how differences in spectral reflectances assist distinguishing leaf colour. (b) Map (Centre longitude: 0.165° , latitude: 50.778°) shows an annual maximum value composite (MVC) for 2018 of the Enhanced Vegetation Index (EVI) as calculated from the Landsat 8 mission. (c) Monthly MVC time series of three example sites (black points highlighted in c) of known land cover (cultivated land, forest, semi-natural grassland).

Land change can be monitored using satellite-based remote sensing. A change on land can occur as either ‘conversion’ or ‘modification’, where the former is usually understood as “complete replacement of one land cover type by another” – i. e. deforestation – while the latter are “subtle changes” – i. e. agricultural intensification – that affect the character of a land cover (Lambin et al., 2003; Lambin and Geist, 2006). Spatial estimates of the Earth’s land cover are commonly derived through a classification of remotely-sensed spectral reflectances (DeFries and Townshend, 1994; Hansen et al., 2000; Di-Gregorio, 2005). However, these spatial estimates could often not be temporally compared because of classification biases and thematic inconsistencies (Verburg et al., 2011; Estes et al., 2018) and – until recently – little progress has been made to quantify land change globally. Novel algorithms and processing frameworks have been developed to quantify land changes from temporal dynamics of spectral reflectances measuring photosynthetic activity (Figure 1.2c, Lhermitte et al., 2011; Gómez et al., 2016; Zhu, 2017). With increasing availability and accessibility of satellite data (Wulder et al., 2016) and computational power (Gorelick et al., 2017) land changes have been quantified globally (Hansen et al.,

2013; Pekel et al., 2016; Li et al., 2018; Song et al., 2018), creating new opportunities to assess impacts of land change on biodiversity.

1.1.2 The impacts of past land change on local biodiversity

Land changes can have immediate and/or delayed impacts on local biodiversity. They can act as disturbance affecting the stability of an ecosystem (Pimm, 1984; Scheffer and Carpenter, 2003), causing an immediate reduction in the number of species and individuals (Nimmo et al., 2015; Ratajczak et al., 2018). In addition, land changes can have delayed impacts on local biodiversity that persist for decades (Martin et al., 2013; Moreno-Mateos et al., 2017) or centuries (Vegas-Vilarrubia et al., 2011; McMichael et al., 2017). Previous studies that investigated lasting influences of past land change – varyingly described as “land-use history” or “landscape history” (Belle-mare et al., 2002; Foster et al., 2003; Ewers et al., 2013) or “management legacies” (Perring et al., 2016) – on biodiversity explained these influences through a number of mechanisms (Figure 1.4, Table 1.1).

Several terms have been proposed to explain lasting impacts of past land change on local biodiversity (Table 1.1). The term “extinction debt” describes the delayed extinction of species following a loss of habitat (Balmford, 1996; Kuussaari et al., 2009; Wearn et al., 2012) and for many vertebrate species an extinction debt is usually “paid off” – e.g. in time until local population is fully extinct – over a few years up to a century depending on the initial population size and species functional traits (Halley et al., 2016). Similarly, local biodiversity can also be influenced by an “immigration credit”, that is the delayed immigration of species from regional source populations after land change (Jackson and

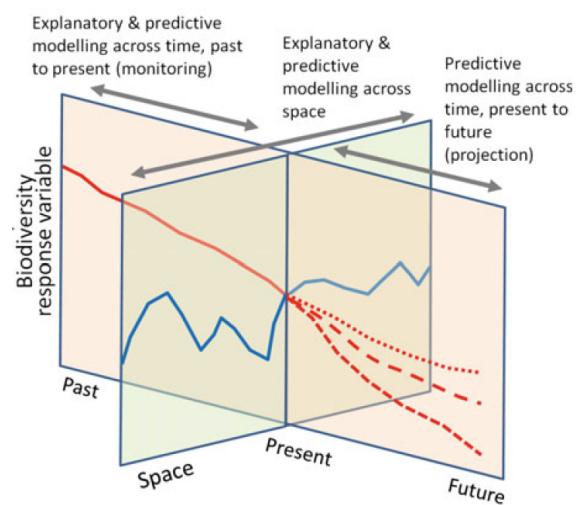


Figure 1.3: Schematic how a biodiversity response variable (red) can be estimated using environmental predictors (blue) in space and time. Adapted from Ferrier et al. (2017).

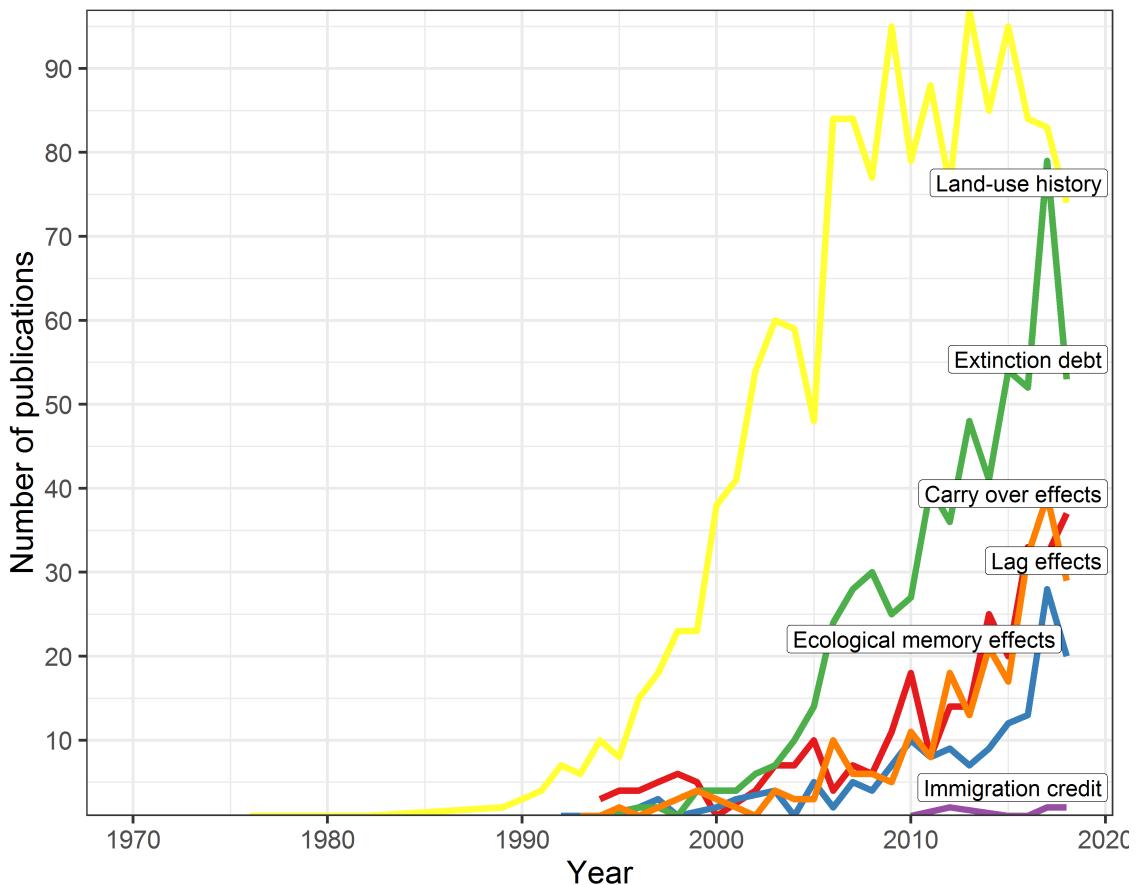


Figure 1.4: Number of publications investigating terms and descriptions referring to biotic lag effects as queried from Web of Science™ (WOS). A WOS search was conducted on the 5th January 2019 limited to Environmental sciences and ecological literature, between 1900 and 2019 including as search topic “land-use histor*” (yellow), “extinction debt*” (green), “lag effect*” (orange), “carry*over effect*” (red), “ecological memory effect*” (blue) and “immigration credit*” (purple).

Sax, 2010; Hylander and Ehrlén, 2013). Many species populations retain an “ecological memory” (Peterson, 2002; Bengtsson et al., 2003; Ogle et al., 2015) of past land changes, reducing population growth and affecting species fitness and survival in subsequent years as “carry over” effect (Harrison et al., 2011). Collectively those terms can broadly be described as “biotic lag” effects (Table 1.1), which are lasting or lagged effects of past changes in environmental factors that continue to influence present biodiversity. Knowledge about lasting impacts of land change can assist in planning management interventions (Standish et al., 2014) and should be considered in broad-scale biodiversity models.

Most existing regional and global assessments, models and scenarios of biodiversity (e.g. those included in the Intergovernmental Science-Policy Platform on Biodiversity

and Ecosystem Services (IPBES) assessments, Alkemade et al., 2009; Pereira et al., 2010; Newbold et al., 2015) ignore lasting impacts of past land change. These assessments usually consider only concurrent differences in land-use/land-cover (Figure 1.3) and may therefore only partially represent biodiversity change. Delayed impacts of past land change may accumulate together with other drivers – such as climate change or species invasions – of biodiversity change (Essl et al., 2015a,b) potentially increasing the number of future species extinctions (Dullinger et al., 2013). To mediate the ongoing loss of biodiversity (Mace et al., 2018), robust estimates of the lasting impacts of land change on biodiversity need to be derived.

Table 1.1: Common terms and descriptions referring to lasting impacts of environmental changes on biodiversity

Term	Description	Reference
Land-use history	“Observed abiotic and biotic properties that are caused by past land use”	(Foster et al., 2003; Per-ring et al., 2016)
Extinction debt	“The number of species committed to delayed extinction following a forcing event”	(Tilman et al., 1994; Kuussaari et al., 2009)
Immigration credit	“The number of species committed to delayed immigration following a forcing event”	(Jackson and Sax, 2010)
Ecological memory	“The degree to which an ecological process is shaped by past modifications of the landscape, biotic and abiotic factors.”	(Padisák, 1992; Peterson, 2002; Bengtsson et al., 2003; Ogle et al., 2015)
Carry-over effect	“Situation in which an individual’s previous history and experience explains their current performance in a given situation”	(Harrison et al., 2011; O’Connor et al., 2014)
Biotic lag	Term summarizing the observed difference in biodiversity caused by lasting or lagged effects of past environmental changes	(De Palma et al., 2018) and this thesis

1.1.3 Linking satellite-based remotely-sensed land change with local biodiversity

Remote sensing data can be useful for biodiversity models. Remotely-sensed land-surface conditions have been used to describe the biophysical state of species habitats (Kerr

and Ostrovsky, 2003), identify critical life-history periods (Pettorelli et al., 2005), map species distributions (He et al., 2015) or as a proxy for predicting biodiversity patterns (Rowhani et al., 2008; Rocchini et al., 2015; Hobi et al., 2017). However, uncertainties remain in the usability of remote sensing data for different measures of biodiversity (Oldeland et al., 2010), for taxonomic groups – where biodiversity measures are sometimes poorly correlated with photosynthetic activity (Adler et al., 2011) or spectral dissimilarity (Schmidlein and Fassnacht, 2017) – or for many, previously unassessed geographic regions. Especially the temporal domain (Figure 1.2b–c), including land change per se, is often ignored (Kennedy et al., 2014). New frameworks are needed to establish links between remotely-sensed land change and local biodiversity.

Land change can be characterized by key attributes that may have varying impacts on local biodiversity (Figure 1.5a). Watson et al. (2014) provided a conceptual framework that distinguishes between four attributes of land change: (1) The magnitude of land-change events, (2) the frequency of land-change events over time, (3) the time span since a land change occurred, and (4) the temporal sequence of land use and/or land cover categories (Figure 1.5a). Ecological theory, experiments and simulations demonstrated that local biodiversity can be affected by these attributes (Figure 1.5b). Land changes of larger magnitude are expected to affect biodiversity more (Scheffer et al., 2001; Dornelas, 2010; Svensson et al., 2012; Ratajczak et al., 2018) and – by removing poor dispersing (Tilman et al., 1997) and specialist species (Christensen et al., 2018) – reduce the stability of species communities (Scheffer et al., 2001; Hautier et al., 2015). In many regions of the world, land changes vary in frequency (Kleyer et al., 2007) impacting local biodiversity (Valtonen et al., 2013; Lawson et al., 2015), especially if those impacts accumulate in a short period of time (Essl et al., 2015a; Ratajczak et al., 2018). Biodiversity measures can often recover to reference levels (i. e. a temporal or spatial baseline) following land change, depending on the time passed (Chazdon, 2003; Laurance et al., 2011; Martin et al., 2013). Lastly, and commonly investigated, is the temporal sequence of land use and/or land cover types (Harding et al., 1998; Chazdon, 2003; Foster et al., 2003), where local biodiversity tends to be more altered at sites with past anthropogenic use. However, the impact of these four attributes of land change on local biodiversity has rarely been comparatively assessed globally and across taxonomic groups.

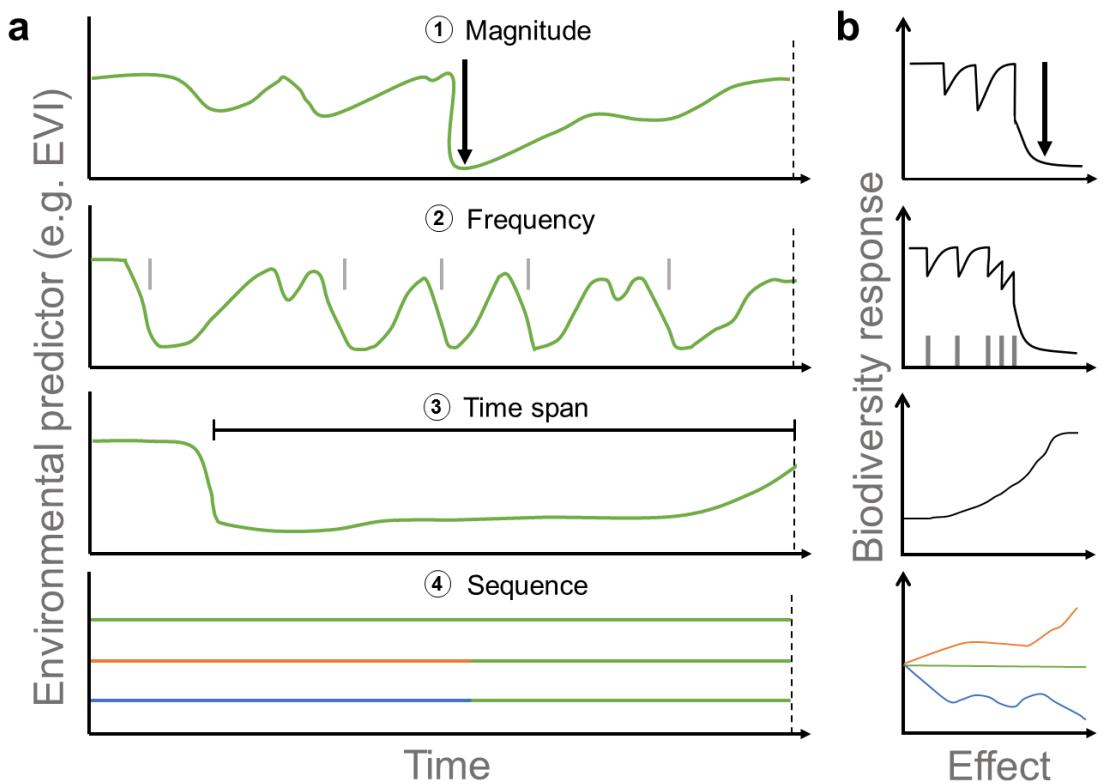


Figure 1.5: (a) Conceptual framework – inspired by Watson et al. (2014) – how sites can differ by attributes of land change, namely (1) magnitude, (2) frequency, (3) time span and (4) sequence. Dashed line indicates the start of biodiversity sampling with the y-axis representing an environmental predictor such as the Enhanced Vegetation Index (EVI). (b) Assumed response of biodiversity to varying land change attributes with x-axis indicating the strength of effect in units of each individual attribute.

1.1.4 Thesis aims and structure

The overall aim of my thesis is to investigate how local biodiversity is impacted by land change globally and whether those impacts vary with attributes of land change (Figure 1.5). I do so by linking satellite-based remotely-sensed estimates of land change with measures of local biodiversity globally (Figure 1.6). The four main analytical chapters (Chapter 2–5) of this thesis each address multiple of the four outlined attributes of land change (Figure 1.6). They each serve as independent articles that have either been published, submitted or are in principle suitable for submission to an academic journal.

Chapter two assesses whether considering past land-surface conditions in the 6 years before biodiversity sampling can assist in explaining differences in local biodiversity. I developed an analytical framework that captures all differences between time series of remotely-sensed land-surface conditions – such as land changes with varying magnitude

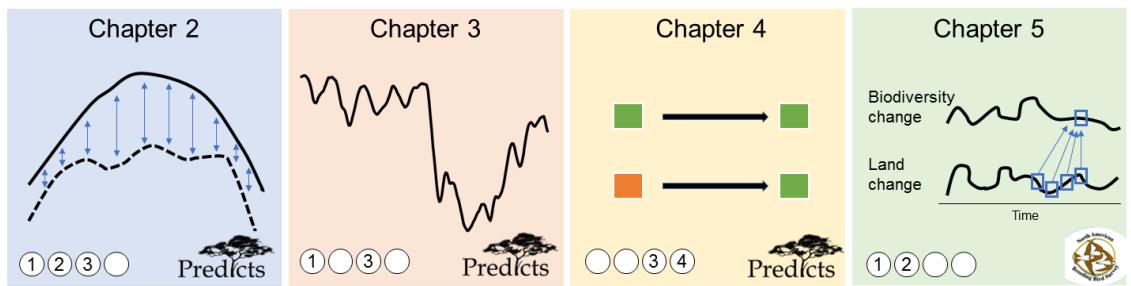


Figure 1.6: Schematic outline of the four approaches (Chapter 2–5) linking local biodiversity with remotely-sensed land change data, with lines and icons representing differences in intra-annual land dynamics (Chapter 2), an abrupt land change of large magnitude (Chapter 3), different land-cover sequences (Chapter 4) and correlating temporal change in land and biodiversity observed at the same sites (Chapter 5). Numbers in circles at the bottom left (1–4) indicate which attributes of land change from Watson et al. (2014) are considered in each approach (see Figure 1.5a), while logos indicate the biodiversity data used (PREDICTS or United States BBS data).

or inter-annual frequency – in a single metric, which was then linked with differences in species assemblage composition across taxonomic and functional groups globally.

The third chapter focusses on how abrupt land changes – characterized by shifts in magnitude or trend and varying time passed – continue to influence local biodiversity. I assembled time series of Landsat imagery globally (Figure 1.1a) and subjected them to a change-detection algorithm to detect abrupt land changes. A hierarchical analysis was conducted to assess if and how strongly local biodiversity differs between sites with and without a land change in the past. The assumption is that local biodiversity is more affected by abrupt land changes of greater magnitude that occurred more recently.

In chapter four I investigated how local biodiversity differs between sites with varying land-cover sequences of land cover change as derived from a global, temporally consistent land-cover product for the years 1992 to 2015. The assumption is that local biodiversity is higher at sites with a past land-cover change compared to those without, if the preceding land cover was less anthropogenically modified. In addition, this chapter investigates how past land-cover sequences can influence global and national biodiversity projections and argues for including estimates of past land change in biodiversity projections.

In contrast to previous chapters, in the fifth chapter I investigate if local biodiversity change can be linked to landscape-wide land changes. Estimates of bird diversity change from repeated breeding bird surveys (BBS data, Figure 1.1) were correlated with estimates of preceding and concurrent land change quantified from time series of Landsat imagery.

I furthermore investigate whether the explanatory power of landscape-wide land changes on bird diversity change varies in space, time and across functional groups of bird species. The assumption is that bird biodiversity declines more in landscapes with a greater proportion of land changes.

The thesis concludes with the sixth chapter, which provides a synthesis of the presented work, discusses all findings in relation to previous studies, and mentions shortcomings and promising directions for future research .

CHAPTER 2

**Local species assemblages are
influenced more by past than current
dissimilarities in photosynthetic
activity**

Most land on Earth has been changed by humans and past changes of land can have lasting influences on current species assemblages. Yet few globally representative studies explicitly consider such influences even though auxiliary data, such as from remote sensing, are readily available. Time series of satellite-derived data have been commonly used to quantify differences in land-surface conditions such as vegetation cover, which will among other things be influenced by anthropogenic land conversions and modifications. Here we quantify differences in current and past (up to five years before sampling) vegetation cover, and assess whether such differences differentially influence taxonomic and functional groups of species assemblages between spatial pairs of sites. Specifically, we correlated between-site dissimilarity in photosynthetic activity of vegetation (the Enhanced Vegetation Index) with the corresponding dissimilarity in local species assemblage composition from a global database using a common metric for both, the Bray-Curtis index. We found that dissimilarity in species assemblage composition was on average more influenced by dissimilarity in past than current photosynthetic activity, and that the influence of past dissimilarity increased when longer time periods were considered. Responses to past dissimilarity in photosynthetic activity also differed among

taxonomic groups (plants, invertebrates, amphibians, reptiles, birds and mammals), with reptiles being among the most influenced by more dissimilar past photosynthetic activity. Furthermore, we found that assemblages dominated by smaller and more vegetation-dependent species tended to be more influenced by dissimilarity in past photosynthetic activity than prey-dependent species. Overall, our results have implications for studies that investigate species responses to current environmental changes and highlight the importance of past changes continuing to influence local species assemblage composition. We demonstrate how local species assemblages and satellite-derived data can be linked and provide suggestions for future studies on how to assess the influence of past environmental changes on biodiversity.

2.1 Introduction

Throughout the Earth's history, land has changed constantly by a combination of natural and anthropogenic forces. Palaeontological evidence indicates that humans have transformed approximately 75% of the land at least once (Ellis et al., 2010; Ellis, 2011), with changes in many land-surface conditions, such as vegetation cover, accelerating since the beginning of the industrial revolution (Lambin and Geist, 2006; Steffen et al., 2015). Changes in vegetation cover may be caused by climatic factors, such as CO₂ fertilization or altered precipitation patterns (Zhu et al., 2016), or anthropogenically caused land conversions, such as deforestation, re- and afforestation (Dupont et al., 2003; Hansen et al., 2013; Müller et al., 2014) or land modifications, such as degradation, intensification (Gibbs and Salmon, 2015; Rufin et al., 2015) or return to less intensive forms of land use (Zomer et al., 2016). Over time, these changes have shaped both land and species assemblages in complex ways (Foster et al., 2003; Watson et al., 2014; Perring et al., 2016).

Most global meta-analyses investigating the influence of differences in vegetation cover on species assemblages have assumed that any difference in vegetation cover at the time of biodiversity sampling is the dominant influence (Stein et al., 2014; Newbold et al., 2014, 2015; Alroy, 2017). However, this assumption might be incorrect as assemblages can be heavily influenced by legacy effects of past changes in vegetation cover (Foster et al., 2003; Watson et al., 2014; Ogle et al., 2015; Perring et al., 2016). For the recent past (e.g., up to five years prior to biodiversity sampling), ecological memory or carry-over effects,

i. e. the capacity of past events to influence present and future ecological assemblages (Harrison et al., 2011; O'Connor et al., 2014; Ogle et al., 2015), have been proposed as mechanisms that shape species assemblages. These effects can arise through site-specific environmental factors, for instance altered conditions because of agricultural practices (Perring et al., 2016, 2018) or different sequences and successional recovery from changes in past vegetation cover (Johnson and Miyanishi, 2008; Walker et al., 2010; Watson et al., 2014). No detailed global analysis to date has explicitly considered the influence of both current and past differences in vegetation cover on current species assemblages.

While some differences in species assemblages can be traced back to changes in vegetation cover in the late quaternary (Vegas-Vilarrúbia et al., 2011; McMichael et al., 2017), there is some evidence that changes in vegetation cover in the more recent past can influence plant (Jakovac et al., 2016), invertebrate (Valtonen et al., 2013) or vertebrate assemblages (Newton et al., 2014; Cole et al., 2015; Graham et al., 2017). However, this has – to our knowledge – not been assessed comparatively across multiple taxonomic groups. Furthermore, it is likely that species with specific traits, such as certain body size and/or trophic level, may be differentially affected by past changes in vegetation cover because of differences in their metabolic rate (for animals), longevity or dispersal abilities (Sutherland et al., 2000; Brown et al., 2004; Speakman, 2005; Thomson et al., 2011; De Palma et al., 2015). Depending on the type and magnitude of a past changes in vegetation cover (as a proxy for land-surface changes) plant assemblages can either be dominated by small, fast sprouting or taller, nutrient-demanding species (Jakovac et al., 2016; Perring et al., 2018). Until now, our understanding of the influence of past differences in vegetation cover on species assemblages has been limited to case studies focused on specific regions or certain taxonomic and functional groups. However, a recently published globally representative dataset on species assemblages of broad taxonomic coverage (Hudson et al., 2017) and globally available satellite-derived data enable us to consider explicitly both current and past differences in land-surface conditions.

Satellite-derived data can provide internally consistent estimates of how land differs across time and space (Pettorelli et al., 2005; Kennedy et al., 2014). Land-surface conditions such as photosynthetic activity of vegetation can be quantified using spectral indicators from satellite-derived data (Gamon et al., 1995; Zhang et al., 2006). Changes in photosynthetic activity of vegetation can be related to both climatic (Fensholt et al., 2012;

Zhu et al., 2016) and anthropogenic factors such as land conversions and modifications (Lambin et al., 2003; Müller et al., 2014). Subtle differences in vegetation dynamics (as measured by various satellite-derived vegetation indices), such as faster greening rate or differing seasonal amplitude, between years have been used to characterize land change (Lambin and Strahler, 1994; Linderman et al., 2005; Lupo et al., 2007). Recent studies have used such differences to identify changes in land use such as pasture use intensity (Rufin et al., 2015), fallow periods in croplands (Estel et al., 2015; Tong et al., 2017), small-scale deforestation (DeVries et al., 2015) and broad scale land degradation and intensification (de Jong et al., 2011; Müller et al., 2014). Dissimilarity metrics describing the entirety of recent land history (e.g. including both differences in land use and land cover as well as climatic and site-specific factors) can be calculated between spatial pairs of time series as the overall dissimilarity in photosynthetic activity (Linderman et al., 2005; Lhermitte et al., 2011). Increasingly such methods have been linked to dissimilarity in local species assemblage composition (Rowhani et al., 2008; Goetz et al., 2014; Nieto et al., 2015; Hobi et al., 2017), however few studies have explicitly distinguished between current and past dissimilarity in photosynthetic activity.

Here we use a time series dissimilarity metric (the Bray-Curtis index) to quantify dissimilarity in a land-surface attribute, e.g. photosynthetic activity of vegetation, among spatial pairs of sites in the Projecting Responses of Ecological Diversity In Changing Terrestrial Systems (PREDICTS) dataset (Hudson et al., 2017). We explicitly distinguish between dissimilarity in current and past photosynthetic activity (BC_{EVI}), defined here as the five years prior to the ‘current’ year, and assess how they influence compositional dissimilarity ($BC_{Biodiversity}$) between species assemblages among paired sites. This pairwise comparison approach allows us to investigate (i) the overall influence of past relative to current dissimilarity in photosynthetic activity on species assemblages where we hypothesize that the influence of past dissimilarity increases with longer past periods considered. Furthermore, we investigate (ii) whether different taxonomic groups respond differently to past dissimilarity in photosynthetic activity, and (iii) if species with particular functional characteristics, i.e., those that are smaller and/or more vegetation-dependent, are more affected by past dissimilarity in photosynthetic activity than others.

2.2 Data and Methods

2.2.1 Remotely-sensed data

A temporal profile of spectral reflectance values was derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor on board NASA's Terra and Aqua satellites. Since the year 2000, MODIS has provided continuous spectral data of medium-scale resolution (nominal ~500 m resolution) with high temporal revisit rates (a global image collection is taken every day) (Schaaf et al., 2002). We used the Bidirectional Reflectance Distribution Function and Albedo (BRDF) product (MCD43A4.005), which aggregates the highest quality daily spectral reflectance values into 8-day composites of seven spectral bands (Schaaf et al., 2002). Google Earth EngineTM was used to download and process temporal profiles of all spectral bands for each site (Gorelick et al., 2017). We calculated a spectral index measuring photosynthetic activity (the two-band Enhanced Vegetation Index – EVI; Jiang et al. (2008)), which is based on a ratio between the near-infrared (nir, 841–876 nm) and red (red, 620–670 nm) spectral band $EVI = 2.5 * \frac{(nir-red)}{(nir+2.4*red+1)}$. We used the EVI as it has been designed to reduce atmospheric contamination and not to saturate in high biomass regions such as tropical rainforests (Huete et al., 2002; Jiang et al., 2008). We applied the following pre-processing steps (also see flowchart in Appendix Figure A.2.1) to the nir and red BRDF bands individually to fill missing observations and filter out extreme data points.

First, we detected and removed extreme outliers in the BRDF data that may have been introduced by cloud shadows, atmospheric haze, inversion errors or sensor failures. We calculated the absolute difference of all values from the median relative to the total median absolute deviation (MAD) of all values (Leys et al., 2013). Pixels which were more than a conservative threshold of two units deviation (but see Leys et al., 2013) away from the MAD as well as greater than 99% of all other difference values were set to missing. This data-defined threshold removed only the most extreme outliers and retained fluctuations that are within the bounds of median conditions. We chose this procedure rather than using the MODIS BRDF quality data set (stored in the separate MCD43A2.005 product) to maintain the maximum number of observations assuming that bad quality inversions of the BRDF product are filtered and smoothed out by subsequent

pre-processing steps.

Second, we interpolated missing values using a Kalman filter, a smoother for estimating missing data points based on preceding data (Kalman, 1960). Previous studies have shown that Kalman filters perform well in filling gaps in BRDF time-series especially in data-poor regions (Samain et al., 2008). The best model for the Kalman filter for a given time-series was estimated using the “forecast” R package (“auto-arima” function) by selecting the model with the lowest Akaike Information Criterion (AIC) (Hyndman and Khandakar, 2008). We only interpolated consecutive gaps ≤ 40 days (i. e. five consecutive 8-day BRDF composites) as longer interpolations would reduce our ability to detect short-term changes in photosynthetic activity. We excluded all time-series from further analyses with more than 50% remaining missing data (average proportion of missing data = $6.32 \pm 10.31\%$) in the time period considered (see Appendix Figure A.2.2).

Lastly, we applied a Savitzky-Golay filter (filter length = 5, “signal” R-package) to reduce the amount of random noise remaining in the time series, but retain small abrupt changes that might occur (Joensson and Eklundh, 2004). The Savitzky-Golay filter performs well relative to other smoothing techniques in removing noise (Kandasamy et al., 2013). Our pre-processing steps aimed to remove influential outliers and random noise from each time series, but we cannot rule out that some non-informative noise has remained in the time series. From these pre-processed BRDF data we calculated the EVI for each 8-day composite (Jiang et al., 2008).

2.2.2 Species assemblage data

We used data on species’ abundance within local-scale assemblages from the PREDICTS database (Hudson et al., 2017, downloaded on 3 February 2016, see A.2.1), which is the largest global database investigating anthropogenic impacts on terrestrial species assemblages to date. The PREDICTS database has collated local-scale species assemblage records from the published literature (henceforth “sources”) comparing observations among at least two localities (henceforth “sites”) with differing land use or related pressures. Sources in the PREDICTS database having multiple sampling methodologies and taxonomic groups were split accordingly into different “studies”. Wherever sampling effort differed among sites within a study, we followed the approach of Newbold et al.

([2014](#)) and adjusted abundance values assuming that recorded abundance increase linearly with effort. Each study was assigned to one of six higher taxonomic groups based on the sampled species identity (Plants, Invertebrates, Amphibians, Reptiles, Birds and Mammals). We grouped plants and invertebrates into single individual groups as there were insufficient data to divide them into smaller groups (e.g., functional divisions such as flying vs ground-living insects). Studies of fungi were dropped from the analyses because of insufficient data.

Of the 25224 sites with abundance data, we removed 6109 sites because their sampling durations spanned more than a year or because the start of biodiversity sampling differed by more than three months among sites within a study. This was done to avoid seasonal effects confounding any link between species assemblage composition and remote-sensing derived estimates. Furthermore, we removed 10248 sites from studies that sampled biodiversity before the 18th of February 2006 to ensure MODIS data availability for at least five years prior to biodiversity sampling. We chose to use a five-year period to allow sufficient MODIS coverage (since year 2000) for the majority of studies in the PREDICTS database (median biodiversity sampling start date = 2007-07-17). In total 8867 sites were suitable to be linked with MODIS remote-sensing data.

The spatial extent of biodiversity sampling at PREDICTS sites typically differs from the resolution of MODIS data. We used the Maximum Linear Extent (MLE) information within the PREDICTS database, which summarises the spatial extent of sampling within a study in metres ([Hudson et al., 2017](#)). Sites from a few studies had large MLE (up to 40 km) and after visual exploration, we decided to keep only those sites that were within the 99% quantile of all MLE values ($\text{MLE} < Q_{99} = 3000 \text{ m}$, removing 249 sites). Some studies had missing MLE information (25% of all studies with abundance data, 728 sites), where no MLE estimate could be obtained during the PREDICTS data curation ([Hudson et al., 2017](#)). We filled missing MLE information with the average MLE estimate of each taxonomic group with corresponding sampling method, and any remaining missing MLE, for which no other combination of taxonomic group and sampling method had MLE estimates, with the average MLE for each taxonomic group. We tested the robustness of this assumption by removing 25% of the existing MLE estimates at random and found interpolated MLE values to be reasonably accurate ($r = 0.73$, $p < 0.001$). We used the centre coordinates for the rest of the sites (mean MLE \pm SD = $256.52 \text{ m} \pm 437.93 \text{ m}$) as

their spatial extent roughly matched the nominal spatial resolution of the MODIS data (~500 m).

We excluded studies from our analyses where all study sites fell within a single MODIS grid cell, to suit our hierarchical statistical approach (see below). Some sites within a study could fall into the same MODIS grid cell, therefore for all further analyses we randomly selected one site per study per grid cell 100 times (See section on analysis – pairwise differences below for description of permutation procedure and Appendix Figure A.2.3 for a schematic), resulting in 100 different subsets that we used for all further analyses. Our final dataset included data from 198 studies with 4053 sites per permutation and model covering all major continents and most taxonomic groups (Figure 2.1).

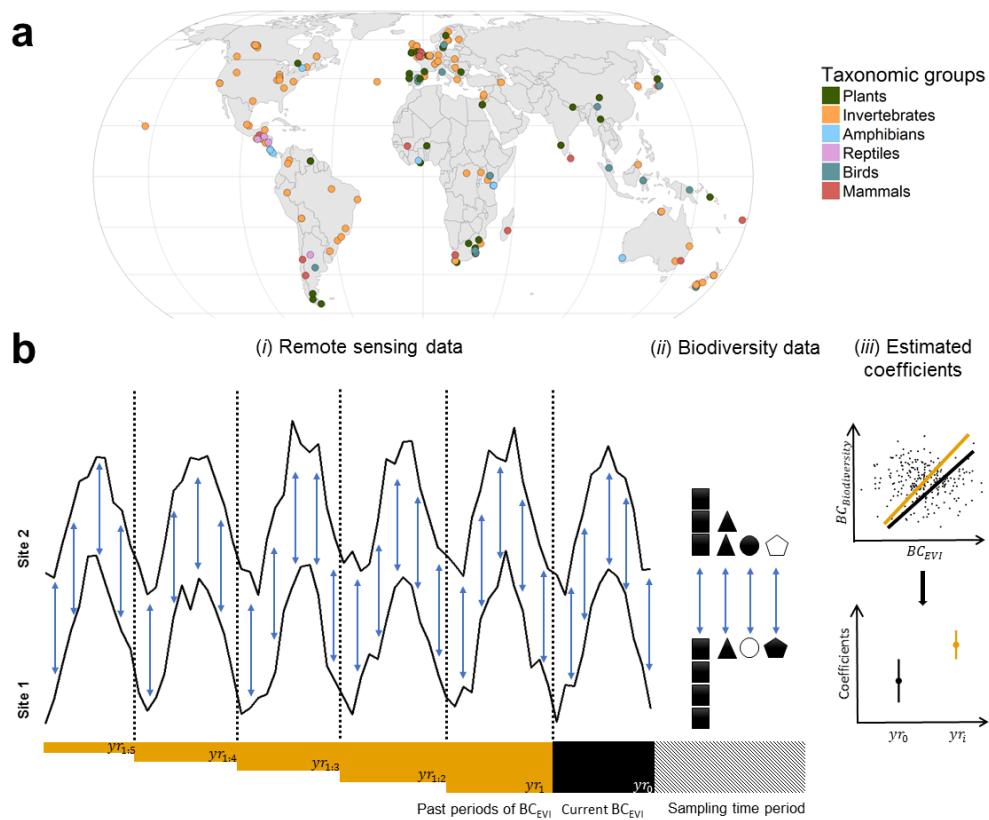


Figure 2.1: (a) Locations of 198 species assemblage studies (centroid of each study) coloured by taxonomic group. (b) Diagram of the modelling approach to investigate influences of current and past dissimilarity in photosynthetic activity on species assemblages. The Bray-Curtis index (BC_{EVI}) was calculated between pairs (blue arrows) of remote-sensing time series (black solid lines) and of species assemblages ($BC_{Biodiversity}$) collected at paired sites. Independent statistical models were constructed for both current (i - black) and past BC_{EVI} of varying length (ii - orange) and their model effects compared (iii – Estimated fixed effects).

2.2.3 Species trait compilation

A species' size and trophic level are two of the most basic traits for understanding differences in species assemblage structure (Speakman, 2005; Terborgh, 2015). We classified studies into size and trophic bins based on a simple majority: small ($>0\text{-}9$ g animal body mass or $> 0\text{-}9$ cm plant height), medium ($10 - 99$ g or $10\text{-}99$ cm) or large species (≥ 100 g or ≥ 100 cm), or predominantly herbivore, omnivore, carnivore or detritivore species, by estimating the dominant number of species (simple sum of measurement) within a study. Studies with species of predominantly unknown size or trophic level were removed from the analysis. We thus classified entire studies to the dominant bins as each study's methodology would likely constrain the average size of animals or plants that can be observed. Data on average adult body mass (in g) were collected for mammals (Jones et al., 2009) and birds (Myhrvold et al., 2015), while for plants we used height (in cm) data from the TRY database (Kattge et al., 2011). The estimates of species trophic levels originate from Kissling et al. (2014), Wilman et al. (2014) and other sources of the literature for invertebrates (obtained from Laura Bentley, Imperial College London, UK). For species for which size or trophic level data were unavailable, we used the genus-wide average for size and the most common trophic level (at least 95% of all species with data within a genus). We excluded studies ($N=8$) from further analyses where no clear majority of species ($> 50\%$) could be assigned to one of the bins (Appendix Figure A.2.4), leaving a total of 65 studies with size information and 130 studies with trophic information.

2.2.4 Analysis - Pairwise dissimilarity

We linked dissimilarity in photosynthetic activity of vegetation with compositional dissimilarity in species assemblages globally. Specifically, we examined the differential influence of "current" (yr_0 , as the 365 days prior to species assemblage sampling) and "past" (yr_i , the i years prior to the current year, where $i = 1, \dots, 5$) dissimilarity in photosynthetic activity between spatial pairs of sites (Figure 2.1b, Appendix Figure A.2.3). We separately considered past periods of increasing lengths (in years, so yr_1 , $yr_{1:2}$, $yr_{1:3}$, $yr_{1:4}$, $yr_{1:5}$). For example, if species assemblage sampling was conducted from the 1st of April until the 15th of July 2008, yr_0 was the 365 days prior to 1st of April 2008, i.e. 1st April 2007 – 31th March 2008, and past i years as the period (number of full years i) before April 1st 2007.

We used the pairwise Bray-Curtis (BC) index, frequently used in community ecology studies, as a metric to quantify dissimilarity in species assemblage composition between sites (Bray and Curtis, 1957; Faith et al., 1987; Su et al., 2004). We also considered the binary version of the BC index, the Sørensen similarity index, to assess whether our results are robust to metric choice. The BC index is a modified Manhattan distance, where the summed distances between values are standardised by the summed values of each site, thus quantifying pairwise dissimilarity from 0 (completely similar) to 1 (entirely different). We used the BC index to measure compositional dissimilarity in local species assemblages ($BC_{\text{Biodiversity}}$) between sites within a PREDICTS study. We also applied the BC index to the EVI time series (BC_{EVI}) to characterize the dissimilarity between sites in (inter- and intra-annual) vegetation dynamics measured through a proxy representing photosynthetic activity of vegetation in current (yr_0) and past years (yr_i , where $i = 1, \dots, 5$), which to our knowledge is the first time the BC index has been applied to assess dissimilarity between remotely-sensed time series.

The BC index is calculated between two pairs of sites with PREDICTS species assemblage records or two EVI time-series from sites x and y as follows:

$$BC_{xy} = \frac{(\sum_{k=1}^n |x_k - y_k|)}{(\sum_{k=1}^n x_k + \sum_{k=1}^n y_k)}$$

For species assemblages, x and y are the abundances of observed species (n = total number of species) at both sites (non-occurring species were assumed to be absent and set to zero), while for the EVI time series x and y are observed EVI values on the same date (n = total number of dates) in the time series at both sites. The BC_{EVI} was calculated on either single or multiple years (yr_i , where $i = 1, \dots, 5$) of EVI time series (Figure 2.1b, Appendix Figure A.2.3).

Compared to other metrics quantifying dissimilarity between time-series based on remotely-sensed data (Lhermitte et al., 2011) the BC_{EVI} index has the advantages of (a) taking the actual spectral values as well as distance between them into account, meaning it can be compared between different land-cover types, and (b) using the same method for assessing dissimilarity between species assemblages and between remote-sensing observations. In remote-sensing terms, for any vegetation index (such as EVI), the BC_{EVI} index can be interpreted as a measure of absolute differences between two sites in the amount and timing of photosynthetic activity scaled by the total amount of

photosynthetic activity available. By calculating the BC_{EVI} index on temporal profiles of EVI measurements, we incorporate all differences in EVI between two sites into a single dissimilarity metric. No further scaling has been done as range and unit of the BC_{EVI} index values were identical for current and past BC_{EVI}.

2.2.5 Analysis - Statistical modelling

The aim of the statistical modelling is to estimate the influence of current and past BC_{EVI} on the BC_{Biodiversity} (Figure 2.1b). For different time periods (0-5 years) we estimated this influence using separate models rather than an interaction term as current and past BC_{EVI} were highly collinear (Random permutation pick: Pearson's $r > 0.9$, $df = 4046$, $p < 0.001$). A hierarchical modelling approach using generalized linear mixed models (GLMMs) with Gaussian link function was used to fit models of current and past BC_{EVI} independently for each time period, taxonomic group, size and trophic bins. GLMMs account for differing sampling methodologies among the PREDICTS studies, by including the "study" as a random intercept in all models. We also allowed the effect of current and past BC_{EVI} to vary for each study by incorporating it as a random slope. From each model, we obtained the fixed effects (estimated slope) of the predicted BC_{Biodiversity} per unit of current and past BC_{EVI}.

As we are primarily interested in the influence of past BC_{EVI} (of different periods) on differences in BC_{Biodiversity}, we incorporated the influence of current BC_{EVI} by transforming the average past BC_{EVI} effects (across all permutations) relative to current effects $\frac{Past}{(Current-1)}$. The resulting ratio describes whether the explicit influence of past BC_{EVI} on BC_{Biodiversity} is larger (> 0) or smaller (< 0) than the influence of current BC_{EVI} (Figure 2.2). The precision estimates (predicted standard errors) of the effect of past BC_{EVI} were also transformed relative to the precision estimates of current BC_{EVI} $\frac{(Imprecision_{past})}{(Imprecision_{current})}$. This helps to visually assess the added imprecision after accounting for the imprecision already present in current BC_{EVI}.

Estimating pairwise comparisons in any regression model would imply substantial pseudo-replication. To account for this, we took the subdiagonal of 100 permuted site-by-site matrices (Appendix Figure A.2.3) to construct the GLMMs of 100 separate permutations. This ensures that for each fitted GLMM, our pairwise comparisons are

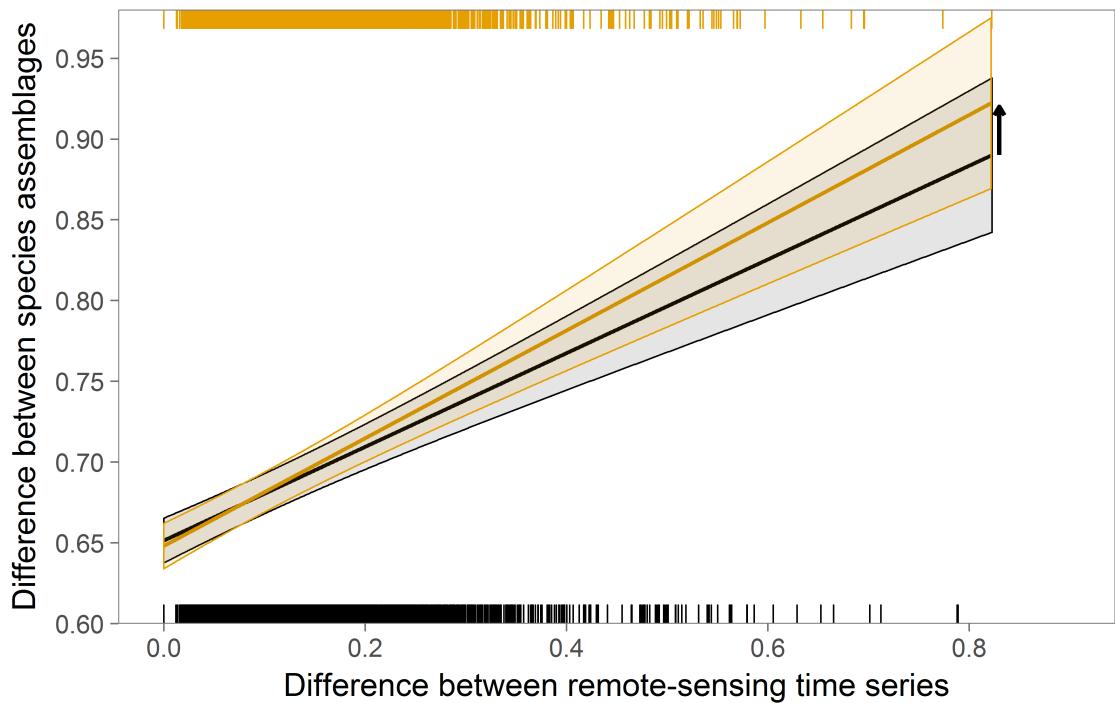


Figure 2.2: Shows the estimated influence of current (black) and past (orange; assessed over the past five years) BC_{EVI} on differences in species assemblages ($N = 198$ studies). Rugs show the distribution of values from a single randomly selected permutation. The difference between the slopes (arrow) is the relative influence (as ratio) shown in Figures 3-6. Shading shows the predicted standard error.

mutually independent subsets (Longacre et al., 2005; Newbold et al., 2016b). Fixed effects and standard errors for both current and past BC_{EVI} were averaged across all permutations. Furthermore, for each model we calculated a marginal and conditional pseudo R-square (Nakagawa and Schielzeth, 2013) and significance estimate Halekoh and Højsgaard (2014), and averaged them across all permutations. As for the fixed effects and precision estimates, the differences in explained marginal variance of past BC_{EVI} were assessed relative to the explained marginal variance of current BC_{EVI}.

All analyses were performed in R (R Core Team, 2018, ver 3.2.2) using lme4 (Bolker et al., 2009; Bates et al., 2015, ver. 1.10) for modelling, and vegan (Oksanen et al., 2015, ver. 2.2.3) for the BC calculation of species assemblages data. The processed MODIS data and R-code for the analyses are available on GitHub (<https://github.com/Martin-Jung/PastLandSurfaceConditions>).

2.3 Results

The compositional dissimilarity of species assemblages ($BC_{Biodiversity}$) increased with between-site dissimilarity in current and past photosynthetic activity (BC_{EVI} ; current: $\beta = 0.289$, $\beta_{SE} = 0.063$, $p < 0.001$; past $yr_{1:5}$: $\beta = 0.334$, $\beta_{SE} = 0.07$, $p < 0.001$; Figure 2.2, Appendix Figure A.2.5). When the influence of past BC_{EVI} was assessed relative to current BC_{EVI} , the $BC_{Biodiversity}$ between sites was more pronounced – although the imprecision also increased - when longer time periods (of up to five years) of past BC_{EVI} were considered (Figure 2.3). Furthermore, the consideration of past BC_{EVI} calculated up to five years prior to current BC_{EVI} increased the relative explained marginal variance by 16.7% (Appendix Table A.2.1). We ensured that the BC index was robust with regards to varying time period lengths (Appendix Figure A.2.6), spatial autocorrelation (Appendix Figure A.2.7) and other temporal and geographic biases (Appendix Figure A.2.8). Similar results were found by using a different metric of species assemblage composition, the Sørensen similarity index, that does not require species abundance estimates (Appendix Figure A.2.9).

The influence of past BC_{EVI} on species assemblages was found to vary among taxonomic groups and time periods considered (Figure 2.4). Dissimilarity in plant, invertebrate, reptilian and bird assemblage composition increased with increasing BC_{EVI} of the past two to five years. In contrast, the influence of past BC_{EVI} on mammalian assemblages was greatest for the first two years relative to the influence of current BC_{EVI} but decreased when longer periods of three to five years of past BC_{EVI} were considered. Meanwhile, amphibian assemblages were more influenced by current than past BC_{EVI} between sites (Figure 2.4). The influence of past BC_{EVI} differed with respect to body size (Figure 2.5). Species assemblages that were dominated by small- ($> 0-9$ g body mass) and medium-sized (10-99 g) mammals were more influenced by differences in BC_{EVI} over the past one to three years, while the influence on assemblages dominated by larger (≥ 100 g) mammals increased with longer time periods. Compared to assemblages dominated by medium-sized birds, assemblages of large bird species were up to five times more influenced by past relative to current BC_{EVI} . For plant assemblages with available information on size, we found that assemblages dominated by medium-sized plants were more influenced by past BC_{EVI} compared to those assemblages dominated by larger plant

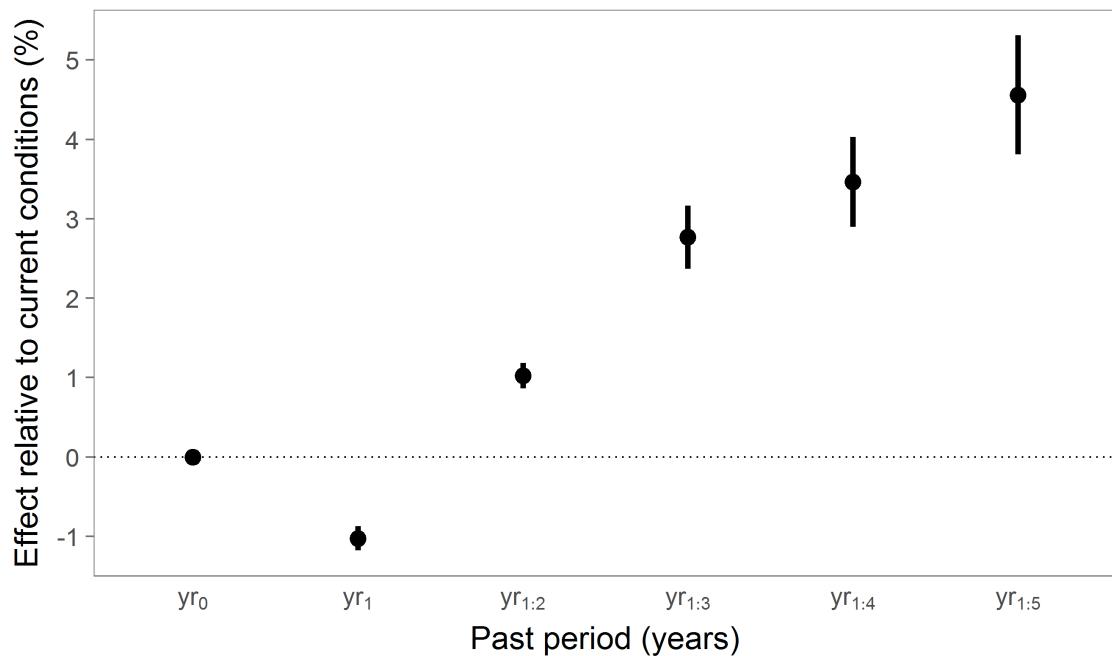


Figure 2.3: Overall influence on species assemblage composition of past BC_{EVI} relative to current BC_{EVI}, estimated individually for past periods of differing length (yr₁ to yr_{1:5}, representing 1 year and up to 5 years current BC_{EVI}). The predicted effects and their precision (standard error) of past BC_{EVI} (yr_{1:5}) on dissimilarity in species assemblages were transformed relative to the effects and precision of current BC_{EVI} (yr₀). Note that error bars indicate the predicted precision of differences in past BC_{EVI} relative to the precision of differences in current BC_{EVI}. Positive values indicate that differences in past BC_{EVI} lead to greater differences in species assemblages than differences in current BC_{EVI}.

species (Figure 2.5). Differences among trophic levels were also seen in the influence of past BC_{EVI} on BC_{Biodiversity} and increased with longer time periods considered (Figure 2.6). Species assemblages dominated by omnivorous and herbivorous assemblages were more influenced by past BC_{EVI} of even one year relative to the influence of current BC_{EVI}, while detritivores assemblages were only more influenced by past BC_{EVI} if periods of the past three years were considered (Figure 2.6). In contrast, studies with predominantly carnivorous species were more influenced by current BC_{EVI} and showed no overall trend with longer time periods of past BC_{EVI} considered (Figure 2.6).

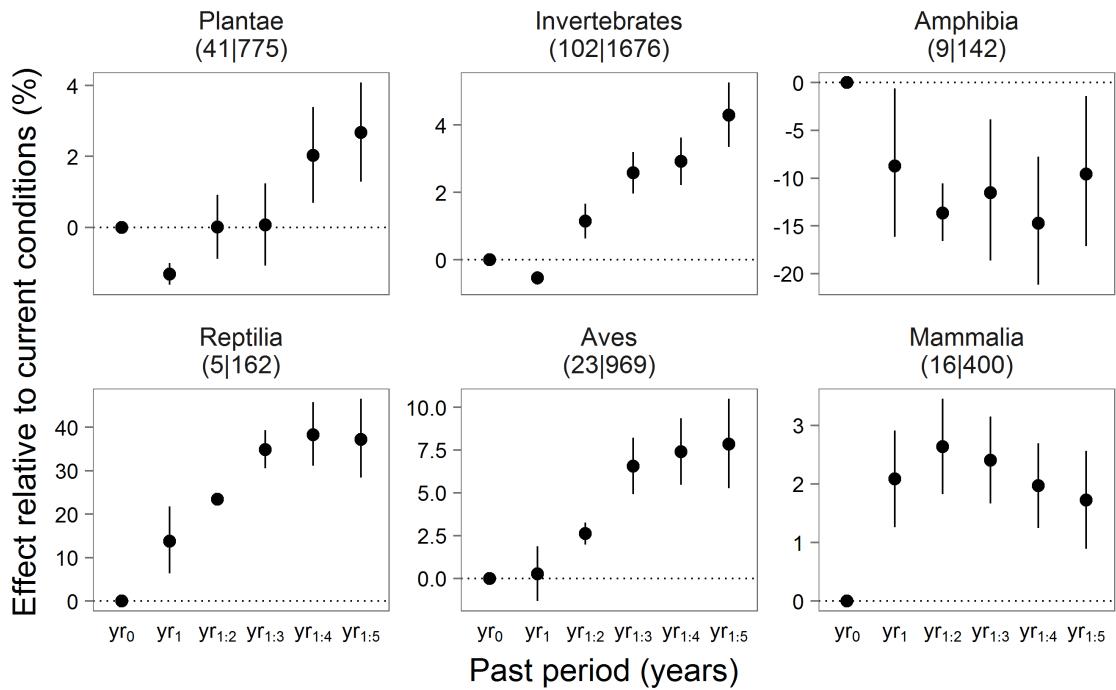


Figure 2.4: Influence of past BC_{EVI} on species assemblage composition across different taxonomic groups. Visualized as relative influence of past BC_{EVI} compared to current BC_{EVI} as described in Figure 2.3. The number of studies and contributing sites (N | N_{Sites}) is indicated for each group.

2.4 Discussion

The main aim of this study was to investigate if between-site dissimilarity in current and past photosynthetic activity of vegetation (BC_{EVI}) can predict compositional dissimilarity in sites' species assemblages (BC_{Biodiversity}). In contrast to previous PREDICTS-based studies that used discrete measures of current land use and land-use intensity (Newbold et al., 2015, 2016b), we used a continuous measure of between-site dissimilarity in remotely-sensed photosynthetic activity that summarises (inter- and intra-annual) vegetation dynamics in a single metric (the BC_{EVI}). We explicitly differentiated between current (the full year prior to species assemblage sampling) and past BC_{EVI} (periods of up to five years before current) that could have influenced compositional dissimilarity in species assemblages. Similar to previous studies using the same dataset to analyse compositional differences with respect to land use (Newbold et al., 2016b), we found that sites with more different current BC_{EVI} also had more different species assemblages (Figure 2.2, Appendix Figure 2.5). However, the BC_{EVI} calculated over five years prior

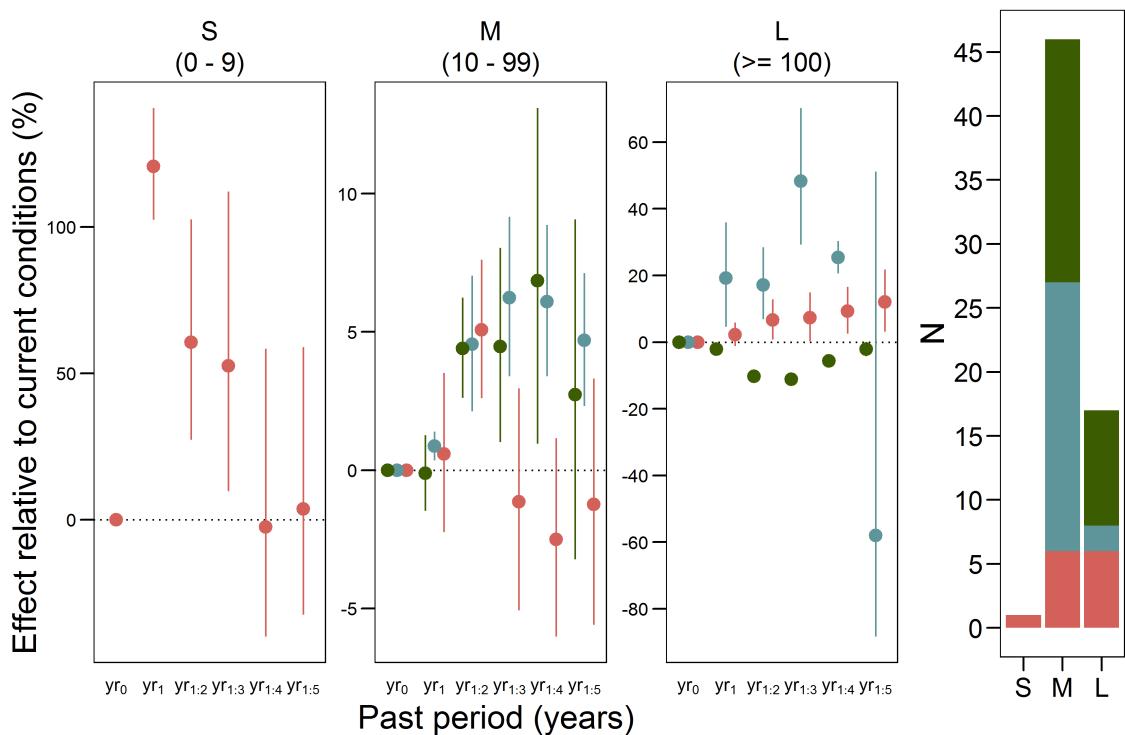


Figure 2.5: Influence of past BC_{EVI} on species assemblages ($N = 65$) of predominantly small ($> 0 - 9$), medium ($10 - 99$) and large sized animals and plants (≥ 100). Available size was measured as adult body mass (in g) for all birds (blue) and mammals (red) and height for plants (green, in cm). Within each study all species were binned into one size group and the study categorized based on which size group is predominant across all sites. The bar chart shows the number of studies that contributed to each taxonomic group and body size bin. Visualized as relative influence of past BC_{EVI} compared to current BC_{EVI} as described in Figure 2.3 and methods.

to biodiversity sampling had, on average, an even greater influence on between-site dissimilarity in species assemblage composition compared to current BC_{EVI} (Figure 2.3). This pattern was consistent across most taxonomic (Figure 2.4) and functional groups (Figure 2.5 and 2.6). Here we discuss potential causes and implications of the observed patterns as well as factors that can affect the BC_{EVI}.

2.4.1 Potential drivers of dissimilarities in photosynthetic activity

Dissimilarities in photosynthetic activity can be caused by many natural (Fensholt et al., 2012; Zhu et al., 2016) and/or anthropogenic factors (Lambin and Geist, 2006; Turner et al., 2007). The latter were likely the dominant cause of current differences between sites in our analyses, given that the PREDICTS database includes only studies of mostly

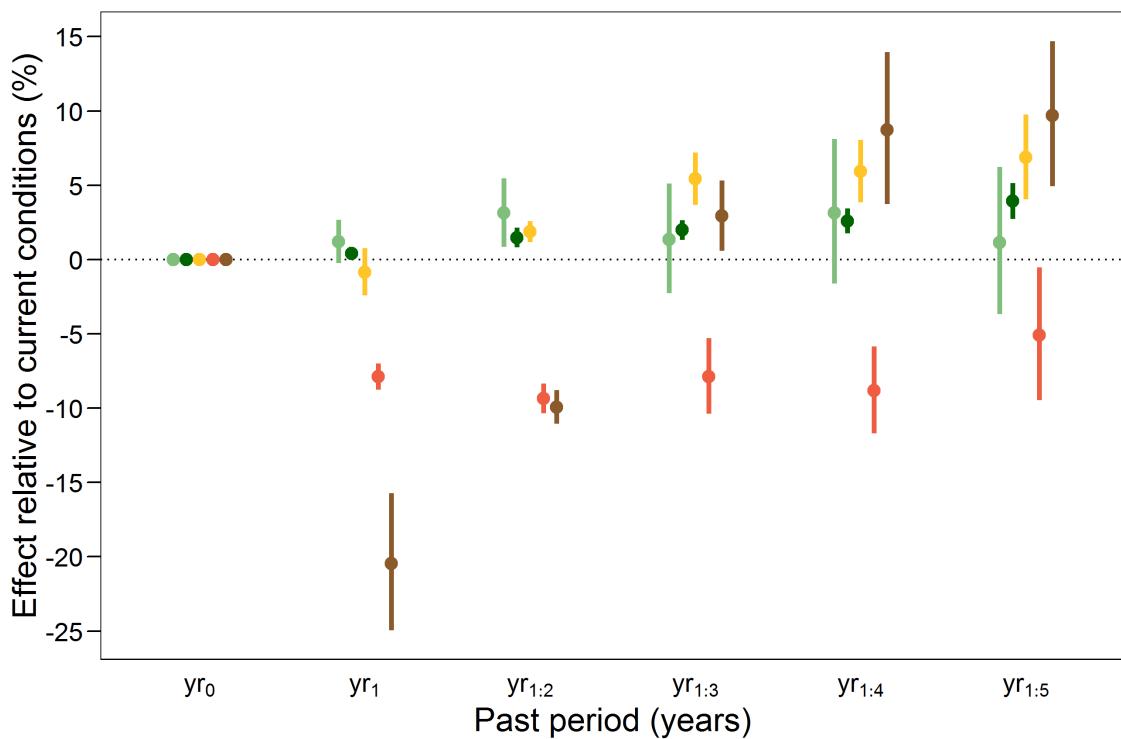


Figure 2.6: Influence of past BC_{EVI} on trophic bins across studies (N = 130). Within each study all species were categorized as one trophic level and the study categorized based on which level is predominant across all sites. Colours indicate the influence of current and past BC_{EVI} for autotroph plants (light green, N=28), herbivores (dark green, N=49), omnivores (yellow, N= 29), carnivores (red, N=13) and detritivores (brown, N=9). Visualized as relative influence of past BC_{EVI} compared to current BC_{EVI} as described in Figure 2.3.

small geographic extent with a difference in current human land use or land-use intensity (Hudson et al., 2017), however climatic factors likely influence the BC_{EVI} as well. Dissimilarity metrics of photosynthetic activity can be considered a coarse approximation of overall differences in land use and land cover as well as in climatic and other abiotic factors between sites (Linderman et al., 2005; Lupo et al., 2007; Lhermitte et al., 2011). Past studies have linked differences in vegetation dynamics with the use intensity of agriculture (Estel et al., 2015; Tong et al., 2017), land-cover change such as deforestation events (Lambin and Strahler, 1994; DeVries et al., 2015), or land degradation and intensification (de Jong et al., 2011; Mueller et al., 2014). The BC_{EVI}, similar to other metrics used to monitor remotely-sensed vegetation dynamics (Linderman et al., 2005; Rowhani et al., 2008; Lhermitte et al., 2011), quantifies dissimilarity in photosynthetic activity across different types of land cover, by exploiting both distance between time series (the absolute difference in EVI data) and amount (area under the time series) of photosynthetic activity.

Besides differences in land use and land cover, dissimilarity metrics such as the BC_{EVI} will also be affected by climatic differences in precipitation and radiation (Fensholt et al., 2012; Zhu et al., 2016), soil properties (Ahmed et al., 2017) or plant species composition (He et al., 2009). The BC_{EVI} thus quantifies dissimilarity in vegetation dynamics caused by both natural and anthropogenic factors affecting EVI time-series.

However, some natural and anthropogenic factors cannot be directly quantified from remotely-sensed time series (Peres et al., 2006; Turner et al., 2007) and the BC_{EVI} is limited to those aspects that affect photosynthetic activity of vegetation. Furthermore, because of the way the BC_{EVI} is calculated, it can only represent overall dissimilarity in photosynthetic activity but cannot be used to infer directionality or timing of change (vegetation regrowth or loss, disturbances such as fires, etc.). By using entire periods (i.e. five full years, instead of the fifth year) it is not possible to disentangle overall dissimilarity and any ‘change’ in photosynthetic activity *per se* (cf. Linderman et al., 2005). Calculating the BC_{EVI} index on longer time periods did not affect the possible range of observed values (Appendix Figure A.2.6), however it likely enhances our ability to capture aspects of past variability in vegetation dynamics caused by either natural and/or anthropogenic drivers. We recommend that future studies evaluate the performance of the BC_{EVI} relative to other time-series dissimilarity metrics.

2.4.2 Influences of current and past dissimilarities in photosynthetic activity on biodiversity

Our results suggest that species assemblage composition was consistently more dissimilar between sites with greater current dissimilarity in photosynthetic activity of vegetation (as quantified by the BC_{EVI}) (Figure 2.2, Appendix Figure 2.5). This is in line with previous studies that have correlated some measurement of dissimilarity in current ‘environmental heterogeneity’ with compositional dissimilarity in species assemblage composition (Buckley and Jetz, 2008; He et al., 2009; Newbold et al., 2016b). However species assemblages might also be explicitly influenced by past dissimilarity in photosynthetic activity (Johnson and Miyanishi, 2008; Watson et al., 2014; Ogle et al., 2015; Perring et al., 2016).

Differences in past BC_{EVI} were on average more correlated with dissimilarity in species assemblages than differences in current BC_{EVI} (Figure 2.2-2.3). This could indicate

that past dissimilarity in photosynthetic activity continues to have a lasting influence or memory effect on species assemblages (Ogle et al., 2015), especially as the effect generally increased as longer periods of past BC_{EVI} were considered (Figure 2.3), therefore increasing the likelihood that past changes in photosynthetic activity of vegetation have been captured. Longer periods of past BC_{EVI} also increased the explained marginal variance (Appendix Table A.2.1), although most of the variance was already explained by differences in study identity (thus by sampling methods and local factors). The marginal variance explained was modest, but comparable to other broad-scale studies using the same species assemblage dataset (Newbold et al., 2014; De Palma et al., 2015; Jung et al., 2017). It is a limitation that we used data from a wide variety of sources (Hudson et al., 2017), which were typically not designed to study lag or memory effects of past changes in land-surface conditions such as photosynthetic activity. At many of the sites in our analyses inter-annual photosynthetic activity could have remained relatively stable during the past five years, which would reduce our ability to differentiate any effects of past BC_{EVI}. Similarly, any dissimilarity in photosynthetic activity among pairs of sites could have been even greater before the monitoring period of MODIS (since year 2000), which we were unable to quantify using these data.

Notably, species assemblages of some taxonomic groups were more dissimilar in composition than others if past dissimilarity in photosynthetic activity was considered (Figure 2.4). The influence of past BC_{EVI} on reptilian species assemblages was large (~35% more different than current) even for the relatively short period of five years (Figure 2.4). Potentially many of the sites of the reptilian studies have been subjected to relatively recent changes in photosynthetic activity of vegetation prior to species assemblage sampling. Indeed, in one of the studies, Woinarski et al. (2009) explicitly suggested an influence of past fires and varying grazing intensity on reptilian species assemblages. In contrast, we found that amphibian species assemblages were less influenced by past compared to current BC_{EVI}, despite being more influenced by current BC_{EVI} than all other taxonomic groups (Appendix Figure 2.5). An explanation could be that most compositional differences between amphibian assemblages that are attributable to past dissimilarities in photosynthetic activity are already explained by current dissimilarity in BC_{EVI}. It may be that amphibian assemblages are more influenced by factors other than past photosynthetic activity (such as microclimatic conditions). Disentangling broad

taxonomic groups into functional groups may assist in highlighting specific responses to past dissimilarities in photosynthetic activity.

Differences in functional traits can influence species responses to dissimilarity in photosynthetic activity (Newbold et al., 2013; De Palma et al., 2015) and we expect that on average smaller species would be more affected by recent dissimilarity in photosynthetic activity (a few years before sampling). Our results confirm this assumption as species assemblages with predominantly small- or medium-sized plants, birds and mammals were relatively more influenced by past BC_{EVI} over two to three years prior to sampling than by current BC_{EVI} (Figure 2.5). Smaller species tend to live shorter lives and disperse less far than larger species (Brown et al., 2004; Thomson et al., 2011; Stevens et al., 2014), which might make them more susceptible to dissimilarity in photosynthetic activity shortly before sampling (Watson et al., 2014). Similar to previous studies (Jakovac et al., 2016) we showed that smaller plant species were more influenced by past dissimilarity in photosynthetic activity over up to five years prior to sampling as quantified by the BC_{EVI} (Figure 2.5). For assemblages dominated by larger plants we did not detect such an influence and it is likely that the considered period (five years) was too short to show measurable influences. Overall our results indicate that assemblages dominated by smaller species might have been more influenced by past dissimilarity in photosynthetic activity, possibly because of carry-over or ecological memory effects (Harrison et al., 2011; Ogle et al., 2015). Other functional traits, such as generation time or dispersal capability (Watson et al., 2014), as well as better coverage of existing traits for underrepresented taxonomic groups could assist in further disentangling these influences especially given the large uncertainty across most influences (Figure 2.5).

The response of species assemblages to dissimilarities in past photosynthetic activity also differed between trophic bins. Except for carnivores, species assemblage composition of all trophic bins were on average more influenced by longer periods of past rather than by current dissimilarity in photosynthetic activity, as measured by BC_{EVI} (Figure 2.6). Yet we found noticeable lags in the observed influence of past BC_{EVI} with varying time periods. Relative to the influence of current BC_{EVI}, the influence of past BC_{EVI} was larger for assemblages dominated by autotrophs, herbivores, omnivores and detritivores (Figure 2.6). Notably, detritivores were more correlated with past BC_{EVI} only if past periods of three to four years were considered. This supports previous studies which

have shown that plant-dependant species are highly sensitive to variability in current and past photosynthetic activity as quantified by remote sensing (Pettorelli et al., 2006; Newton et al., 2014). In contrast, we found predominantly carnivorous assemblages to be less influenced by past BC_{EVI} compared to current BC_{EVI} regardless of the considered time period. Possibly, carnivore abundance was more influenced by contemporary prey density (Terborgh, 2015) than past dissimilarity in photosynthetic activity (Figure 2.6). Because of a lack of data for carnivores and herbivores co-occurring at the same site, we were unable to investigate such interactions.

2.5 Study implications and conclusions

Knowledge about past dissimilarities in land-surface conditions, such as photosynthetic activity, and their influence on species assemblages is important for both the design of ecological studies and interpretation of dissimilarities in current composition of species assemblages. We found that sites with more dissimilar past than current photosynthetic activity (as quantified by the BC_{EVI}) were more strongly correlated with compositional dissimilarity in local species assemblages among spatial pairs of nearby sites. Ignoring such past influences can lead to biased biodiversity estimates by not accounting for extinction debts or immigration credits still to be paid (see Tilman et al., 1994) or lasting ecological memory and carry-over effects because of higher variability in past photosynthetic activity (Rowhani et al., 2008; Cole et al., 2015; Ogle et al., 2015). We suggest that future broad scale studies investigating biodiversity responses to environmental changes should explicitly consider legacy effects that influence species assemblages in a study area and we demonstrate how remote sensing can help to quantify such effects globally. Our approach could be extended to incorporate differences in the vegetation dynamics of the surrounding landscape. There is some evidence that landscape-wide temporal differences in photosynthetic activity can affect species assemblage composition in the wider landscape (Manning et al., 2009; Fernández et al., 2016). In conclusion, we have demonstrated that compositional dissimilarity of species assemblages, of various taxonomic and functional groups, are not only influenced by dissimilarity in current photosynthetic activity, but also by dissimilarity in past photosynthetic activity over the last five years. Future studies should investigate the influence of disturbance events and

directionality of changes in photosynthetic activity for more than five years before local biodiversity sampling.

2.6 Data availability

Extracted MODIS data and pairwise biodiversity permutations are available on GitHub. A 2016 snapshot of the PREDICTS database has been openly released earlier (doi:[10.5519/0066354](https://doi.org/10.5519/0066354)).

CHAPTER 3

Impacts of past abrupt land change on local biodiversity globally

Abrupt land change, such as deforestation or agricultural intensification, is a key driver of biodiversity change. Following abrupt land change, local biodiversity often continues to be influenced through biotic lag effects. However, understanding of how terrestrial biodiversity is impacted by past abrupt land changes is incomplete. By combining geographically- and taxonomically-broad data on local biodiversity with quantitative estimates of abrupt land change detected within time series of satellite imagery from 1982 to 2015, here we show that abrupt land change in the past continues to influence present species assemblages globally. Species richness and abundance were reduced by 4.2% and 2%, respectively, and assemblage composition was altered at sites with an abrupt land change compared to unchanged sites, although impacts differed among taxonomic groups. Biodiversity recovered to levels comparable to unchanged sites after >10 years. Ignoring delayed impacts of abrupt land changes likely results in incomplete assessments of biodiversity change.

3.1 Introduction

Natural and anthropogenic processes change the terrestrial surface of the Earth (Ellis et al., 2013b; Song et al., 2018), which have been shown to impact biodiversity (Newbold et al., 2015; Jung et al., 2018) and ecosystem services (Isbell et al., 2015). Previous studies have found that present differences in land-surface conditions reduce local biodiversity

globally (Gibson et al., 2011; Newbold et al., 2015). However, these studies often ignore the impacts of past land change (Foster et al., 2003; Watson et al., 2014). Simulations and experiments have demonstrated that land changes of greater magnitude have larger impacts on the number of species and individuals (Dornelas, 2010; Hautier et al., 2015; Santini et al., 2017). Yet, few studies have quantified the impacts of land change in the past on local biodiversity globally.

Local biodiversity continues to be influenced by past land change through biotic lags. Biotic lags—including ecological processes such as extinction debt (Tilman et al., 1994; Kuussaari et al., 2009; Halley et al., 2016), colonization credit (Hylander and Ehrlén, 2013) and ecological memory effects (Ogle et al., 2015)—negatively affect the number of species and individuals present within local assemblages (Halley et al., 2016; Jung et al., 2018; Perring et al., 2018), and potentially reduce resilience (Hautier et al., 2015; Nimmo et al., 2015). The impacts of land change on species assemblages through biotic lag depend on species' abilities to persist (Turner et al., 1998) and recover (Martin et al., 2013; Fu et al., 2017; Moreno-Mateos et al., 2017). Most previous global studies (Supp and Ernest, 2014; Fu et al., 2017; Moreno-Mateos et al., 2017; Shackelford et al., 2017) investigating abrupt land changes in the past have used descriptive study-specific categories of “land changes”, e.g. wild fire, flooding or cultivation, thus hindering comparisons among studies, and preventing predictions. To assess the impacts of abrupt land change on local biodiversity more generally, comparable quantitative measures of “land change” are needed.

The availability of time series of satellite imagery enables the detection and quantification of land changes globally (Kennedy et al., 2014; Song et al., 2018). Land change can be defined as abrupt shifts in intra- and inter-annual dynamics of remotely-sensed photosynthetic activity quantified through vegetation indices (Linderman et al., 2005; Pettorelli et al., 2005). Abrupt shifts in magnitude (Kennedy et al., 2012; Watson et al., 2014; DeVries et al., 2015) and/or trend (de Jong et al., 2013) of photosynthetic activity, and the time passed since such shifts (Potter et al., 2003; Kennedy et al., 2012) are three key attributes of land change (Watson et al., 2014). Several algorithms have been developed to detect abrupt land change (Zhu, 2017) and measure these attributes. However, attributes of remotely-sensed abrupt land change have never before been used to assess biotic lags in local biodiversity.

Here we investigate the impacts of abrupt land change in the past – defined as the

single largest shift in magnitude and/or trend of photosynthetic activity (Verbesselt et al., 2010a; de Jong et al., 2013; Song et al., 2018) – on local biodiversity globally. We used data on local biodiversity of unprecedented geographic and taxonomic coverage from the Projecting Response of Ecological Diversity in Changing Terrestrial Systems (PREDICTS) database (Hudson et al., 2017). At each site, where local biodiversity was sampled, we assessed time series of high spatial resolution (nominal ~30m) Landsat satellite imagery from 1982-2015 for the presence of an abrupt land change (Figure 3.1a) and, where detected, we quantified key attributes, i. e. , shifts in magnitude, trend and time passed. Using hierarchical analyses, we compared four measures of local biodiversity (species richness, total abundance, evenness and species turnover) between paired sites (5,563 sites with and 10,102 without an abrupt land change) from 377 studies (Figure 3.1b). We expect that abrupt land changes with larger shifts in magnitude and trend have greater impacts on local biodiversity through biotic lag effects and that with more time passed local biodiversity can recover from the impacts of abrupt land change.

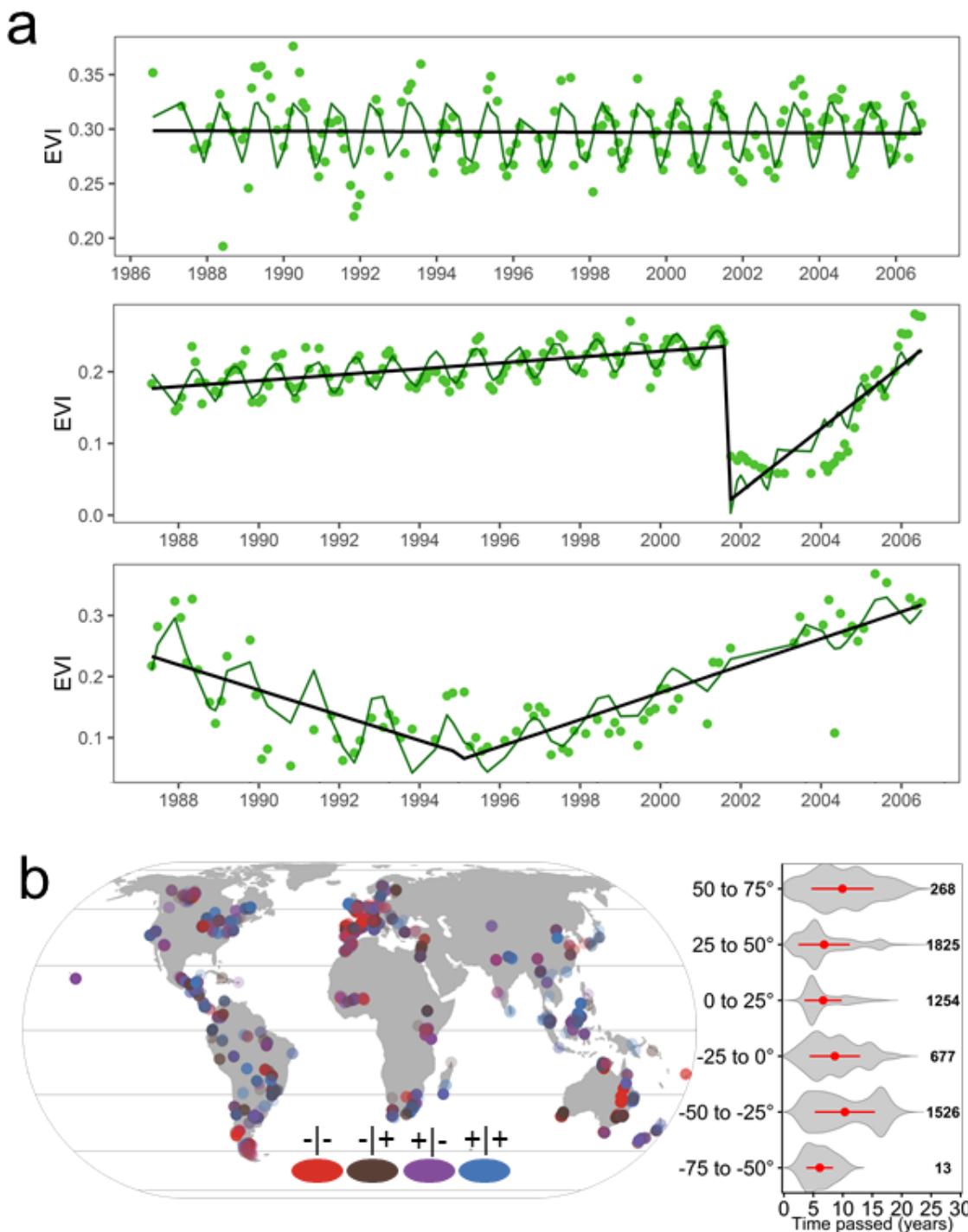


Figure 3.1: Examples and distribution of sites without and with abrupt land change. (a) Remotely-sensed time series of monthly Enhanced Vegetation Index (EVI; green points) at an unchanged site; a site with an abrupt shift in magnitude, i.e., loss in EVI; and a site with a shift in EVI trend, i.e., an increase in annual EVI. Linear (black lines) and seasonal (dark green lines) fits of the change detection algorithm (Verbesselt et al., 2010a) are shown. (b) Location of 5,563 sites from 377 studies in the PREDICTS database with an abrupt land change in the monitoring period (since 1982) of the Landsat 4-8 missions. Colours indicate sites with abrupt land change that had a magnitude gain (+) or loss (-) and/or trend increase (+) or decrease (-); (magnitude | trend). For ease of viewing, the location of 10,102 sites without an abrupt land change has been omitted. Latitudinal distribution of sites with an abrupt land change and time passed between abrupt land change and biodiversity sampling (in years, mean and standard deviation shown in red) by 25° latitudinal bands. Map shown in Eckert IV equal-area projection.

3.2 Methods

3.2.1 Biodiversity data

We used data from the Projecting Responses of Ecological Diversity In Changing Terrestrial Systems (PREDICTS) database (Hudson et al., 2017), which includes species' presence and abundance data from 'studies' with at least two spatially-explicit 'sites', information on the date of sampling, and local land-use and/or land-use intensity (Hudson et al., 2017). We simplified the original PREDICTS land use and land-use intensity information (Hudson et al., 2014, 2017) by allocating each site to one of three broad land-use categories: primary vegetation (**PV**, i. e. primary [non-] forest), secondary vegetation (**SV**, i. e. mature, intermediate, young and indeterminate age secondary vegetation) or human-dominated vegetation (**HDV**, i. e. , plantation forest, cropland, pasture, urban). Studies were grouped into eight broad taxonomic groups based on the sampled taxa: plants, fungi, ground dwelling invertebrates (e. g. , soil-fauna, snails, beetles), flying invertebrates (e. g. , butterflies, bees, dragonflies), amphibians, reptiles, birds or mammals.

We assessed four measures of local biodiversity that complement each other and have previously been shown to be sensitive to abrupt land change (Supp and Ernest, 2014; Santini et al., 2017). For each site in the PREDICTS database, we calculated within-sample species richness and, where data on abundance were available, \log_{10} total abundance of individuals, adjusted by sampling effort following Newbold et al. (2014). After visual inspection, we removed one outlier study (a study of soil biomass, ID = DL1_2012_CalvinoCancela) from further analyses because of very large abundance estimates ($> 3 \times 10^6$ individuals). As a measure of assemblage evenness, we calculated the arcsine square root transformed probability of an interspecific encounter (PIE), which quantifies the probability of two individuals randomly chosen from an assemblage representing different species (Hurlbert, 1971). As a measure of turnover in species assemblage composition within studies, we calculated the Sørensen similarity index among spatial pairs of sites within each study and land-use category (Magurran, 2004).

Species assemblages were sampled at various spatial extents defined by each study's sampling method and land use. Following the PREDICTS data curation protocol we assumed the allocated land use to be dominant within the reported sampling extent

(maximum linear extent [MLE], in meters) of each site (Hudson et al., 2014, 2017). For studies without reported MLE (4779 sites, 18.3% of all sites), we used either the mean MLE for each taxonomic group and corresponding sampling method, e.g., mist netting, pitfall trapping, or the mean MLE within the same taxonomic group. To test whether these interpolated MLEs are consistent among taxonomic groups and sampling method, we randomly removed 25% of the reported MLEs and found the interpolated MLEs to be reasonably correlated (Pearson's $r = 0.73$, $p < 0.001$). We included all studies with a MLE $< 3000\text{m}$ (98.3% of all sites), approximately 100 times the nominal resolution ($\sim 30\text{m}$) of the remotely-sensed data used in this study, and removed four studies with sites located in water (rivers, coastal areas or ponds), identified by intersecting all sites with a global permanent water surface mask (Pekel et al., 2016), as a precaution as sites within these studies likely have low positional accuracy. To spatially link species assemblage with remote sensing data, we calculated a rectangular buffer with MLE as radius ($\text{MLE}_{\text{mean}} = 412.1 \text{ m } pm 1,661.82\text{m SD}$) around each site's coordinates as the smallest area that fully captures all grid cells of varying sampling units (e.g., point counts, line transects).

3.2.2 Remote sensing data

We used land-surface reflectance products derived from the sensors of the Landsat 4 (1982 – 1993), 5 (1984 – 2012), 7 (1999 – ongoing), and 8 (2013 – ongoing) missions available within Google Earth Engine (GEE) (Gorelick et al., 2017), based on raw United States Geological Service Landsat Collection images (Tier 1) to calculate the Enhanced Vegetation Index (EVI, as two-band version Jiang et al. (2008)) as a proxy of photosynthetic activity. We masked all cloud-covered grid cells ($\sim 30 \text{ m}$ nominal resolution) using the cloud-detection output in the 'cfMask' band (Zhu and Woodcock, 2012) and removed occasional snow- and water-covered grid cells, i.e. those with negative EVI values. All data preparation and extraction were performed within GEE (Gorelick et al., 2017).

For each Landsat image and PREDICTS site we calculated the mean EVI within the rectangular buffer (\bar{y}) and extracted time series of all EVI values. We removed outliers introduced by satellite sensor errors, missed cloud shadows or bad quality estimates by calculating the absolute difference of all \bar{y} values from the median absolute deviation (MAD) per EVI time series (Leys et al., 2013). EVI values more than a conservative

threshold of two units of deviation away from the MAD or in the top 1% of all MAD estimates were set to NA (Leys et al., 2013). Time series of EVI data were temporally aggregated to monthly maximum value composites to ensure equal intervals between data points and to reduce the amount of noise and missing data. Because of the ongoing consolidation of the global Landsat archive (Wulder et al., 2016), there can be periods of consecutively missing data, particularly before the launch of Landsat 7 in 1999 (Appendix Figure A.3.1a). To remove gaps of ≥ 5 years of consecutively missing data, which might affect the precision of land change attribute calculations, we identified and then truncated time series to include only the years from 1999 onwards in subsequent analyses (see Appendix Figure A.3.1b). In total 25,656 sites had suitable EVI time series, with an average 18.83 (± 6.7 SD) years duration containing on average 1.82 years (± 1.57 SD) of consecutively missing data.

3.2.3 Abrupt land change detection

To identify the presence of abrupt land change and its attributes in EVI time series, we used the Breaks For Additive Season and Trend (BFAST) algorithm (Verbesselt et al., 2010b) modified to work with missing data and optimized to find the single most influential abrupt land change in a time series (de Jong et al., 2013). BFAST accurately detects abrupt land changes (Verbesselt et al., 2010a; DeVries et al., 2015) by using a multiple regression model to estimate both trend and seasonal components of a time series (de Jong et al., 2013): $\bar{y}_t = \alpha_s + \beta_s t + \sum_{p=1}^k \gamma_p \sin\left(\frac{2\pi p t}{h} + \delta_p\right) + \varepsilon_t$, where \bar{y}_t is the mean EVI at time t , s the segment in the time series, α_s the intercept, β the slope (i.e., trend), p and k the order of the seasonal term ($k = 2$), γ the amplitude, δ the phase and ε the residual error. The expected frequency to detect an abrupt land change in a time series is determined by h and, following previous studies (Verbesselt et al., 2010a,b), was set as the ratio of the number of data points per year (12 months) to the total length of the individual time series (in months). Whenever the inclusion of the seasonal component caused the model to fail to converge (17% of all fitted models), we removed the seasonal component by time series decomposition ('stlplus' package, Hafner (2016)) prior to fitting BFAST with a trend component only. BFAST detects abrupt land change when model residuals depart significantly ($p < 0.05$) from a statistical boundary (Zeileis, 2005). To test for

significant departure we used two complementary approaches (Zeileis, 2005; Verbesselt et al., 2010a,b) using first, a moving sum of residuals (MOSUM) test within the monitoring period (determined by h) and second, an information-theoretic approach, the Bayesian Information criterion (BIC). All BFAST models were fitted using the ‘bfast’ package (ver. 1.5.7, Verbesselt et al. (2010a)) in R (ver. 3.5, R Core Team (2018)).

For the single most influential abrupt land change detected in each time series, we calculated the relative shift in magnitude as the immediate change in EVI [$\frac{(\hat{y}_j - \hat{y}_{j-1})}{|\hat{y}_{j-1}|}$, where \hat{y}_j is the first monthly estimate of \hat{y} predicted by the BFAST model after an abrupt land change has been identified and \hat{y}_{j-1} the predicted estimate one month before], the difference in linear trend as increase/decrease in EVI before and after the abrupt land change ($\beta_{\text{after}} - \beta_{\text{before}}$, where β_{after} and β_{before} are the predicted linear trends in EVI from the BFAST model, before and after the abrupt land change), and the time passed (in months, $t_n - t_j$) between the date of the abrupt land change (t_j) and the start of biodiversity sampling (t_n). Attributes of abrupt land change were grouped into bins as follows (Appendix Figure A.3.2 and Table A.3.1): for shifts in magnitude (> 50%, > 25% and \leq 50%, and \leq 25% EVI loss or gain, Appendix Figure A.3.2a), for shifts in trend (0.01, 0.05, and $>$ 0.05 lower or higher EVI trend change, Appendix Figure A.3.2b) and time passed (<5, 5-10, and $>$ 10 years ago, Appendix Figure A.3.2c). The three attributes of abrupt land change were only marginally correlated among each other (mean Pearson’s $|r| < 0.07$, Appendix Figure A.3.3). Sites without an abrupt land change detected by BFAST are referred to as “unchanged” sites (o) and all studies containing only unchanged sites (10,196 sites of 262 studies) were excluded from further analyses.

3.2.4 Statistical analyses

We built hierarchical models comparing biodiversity measures between paired sites without and with an abrupt land change in the past. Hierarchical generalized linear mixed effects (LME) models were fitted separately for species richness (using a Poisson error distribution), total abundance, and the PIE (using a Gaussian error distribution). For models of species richness we included an observation-level random effect (i. e. , site ID) to account for overdispersion (Harrison, 2015). For each LME model we compared several candidate random-effect structures by fitting null models with combinations of different

random intercepts and random slopes to determine the structure with the lowest overall Aikake Information Criterion (AIC). Random effects always included the study ID to account for study-level differences in sampling methods, optionally a spatial block ID in which sites were located, the site's land-use category (PV, SV, HDV), the presence of an abrupt land change (yes|no), as well as the studies climatic zone (tropical, arid, temperate or continental climate) according to the Koeppen Geiger classification (Peel et al., 2007). Whenever a climatic zone could not be determined (for instance on small islands), we attributed studies to a zone based on latitude and a site's terrestrial biome (1369 sites). The most parsimonious random-effect structure by AIC was identical among response variables and included –besides the study ID –the spatial block and land-use category as random intercept as well as the presence of an abrupt land change as random slope. We included the binned attributes of abrupt land change, e. g. shifts in magnitude, trend, and time passed, as fixed effects in our models with the unchanged sites (0) as paired reference comparison. Separate models were fitted for each taxonomic group using the direction (positive or negative) of magnitude and trend shifts because of limited data availability. Full LME models were tested for significant differences ($p < 0.05$) from a null model using likelihood ratio tests, while significant differences between bins were approximated by Wald statistics (Bates et al., 2015). To compare impacts of a shift in magnitude against shift in trend, we assessed the difference in Akaike's Information criterion (AIC), a difference of $\Delta\text{AIC} < 7$ commonly indicates little improvement in model fit, and calculated ordinary Pearson correlation coefficients between their effects as models were otherwise not comparable because of equal fixed structures. All models were fitted using the 'lme4' package (ver. 1.1-14 in R ver. 3.5, Bates et al. (2015); R Core Team (2018)).

To estimate differences in species assemblage composition we calculated the mean compositional similarity (as quantified by the Sørensen similarity index) between all pairs of sites without and with an abrupt land change in the same study and land-use category. To visualize the mean similarity for each land change attribute bin, we performed hierarchical complete-linkage clustering ('hclust' function in R) on Manhattan distances between estimates of compositional similarity transformed relative to the mean difference between pairs of unchanged sites.

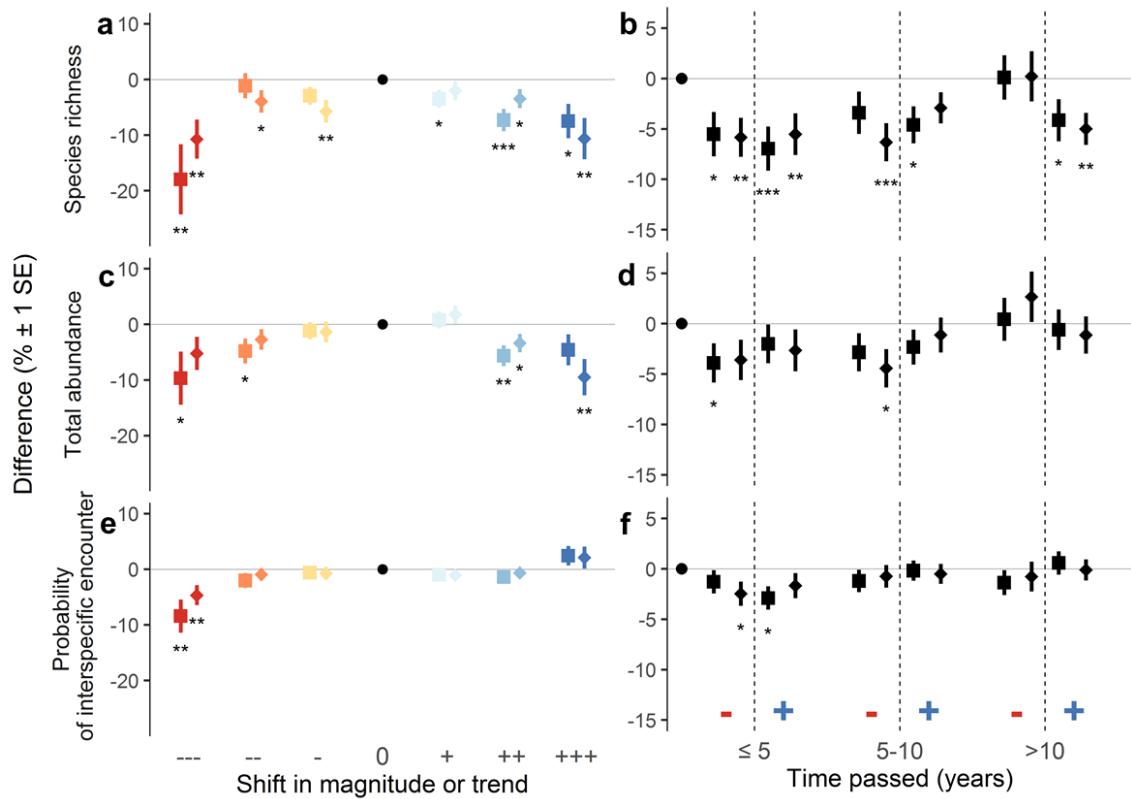


Figure 3.2: Local biodiversity impacts varied with attributes of abrupt land change. Differences in three measures of local biodiversity, (a,b) species richness, (c,d) total abundance, and (e,f) the probability of interspecific encounter (PIE) at sites with an abrupt land change (squares, diamonds) relative to unchanged sites (0, black points). (a,c,e) Estimates are given separately for shifts in magnitude (squares; > 50%, > 25% to \leq 50%, and \leq 25% EVI loss [--- to -, coloured red to orange] or gain [+++ to +, blue to light blue], Appendix Figure A.3.2a) or in EVI trend (diamonds; from --- to +++ for negative to positive trend differences, Appendix Figure A.3.2b). (b,d,f) Impacts on biodiversity measures of time passed between an abrupt land change (gain/increase [+]) or loss/decrease [-] in EVI shift in magnitude [squares] or trend [diamonds]) and sampling of biodiversity. Separate models were fitted for shifts in magnitude and in trend relative to unchanged sites (points). Error bars show fitted standard errors and asterisks statistical significance (* $p < 0.05$, ** $p < 0.01$, *** < 0.001) from the hierarchical models. For number of sites and studies for each bin and biodiversity measure see Appendix Figure A.3.4 and Table A.3.1

3.3 Results

Local biodiversity measures are lower at sites with an abrupt land change in the past. Sites at which an abrupt land change was observed contained on average 4.2% fewer species (SE: 1.3%, $\chi^2 = 10.27$, df = 3, $p < 0.01$), 2% fewer individuals (SE: 1.3%; $\chi^2 = 72.9$, df = 3, $p < 0.001$), and species assemblages were 1% less even (SE: 0.6%; $\chi^2 = 42.79$, df = 3, $p < 0.001$) compared to unchanged sites (Figure 2). Sites with larger abrupt shifts in

magnitude and trend had fewer species and individuals than unchanged sites regardless of direction of abrupt land change (Figure 3.2a,c). Sites with > 50% loss or gain in EVI had on average 18% (SE: 6.4%) or 9% (SE: 3.2%) fewer species, and 10% (SE: 5%) or 5% (SE: 3%) fewer individuals than unchanged sites (Figure 3.2a,c). Compared to unchanged sites, species assemblages were less even at sites with larger abrupt losses in EVI, but not at sites with larger gains in EVI (Figure 3.2e). We found similar impacts of shifts in magnitude and trend on species richness ($\Delta AIC = 3.22$, Pearson's r between impacts = 0.71), abundance ($\Delta AIC = 2.64$, $r = 0.61$), and evenness ($\Delta AIC = 5.66$, $r = 0.98$).

Biodiversity can recover after an abrupt land change depending on time passed. We hypothesize that with more time passed local biodiversity recovers to levels comparable to unchanged sites. In line with our expectation we found that sites with an abrupt land change up to five years before biodiversity sampling had on average 6.6% fewer species (SE: 1.8%), 3% fewer individuals (SE: 1.8%) and were 2% less even (SE: 0.1%) than unchanged sites (Figure 3.2b,d,f). After more than 10 years had passed, biodiversity measures were comparable to unchanged sites (Figure 3.2b,d,f), except for local species richness at sites with positive shifts in magnitude or trend (-4%; Figure 3.2b). Overall, we found similar impacts of shifts in magnitude and trend and varying time passed for species richness ($\Delta AIC = 2.85$, Pearson's r between impacts $r = 0.66$), abundance ($\Delta AIC = 2.46$, $r = 0.42$), and evenness ($\Delta AIC = 3.03$, $r = 0.65$).

Abrupt land change affects the composition of species assemblages. Species assemblages at sites with larger abrupt shifts in magnitude were less similar in composition to unchanged sites (Figure 3.3a, c). Especially sites with a shift in magnitude of > 50% EVI loss or gain were on average less similar (-0.12 / -0.03, respectively) in assemblage composition to unchanged sites (Figure 3.3a). Furthermore, the composition of species assemblages was most dissimilar to unchanged sites if an abrupt land change occurred less than five years ago (Figure 3.3b,d). After more than five years had passed between an abrupt land change and biodiversity sampling, species assemblages were on average more similar in composition (0.04 / 0.001 for loss and gain in EVI, respectively) to unchanged sites (Figure 3.3b). The composition of species assemblages was on average more similar among sites of comparable shifts in magnitude or with time passed (diagonals in Figure 3.3a,b) relative to unchanged sites. The impacts of abrupt shifts in magnitude were broadly comparable to shifts in trends although negative shifts in trend impacted

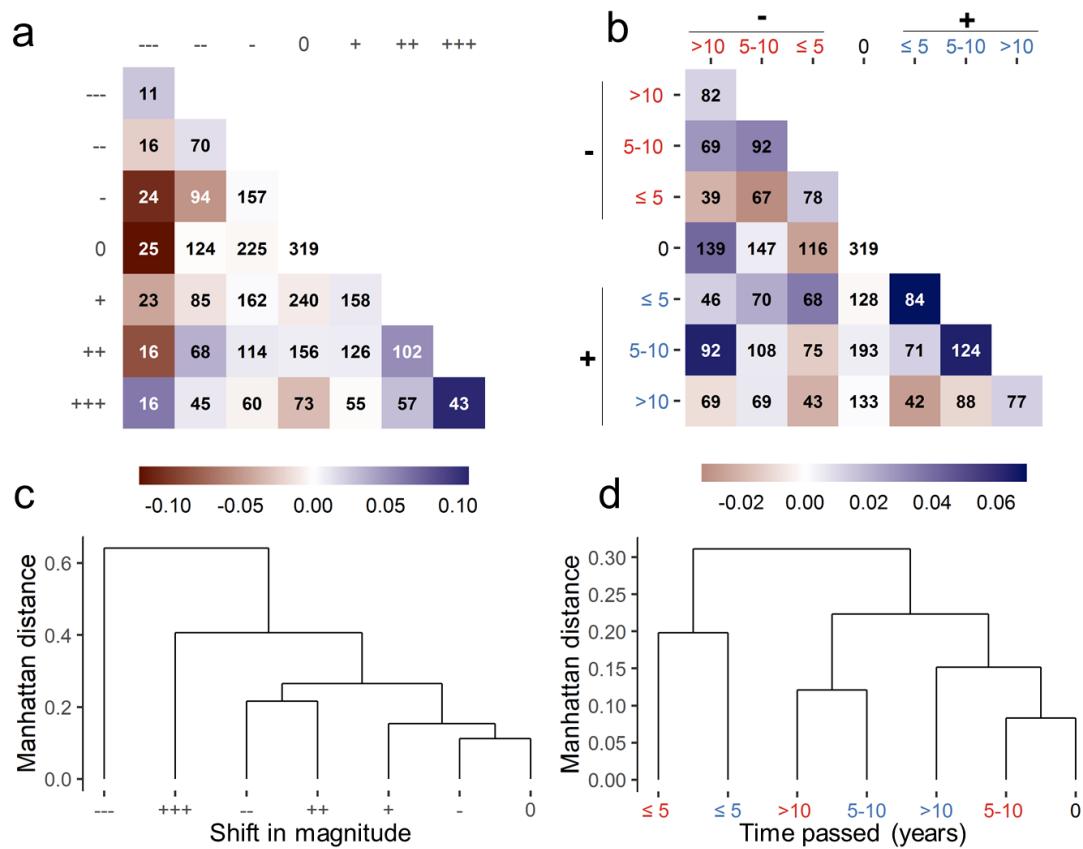


Figure 3.3: Reduced compositional similarity between sites without and with an abrupt land change. Mean similarity in species assemblage composition (Sørensen similarity index) calculated between pairs of sites within the same study and land-use category without (0) and with an abrupt land change of (a, c) varying shifts in magnitude, or (b, d) loss or gain in EVI (– and +) and time passed between abrupt land change and biodiversity sampling (axis labels as in Figure 3.2). Colours indicate whether similarity of species assemblages was on average greater (purple) or smaller (brown) relative to unchanged sites. Numbers (in a,b) indicate the total number of studies for which pairwise comparisons between sites could be made. All estimates are transformed relative to the compositional similarity between pairs of sites without a land change (0 – 0). (c,d) Dendograms show hierarchical clustering of all pairwise similarities based on the average Manhattan distance between pairs of sites; sites with more similar assemblage composition are in branches of closer proximity.

assemblage composition more (Appendix Figure A.3.5).

Impacts of abrupt land changes in the past varies among taxonomic groups. Sites with a positive shift in magnitude had significantly fewer species of plant (9.7%), bird (4.2%), ground dwelling invertebrate (6.4%), and reptile (10.4%) compared to unchanged sites (Figure 3.4a). Particularly sites with a negative shift in trend had significantly fewer species of plant (8.2%, Figure 3.4a) and fungi (29.6%), and fewer individuals of fungi (17.8%, Figure 3.4b) compared to unchanged sites. The number of individuals and assemblage evenness was overall lower at sites with an abrupt land change compared to unchanged

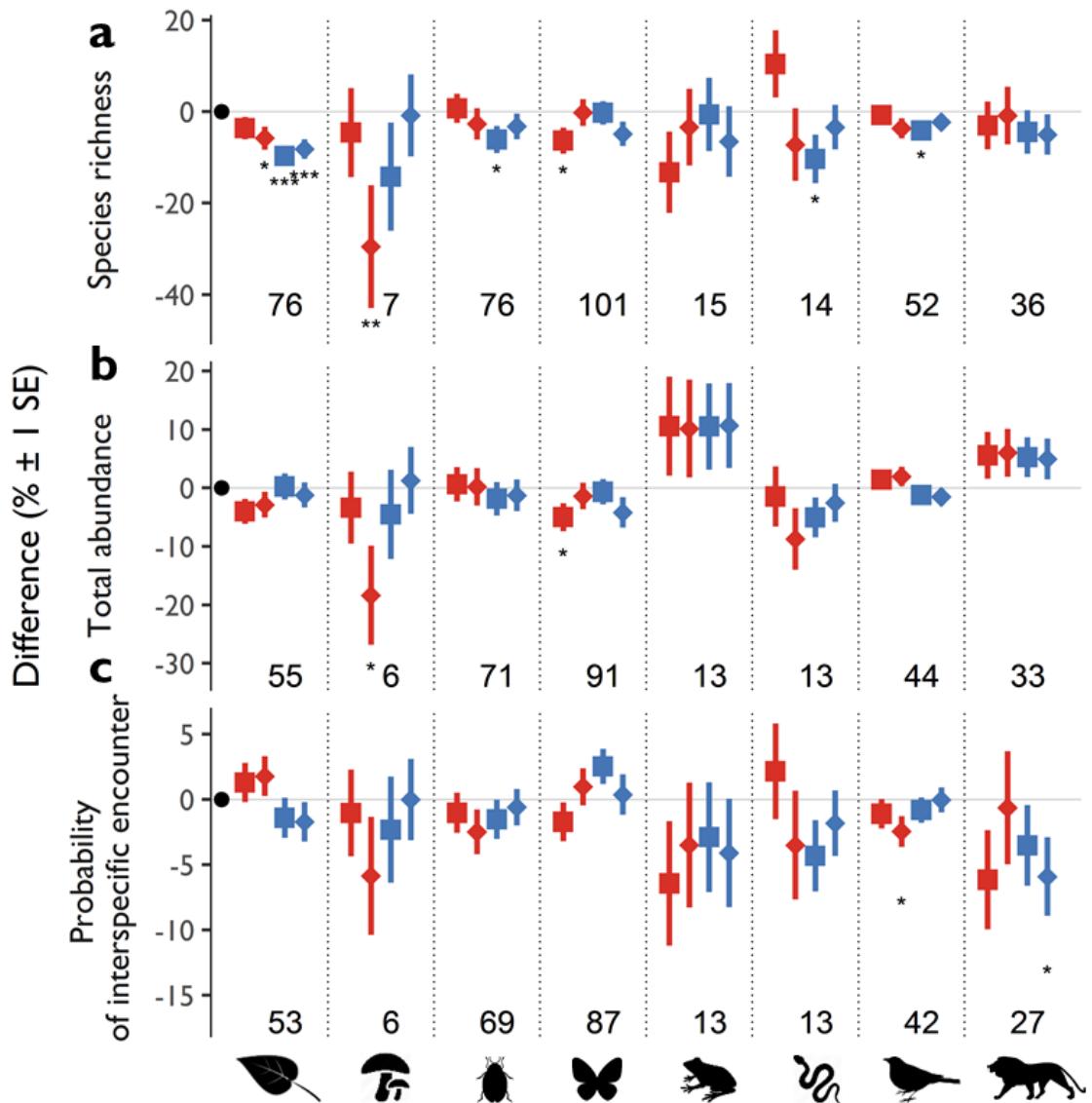


Figure 3.4: Abrupt land change affects taxonomic groups differently. Difference in (a) species richness, (b) total abundance, and (c) assemblage evenness for taxonomic groups (plants, fungi, ground dwelling invertebrates, flying invertebrates, amphibians, reptiles, birds, and mammals) between sites without and with an abrupt land change. Separate models were fitted for taxonomic groups comparing sites with shifts in magnitude (squares) and trend differences (diamonds) where colours indicate negative (red) and positive (blue) direction and sites without abrupt land change (black points, grey line). Error bars show standard errors and asterisks indicate statistical significance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Numbers give the number of studies included per taxonomic group.

sites, although amphibian and mammal abundance as well as evenness of flying insects was higher at sites with an abrupt land change (Figure 3.4b,c). For most taxonomic groups, except fungi and reptiles, there was little difference between the impacts of shifts in magnitude or trend on biodiversity measures (Figure 3.4).

3.4 Discussion

We found species assemblages to be negatively impacted by past abrupt land change. Larger changes on land caused greater reductions in local biodiversity (Figure 3.2a-c) regardless of whether shifts in magnitude or trend of photosynthetic activity (EVI) were positive or negative, suggesting general impacts of past abrupt land change on biodiversity (Dornelas, 2010; Hautier et al., 2015) likely caused by biotic lag effects (Hylander and Ehrlén, 2013; Ogle et al., 2015; Jung et al., 2018). Abrupt land changes with large (>50%) losses or gains in EVI have caused immediate and time-delayed local extinctions (Krauss et al., 2010; Halley et al., 2016; Wood et al., 2017), and reduced the abundance and dominance of persisting species (Figure 3.2b-c), which may ultimately affect ecosystem functioning (Hautier et al., 2015; Isbell et al., 2015). Previous studies predicted assemblage evenness to increase with change magnitude (Svensson et al., 2012), however our results demonstrate this to be only the case for positive changes in photosynthetic activity (i.e. a gain or positive trend shift in EVI). Abrupt land changes can alter the composition of species assemblages with early colonizing and non-native species often outperforming or replacing many persisting species (Fraterrigo et al., 2006; Turner, 2010; Jauni et al., 2015), which could explain the observed impacts on species assemblage evenness (Figure 3.2c) and compositional similarity (Figure 3.3).

The recovery from abrupt land change is of important concern for biodiversity conservation (Chazdon, 2003). We found biodiversity measures to be lower (Figure 3.2b,d,f) and the composition of species assemblages altered more compared to unchanged sites (Figure 3.3b,d) if an abrupt land change occurred relatively recently (< 5 years). An explanation could be that some, disturbance sensitive, species are immediately lost from local assemblages because of an abrupt land change (Devictor et al., 2008; Supp and Ernest, 2014). However local biodiversity can recover from an abrupt land change with biodiversity measures being comparable to unchanged sites after >10 years (Martin et al., 2013; Moreno-Mateos et al., 2017), although local species richness did not recover at sites where EVI had increased (Figure 3.2b). Land changes causing an abrupt positive shift could be related to increase or sudden cessation of anthropogenic use intensity (Eastman et al., 2013; Müller et al., 2014), which may have caused further local species loss (Tilman et al., 1994; Balmford, 1996; Hylander and Ehrlén, 2013). Nevertheless, the time passed

since an abrupt land change occurred can be a poor predictor of biodiversity recovery as land trajectories are often highly unpredictable (Norden et al., 2015) or include multiple land changes (Watson et al., 2014). We suggest future analyses to consider how additional attributes, such as trajectories or frequency of land change (Watson et al., 2014), influence local biodiversity recovery.

A number of other factors mediate the response of local biodiversity to land change (Arroyo-Rodríguez et al., 2015). Previous studies demonstrated local biodiversity to recover quicker from an abrupt land change with a greater availability of undisturbed land in the wider landscape (Turner, 1989; Chase, 2003; Shackelford et al., 2017). In addition, site-specific factors and a long history of human modification can mediate the impact of abrupt land change on local biodiversity (Ellis, 2015; Jung et al., 2017), especially since the majority of sites in the PREDICTS database are in regions that have long been subjected to human influence (Newbold et al., 2016a; Hudson et al., 2017). It is likely that some species – those particularly sensitive to land changes – have been lost from local assemblages long before the availability of Landsat data (< 1982) and we expect the found impacts of abrupt land change on biodiversity to be conservative (Mihoub et al., 2017). Land changes can also be characterized by attributes not considered in this study, such as frequency and trajectory (Watson et al., 2014), which have been shown to influence local biodiversity (Tiemann et al., 2015; Wood et al., 2017) and for many types of land change events – such as harvests, grazing or fallow period cycles (Kleyer et al., 2007; Ray and Foley, 2013) – are often similar in shifts of magnitude and trend. Future studies should evaluate the influence of differing land trajectories and frequencies of land change on local biodiversity.

What drives abrupt land change events? Abrupt land change, identified by shifts in magnitude and/or trend of photosynthetic activity, can be caused by anthropogenic deforestation (DeVries et al., 2015), land intensification (Fensholt et al., 2012; Müller et al., 2014), or degradation (Tian et al., 2015; Aguiar et al., 2017). In this study we did not separate between natural and anthropogenic drivers of abrupt land change and changes in photosynthetic activity can also be caused by rainfall-driven anomalies (Papagiannopoulou et al., 2017) or changing nitrogen deposition and CO₂ fertilization (Zhu et al., 2016). Most PREDICTS sites are modified by humans (Newbold et al., 2016a; Hudson et al., 2017) and it is therefore likely that most detected land changes were caused

by humans. Future studies should attempt to distinguish and disentangle the impacts of natural and anthropogenic abrupt land changes (Curtis et al., 2018).

Detecting and quantifying abrupt land changes is challenging. Here we focussed on detecting abrupt land change as shifts in magnitude or trend (Verbesselt et al., 2010a), but not all land change is abrupt (Vogelmann et al., 2012) or – such as understory thinning and selective logging – can be detected in time series of remotely-sensed photosynthetic activity (Asner, 2005; Peres et al., 2006). Similar to previous studies we assessed only the impact of the single largest shift in magnitude or trend (de Jong et al., 2013; Song et al., 2018), while different sequences of land change may also affect local biodiversity (Watson et al., 2014). Future studies quantifying abrupt land change globally could benefit from better access to, or fusion of, available satellite data to reach higher temporal and spectral resolution (Reiche et al., 2015; Wulder et al., 2016).

In conclusion, we demonstrate that compared to unchanged sites local biodiversity is considerably reduced because of abrupt land changes in the past, potentially affecting the stability and functioning of ecosystems (Hautier et al., 2015). Ignoring delayed biodiversity responses to abrupt land changes means that contemporary biodiversity changes, loss and recovery, are underestimated (Kuussaari et al., 2009; Essl et al., 2015a). Conservation practitioners need to consider the impacts of biotic lag effects to ensure global and regional assessments (e.g. those by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services [IPBES]) fully capture biodiversity change (Essl et al., 2015a). Remote sensing can assist in quantifying attributes of abrupt land change over large spatial and temporal scales. Our analytical framework can be expanded to assess spatial prioritization of habitat restoration plans or to support scenario-based modelling (Ewers et al., 2009) to predict the impacts of abrupt land change on local biodiversity.

3.5 Data and code availability

The PREDICTS biodiversity data are publicly available in the Natural History Museum Data Portal ([doi:10.5519/0066354](https://doi.org/10.5519/0066354), Hudson et al. (2017)). All remote sensing data are accessible via Google Earth Engine (earthengine.google.com/) (Gorelick et al., 2017) and pre-processed time series will be deposited on GitHub (<https://github.com/Martin->

Jung/PastDisturbance) on publication. Data and code to reproduce the results will be made available in a GitHub repository (<https://github.com/Martin-Jung/PastDisturbance>) on publication.

CHAPTER 4

**Incorporating land-cover changes
between 1992 and 2015 into
biodiversity projections**

Changes in global land cover are important factors that determine past and present biodiversity patterns. It has been proposed that attributes of land-cover change, such as the time passed or the sequence in land cover – i. e. from forest to agriculture – likely affect local biodiversity differently. Local biodiversity might continue to be affected by past land-cover change depending these attributes, which need to be considered to assess biodiversity change, especially in global and national biodiversity projections. Yet, the impacts of attributes of past land-cover change on local biodiversity have not been fully determined globally and most existing biodiversity projections remain largely uninformed of past land-cover change. Here, we combine time series of annual land cover from the period 1992 to 2015 with data of local biodiversity globally. Using hierarchical models comparing sites with and without a land-cover change in the past, we ask whether biodiversity differences vary with the time passed or the sequence after a land-cover change occurred and how this affects global and national biodiversity projections. Overall, we found local biodiversity to be consistently lower in sites with a past land-cover change. However, with increasing time passed after land-cover change local biodiversity recovered to levels comparable to unchanged sites. Furthermore, depending on the land-cover sequence, we observed either increases or decreases in local biodiversity and we demonstrated how a consideration of past land-cover change affects global and national

biodiversity projections, especially so in tropical and economically developing countries. Our findings have implications for global biodiversity models given that most past and future projections of biodiversity ignore lasting influences of past land-cover changes.

4.1 Introduction

The terrestrial surface of the Earth is shaped by natural and anthropogenic processes (Foley et al., 2005). The outcomes of these processes alter soil, plant and human structures, which collectively define terrestrial land cover (Di-Gregorio, 2005; Lambin and Geist, 2006). Land cover – quantified as either continuous or categorical estimate of the Earth land surface conditions – is commonly derived from remotely-sensed spectral measurements with many studies having mapped the distribution of land-cover categories globally (DeFries and Townshend, 1994; Hansen et al., 2000; Tuanmu and Jetz, 2014; Grekousis et al., 2015). Knowledge of land-cover change is important to help understand biodiversity change and create future projections and scenarios (Harfoot et al., 2014; Titeux et al., 2016; Kehoe et al., 2017a). Yet, with exception of vegetation (Hansen et al., 2013; Song et al., 2018) or water-covered areas (Pekel et al., 2016), few temporally consistent estimates of global land-cover change exist.

Quantifying change in remotely-sensed land cover is challenging. For continuous representations of land cover, remotely-sensed changes are commonly detected by exploiting differences in timing, amplitude and direction of remotely-sensed spectral measurements (Coppin et al., 2004; Lhermitte et al., 2011; Zhu, 2017). There have been initial attempts to incorporate land-cover changes detected from these differences into categorical land-cover maps (Zhu and Woodcock, 2014; Hermosilla et al., 2018), but the majority of land-cover maps remain uninformed of preceding land cover. Quantifying temporal change in categorical representations of land cover has been problematic because of inconsistencies in thematic resolution that lead to unrealistic estimates of land-cover change (Verburg et al., 2011; Cardille and Fortin, 2016; Abercrombie and Friedl, 2016). A new generation of temporally consistent time series of land cover (ESA CCI, 2017; Hermosilla et al., 2018; Nowosad et al., 2018; Sulla-Menashe et al., 2019) are beginning to emerge that allow the investigation of land-cover change globally and its impacts on biodiversity.

Biodiversity is impacted by past and present differences in land cover (Newbold et al., 2015, 2016a; Jung et al., 2018). Local species richness has been estimated to be up to 31% lower globally in the most anthropogenically modified land compared to “primary vegetation” sites (Newbold et al., 2015). However most previous global studies have considered only differences in land use and/or land cover at the time of biodiversity sampling (Gibson et al., 2011; Murphy and Romanuk, 2014; Newbold et al., 2015), thus ignoring lasting influences of past changes in land cover. There is evidence that the occurrence and abundance of species is not only determined by differences in present but also past land cover (Chapter 3) through so called ‘biotic lag’ effects, such as ecological memory effects (Ogle et al., 2015) or extinction debts (Kuussaari et al., 2009). The impact of past land-cover change on biodiversity likely depends on certain attributes such as magnitude and time passed since land-cover change (Chapter 3, Martin et al., 2013; Watson et al., 2014; Fu et al., 2017) or the sequences of land-cover (Watson et al., 2014; Nowosad et al., 2018).

Land-cover change causes varying sequences of land cover (Nowosad et al., 2018), which often have differing impacts on local biodiversity (Foster et al., 2003). Bremer and Farley (2010) reported an average loss of species richness globally for land changing from grass- or shrubland to forest cover, but not for land changing from secondary vegetation to forest cover. Meanwhile, biodiversity in secondary vegetation has been shown to recover more quickly if land was previously covered by grassland rather than agriculture (Dyer, 2010), although among taxonomic groups, especially plant diversity, abundance and growth have been shown to be influenced by lasting influences of an agricultural past (Chazdon, 2003; Fraterrigo et al., 2006; De Frenne et al., 2010; Perring et al., 2018). Other studies have highlighted the lasting effect that changes in forest (Gonzalez et al., 2016) or wetland cover (Halstead et al., 2014) might have on biodiversity. While these studies suggest that land-cover sequences need to be considered for explaining differences in local biodiversity, little is known about the influence of land-cover sequences across taxonomic groups and at global and national scales, which could affect projections of biodiversity.

To guide decision making, projections of global and national biodiversity change are often useful to inform policy (Pereira et al., 2010; Visconti et al., 2016). Biodiversity projections can be used to create scenarios of biodiversity change in response to pressures

such as land change (Newbold et al., 2015, 2016a; Titeux et al., 2016), which can inform science-policy platforms (Harfoot et al., 2014; Visconti et al., 2016; Purvis et al., 2018) like as the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES). However most existing biodiversity projections ignore lasting effects of past land-cover change. This is especially problematic for tropical, developing nations, where much land has been converted from forest to agriculture or pasture covered land in recent decades (Curtis et al., 2018) and that are recognized as global biodiversity hotspots (Brooks et al., 2002; Laurance et al., 2014). Under a business-as-usual scenario of future biodiversity change, especially less economically developed countries will suffer the greatest losses in local biodiversity (Newbold et al., 2015; Visconti et al., 2016), however these projections might – depending on attributes of land-cover change – over- or underestimate impacts on biodiversity.

The overall aim of this study is to investigate (*i*) how local biodiversity is impacted by a land-cover change in the past as derived from a global remotely-sensed land cover product, (*ii*) if impacts on local biodiversity differ with attributes of land-cover change such as differing sequences of land cover or time passed (Watson et al., 2014), and (*iii*) how particularly differing sequences of land cover affect global and national biodiversity projections. Overall, this study adds to our knowledge of how attributes of land-cover change affect local biodiversity and demonstrates how these attributes can be incorporated into global and national biodiversity projections.

4.2 Methods

4.2.1 Species assemblage data

The local biodiversity data were derived from a snapshot (obtained Feb 2016) of the Projecting Responses of Ecological Diversity In Changing Terrestrial Systems (PREDICTS) database which collated data on species' presence and abundance at sampled 'sites' from published 'studies' (Hudson et al., 2017). Each PREDICTS site has associated spatial coordinates – usually obtained from the text or author of a published study – and a record of when and how long biodiversity sampling took place. Species assemblages in the PREDICTS database were sampled at various sampling extents (maximum linear

extent, MLE) which are defined by methodology and taxonomic group (Hudson et al., 2014). To link local biodiversity with remotely-sensed land cover data (see 4.2.2), we used the spatial coordinates of all sites provided by the PREDICTS database as for the majority of sites the MLE is fully contained (median MLE = 40 ± 56.49 MAD) within the used grid cell size (~300m, see methods 4.2.2).

Similar to previous analyses using the same data (e. g. Chapter 2 in this thesis), we calculated several biodiversity measures including the total number of species, individuals and the species assemblage evenness at the site level. We calculated local species richness and – where data on species abundance was available – the total abundance for each PREDICTS site. For those studies in PREDICTS with differing sampling effort among sites we corrected estimates of total abundance by assuming that total abundance increases linearly with sampling effort (Newbold et al., 2014, 2015). As a measure of assemblage evenness, we calculated the probability of an interspecific encounter (PIE), which quantifies the probability of two individuals randomly chosen from an assemblage representing different species (Hurlbert, 1971).

4.2.2 Annual land cover data

We used estimates of land cover (LC) from a global dataset produced by the European Space Agency Climate Change Initiative (ESA CCI, 2017, ver. 2.0.7 obtained from <http://maps.elie.ucl.ac.be/CCI>). The ESA LC product quantifies global land cover annually from 1992 to 2015 with a spatial resolution of ~300m (ESA CCI, 2017) and a thematic resolution of 22 land-cover categories (75.38% global accuracy, ESA CCI, 2017) at two different hierarchies (level 1 and 2), that follow the Land Cover Classification System (LCCS, Di-Gregorio, 2005) of the United Nations Food and Agriculture Organization. Compared to many existing LC products (Grekousis et al., 2015), we used the ESA LC product because of its comparably long availability (1992 to 2015) and ability to detect land-cover changes (ESA CCI, 2017). However the change detection algorithm in the ESA LC product does not come without caveats as only land-cover changes persistent over at least two years are detected and therefore “short-lived” land-cover changes (Lambin and Geist, 2006) are generally poorly captured. Furthermore abrupt land-cover changes (such as forest to agriculture) tend to be better captured than gradual land changes (ESA

CCI, 2017) and in the years 2014 and 2015 only changes in forest cover could be reliably detected (ESA CCI, 2017). Despite these caveats, estimates of land-cover change from the ESA LC product have good agreement with other, independently developed, land-cover change products (Li et al., 2018).

For this study, we extracted for each PREDICTS site the land-cover sequence from the ESA LC product (Figure 4.1c-d). Before extracting these sequences, we reclassified the original ESA LC level 2 categories (22 categories based on the LCCS) to the level 1 hierarchy (10 LC categories, namely: forest, shrubland, grassland, sparse vegetation, agriculture, urban, bare area, wetland, water, and other) to reduce inaccuracies caused by misclassifications and because temporal changes between ESA LC level 2 categories can be poorly captured (ESA CCI, 2017). PREDICTS sites where the extracted ESA LC level 1 categories indicated “water” or “other” (such as snow and ice) at the start of biodiversity sampling were removed from further analyses ($N = 262$ sites). In this study we focussed only on sequences of land cover with a single land-cover change before biodiversity sampling as two or more land-cover changes were rarely observed globally (Figure 4.1a) and did only occur at two PREDICTS sites, which were excluded from further analyses.

4.2.3 Analyses

The statistical analysis for this study had two main aims. First, we aimed to quantify whether biodiversity measures were different at sites with a past land-cover change compared to sites without any land-cover change in the period 1992 to the start of biodiversity sampling. To do so, we fitted generalized linear mixed effects models (GLMMs) using Poisson distributed errors for species richness and a Gaussian error distribution for total abundance (\log_{10} transformed) and the probability of an interspecific encounter (PIE, asin-squareroot transformed). Following previous studies (Newbold et al., 2015; Jung et al., 2017) all models included the study identity and a spatial block of sampling design and additionally the ESA LC category at the time of biodiversity sampling as random intercept. We fitted separate GLMMs to assess the difference in local biodiversity measures between sites with and without (i) a past land-cover change overall, (ii) a categorical representation of the time passed since a land-cover change occurred (unchanged, i. e. 0 years, or ≤ 5 , 5-10, >10 years), (iii) distinguishing sites with and without a past

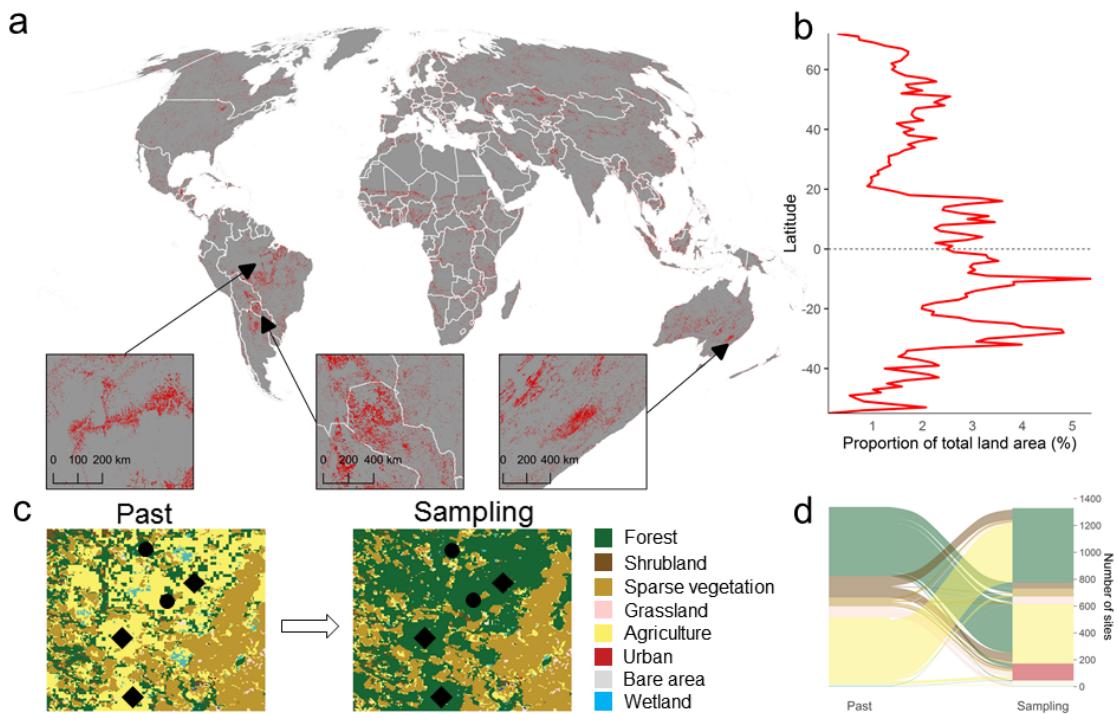


Figure 4.1: (a) Global map depicting the grid cells of the ESA LC product that had ≥ 1 land-cover change (red) in the period 1992 to 2015. Inset maps focus – from left to right – on the deforestation in the eastern Amazon basin, expanding soy plantations in Paraguay as well as shrubland loss in south east Australia. Map is projected in an equal-area Mollweide projection (b) Mean proportion of land with a land-cover change (in %) in the period 1992 to 2015 averaged per 1° of latitude. (c) Example land cover maps of the past and at the time of biodiversity sampling for a single study. Black symbols indicate sites with (diamond) and without (circle) land-cover change. (d) Flow diagram showing the sequence of land cover of all PREDICTS sites with a past land-cover change. Colours as in c.

land-cover change by their land-cover sequence, for which we fitted separate GLMMs for each ESA LC category at the time of biodiversity sampling using the extracted sequence of land-cover (those with at least 10 sites to ensure robustness of coefficients) categories as fixed effect (Figure 4.1b). Lastly (iv) we fitted a GLMM using the ESA LC categories at the time of biodiversity sampling and as interacting covariate, human population density data from the global human settlement (GHS) project (Pesaresi et al., 2013, 2016). We used data from the GHS project as it is available at a spatial ($\sim 250\text{m}$) and temporal (1975–2015) resolution that matches the resolution of the ESA LC data. All GLMMs were fitted using the ‘lme4’ package (ver. 1.1-18-1, Bates et al., 2015) in R (ver. 3.5, R Core Team, 2018).

Second, we constructed global and national projections of biodiversity. We used the model described above (iv) to project the mean coefficients of local biodiversity onto the global ESA LC map for the year 2015 only, which we resampled to $\sim 3 \times 3\text{ km}$ spatial

resolution by assigning the most dominant ('modal') LC value to each grid cell. All predicted estimates were transformed relative to the predicted estimate of a 'forest' site with zero human population density in the year 2015 (Newbold et al., 2015). Biodiversity sampling in the majority of PREDICTS sites (96.2%) occurred between 2000 and 2013 and from the ESA LC maps of the years 2000 and 2015 we constructed a new global map for the year 2015 with each grid cell set to a unique categorical code of the sequence of land-cover (using Cantor's pairing function). For each separate model (see *iii* above) and unique sequence of land-cover categories a new spatial projection was created for those grid cells with the respective sequence. We then added (to the mean coefficients) those separate spatial projections to the projection of the global mean difference in local biodiversity for the year 2015 (see above), thus "updating" the projected difference in those grid cells only where a past land-cover change has occurred (see Appendix Figure A.4.1 for a schematic). Some land-cover sequences were not available among PREDICTS sites and here we used the global average impact (see model *i*) in place of no better data available. Because of data limitations, we were also not able to investigate the impact of interactions between land-cover sequences and time passed on local biodiversity. Globally each grid cell has a different baseline level of local biodiversity – e.g. deserts being less species richness than shrublands – and we followed Newbold et al. (2015) by weighting all grid cells using either a global layer of terrestrial vertebrate diversity (summed range-of-occurrence maps for bird, mammal and amphibian species, Birdlife International, 2015; IUCN, 2016) for species richness or a layer of global photosynthetic activity (average photosynthetic activity as measured by MODIS NDVI in the period 2000–2015) for total abundance and assemblage evenness (Newbold et al., 2015).

Global biodiversity projections were visualized in a way that emphasises model uncertainty by suppressing estimates with large uncertainty (Correll et al., 2018). We refitted the GLMM models using the 'mgcv' package (ver. 1.8-24, Wood, 2011) because of their ability to obtain estimates of prediction uncertainty for hierarchical models. For each grid cell we predicted the standard error from the Bayesian posterior covariance matrix of the 'mgcv' model (Wood, 2011) and used it to calculate the absolute error in the predicted difference of local biodiversity (known as mean absolute error or MAE). To use the MAE for visual suppression of uncertain projected estimates, we excluded the 1% lowest and highest MAE estimates and furthermore normalized ($\frac{(MAE - \min(MAE))}{(\max(MAE) - \min(MAE))}$) the MAE

globally. To assess whether accounting for past land-cover sequences affects national biodiversity projections, we calculated the area-weighted relative mean difference in biodiversity at the national scale compared to a spatial projection where past land-cover changes are not taken into account ($\frac{x_{Sequence} - x_{without}}{|x_{without}|}$, where x is the mean area-weighted predicted national difference in biodiversity). We differentiated countries into groups of high (black), middle (orange) or low (blue) income (according to <http://data.un.org>) and assessed differences between those groups using ordinary analysis of variance (ANOVA) tests.

4.3 Results

Across all sites in the PREDICTS database, 1326 sites had a single land-cover change in the years before biodiversity sampling compared to 13696 sites without any change (number of studies: 238). The greatest number of PREDICTS sites with a past land-cover change were forest covered (552), followed by agriculture (442) and urban covered (126) sites (Appendix Figure A.4.2). Overall, sites with a past land-cover change had on average 5.3% (± 0.01 SE, $p < 0.001$) fewer species, 6.1% (± 0.03 SE, $p < 0.001$) fewer individuals and were 1.1% (± 0.01 SE, $p = 0.217$) less even compared to a site without a past land-cover change. With increasing time passed after a land-cover change occurred, local species richness and total abundance recovered to levels comparable to unchanged sites (Figure 4.2). If a land-cover change occurred in the five years before biodiversity sampling, sites had on average 5.6% (± 0.01 SE, $p < 0.001$) fewer species and 8.5% (± 0.04 SE, $p < 0.05$) fewer individuals than sites without a land-cover change in the past. Compared to unchanged sites, assemblage evenness was not significantly different ($1.6\% \pm 0.01$ SE, ns) for sites with a land-cover change less than 5 years ago but was significantly lower ($4.4\% \pm 0.01$, $p < 0.01$) after 5 to 10 years had passed.

Local biodiversity varied between sites with and without a past land-cover change depending on past land-cover sequences (Figure 4.3). The number of species ($11.4\% \pm 4$ SE) and individuals ($13.4\% \pm 12.9$ SE) of forest sites was lower if the site had been shrub covered before biodiversity sampling compared to forest sites without a land-cover change in the past (Figure 4.3a), while the number of species was higher ($17.4\% \pm 5.51$ SE) if the preceding land cover had been grassland. More species ($10.83\% \pm 5.51$ SE) and individuals ($26.1\% \pm 15.1$ SE) were found in previously forest covered sites compared to shrubland sites without a past land-cover change (Figure 4.3b). The number of species and individuals in agricultural sites was lower if the preceding land cover was forest ($8.81\% \pm 2.1$ SE for species and $6.93\% \pm 6.9$ SE for individuals) or shrubland ($23.93\% \pm 3.9$ SE and $35.8\% \pm 18.4$ SE) compared to sites without a land-cover change in the past (Figure 4.3e). Sites with urban land cover had in most cases higher number of species, individuals and assemblage evenness (up to $80.2\% \pm 30$ SE for abundance in agriculture, Figure 4.3f) compared to urban sites without a past land-cover change, with only species assemblages in previously agricultural sites being less even (Figure 4.3f).

Local biodiversity varied globally with land cover in the year 2015 as estimated from spatial projections (Figure 4.4a). Estimates of projected grid cells had a range from 41% to 0% fewer species, -10% to 13.3% fewer individuals and 30.3% to 46.1% less even assemblages. Globally projected differences in species richness had considerable uncertainty ranging between $\pm 0.1\%$ and $\pm 29\%$ MAE in the most extreme cases (grid cells

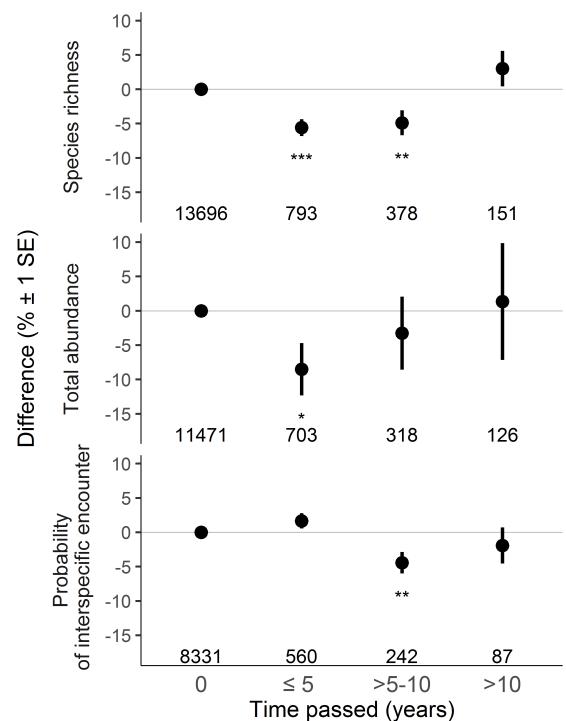


Figure 4.2: Difference in local biodiversity measures between sites without (o) and sites with a past land-cover change that occurred ≤ 5 years, $> 5-10$ or over 10 years ago. The error bars show the predicted standard error and stars (*) indicate whether the difference was statistically significant ($p < 0.05$). The total number of sites is indicated.

with over 5.5% MAE occurred in less than 1% of all land grid cells). Informed by past land-cover sequences (Figure 4.3), we found the predicted number of species to be up to 17.1% lower or 20.1% higher than estimates that do not take sequences of past land cover into account (Appendix Figure A.4.3). This is especially the case for locations in the Amazon and Gran Chaco (Figure 4.1b), where after – accounting for land-cover change between 2000 and 2015 – high losses of species are expected (Figure 4.4b). Projections were created using human population density as spatial covariate and we found that a greater human population density increased species richness in sparse vegetation, agriculture and urban covered sites relative to forest covered grid cells, while total abundance increased with population density across all land-cover categories relative to forest covered grid cells

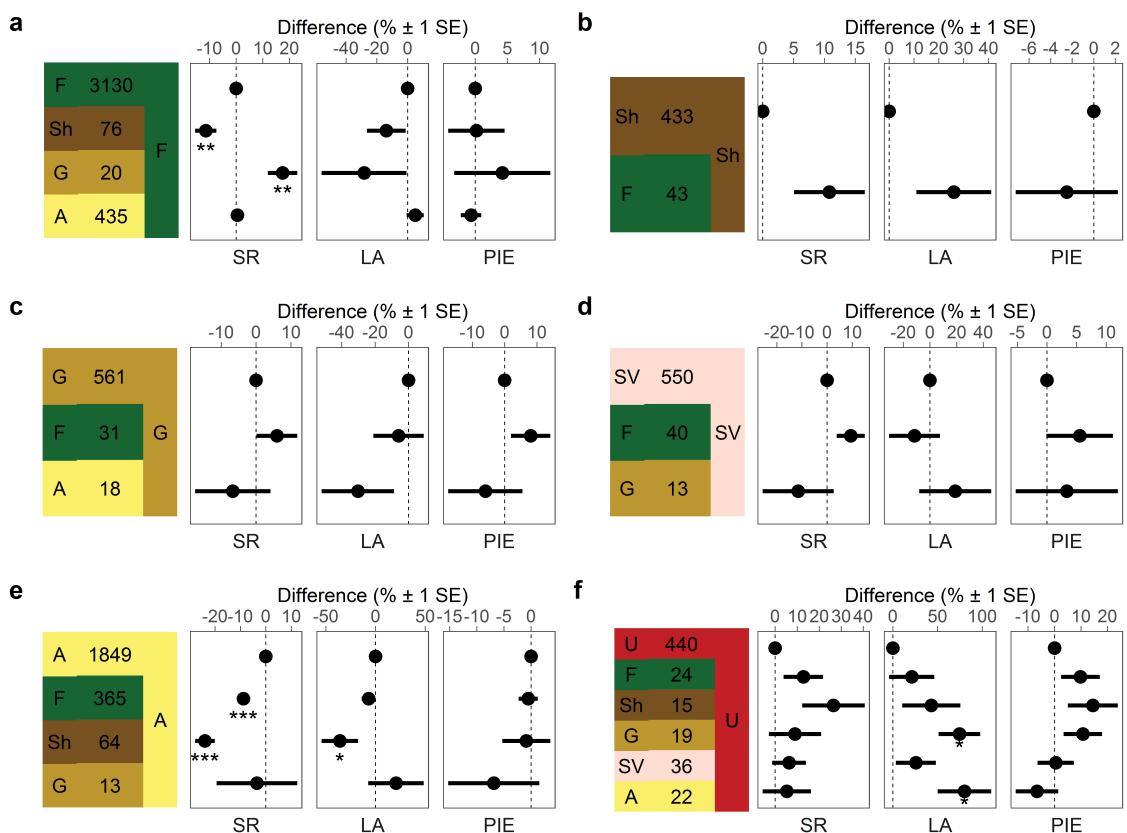


Figure 4.3: Difference in local biodiversity measures between sites with varying sequences of land cover relative to sites without any past land-cover change (dotted line) in the period 1992 to biodiversity sampling start. Separate models were fitted for each biodiversity measure and land cover at the time of biodiversity sampling as indicated by colour and abbreviation, namely forest (F, a), shrubland (Sh, b), grassland (G, c), sparse vegetation (SV, d), agriculture (A, e) and urban (U, f). Abbreviations on the x-axis show the difference in local biodiversity (SR = Species richness, LA = Total abundance, PIE = Species assemblage evenness). Number of sites contributing to each fitted land-cover sequence are indicated. The error bars show the predicted standard error and stars (*) indicate whether the difference is statistically significant ($p < 0.05$).

(Appendix Figure A.4.4).

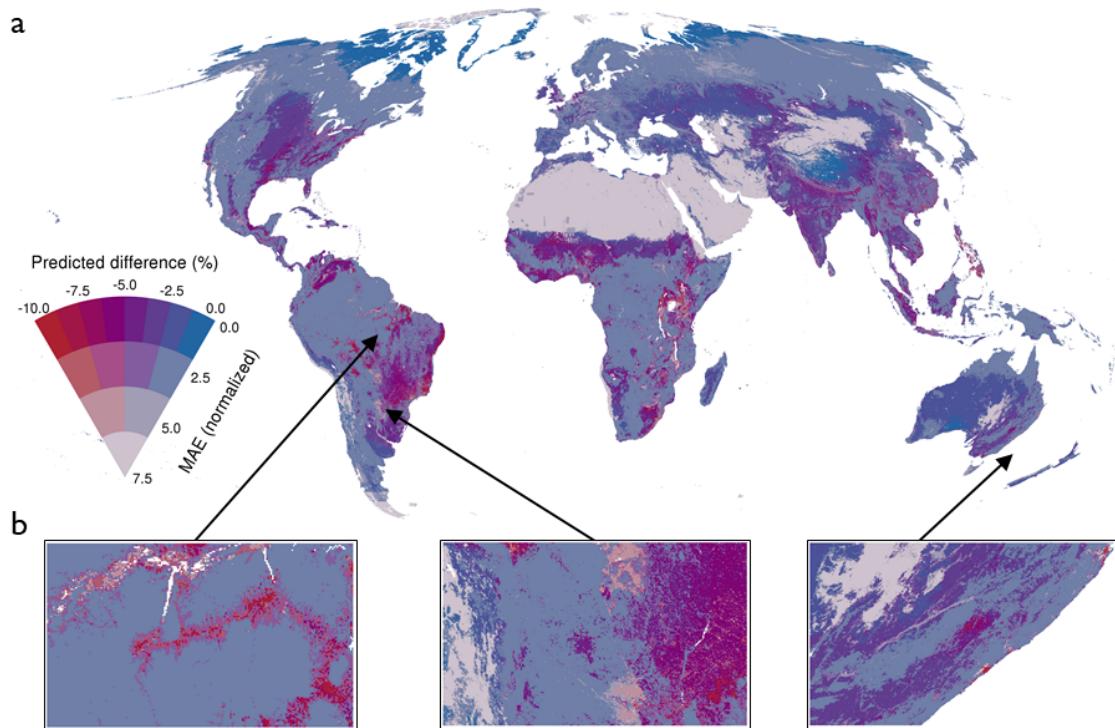


Figure 4.4: (a) Global projection of the difference in local species richness with land cover – relative to a forest site with zero human population – and informed by land-cover sequences in the past. Projected estimates are visualized relative to their uncertainty (normalized mean absolute error (MAE) from the predicted difference), where values of higher uncertainty visually suppressed in hue. Most extreme values (lowest 1% and highest 1% percentile) were excluded from the visualization and are displayed as inland white colour. (b) shows examples (as in Figure 4.1) how projections of local species richness loss differ because of prediction uncertainties and land-cover sequences. Inland white pixels are within the 1% of highest estimates of projected species richness loss after accounting for past land-cover sequences. Map is displayed in a global equal-area Mollweide projection and aggregated ($\sim 3000 \text{ m}^2$) for this visualization. Predicted difference and uncertainty (unweighted) are in Appendix Figure A.4.3 individually.

Land cover changes continue to influence biodiversity estimates at the national scale. On average $4.04\% \pm 3.73$ SD of land across all countries had a land-cover change relative to their total land area in the period from 2000 to 2015. Singapore with 31.7%, Malawi with 17.7% and Paraguay with 16.4% had the highest proportion of land with a land-cover change in the period 2000 to 2015 (Appendix Figure A.4.5). Although there were no significant differences in the proportion of land with a land-cover change among countries ($F_{2,201}=0.477, p=0.621$, Appendix Figure A.4.5), considering past land-cover change affected biodiversity more in tropical, lower-income countries (Figure 4.5, Appendix Figure A.4.6-A.4.7). The area-weighted difference in projected national biodiversity estimates –

relative to a projection that did not account for land-cover sequences – was significantly lower in low income countries for species richness ($F_{2,200}=9.131, p<0.001$, Figure 4.5), total abundance ($F_{2,198}=13.48, p<0.001$, Figure A.4.6) and evenness ($F_{2,198}=6.644, p<0.01$, Appendix Figure A.4.7).

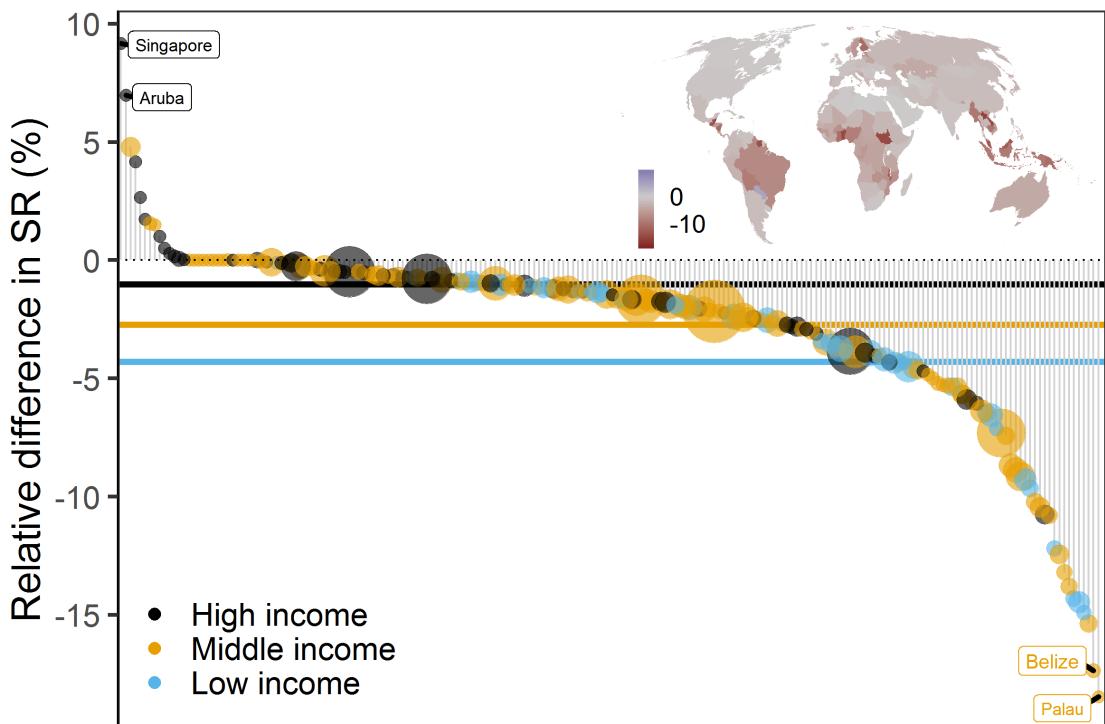


Figure 4.5: Area-weighted relative difference – compared to a projection where past land-cover sequences were not considered – in mean national species richness (SR) from 2000 to 2015. Points represent the country-wide average in SR (area-weighted) with the size of the points scaled with land area (small to large). Colours indicate whether countries are considered high (black), middle (orange) or low (blue) income. Outlier countries and overall averages per income group (vertical lines) are indicated. Inset map shows the relative difference in SR from low (red) to high (blue) per country. Plots for total abundance and assemblage evenness are broadly comparable (Appendix Figure A.4.6 - A.4.7).

4.4 Discussion

Biodiversity differs with attributes of past land-cover change (Watson et al., 2014). We found local biodiversity at sites with a past land-cover change to be on average lower than at sites without any land-cover change in the period 1992 to biodiversity sampling start. Local biodiversity recovered to levels comparable to sites without land-cover change after

more than ten years had passed (Figure 4.2). These results are in line with a previous study on the same biodiversity dataset that found abrupt land changes to consistently reduce local biodiversity (Chapter 3 in this thesis). We furthermore found that the impacts of land-cover change on biodiversity varied with different sequences of past land cover (Figure 4.3) and that these impacts affect global (Figure 4.4) and national (Figure 4.5) biodiversity projections. We discuss how our results relate to those of previous studies and make recommendations how to incorporate lasting influences of past land-cover change into biodiversity projections.

4.4.1 The influence of land-cover sequences on local, national and global biodiversity

Depending on the sequence of land cover, local biodiversity estimates are considerably altered after a land-cover change. Forest covered sites, that were previously covered by agriculture, had about the same number of species and individuals as forest covered sites without a land-cover change in the period 1992 to biodiversity sampling start (Figure 4.3a), which contrasts with findings of previous studies investigating the impact of an agriculture to forest transition on local biodiversity (Bellemare et al., 2002; Hermy and Verheyen, 2007; Dyer, 2010). It could be that many of the reference forest-covered sites had an agricultural history long before 1992 – which we were unable to quantify using the ESA LC product – potentially weakening the impacts of land-cover change as local biodiversity has already been altered before the start of satellite-based earth observation (Ellis et al., 2010; McMichael et al., 2017). A previous meta-analysis has shown that forests, which were previously covered by shrublands had on average lower species richness (Bremer and Farley, 2010) and we found similar results with previously shrub covered sites, having on average 11% fewer species and 14% fewer individuals (Figure 4.3a). In contrast, previously forest covered shrubland sites had on average 11% more species and 26% more individuals than a shrubland site without a past land-cover change (Figure 4.3b). Likely these sites still support a high number of species typical at low vegetation height and structural complexity (Chazdon et al., 2016).

In more anthropogenically altered land cover, a past land-cover change caused varying “biotic lag” effects (Figure 4.3e-f). Urban sites with a past land-cover change had a higher

number of species and individuals than sites without land-cover change (Figure 4.3f). It could be that local biodiversity in these sites is inflated because of pending extinction debt and thus these sites likely have local extinctions of native species in the future (Tilman et al., 1994; Kuussaari et al., 2009; Hylander and Ehrlén, 2013). This is supported by a global meta-analysis which has found that preceding land cover together with city age is one of the best predictors of (native) bird and plant occurrence in urban areas (Aronson et al., 2014). However, similar effects could not be observed for agricultural sites previously covered by forest or shrubland, where the number of species and individuals was on average lower compared to an agricultural site without a past land-cover change (Figure 4.3e). One possible explanation could be that this pattern is mostly driven by (pollinating) invertebrates, which compose 64.8% of all previously forest or shrub covered agricultural sites in our dataset. Pollinating invertebrates have previously been shown to have higher numbers of species and individuals in agricultural land compared to forests (Winfrey et al., 2009). It should be mentioned that many of our findings could be rather imprecise given the low number of sites with a past land-cover change (Appendix Figure A.4.2), which prevented us from robustly assessing the impact of land-cover sequences across taxonomic or functional groups (Jung et al., 2018) or in interactions with other attributes of land-cover change such as time passed (Figure 4.2). Nevertheless, these estimates are to our knowledge the first comprehensive and comparative assessment of the impact of past land-cover sequences on local biodiversity measures.

The consideration of past land-cover change can also affect global and national biodiversity projections (Figure 4.4, 4.5). Although only 4.04% of the terrestrial land surface globally had a land-cover change in the period 1992 to 2015 occurring predominantly in the global south (Figure 4.1), which is in line with previous studies that analysed the spatial distribution and drivers of land-over change (Curtis et al., 2018; Nowosad et al., 2018) and found the expansion of agricultural and pastoral land to be the most likely cause (Phalan et al., 2013). Those areas are often globally irreplaceable for biodiversity (Brooks et al., 2002; Laurance et al., 2014; Pimm et al., 2014). Comparing national biodiversity projections with and without a consideration of past land-cover change, we find that a consideration of land-cover sequences led to even lower biodiversity estimates in most, but especially so in tropical and low-income countries (Figure 4.5, Appendix Figure A.4.6-A.4.7). In those countries anthropogenically caused land-cover change is commonly

linked to attempts to close yield-gaps in agricultural production (Mueller et al., 2012) or increase the output of export commodities (Byerlee et al., 2014; Meyfroidt et al., 2018). Our results indicated that not accounting for lagged effects of past land-cover change can cause an over- and/or underestimation of biodiversity change in global projections.

4.4.2 Model and land cover data uncertainties in biodiversity projections

There are several factors that need to be considered when our results are compared to those of previous studies (Newbold et al., 2015). The PREDICTS database was set up to compare biodiversity measures between sites of varying land-use and land-use intensity derived from study descriptions (Newbold et al., 2015; Hudson et al., 2017), while this study used remotely-sensed estimates of land cover. Land use and land cover are intertwined in a land system (Lambin and Geist, 2006; Turner et al., 2007), however not all differences between two PREDICTS sites can likely be explained by land cover (and human population density, Appendix Figure A.4.3) alone. Differences in impact can arise because of inaccuracies in characterizing land cover (ESA CCI, 2017), scale mismatches (Estes et al., 2018) or local factors that mediate biodiversity responses to differences in land cover (Jung et al., 2017). Furthermore because of sampling size limitations, we were not able to incorporate other attributes of land-cover change that could be important in determining differences in local biodiversity (Watson et al., 2014), such as the frequency (Watson et al., 2014; Griffiths et al., 2015) or magnitude of land-cover change (Chapter 3 in this thesis). Future studies should attempt to incorporate interactions between attributes of land-cover change into biodiversity projections, pending greater biodiversity and land-cover data availability.

Remotely characterizing land-use and/or land-cover at global extents is challenging (Verburg et al., 2011; Kuemmerle et al., 2013). In this study we used time series (period 1992-2015) of remotely-sensed land cover instead of the modelled estimates (1500-2100) of land use and land cover (Hurtt et al., 2011; Klein Goldewijk et al., 2016) used by previous studies (Newbold et al., 2015, 2016b; De Palma et al., 2017). Most of the terrestrial land surface has been altered by humans long before the availability of Earth observation data (Ellis et al., 2010) and modelled estimates of land use and land cover change are often the

only available data at global scales. However, these estimates are only available at coarse spatial resolution ($\sim 10 \text{ km}^2$ at the equator) and are dependent on model assumptions and accompanied uncertainties (Gaillard et al., 2010; Klein Goldewijk and Verburg, 2013), with previous independent validations having shown that they can misrepresent pre-industrial land use substantially (Kaplan et al., 2017). Remotely-sensed land-cover products, despite classification errors and thematic differences that can affect subsequent analyses (Sexton et al., 2015; Estes et al., 2018), remain some of the best directly measured estimates of global land cover, but not land use. Promising case studies have quantified proxies of land use for agricultural (Estel et al., 2015), pasture (Rufin et al., 2015) or forest use intensity (Pflugmacher et al., 2012) from time series of remotely-sensed data at the regional scale. We suggest that in order to improve future biodiversity models and projections, new time series of proxies of land use need to be developed at the global scale.

4.4.3 Conclusion

This study investigated the impacts of past land-cover change – differentiated by attributes such as time passed or the sequence of land cover – on local biodiversity. We found local biodiversity to be significantly reduced shortly after a land-cover change but being able to recover with longer time passed (Figure 4.2). Depending on the sequence of past land cover, local biodiversity either increased or decreased compared to sites without a land-cover change (Figure 4.3). If those lasting influences of past land-cover change are ignored in global and national biodiversity projections, we find that they can considerably misrepresent projected biodiversity change, especially so in tropical and low-income countries (Figure 4.4 - 4.5). There are several ways to improve biodiversity projections beyond what has been presented in this study. We emphasize the need to consider interactions between attributes of land-cover change such as between the time passed (Figure 4.2) and land-cover sequences (Figure 4.3), which might affect the estimated impacts on biodiversity given evidence from previous studies (Chazdon, 2003; Martin et al., 2013). The impacts of land-cover change could furthermore be estimated using before and after biodiversity measures (De Palma et al., 2018) and time series of land cover could be useful to identify sites for resurveying local biodiversity (see discussion 6) or to establish links with time series of biodiversity measures (Dornelas et al., 2018).

Overall, our study highlights the usefulness of remotely-sensed time series of land cover for biodiversity projections and models, particularly in quantifying lasting impacts of past land cover change.

CHAPTER 5

Landscape-wide land changes correlate with, but rarely explain local bird diversity change

There is an ongoing debate whether biodiversity at local scales is declining and what might drive this change. Land changes are suspected to impact local biodiversity change. However, there is little evidence across spatial and temporal scales and for multiple functional groups of species, thus limiting our understanding of the causes of local biodiversity change. Here we investigate whether landscape-wide land changes, opposed to those at the local scale, are driving local bird diversity change. We link time series of 34 years of breeding bird survey (BBS) data (1984-2017) at 2745 routes across the continental United States of America with remotely-sensed satellite imagery (~30m resolution) from the Landsat missions. Specifically, we assessed for each year what proportion of the landscape surrounding the BBS routes had a land change – defined as abrupt shift in magnitude or trend of photosynthetic activity as detected by the Breaks for Additive Seasonal and Trend (BFAST) algorithm – and tested whether large proportions of concomitant or preceding landscape-wide land changes explain changes in bird diversity, quantified as either geometric mean of relative abundance (GM) or progressive Bray-Curtis index (pBC). We found that the GM was negatively and the pBC positively correlated with a large proportion of land changes in the wider landscape. Furthermore, the consideration of preceding – instead of concomitant – landscape-wide land changes explained on average more variation in bird diversity change. Overall, landscape-wide land changes failed to

explain most of the variation in local bird diversity change for most BBS routes regardless if bird diversity change is differentiated by functional groups or geographic regions. This study is one of the first studies attempting to link land and biodiversity change. It highlights the influence of preceding and concomitant land change on biodiversity and makes suggestions for promising directions of future research.

5.1 Introduction

Ongoing human alteration of the Earth surface causes changes in biodiversity across scales (Gibson et al., 2011; Murphy and Romanuk, 2014; Newbold et al., 2015). Globally, about 32% of all known vertebrate species show decreasing population sizes and range contractions (Ceballos et al., 2017; WWF, 2018) with reported species extinction rates being several times higher than expected naturally (Brooks et al., 2002; Pimm et al., 2014). Yet, any change in biodiversity is scale and measure dependent (Sax and Gaines, 2003; Chase and Knight, 2013) and, perhaps surprisingly, there is still a debate whether local – opposed to global – biodiversity is truly changing (Thomas, 2013; McGill et al., 2014).

A number of global meta-analyses demonstrated that some biodiversity measures, notably species richness, have not changed at the local scale (Vellend et al., 2013, 2017; Dornelas et al., 2014). However, these results have been questioned, particularly on whether the data are spatially and temporally biased (Gonzalez et al., 2016) or if sites with and without land change were differentiated (Cardinale et al., 2018). This raises the question whether changes on land can explain changes in local biodiversity measures across space and time.

Present differences on land influence local biodiversity globally. Previous studies found local biodiversity to be consistently reduced at sites with more intensively used land (Murphy and Romanuk, 2014; Newbold et al., 2015; Alroy, 2017), where on average 13.6% fewer species and 10.7% fewer individuals were observed compared to undisturbed primary vegetation (Newbold et al., 2015). However, these analyses relied on spatial comparisons of local biodiversity and therefore do not capture temporal biodiversity change. In addition, they ignored the influence of past land changes (Perring et al., 2018; Jung et al., 2018) and did not consider landscape-wide land changes, which can influence

local biodiversity (Tscharntke et al., 2012; Turner et al., 2015; Miguet et al., 2015).

Local biodiversity is influenced by the variability of resources, such as food or nesting material, or through ecological processes, such as migration or fear of predation, at the landscape scale (Hanski and Ovaskainen, 2000; Chase, 2003; Turner et al., 2015; Fernández et al., 2016). However these influences are not static and landscapes are constantly changing because of natural and anthropogenic factors (Pickett and White, 1985; Manning et al., 2009; Turner et al., 2015). Previous studies have shown that landscape-wide land changes may have a lasting influence on local biodiversity through ‘biotic lag’ effects (Metzger et al., 2009; Ewers et al., 2013). Yet, most studies focussed on small geographic regions and changes in forest cover (Rittenhouse et al., 2010) and did not investigate general impacts of landscape-wide land changes on local biodiversity across spatio-temporal scales. A lack of data on local biodiversity and landscape-wide land change has so far prevented comparative assessments (De Palma et al., 2018).

Increasing availability of satellite imagery enables the assessment of land change at broad spatial and temporal scales (Kennedy et al., 2014; Pasquarella et al., 2016). Long-running satellite missions, such as Landsat, provide one of the best sources to monitor land-surface conditions (Kennedy et al., 2014; Vogelmann et al., 2016; Hermosilla et al., 2018; Song et al., 2018). Time series of land-surface conditions, such as photosynthetic activity, can measure intra- and inter-annual vegetation dynamics (Pettorelli et al., 2005; Fisher et al., 2006) and specific algorithms have been developed to detect land changes as changes in photosynthetic activity (Verbesselt et al., 2010b; Zhu, 2017). Land changes can be differentiated by attributes (Watson et al., 2014), such as abrupt shifts in magnitude, causing an immediate loss or gain of vegetation (DeVries et al., 2015), or shifts in trend, causing either greening or browning over time (de Jong et al., 2013; Müller et al., 2014). These attributes can be robustly quantified at the landscape scale and linked to changes in local biodiversity.

Birds are one of the best surveyed taxonomic groups globally. Local biodiversity change quantified from repeated breeding bird surveys (BBS) has been widely studied (Harrison et al., 2014; Pardieck et al., 2018). Previous studies have shown that changes in bird diversity are dependent on the specific biodiversity measure considered (Schipper et al., 2016; Jarzyna and Jetz, 2017) and are often non-linear (Gutzwiller et al., 2015; Barnagaud et al., 2017). Bird diversity change also varied spatially (Harrison et al., 2014;

Jarzyna and Jetz, 2017) with many birds of particular functional traits, such as migratory or grassland dependent species, declining in developed countries (Fewster et al., 2000; Sanderson et al., 2006; Stanton et al., 2018). Land changes are most likely a driving factor of these declines (Harrison et al., 2014, 2016), and yet most studies investigated only spatial correlations between remotely-sensed attributes of land change and local bird diversity (Rowhani et al., 2008; Goetz et al., 2014; Hobi et al., 2017). Notably Rittenhouse et al. (2010) found bird assemblage composition to be altered in landscapes with more “disturbed forests”, which they assessed using remotely-sensed time series. However, to our knowledge, no previous study has investigated whether landscape-wide land changes correlate with and explain changes in local bird diversity.

Consequently, this study hypothesizes that (i) changes in local bird diversity are driven by landscape-wide land changes varying by land change attributes, (ii) local bird diversity change can best be explained by past land changes, and (iii) the explanatory power of landscape-wide land changes on local bird diversity change varies across geographic regions and functional groups of bird species. We combine 34 years (1984–2017) of annual BBS records collected at sites across the continental United States of America with time series of medium-high resolution (nominal ~30m) satellite imagery from the Landsat missions. Using Breaks for Additive Seasonal and Trend (BFAST), a generic change detection algorithm, we detect abrupt shifts in magnitude (immediate gain or loss in photosynthetic activity) and trend (greening or browning) of photosynthetic activity in the landscape surrounding each BBS route. Non-linear spatio-temporal models were used to correlate the proportion of changing land in the wider landscape with changes in local bird diversity.

5.2 Methods

5.2.1 Bird diversity time-series preparation

Time series of local bird count records (1984 – 2017) were obtained from the North American Breeding Bird Survey (BBS, available from <https://www.pwrc.usgs.gov/bbs/>, Pardieck et al., 2018) dataset. Bird counts were conducted annually during the breeding season (April to August with > 83.3% sampled in June) along approximately 39.4km long

roadside survey routes and usually follow a standard protocol that involves fifty 3min stops at evenly spaced intervals (approximately 0.8km) (Ralph et al., 1995). At each 3min stop, volunteer observers record the number and identity of every bird species seen or heard within approximately 400m distance from the route. For our analyses we only included routes that followed the standard BBS protocol of fifty randomly selected stops (94.4% of all routes) and had at least ten years of sampling between 1984 and 2017, as many BBS routes were not sampled every year (mean proportion of missing years = 19.7%). The period from 1984 to 2017 was chosen to align to the availability of satellite data (but see 5.2.2). We removed routes from the analyses with non-acceptable weather conditions according to BBS standards (Ralph et al., 1995) and excluded all nocturnal, crepuscular and aquatic species from the analysis as they are not well sampled by BBS methods (Gutzwiller et al., 2015; Jarzyna and Jetz, 2017). All partially identified species (e.g. “sp.”), hybrids and species with unclear taxonomy (e.g. “A x B”) were removed from further analyses. In total, time-series from 2745 routes (out of 5248 in the entire BBS dataset) had suitable data for further analyses.

We calculated two different biodiversity measures commonly applied to BBS data. First, we calculated the geometric mean of relative abundance (GM), which quantifies relative changes in both abundance and evenness (Buckland et al., 2011, 2017; Harrison et al., 2014). The GM for the year y is defined as $GM_y = \exp(\frac{1}{S} \sum_{i=1}^S \log(\frac{A_{iy}+1}{A_{iy_0}+1}))$, where S quantifies the total number of species with i being an individual species, A_{iy} the abundance of species i in year y . The GM is unaffected by species detectability as it is based on within-species abundance trends, however it cannot be quantified for absent species and is unable to reflect changes in assemblage composition (Buckland et al., 2011). We added a constant (1) to all abundance values before calculating the annual GM to account for the species being absent in some years. The first four years of BBS data (1984 – 1987) were used to define the baseline years y_0 (calculated from the median number of individuals for each observed species) and to align the analyses with the baseline years used in the land change detection (but see Methods 5.2.3). Whenever no BBS was conducted in the years between 1984 and 1987 on a given route, we used the first year of available BBS data to define the baseline year y_0 . Second, as measure of change in assemblage composition, we calculated the progressive Bray-Curtis index (pBC, Bray and Curtis, 1957; Rittenhouse et al., 2010) as the difference in composition between a

baseline and all following years of sampled bird assemblages (Rittenhouse et al., 2010). The pBC is defined as $= 1 - \sum_{i=1}^S \frac{|A_{iy} - A_{iy_0}|}{(A_{iy} + A_{iy_0})}$, where A_{iy} is the abundance of species i in year y and A_{iy_0} the estimated abundance in the baseline y_0 (defined as for the GM, calculated from the median number of individuals for each observed species).

5.2.2 Time series of annual photosynthetic activity at the landscape scale

Following previous studies, we define the “landscape” as the 19.7km radius buffer around the centroid of each BBS route because it fully encompasses the majority of BBS routes and approximates the median natal dispersal distance of North American bird species (Sutherland et al., 2000; Pidgeon et al., 2007; Albright et al., 2011). Grid cells with permanent open water, ice or snow cover were excluded using a land mask derived from the 2011 National Land Cover Database (NLCD) land-cover map at ~30m resolution (Homer et al., 2015). In addition, BBS routes with less than 50% land area ($N = 18$) within the surrounding landscape were excluded from further analyses, assuming that in those routes breeding birds are less influenced by landscape-wide changes in terrestrial photosynthetic activity.

To quantify land changes in the landscape surrounding each BBS route, we used imagery from the Landsat 4, 5, 7 and 8 satellites (1984 to 2017, ~30m nominal resolution) supplied by the United States Geological Service (USGS) available through Google Earth Engine (Gorelick et al., 2017). All Landsat images were radiometrically (Chander et al., 2009) and atmospherically calibrated to surface reflectances (Masek et al., 2006). For each surface reflectance image, we masked out non-land grid cells, including clouds and cloud shadows as identified by the ‘cFMask’ algorithm (Zhu and Woodcock, 2012), areas permanently covered with water (> 90% water occurrence probability in the period 1984 – 2016, Pekel et al., 2016). A spectral index of photosynthetic activity (the two-band enhanced vegetation index (EVI), Jiang et al., 2008) was calculated for each surface reflectance image. We composited all EVI data up to three months before the Summer solstice (20th of March to 20th June of each year) into a single annual image (1984, 1985, ..., 2017) that retains the greenest (95% percentile) EVI value. We used three months of EVI data to capture the greening onset in annual vegetation dynamics (Appendix Figure

[A.5.1](#)), a period that can assist in distinguishing between land cover types ([Pettorelli et al., 2005](#); [Fisher et al., 2006](#); [Zhang et al., 2006](#)) and that matches the sampling period during which most BBS were conducted (March to June). All data pre-processing and compositing was done using the Google Earth Engine platform ([Gorelick et al., 2017](#)).

A lack of clear-sky images in certain years can lead to missing data for parts of the buffered BBS routes. Routes with more than 50% missing data ($N = 2$) over the period from 1984 to 2017 were excluded from further analyses assuming that the Landsat satellites have missed most land changes (median proportion of missing data = $1.06\% \pm 1.54$ median absolute deviation [MAD], Appendix Figure [A.5.2](#)).

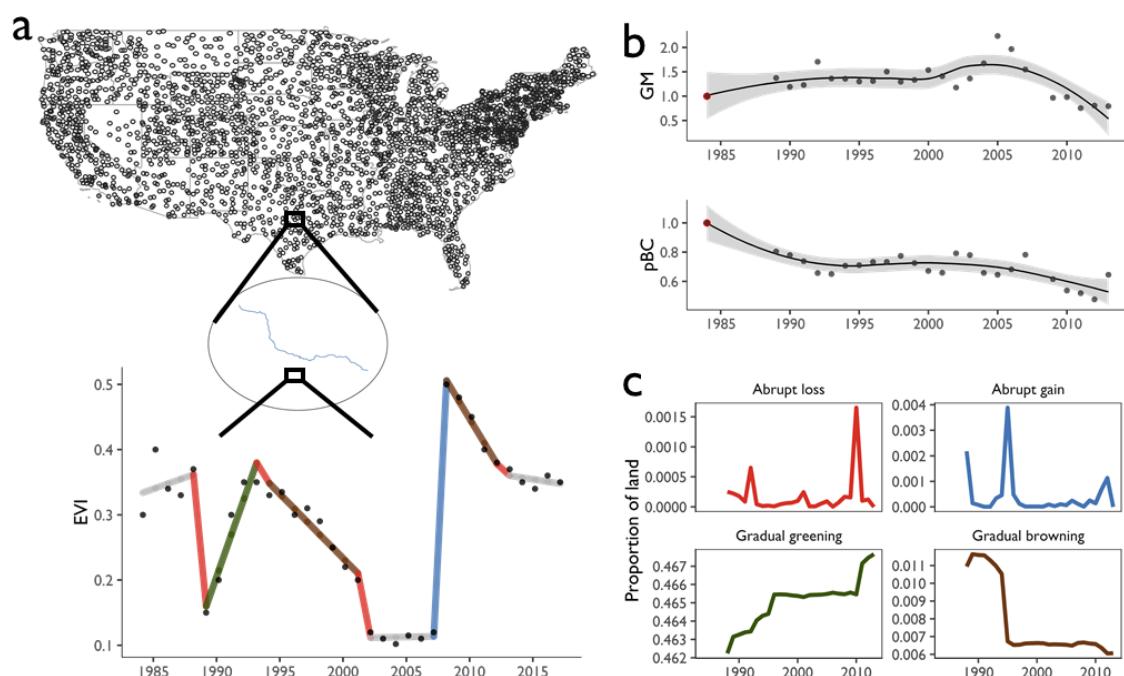


Figure 5.1: (a) Schematic how landscape-wide land changes are quantified in a hypothetical BBS route. For each grid cell within the landscape (buffered circle around the BBS route) time series of annual March-June EVI were tested for a single or multiple land changes (see Methods [5.2.3](#)). If a land change has been detected, we determined the position of all shifts in magnitude (abrupt loss in [“red”] or gain [“blue”]) or trends (greening [“dark green”] or browning [“brown”]) of photosynthetic activity (as measured by the EVI). (b) Changes in local bird diversity (as quantified by the GM and pBC) relative to a baseline year y_0 (highlighted in red) for an example BBS route. (c) Summarised proportion of all grid cells within the landscape with either a shift in magnitude or trend in EVI (colours as in a) per year. Map shown in the Albers equal area conic projection (NAD83).

5.2.3 Detection of landscape-wide land changes as changes in annual photosynthetic activity

Landscape-wide land changes were quantified as the proportion of grid cells showing a shift in magnitude or trend of photosynthetic activity (Figure 5.1a). Among all algorithms proposed to detect changes in remotely-sensed time series (Zhu, 2017), we relied on the generalized fluctuation framework originally developed for econometrics (Bai and Perron, 2003; Zeileis, 2005), later adapted for remote sensing as the Breaks for Additive Seasonal and Trend (BFAST) algorithm (Verbesselt et al., 2010b). For each annual EVI time series, we tested for single or multiple structural breaks in linear trend using a recursive Moving Sum of Residuals (Rec-MOSUM) test over each four year window period (Zeileis, 2005). A statistically significant ($p < 0.05$) structural change test indicates whether at least a single structural break exists, in which case we iteratively fitted segmented linear regression models over the entire time series. The optimal number and position of all structural breaks were detected by minimizing both the Bayesian Information Criterion (BIC) and residual sum of squares (RSS) of the segmented regression models (Zeileis, 2005; Verbesselt et al., 2010b). The framework requires a gap-free time series (“strucchange” package in R, ver. 1.5-1) and similar to previous studies we filled missing data using linear interpolation between adjacent years (Verbesselt et al., 2010b).

Per grid cell and year, we differentiated all detected land change events as either abrupt shifts in magnitude or trend (Figure 5.1). Shifts in magnitude were quantified using the predicted EVI data (from the segmented linear regression model) before and after the detected change date ($EVI_{After} - EVI_{Before}$) and categorized as either immediate loss or gain in photosynthetic activity in a given year if negative or positive, respectively. For shifts in trend, we assessed for each year whether the linear trend in annual EVI was significantly ($p < 0.05$) increasing ('greening'), decreasing ('browning') or flat ('stable'). Similarly, for time series with non-significant structural change tests, we fitted simple linear regression models to test whether the overall trend in EVI (across all 34 years) significantly increased or decreased.

For each BBS route and year (Figure 5.1c), we summarized the amount of land that had either an abrupt shift in magnitude (loss or gain in EVI) or trend (greening or browning). Because the total land area differed among BBS routes, we calculated proportions relative

to the total land area (see Methods 5.2.2). The change detection algorithm relies on a moving window (four years) and thus no land changes could be detected in the first (1984 - 1987) and last four (2014 - 2017) years of each EVI time series. In case a land change occurred within these years, the algorithm would set the date to the latest, respectively earliest, year possible (e. g. 1987 and 2014) causing an inflated number of incorrectly dated land change events at the start and end of each time series. We therefore considered the first four years as ‘baseline’ ($year_0$) and the last four as ‘overhang’ and removed them from further analyses.

5.2.4 Additional predictors and bird trait data

At continental scales, bird diversity at BBS routes has been shown to be influenced by a number of environmental variables (Rowhani et al., 2008; Goetz et al., 2014; Hobi et al., 2017; Barnagaud et al., 2017). For a coarse measure of overall vegetation activity (Rowhani et al., 2008; Hobi et al., 2017), we calculated the mean EVI across all 34 years of annual Landsat composites per buffered BBS route (see Methods 5.2.2). Previous studies have shown that the number of bird species varies with elevation (Jarzyna and Jetz, 2017) and we extracted the mean elevation of the buffered BBS route from the global GMTED (~1km resolution) product (Danielson and Gesch, 2011). Precipitation-driven anomalies have been shown to affect the number and abundance of bird species (Barnagaud et al., 2017). We used the Standardized Precipitation-Evapotranspiration Index (SPEI), which quantifies anomalies relative to the conditions observed in a moving window before a given month (Vicente-Serrano et al., 2010, 2012). For each BBS route we extracted the monthly SPEI from SPEIbase (ver. 2.5, <http://spei.csic.es>, Vicente-Serrano et al., 2010) calculated on a climatology from 1901 to 2015 and over a moving window of three months from January to March of each year (Vicente-Serrano et al., 2010), thus capturing precipitation anomalies in the winter months.

Similar to previous studies we used four functional trait groups – nesting status, migratory behaviour, habitat guild and body mass – to differentiate all bird species (Schipper et al., 2016; Barnagaud et al., 2017). Data on nesting (ground or canopy) and migratory behaviour (resident, short-distance and neotropical migrants) were obtained from Albright et al. (2011), while data on bird species habitat guilds (e. g. wood-

land, shrubland, grassland and urban birds) were extracted from the USGS website <https://www.mbr-pwrc.usgs.gov/bbs/guild/guildlst.html>. The mean body mass (bm , measured in g) for all bird species was extracted from the Amniote database (Myhrvold et al., 2015) and grouped into terciles of all estimates, e. g. small, medium and large birds ($bm < 33\%$, $bm \geq 33\% \& bm < 66\%$, $bm \geq 66\%$). For species without trait estimates, we filled the missing data with the most common (mode) trait within the same bird genus, provided more than 50% of all species within that genus had existing body mass estimates or identical categorical trait. For each BBS route and trait group we calculated separate GM estimates, but only for routes with at least 10 years of data and at least 3 different species within a trait group.

5.2.5 Spatio-temporal models

The aim of the statistical analyses was to investigate whether changes in local bird diversity (measured by GM and pBC) and landscape-wide land changes are correlated. To do so we relied on generalized additive regression models (GAMs), which are commonly used to model species population trends (Fewster et al., 2000) and can handle complex non-linear, spatio-temporal and hierarchical datasets (Kneib et al., 2009; Wood, 2011). All considered variables were included as thin-plate smooth (fixed to 4 residual degrees of freedom to prevent overfitting) in the GAMs and we applied a smoothing penalization for variable selection (Wood, 2008, mgcv parameter: select = TRUE). The approximate significance of non-linear model terms was assessed using an approach by Wood (2013). All GAMs were fitted using the ‘mgcv’ package (Wood, 2011, ver. 1.8-24) in R (R Core Team, 2018, ver. 3.5.0).

We distinguished between four groups of variables to be included as thin-plate smooths in the full GAM. (1) As “local” factors (f_{local}) we considered the mean EVI, elevation and, for each year, the SPEI. (2) For landscape-wide land changes ($f_{landscape}$), we included for each year the proportion (arcsine square root transformed) of abrupt shifts in magnitude (immediate loss and gain in EVI) and trend (browning or greening) in the landscape (Figure 5.1c). (3) Incorporating spatial autocorrelation into regression models can improve predictive power (Kneib et al., 2009; Dornelas et al., 2012), especially when local biodiversity was surveyed over large scales such as the continental U.S. . We

followed an approach by Kneib et al. and included the spatial coordinates ($f_{spatial}$) of each BBS route using a non-linear smooth surface function $g(x_{Northing}, x_{Easting})$ with a tensor product P-spline (Kneib et al., 2009). Northing and easting coordinates were obtained by projecting the centroid of each buffered BBS route to an Albers equal area conic projection (NAD83). (4) For comparing biodiversity measures among BBS routes, species detectability or misidentification by different BBS observers has to be accounted for (Sauer et al., 1994; Harris et al., 2018). We included the BBS route ID (f_{obs}) as random intercept in all models, therefore estimating the effect of f_{local} , $f_{landscape}$ and $f_{spatial}$ on local biodiversity measures (GM and pBC) across all BBS routes. We acknowledge that using the route ID does not fully account for differences in observer abilities (there can be multiple observers for a single route), but previous studies found limited influence of varying observers over large scales (Jarzyna and Jetz, 2017; Barnagaud et al., 2017). All biodiversity time series were detrended by including time (year) as linear predictor to avoid spurious correlations. To account for temporal autocorrelation, we included an autoregressive error structure (AR1), which we parametrized by visually assessing the autocorrelation function of the full model residuals at lag 1 ($\rho = 0.5$).

We tested if past (e. g. the years before a BBS) landscape-wide land changes continued to influence bird diversity change in subsequent years. A ‘lagged’ correlation between two time series is commonly known as “Granger causality”, where one “time series x_t contains information in past terms that helps the prediction of y_t ” (Granger, 1969). We followed an approach by Papagiannopoulou et al. (2017) and assessed the relative improvement in explanatory power of models including preceding instead of concomitant land changes. Preceding land changes with abrupt shifts in magnitude (loss or gain in EVI) of up to five years were included either individually, thus adding estimates for the preceding year $i = 1, \dots, 5$ only; or cumulatively, where aggregated estimates for the preceding years $1 : i$ were included in the model (Jung et al., 2018). The relative improvement in explanatory power was assessed using out-of-bag (OOB) coefficients of determination (R^2). To do so we split all time series into training and test datasets (50/50) 100 times at random. All models included the f_{local} and $f_{spatial}$ variables to account for variation not directly attributable to landscape-wide land changes.

Lastly, we assessed the explanatory power of each group of variables (f_{local} , $f_{spatial}$, $f_{landscape}$) in spatio-temporally and for birds grouped by functional traits. To do so we

fitted several GAMs using the GM (log-transformed) or pBC as response variable with a gaussian log-link distribution. We first fitted a “full” GAM including all variables, followed by separate GAMs where groups of variables (f_{local} , $f_{spatial}$, $f_{landscape}$) were explicitly excluded from the model. Models for both GM and pBC converged well (Appendix Figure A.5.3-A.5.4), although the largest changes in pBC were generally poorly predicted by the models (Appendix Figure A.5.4). The explanatory power of all models was assessed by calculating the R^2 of each model. The group of variables (f_{local} , $f_{spatial}$, $f_{landscape}$) explaining the most variation was then identified from the largest reduction (partial R^2 , relative to the full model) in R^2 (Papagiannopoulou et al., 2017). We assessed patterns of the most important group of variables spatially and in relation to robust linear trends in biodiversity measures (fitted using the MASS package, ver. 7.3-49, Venables and Ripley, 2002). Lastly, we investigated if the explanatory power of landscape-wide land changes ($f_{landscape}$) varied with either bird species being differentiated by functional trait groups (see 5.2.4) or with BBS routes grouped by U.S. ecoregions (Level 1, Omernik, 1987), which we derived by intersecting the centroid of each buffered BBS route with the U.S. ecoregions layer. For each functional trait group, we fitted two separate GAMs either including or excluding all $f_{landscape}$ variables before calculating the difference in R^2 attributable to $f_{landscape}$ variables. For U.S. ecoregions we assessed the contribution of $f_{landscape}$ variables to the total R^2 on overall GM change.

5.3 Results

Both local bird diversity and landscapes have changed across the continental USA. Across all BBS routes the geometric mean of relative abundances (GM) increased by $0.01\% \pm 0.002$ standard error (SE) per year (mean first derivative) in the first two decades from 1984 to 2005, after which annual decreases of $0.01\% \pm 0.003$ SE were observed (Appendix Figure A.5.5a). The compositional similarity of bird assemblages (pBC) decreased by $0.006\% \pm 0.001$ SE per year (Appendix Figure A.5.5b). Landscapes surrounding each BBS route had on average $6\% \pm 6.42$ SD (range $0.02\% - 78.96\%$) of land experiencing at least one land change in the period 1984 to 2017 (Appendix Figure A.5.6). Over the same period a decrease in landscape-wide land changes were observed (mean robust linear trend = -0.00015 ± 0.0198 SD, range -0.545 to 0.112) but with large spatial variability

(Appendix Figure A.5.7). Across all BBS routes the mean proportion of land experiencing a land change with an abrupt shift in magnitude (loss or gain in EVI) fluctuated strongly (Appendix Figure A.5.8a), while shifts in trend showed an inverse hump-shaped pattern for greening and a continuous decrease for browning (Appendix Figure A.5.8b). Shifts in magnitude or trend were little correlated among each other (Appendix Figure A.5.9) and across ecoregions (Appendix Figure A.5.10).

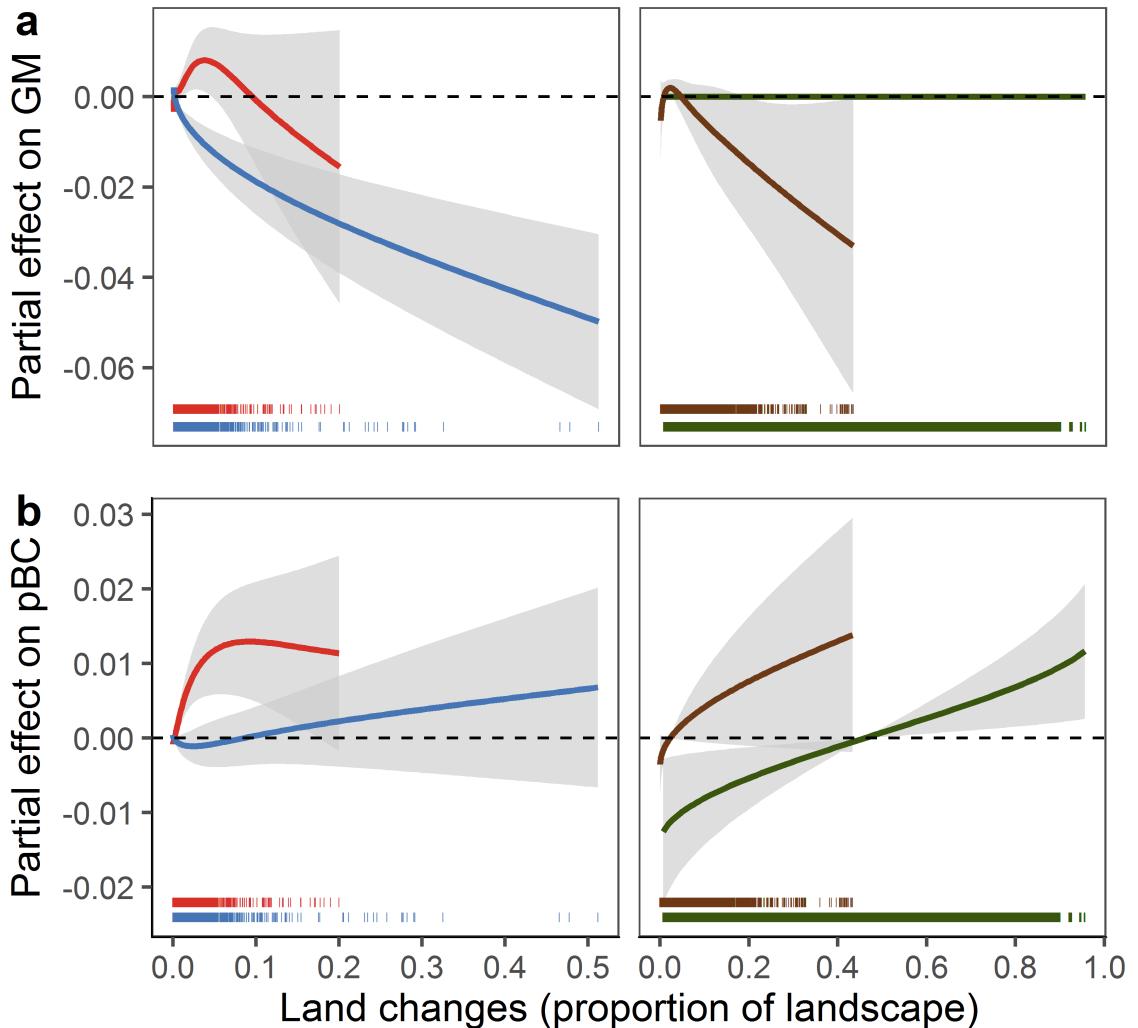


Figure 5.2: Partial effects of landscape-wide land changes (proportion of landscape) per unit of change in (a) the geometric mean of relative abundance (GM) and (b) the progressive Bray-Curtis index (pBC). Colours indicate either abrupt shifts in magnitude with losses (red lines) or gains (blue) in EVI or trend with greening (green) or browning (brown) land. Error margins show the estimated standard error of the partial effect (grey shading) and rugs the observed proportion of landscape-wide land changes across all BBS routes. Flat lines without error margins indicate that the term was penalized out during model fitting and thus had no effect on the biodiversity measure.

Bird diversity change is correlated with landscape-wide land changes. The GM

significantly decreased ($F_4 = 10.8, p < 0.001$) in years with a large proportion of landscape-wide abrupt gains of EVI (Figure 5.2a, blue line). More landscape-wide abrupt losses of EVI led to a significant decrease in GM ($F_4 = 6.44, p = 0.001$), but only after ~10% of the landscape had abrupt losses in a given year (Figure 5.2a, red line). The GM also decreased with more land in the landscape browning ($F_4 = 37.89, p = 0.057$), while a high proportion of greening land in the landscape had no effect ($F_4 = 0, p = 0.529$) on changes in GM (Figure 5.2a). The pBC significantly increased with a large proportion of landscape-wide abrupt losses ($F_4 = 8.25, p < 0.001$) or gains ($F_4 = 0.614, p = 0.1$) in EVI (Figure 5.2b). The pBC also increased with a large proportion of browning ($F_4 = 13.81, p = 0.038$) or greening land ($F_4 = 74.25, p = 0.005$) in the wider landscape (Figure 5.2b).

Local factors strongly influence local bird biodiversity change. The GM significantly increased ($F_4 = 1789.06, p < 0.001$, Appendix Figure A.5.11a) and the pBC significantly decreased ($F_4 = 1923.71, p < 0.001$, Appendix Figure A.5.11b) at BBS routes of high mean elevation. GM significantly increased ($F_4 = 291.05, p < 0.001$) in landscapes with overall low photosynthetic activity ($\text{EVI} < 0.4$) but decreased in landscapes with high photosynthetic activity; a pattern that was reversed for pBC (Appendix Figure A.5.11). Years of abnormal precipitation between January and March had no effect on GM or pBC change (Appendix Figure A.5.11).

Land changes in one year continued to influence local bird diversity in subsequent years. The mean explanatory power (out-of-bag [OOB] R^2) of abrupt shifts in magnitude in concomitant years (Lag 0, Figure 5.3) was 0.03 (0.047 cumulatively) for GM and 0.126 (0.122) for pBC. A consideration of abrupt shifts in magnitude in preceding years explained modestly more variation than those in concomitant years (Figure 5.3). The individual inclusion of one to five preceding years of abrupt shifts in magnitude explained similar amounts of variation (mean OOB $R^2 = 0.031$) in GM, whereas for pBC only preceding abrupt shifts in magnitude more than three years ago increased explanatory power (mean OOB $R^2 = 0.129$, Figure 5.3). Considering cumulatively preceding abrupt shifts in magnitude increased the mean explanatory power for both GM and pBC (Figure 5.3), although for pBC the relative improvement in explanatory power was highest at three cumulatively included preceding years (mean OOB R^2 of year three = 0.128).

We assessed whether the explanatory power of all variables varied in space (Figure

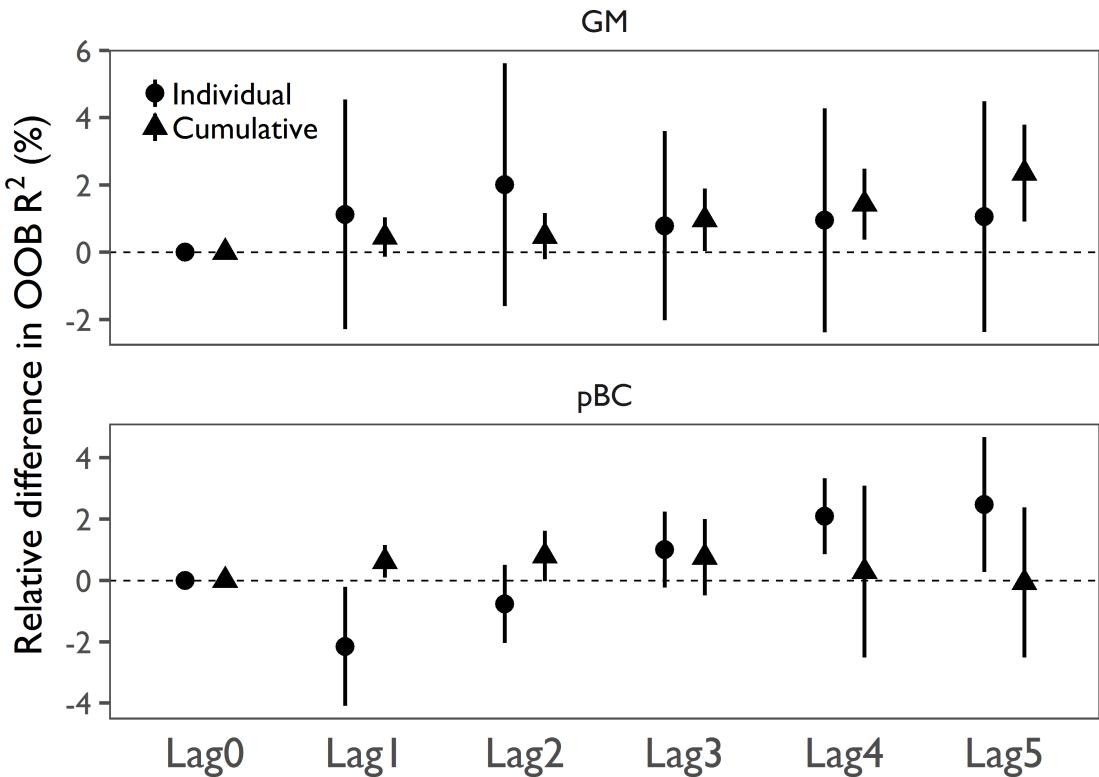


Figure 5.3: Preceding landscape-wide land changes of one to five years improve predictions of GM and pBC. Bird diversity time series for all BBS routes were randomly split (100 times) into training and test datasets and the explanatory power (R^2) was assessed relative to a model that only included concomitant abrupt shifts in magnitude (gain or loss of EVI) averaged across all random subsets. Symbols differentiate between two types of model structures, where past land changes were either added individually (circles) or aggregated cumulatively (triangles). Error bars show the standard deviation of the out-of-bag (OOB) R^2 values.

5.4a,c) and for linear trends of bird diversity change (Figure 5.4b,d). The full model including all variables explained 64.7% of the total variation of changes in GM (69.3% for pBC), with most of the variation explained by unknown differences among BBS routes (partial R^2 of $f_{obs} = 58.5\%$ for GM and 39.8% for pBC). Of all variables considered, landscape-wide land changes were the most important predictor of GM change for 34.83% of BBS routes (partial R^2 range 0 – 54%, Figure 5.4a) and for pBC in 46.6% of BBS routes (partial R^2 range 0 – 7%, Figure 5.4c). Incidentally, landscape-wide land changes were the best predictor for some of the greatest changes (increase/decrease per year) in local bird diversity measures (Figure 5.4b,d).

The explanatory power of landscape-wide land changes on changes in GM differed among bird species of varying functional traits and across ecoregions (Figure 5.4, Ap-

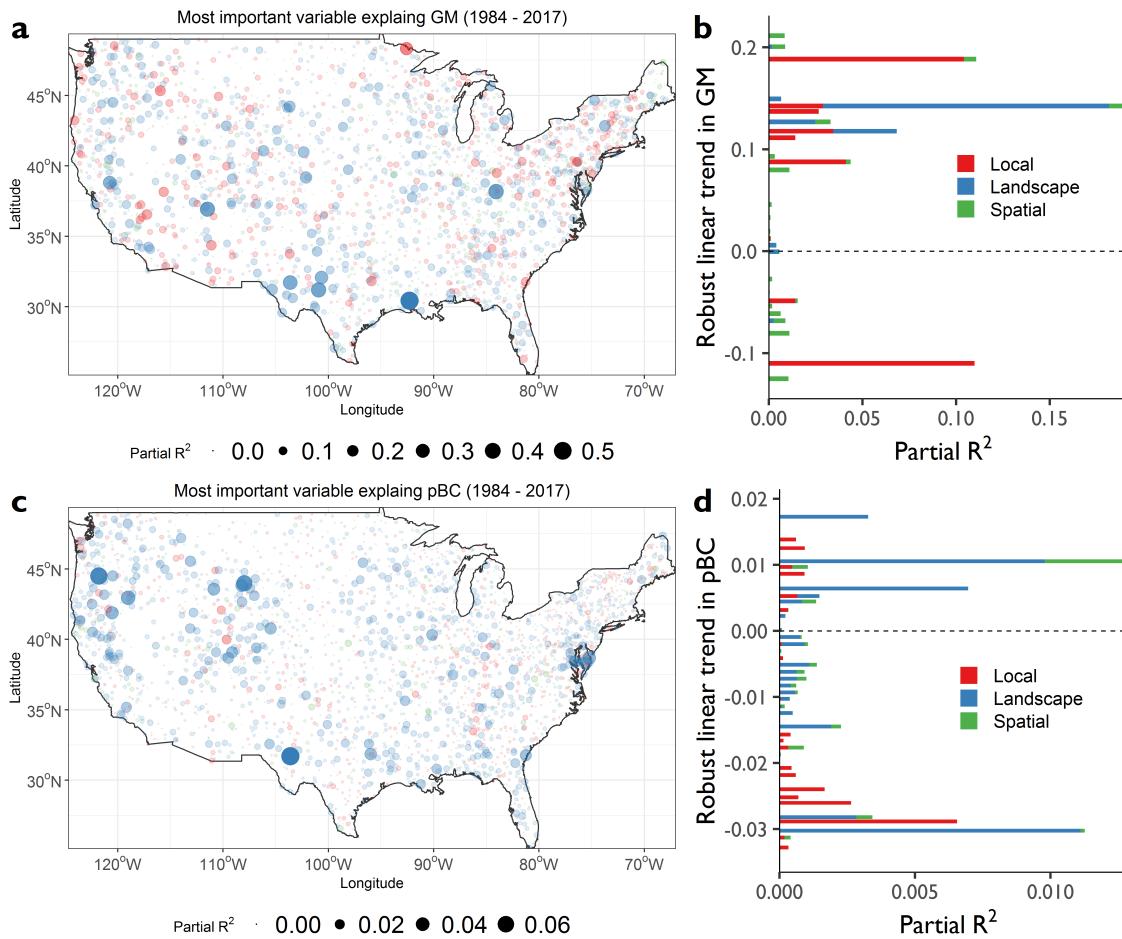


Figure 5.4: Most important group of variables explaining changes in the (a) GM and (c) pBC at 2745 BBS routes across the United States of America. Point sizes in (a,c) indicate larger partial R² of the most important variable group. Colours indicate which of the considered variable groups, f_{local} (red), $f_{landscape}$ (blue) or $f_{spatial}$ (green), explained most of the variation (greatest partial R²) in the full model. (b,d) Partial R² of the most important variable group averaged per increase or decrease (robust linear trend per year) in GM or pBC.

pendix Figure A.5.12). On average landscape-wide land changes did not explain (mean partial R² = $-.02 \pm 0.09$ SD) changes in GM for birds of varying trait groups (Figure 5.5a). Similar to spatial patterns of the most important group of variables (Figure 5.4), landscape-wide land changes were only important for a subset of BBS routes (Figure 5.5a, blue outliers) in which they explained up to 71.9% of the total R². For many BBS routes the inclusion of landscape-wide land changes did not increase but decreased the R² for explaining changes in GM (Figure 5.5a, red outliers). A visual exploration could not identify any spatial patterns in these outlier BBS routes and there were also no distinguishable differences between ecoregions (Figure 5.5b) and especially in Southern Semi-Arid Highlands landscape-wide land changes did not increase the explained varia-

tion in GM change, despite the on average large proportion of browning land (Appendix Figure A.5.10).

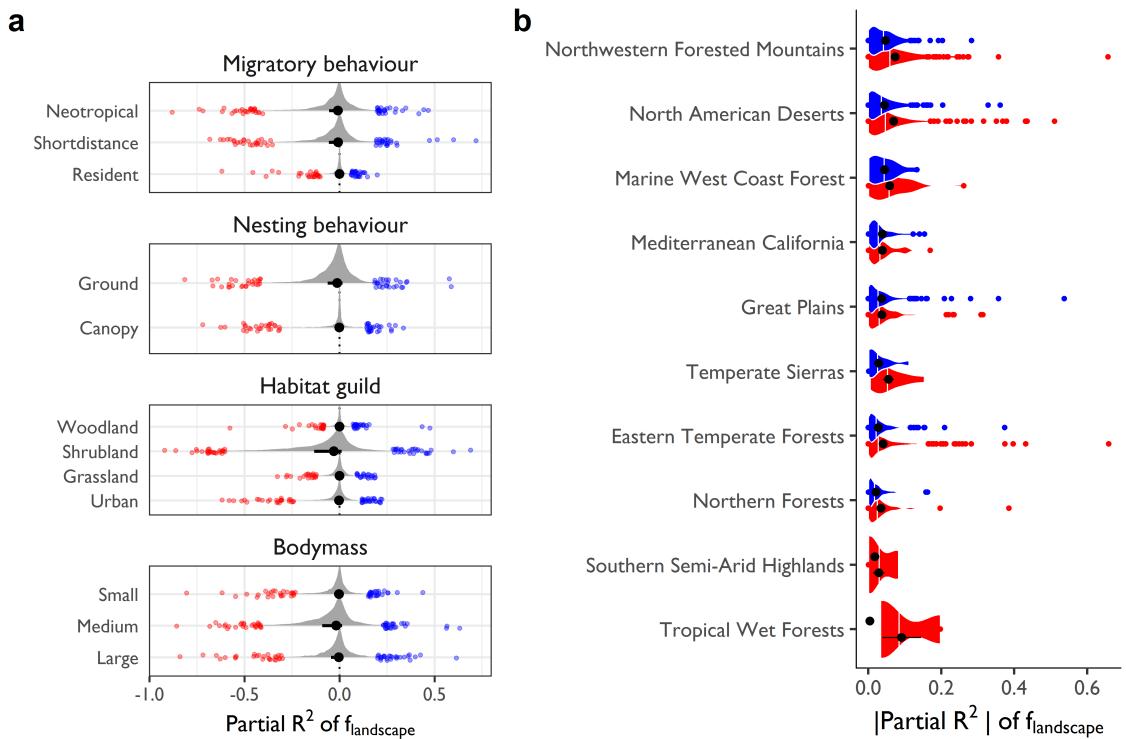


Figure 5.5: (a) Partial R^2 of landscape-wide land changes (difference in explanatory power after excluding $f_{landscape}$ variables) for explaining changes in GM grouped by functional trait group. Shown is the distribution (grey), median and 50% quantile (black) for each response variable. Red and blue points indicate outliers (1% smallest / biggest partial R^2 values). (b) Shows the absolute partial R^2 of landscape-wide land changes in explaining trends in GM grouped by U.S. ecoregions. Coloured depending on whether landscape-wide land changes increased (blue) or decreased (red) overall R^2 . Black points and error bars show the mean and standard error of the mean.

5.4 Discussion

The aim of this study was to investigate whether land changes (as measured by abrupt shifts in magnitude or trend of photosynthetic activity) in the landscapes surrounding the U.S. breeding bird survey (BBS) routes are correlated with changes in local bird diversity. We found that a great proportion of landscape-wide abrupt shifts in magnitude were correlated with a decrease of the geometric mean of relative abundances (GM, [Buckland et al., 2011](#)) and an increase in the progressive Bray-Curtis index (pBC, [Rittenhouse et al., 2010](#)). A great proportion of browning land was correlated with a decrease in GM and an

increase in pBC, while more greening land increased pBC only (Figure 5.2). Confirming previous studies, some local factors (e.g. mean elevation and photosynthetic activity) influenced local bird diversity change. Changes in GM and pBC were not only influenced by concomitant abrupt shifts in magnitude, but also by individual and cumulative effects of preceding land changes (Figure 5.3). On average, landscape-wide land changes had high explanatory power ($R^2 > 0.1$) only for a few selected routes without any clear pattern in space (Figure 5.4), across trait groups (Figure 5.5a) or ecoregions (Figure 5.5b). We discuss how these results link to previous studies of local biodiversity change and landscape ecology.

5.4.1 Landscape-wide land changes as drivers of biodiversity change

Land changes have previously been linked to local biodiversity change (Brooks et al., 2002; Ewers et al., 2013; Cousins et al., 2015). Like previous studies at the local scale (Chapter 3 in this thesis), we found local biodiversity measures to be more affected by larger abrupt shifts in magnitude at the landscape scale (Figure 5.2). A greater proportion of abrupt shifts in magnitude and trend (for ‘browning’) in the wider landscape were associated with a significant decline in GM (Figure 5.2a), potentially indicating local bird population collapse as fewer individuals across species are observed (Loh et al., 2005; Buckland et al., 2011). Meanwhile more abrupt shifts in magnitude and trend in the wider landscape increased the pBC (Figure 5.2b). Because we found the relative mean abundance of bird species (GM) to decline with a greater proportion of landscape-wide land changes, it is likely that the changes in pBC are caused by an increase in species richness, a pattern shown before for the BBS data (Schipper et al., 2016). Previous studies found compositional changes in bird assemblages to be particularly associated with changes in the occurrence of rare and specialist species, leading to a “homogenization” of assemblages (McKinney and Lockwood, 1999; Olden, 2006; Newbold et al., 2018). It could be that landscape-wide land changes increase the heterogeneity of resources and bird habitats available, thus allowing a greater number of bird species, but fewer individuals overall, to thrive (Holt, 2009; Stein et al., 2014), for instance through increased competition (Randall Hughes et al., 2007).

Changes in GM and pBC differed with local environmental gradients (Appendix Figure A.5.11). Consistent with previous studies (Lomolino, 2001; Jarzyna and Jetz, 2017), the GM increased at BBS routes of high elevation (Appendix Figure A.5.11a), indicating that bird species increasingly utilize high elevation regions, likely because of climate change. Those species appear to be different from the species previously inhabiting BBS routes at high elevations, given the strong negative effect of elevation on pBC (Appendix Figure A.5.11b). Furthermore, we found changes in GM to decrease and “flatten” in BBS routes with high average photosynthetic activity (EVI > 0.4, Appendix Figure A.5.11a), in contrast to the pBC, which increased in BBS routes of high photosynthetic activity (Appendix Figure Appendix Figure A.5.11b). This is in line with previous studies that demonstrated that high photosynthetic activity is negatively correlated with bird abundance (Barnagaud et al., 2017) but positively with richness (Rowhani et al., 2008; Goetz et al., 2014), which could drive changes in pBC. Similar to previous studies (Barnagaud et al., 2017), we found no strong effect of precipitation anomalies prior to a BBS on GM or pBC (Appendix Figure A.5.11).

5.4.2 Lag effects of preceding land changes

Land changes can have immediate and delayed impacts on local biodiversity (Kuussaari et al., 2009; Hylander and Ehrlén, 2013). Theory suggests that – single and cumulative – preceding land changes are correlated with larger changes in local biodiversity (Scheffer et al., 2001; Andersen et al., 2009; Watson et al., 2014; Ratajczak et al., 2018). We demonstrated that considering preceding landscape-wide land changes helps explain local GM and pBC changes (Figure 5.3). Increasing explanatory power of individual preceding years could be linked to an average “ecological memory” effect for birds, particularly for the 4th and 5th year prior and changes in pBC (Figure 5.3) and is similar to what has been shown for plant species (Ogle et al., 2015). The impacts of cumulative preceding land changes depended on their duration (Essl et al., 2015a) and frequency (Watson et al., 2014; Ratajczak et al., 2018) and a recent study found that considering cumulative preceding – relative to concomitant – land-surface differences explained more differences in local (bird) biodiversity (Jung et al., 2018). Similarly, we find that a consideration of cumulative periods of preceding land changes assists in explaining differences in local biodiversity

(Figure 5.3). Preceding land changes may have affected the resources available to birds thus directly influencing their fitness and persistence in subsequent years (Holt, 2009; Harrison et al., 2011; Ogle et al., 2015).

Our understanding of “lagged” effects of land change on biodiversity change are still in their infancy. The majority of previous studies investigated climatic influences on richness and abundance change (Albright et al., 2011; Lindström et al., 2013; Valtonen et al., 2013; Martay et al., 2017), but little is known about the influence of past land change. Rittenhouse et al. (2012) investigated differences in the proportion of landscape-wide land cover on bird diversity, but only used bi-annual, thematically non-consistent estimates of land cover. Other studies investigated the link between preceding land change and local biodiversity (Chapter 2-3 in this thesis, Jung et al., 2018), but only for spatial differences in local biodiversity rather than biodiversity change *per se*, which might mask lasting impacts (França et al., 2016; De Palma et al., 2018). We show that a consideration of preceding land change better explains biodiversity change than concomitant land change (Figure 5.3), indicating a biotic lag towards land change for bird species. Future studies could benefit from analysing impacts of preceding land change on both mean and variance of biodiversity change (Leung et al., 2017; Christensen et al., 2018) as well as considering varying trajectories of remotely-sensed land change (Watson et al., 2014).

5.4.3 Variability in explanatory power in space and functional traits

Quantifying local biodiversity change and identifying drivers of these changes is not trivial (Dornelas et al., 2012; Cardinale et al., 2018). Drivers of local biodiversity change are often unknown or cannot be reliably quantified (Hallmann et al., 2017). In an attempt to forecast local bird richness change, Harris et al. (2018) parametrized models with and without ('naïve') including remotely-sensed photosynthetic activity and climatic data. Surprisingly, they found naïve models to predict bird richness change better than those including such variables, which they attributed to a lack of abrupt biodiversity changes. Opposed to bird richness, which has been found to increase in the BBS data (Schipper et al., 2016), we found GM and pBC to decline (Appendix Figure A.5.5), but it is unclear what is driving those changes.

Bird biodiversity can be constrained by “thresholds” of land-surface conditions – such as vegetation availability – in the wider landscape (Andersen et al., 2009; Gutzwiller et al., 2015). A global review of threshold responses towards landscape-wide land changes suggests, that bird diversity is most affected if more than 27.9% of the landscape is changing (Melo et al., 2018). With exception of a few BBS routes (Figure 5.4, Appendix Figure A.5.6), the average proportion of land changes within landscapes was only 6% (Appendix Figure A.5.6-A.5.7 & A.5.10), which could explain why $f_{landscape}$ variables in our models explained on average little variation in bird diversity change and were important for a few BBS routes only (Figure 5.4). However, it could also be that impacts of landscape-wide land changes on bird diversity are poorly generalizable and depend on local context and functional traits of bird species.

Changes in local bird diversity differ by functional trait groups (Appendix Figure A.5.12, Jarzyna and Jetz, 2017; Barnagaud et al., 2017). Yet, the explanatory power of landscape-wide land changes on bird diversity change did not vary by functional groups of traits (Figure 5.5a). Many birds are migratory and as such are affected by human persecution and climatic anomalies on their migration paths (Sanderson et al., 2006; Tottrup et al., 2012). Although we did not find any difference in explanatory power between migratory and non-migratory birds (Figure 5.5a), our analysis only considered land changes in bird breeding grounds with the location of wintering grounds being unknown. In contrast to previous studies (Schipper et al., 2016), a distinction into habitat guilds also did not assist in identifying differences in explanatory power (Figure 5.5a), which is surprising given the difference in trend between for instance woodland and grassland birds (Appendix Figure A.5.12). It could be that land changes specific to certain bird habitats, e. g. changes in vegetation height (Goetz et al., 2014), are a better predictor of bird diversity change.

In this study we investigated the influence of landscape-wide, rather than local, land changes on biodiversity trends. Landscapes surrounding the BBS routes are constantly changing (Appendix Figure A.5.6-A.5.7) and such changes are expected to influence local biodiversity (Manning et al., 2009; Turner et al., 2015; Seppelt et al., 2016). However, the processes influencing local biodiversity at the landscape scale are difficult to quantify (Chase, 2003), dependent on spatial scale (Miguet et al., 2015) and local context (elevation, terrain, climatology). Regular natural disturbances – such as wild fires – can occur

in many U.S. ecoregions (Morgan et al., 2001), but there were no differences in the explanatory power of landscape-wide land changes among U.S. ecoregions (Figure 5.5b). Possibly bird diversity change is primarily driven by land changes not detectable in annual remotely-sensed photosynthetic activity and requires different spectral information (Zhu and Woodcock, 2014). Overall, for most BBS routes, the drivers explaining local bird diversity change remain unknown (Figure 5.4-5.5) and we suggest future studies to consider alternative attributes of remotely-sensed land change at the landscape-scale (Watson et al., 2014) or other spatio-temporal variables not quantifiable from optical remote sensing.

5.5 Conclusion

Overall our results indicate that landscape-wide land changes are correlated with (Figure 5.2) but did on average not explain bird diversity change across spatial scales (Figure 5.4), functional groups (Figure 5.5a) and ecoregions (Figure 5.5b). Preceding land changes assisted in explaining changes in bird diversity (Figure 5.3), highlighting the importance of biotic lag effects. We demonstrate that measures of biodiversity change are correlated with remotely-sensed landscape-wide land changes and highlight the need to better understand drivers of biodiversity change. Future studies investigating biodiversity change should consider changes in other remotely-sensed variables or variables not quantifiable through remote sensing (e.g. pesticide use, human persecution, etc.). We furthermore suggest that more research is needed on scale-dependent effects (local vs landscape changes) of biodiversity change.

CHAPTER 6

Synthesis

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Appendix

Appendix - Chapter 2

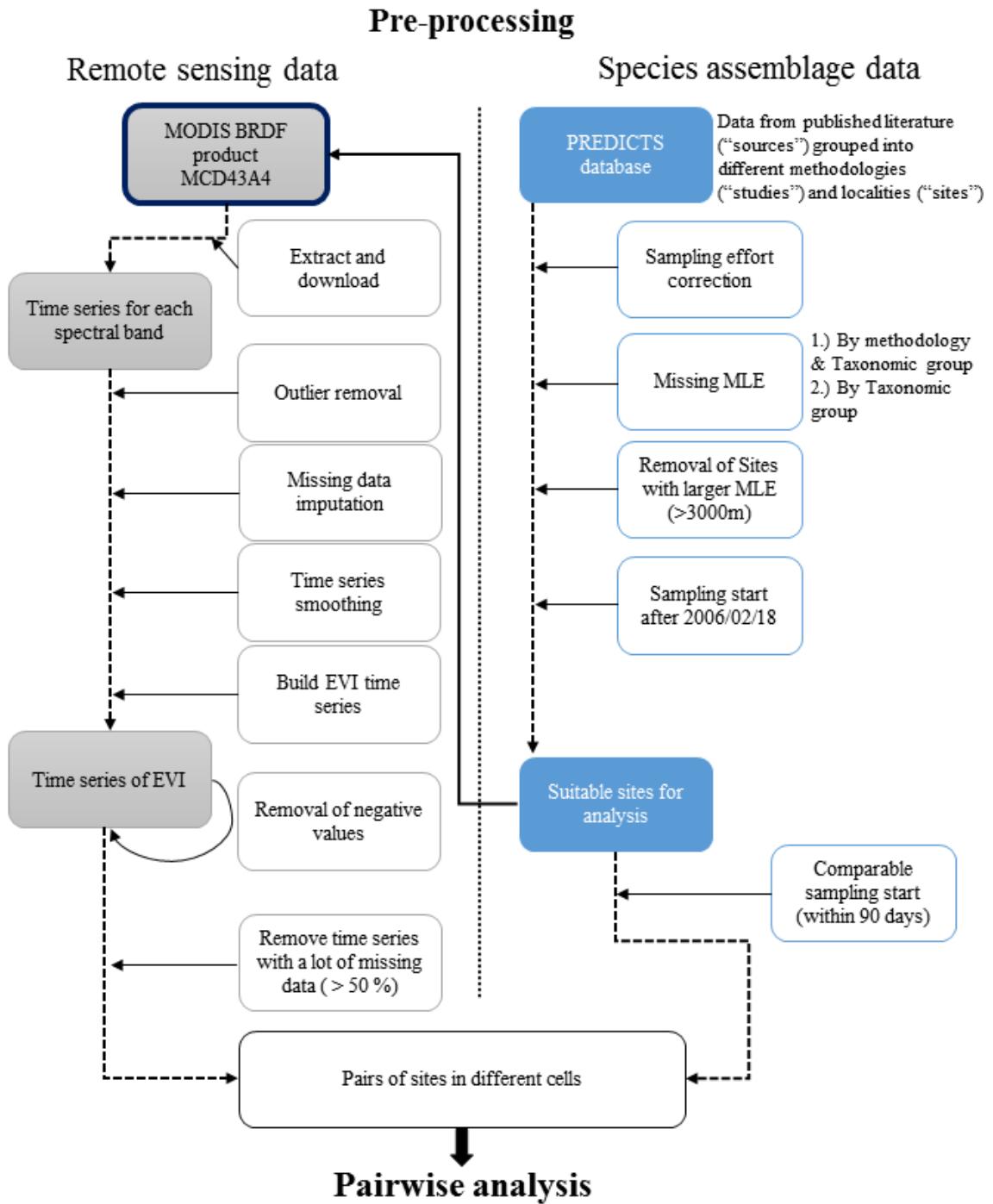


Figure A.2.1: Flow chart showing all pre-processing steps of the analysis for both remote sensing and species assemblage data. Remote sensing data were derived from the MODIS Bidirectional reflectance distribution function (BRDF) MCD43A4 product (<https://tinyurl.com/mcd43a4-voo6>) and time series of the Enhanced Vegetation Index (EVI) were calculated for the analysis (see methods 2.2). Species assemblage data originates from the Projecting Responses of Ecological Diversity In Changing Terrestrial Systems project (PREDICTS, <http://www.predicts.org.uk/>). MLE stands for the Maximum Linear Extent as defined by (Hudson et al., 2017).

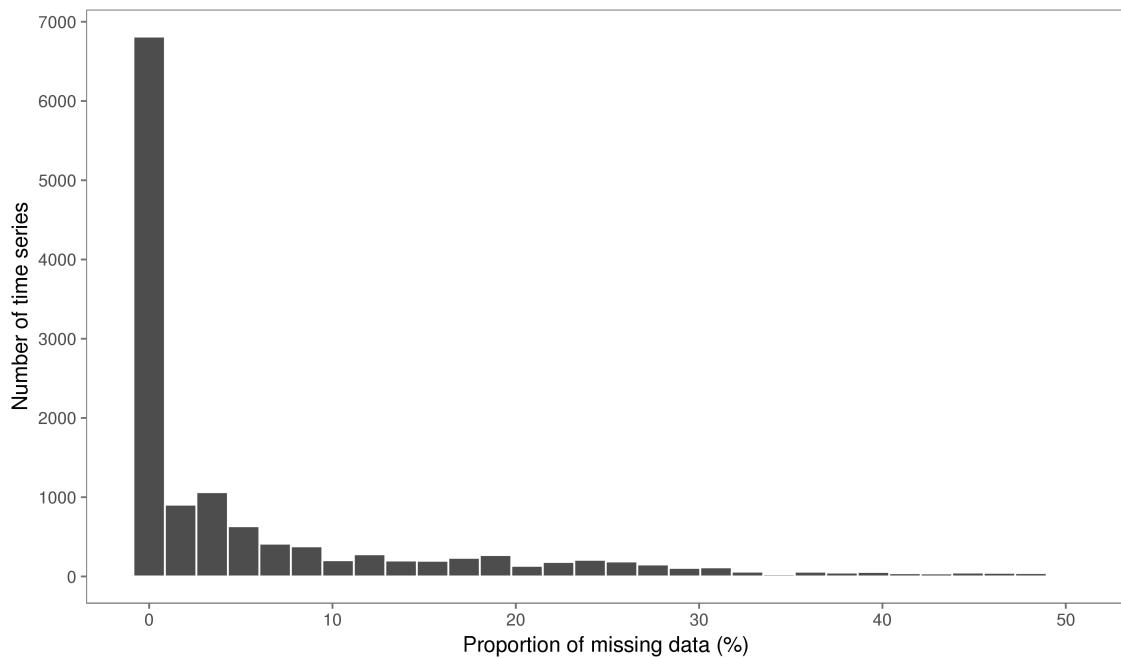


Figure A.2.2: Distribution of proportion of missing data (not interpolated) across all time series used.

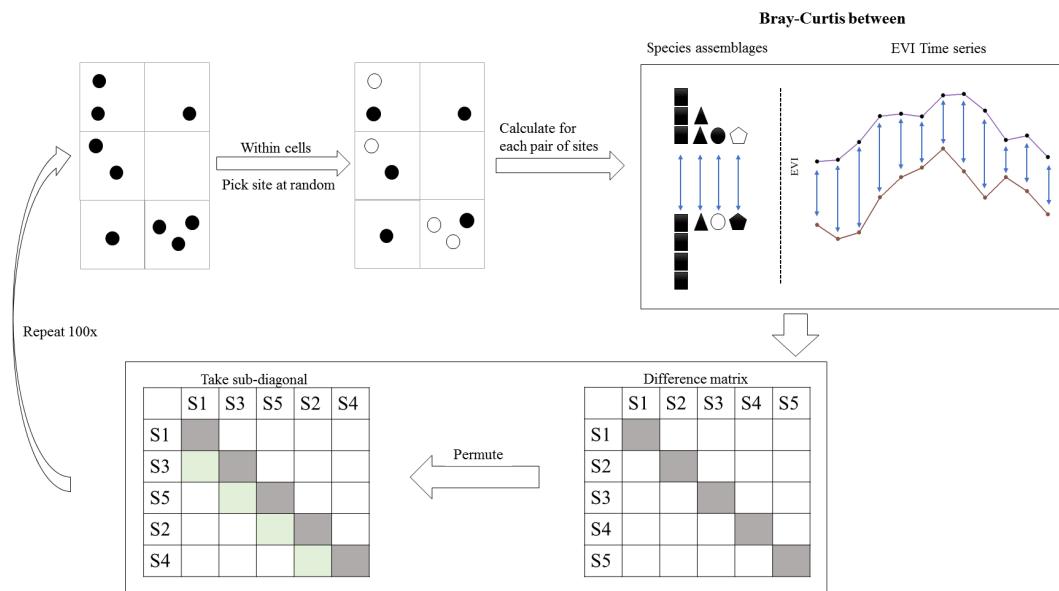


Figure A.2.3: Diagram of how the permutations of mutually independent pairwise comparisons were generated. Black dots represent 9 theoretical sites of a study within MODIS grid cells of which one site (S1 – S5) per grid cell was randomly selected. We then calculated two dissimilarity matrices one matrix for the dissimilarity between species assemblages in that grid cell and all other grid cells within the study, and the other matrix for the dissimilarity between time series of the EVI of these grid cells. For the time series, the Bray-Curtis index was calculated between the EVI values at each time step. For both species assemblages (symbols of varying number and shape) and EVI time series, the obtained dissimilarity matrix was permuted and the sub-diagonal taken for subsequent analysis.

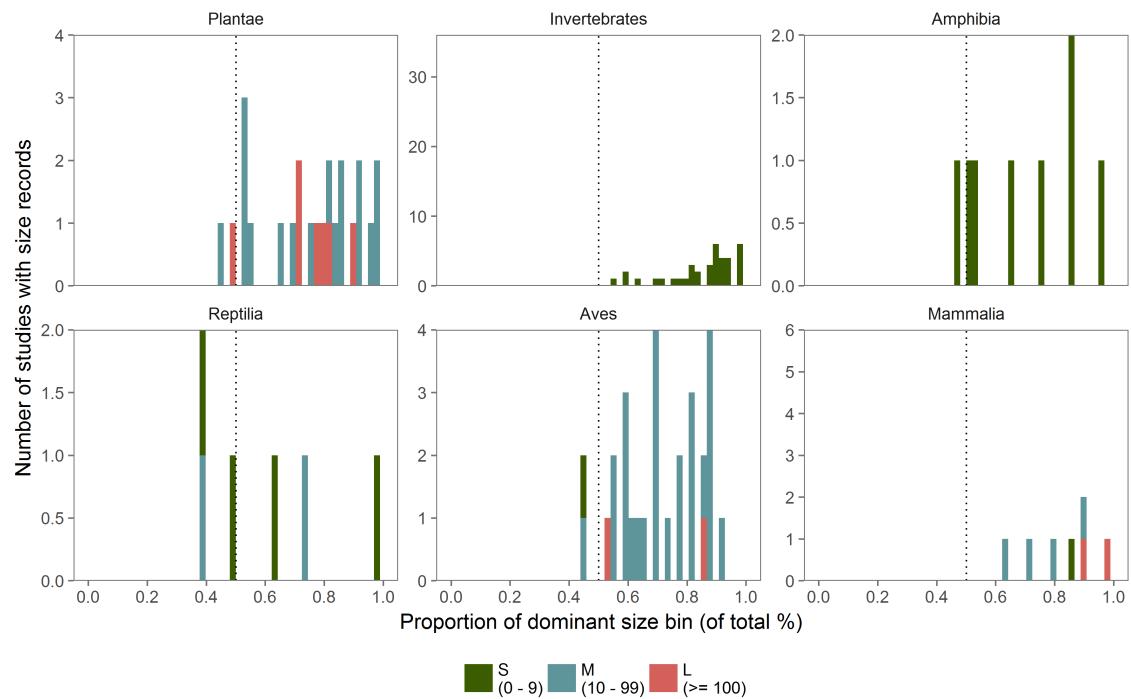


Figure A.2.4: The proportion of species that contributed to a study being classified as either predominantly inhabited by small, medium or large species. The dotted line is a visual aid to assess simple majority (50%) indicating whether a study classification is based on the majority of species within an assemblage. The y-axis shows the number of studies with similar proportions (note the difference in y-axis scale per taxonomic group).

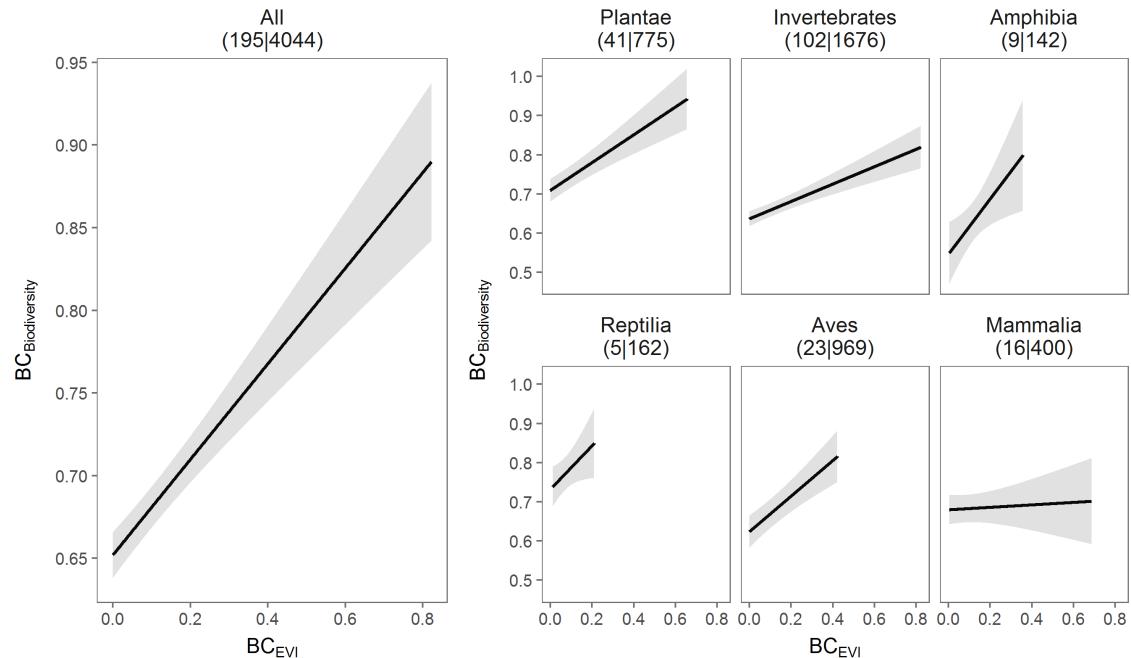


Figure A.2.5: Effect of differences in current BC_{EVI} in the first year before biodiversity sampling against their pairwise differences in species assemblages (BC_{Biodiversity}). The number of studies and contributing sites (N|N_{Sites}) is indicated for each taxonomic group.

Table A.2.1: Averaged fixed effect, standard error (SE), marginal and conditional R^2 estimates as well as relative change in R^2 to current BC_{EVI} of the overall average model (Figure 2.3). N and N_{sites} indicate the maximum number of studies and sites across permutations contributing to these estimates.

Time Period	Slope	SE	Marginal R^2	Conditional R^2	Relative difference R^2	N	N_{sites}
yr ₀	0.289	0.064	0.012	0.464	0	198	4053
yr ₁	0.279	0.062	0.011	0.460	-9.6	198	4053
yr ₁₋₂	0.299	0.065	0.012	0.462	0.4	198	4053
yr ₁₋₃	0.316	0.067	0.013	0.462	9.1	198	4053
yr ₁₋₄	0.323	0.069	0.013	0.463	11.2	198	4053
yr ₁₋₅	0.334	0.071	0.014	0.463	16.7	198	4053

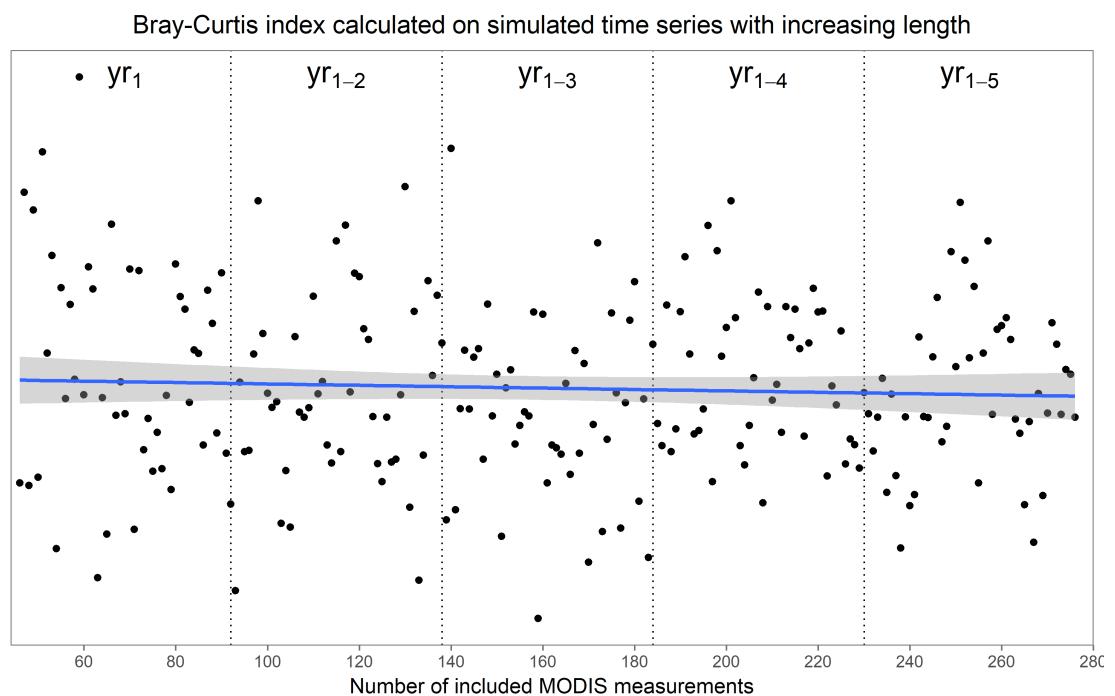


Figure A.2.6: Simulation of how the Bray-Curtis index (BC_{EVI}) between two time series changes with increasing time series length. Calculated on pairs of randomly generated time series for each past period. Vertical dotted lines indicate periods of full past years of theoretical possible MODIS measurements (46 each, increasing from 46 initially for current BC_{EVI}). There is no overall bias that the Bray-Curtis index increases with time series length (blue line shows a linear regression fit; $\beta < 0.0001$, $df = 229$, $p = 0.44$).

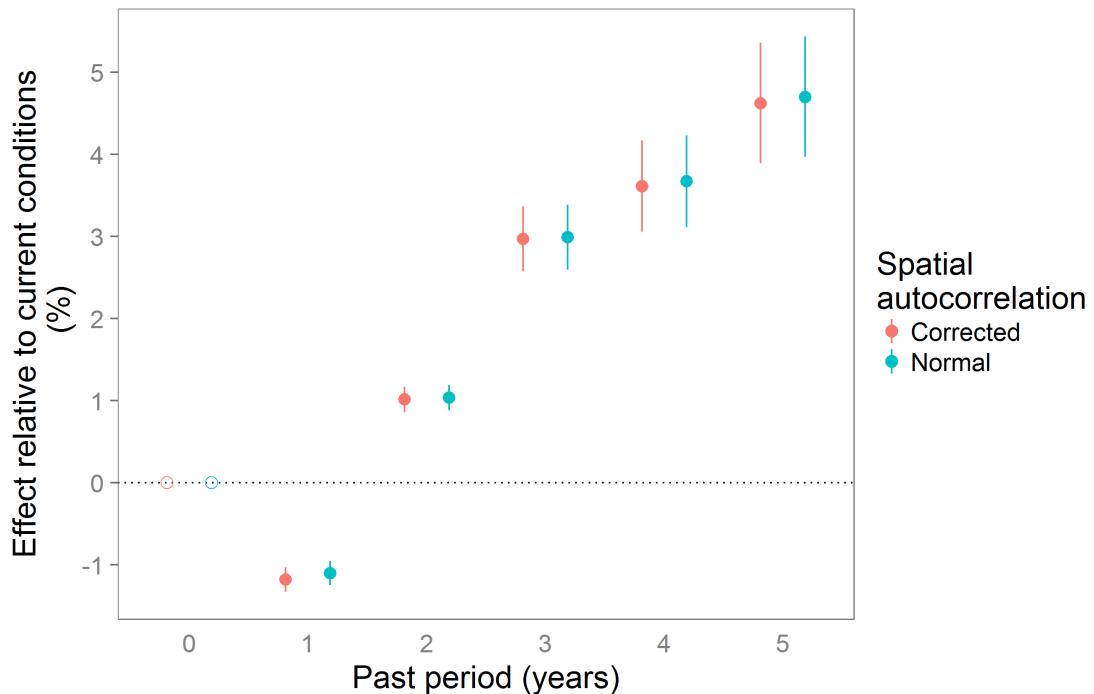


Figure A.2.7: Difference in overall fit if studies with significant residual correlation with spatial distance ($N=1$) are removed. X-axis shows the current (o) and past periods (yr_{1-5}), while the y-axis shows the difference in effect relative to the effect of current BC_{EVI} .

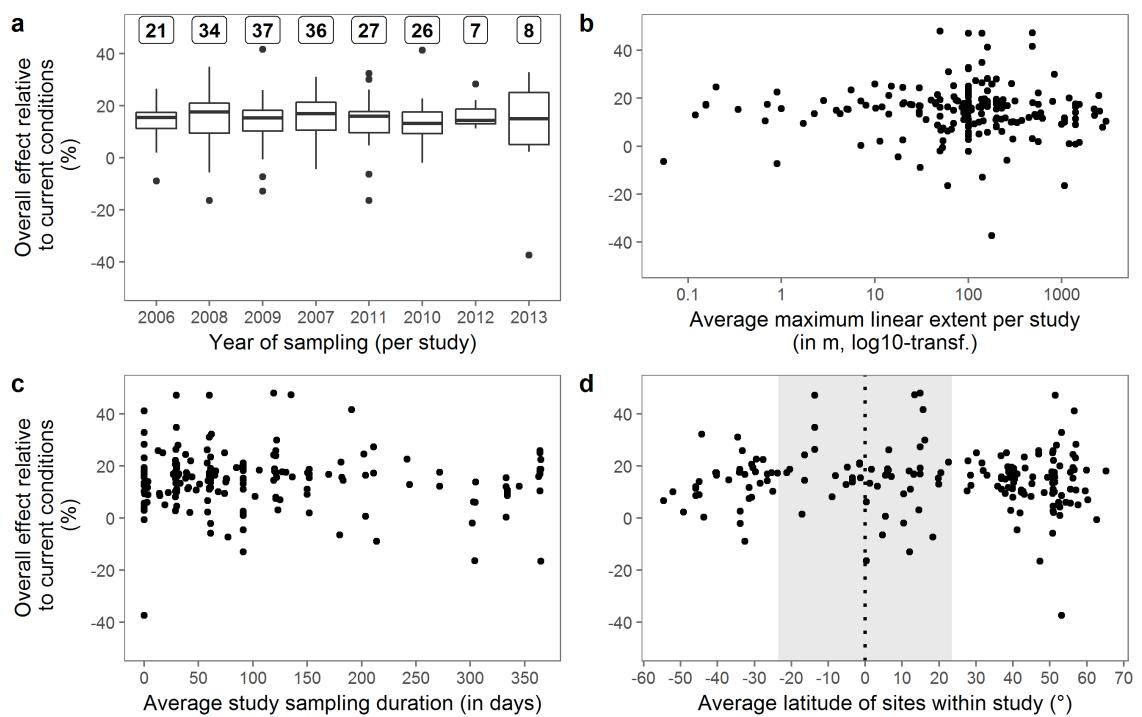


Figure A.2.8: Investigation of potential broad-scale biases of the full model coefficients (5-year period). There is no bias in the permuted model effects with regards to (a) year of biodiversity sampling, (b) spatial scale of sampling, (c) average sampling duration, or (d) average latitude of study (grey shading indicates tropic belt).

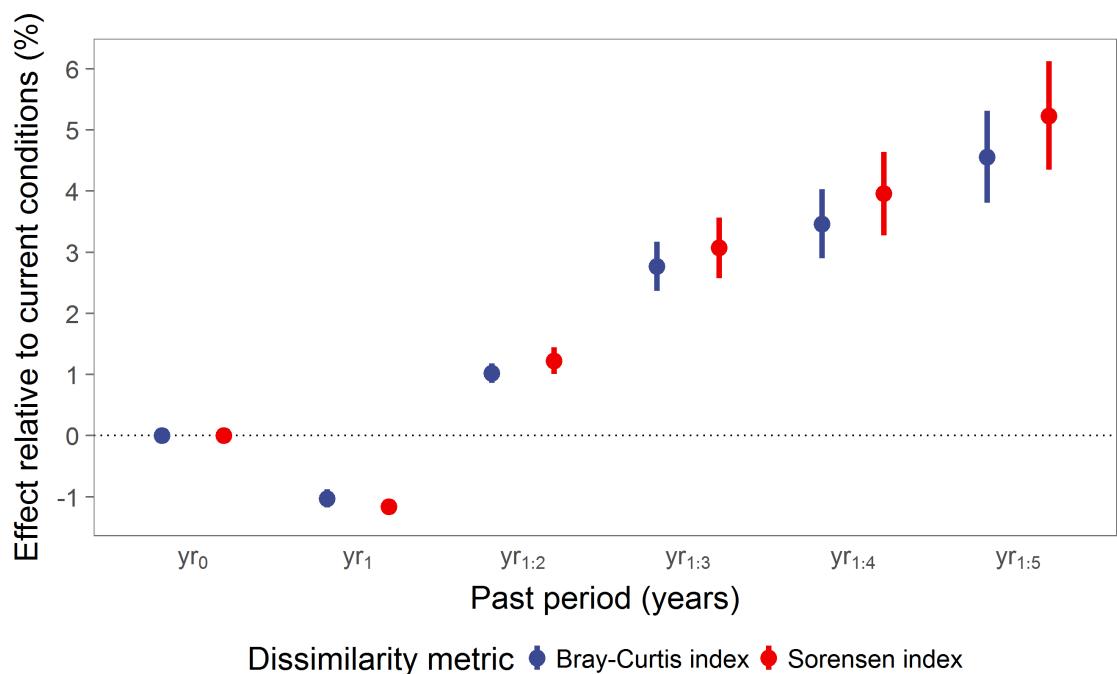
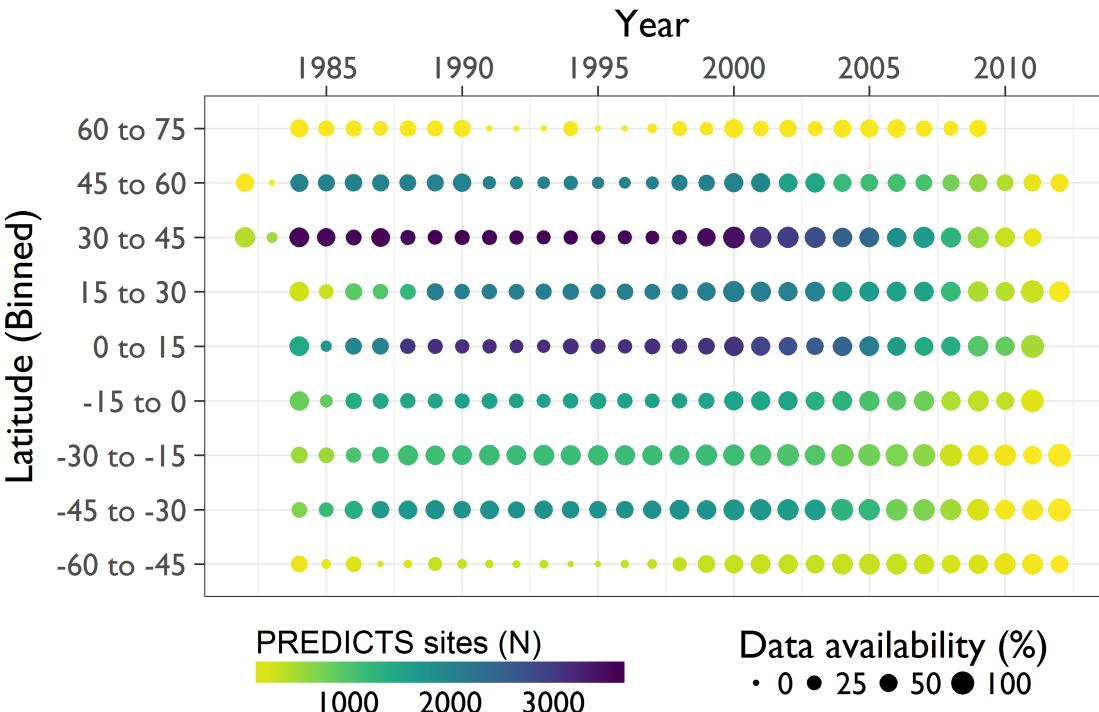


Figure A.2.9: Overall influence of past periods of BC_{EVI} on species assemblage composition as in Figure 2.3, however shown for both Bray-Curtis index and as alternative the Sørensen index. Axis labels as in Figure 2.3.

Appendix - Chapter 3

a



b

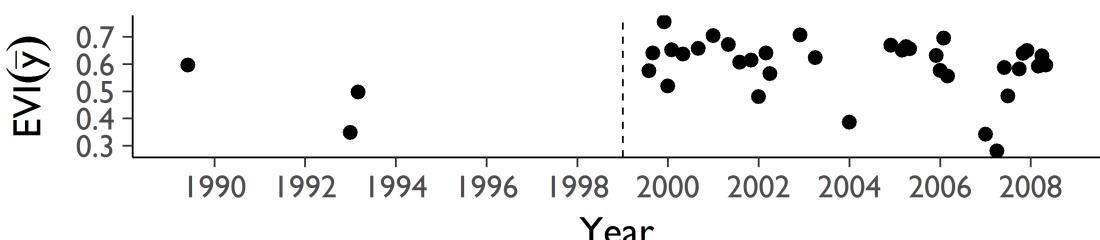


Figure A.3.1: Average temporal distribution of Landsat data and an example times series of Landsat data. (a) Distribution of available Enhanced Vegetation Index (EVI) data in years covered by the Landsat missions. Points show the average monthly EVI data availability per year (0 to 12 months of data) across time series and PREDICTS sites grouped by 15° latitude bins. The size of points indicates the mean data availability (0 to 100% with 100% having 12 months of available data in a given year), while the colour shows the number of PREDICTS sites contributing to the mean (as PREDICTS sites were sampled in varying years). (b) Example time series for one PREDICTS site with a high proportion of missing data before 1999. In all analyses such time series were truncated to the period from 1999 onwards (indicated by the dashed line).

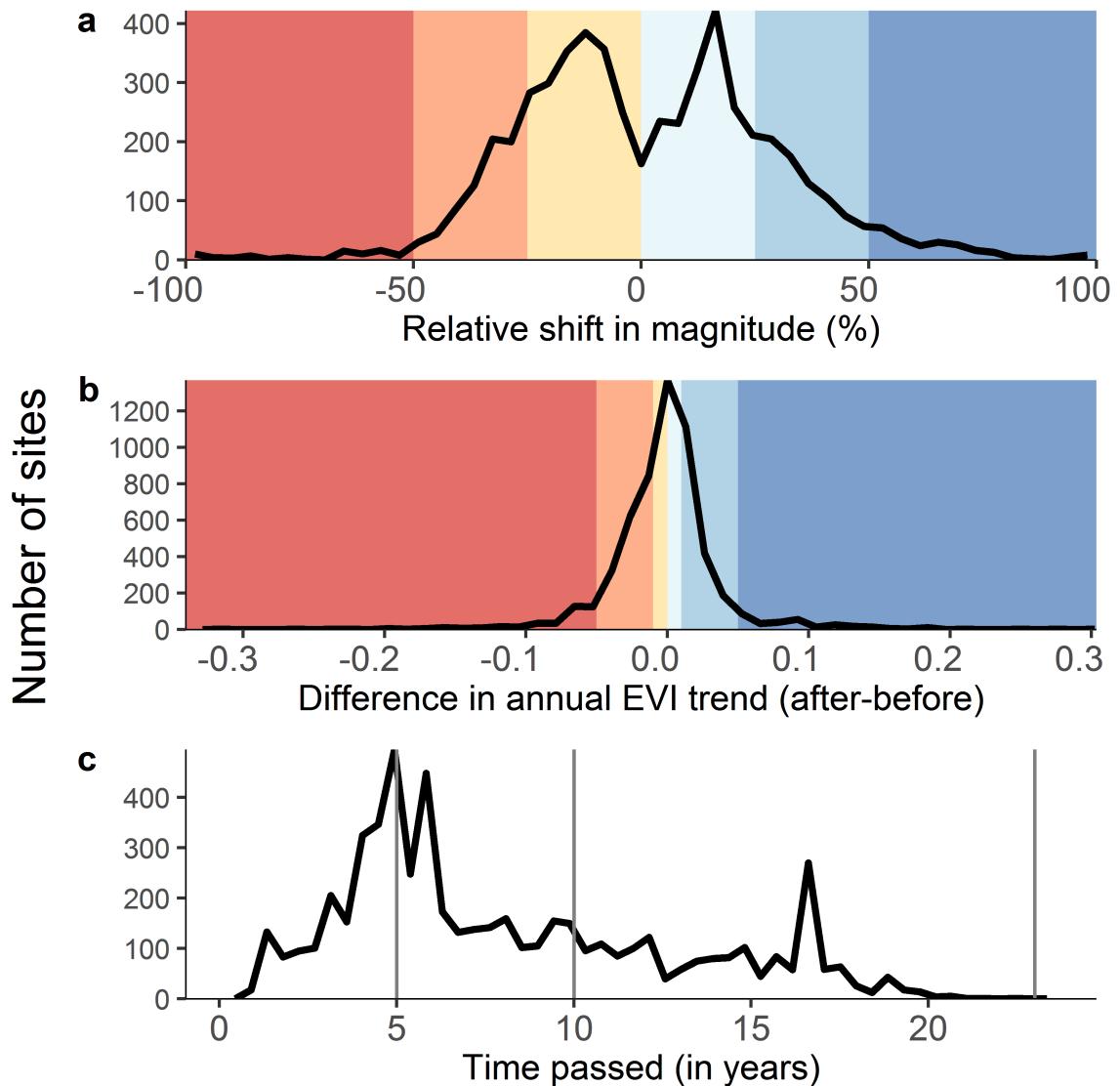


Figure A.3.2: Number of sites with abrupt land change per attribute. Number of sites (black line) per attribute of abrupt land change with (a) the relative shift in magnitude, (b) the shift in trend as difference in annual EVI trend, and (c) the time passed between abrupt land change and biodiversity sampling. Background colours in (a) and (b) indicate the binning into six groups for shifts in magnitude ($> 50\%$, $> 25\% \text{ to } \leq 50\%$, and $\leq 25\%$ EVI loss [--- to -] or gain [++ to +]), and in trend (0.01, 0.05, and > 0.05 annual negative [--- to -] to positive [+++ to +] EVI trend differences). Gray lines in (c) delineate bins of time passed (≤ 5 years, > 5 and ≤ 10 years, and > 10 years). Colours as in Figure 3.2.

Table A.3.1: Number of PREDICTS sites and studies with an abrupt land change. Shown as either a change in magnitude (columns) and/or change in trend (trend). Symbols as in Figure 3.2.

		Shift in magnitude							Total sites	Studies
	Shift in trend	- - -	- -	-	0	+	++	+++		
	- - -	2	8	192	NA	73	26	22	323	57
	- -	7	281	642	NA	497	158	53	1638	175
	-	7	88	256	NA	231	154	53	789	184
	0	NA	NA	NA	10102	NA	NA	NA	10102	358
	+	9	102	399	NA	410	205	49	1174	237
	++	47	172	342	NA	465	254	86	1366	224
	+++	12	137	47	NA	34	12	31	273	56
Total sites		84	788	1878	10102	1710	809	294		
Studies		34	135	246	358	263	171	83		

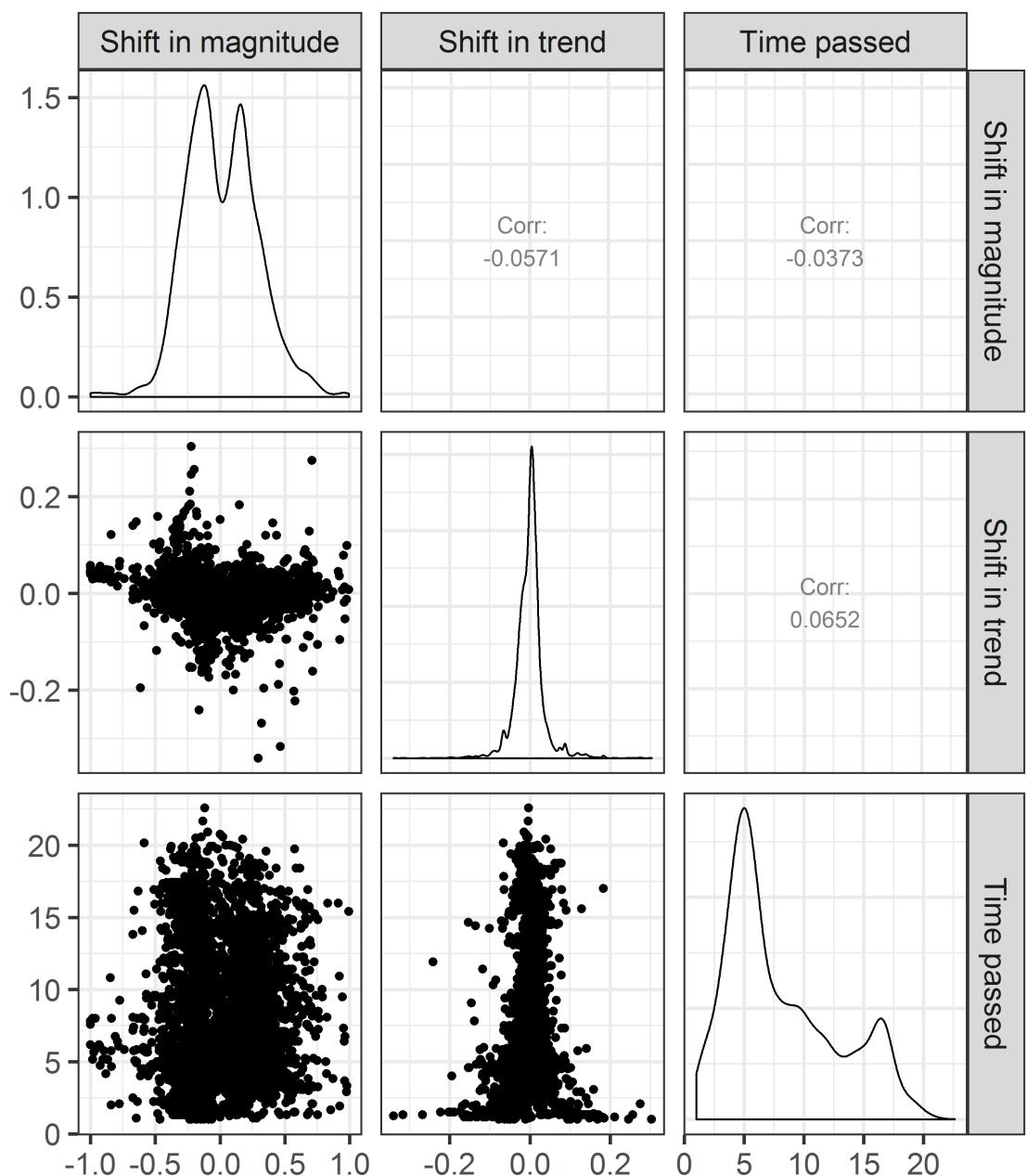


Figure A.3.3: Correlations between attributes of abrupt land change. Showing shifts in magnitude, trend and time passed (see Methods). The lower facets show a point density plot, the upper facets the Pearson correlation coefficient between pairs of attributes and the diagonal a density plot.

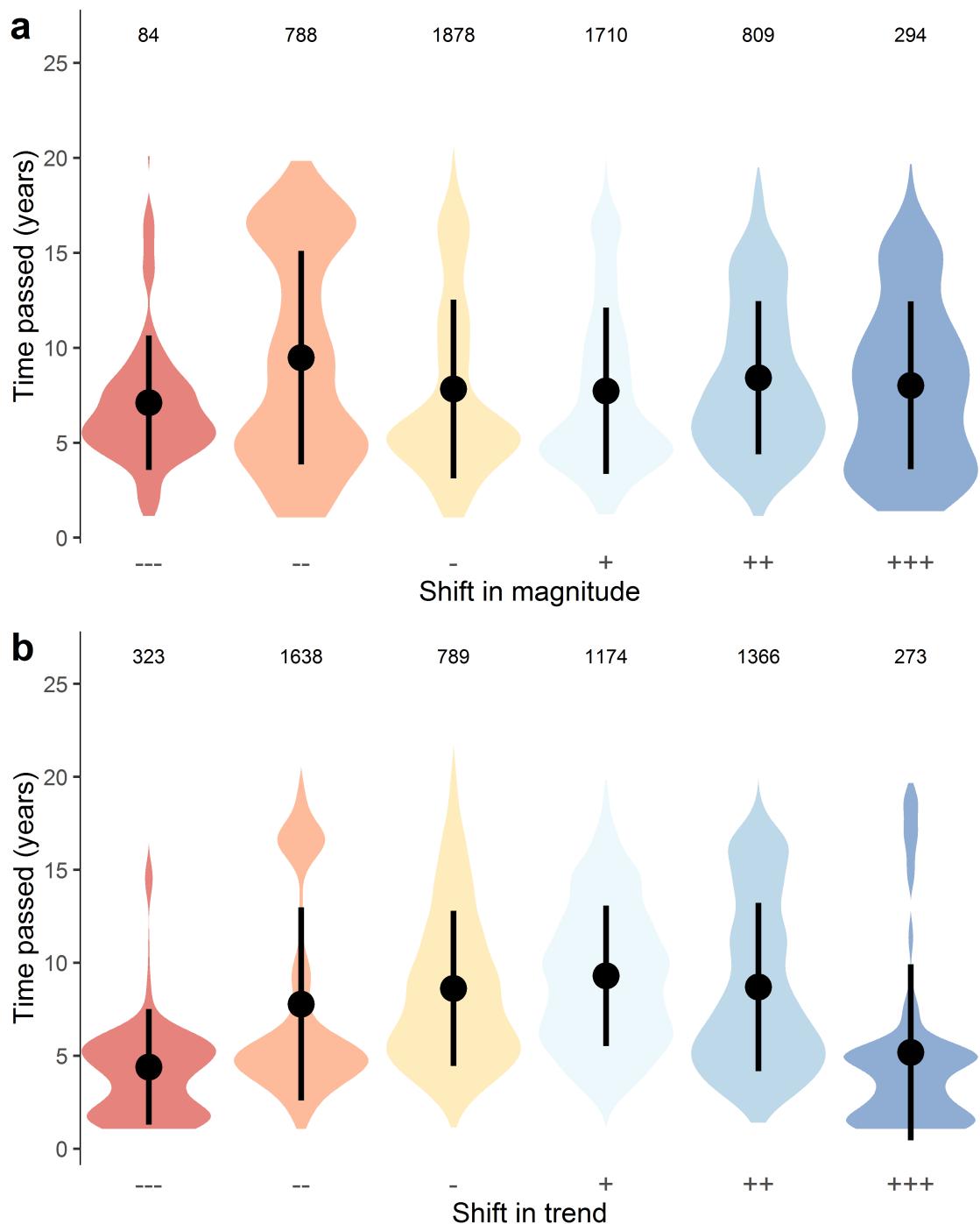


Figure A.3.4: Distribution of time passed between abrupt land changes and start of biodiversity sampling. Shown for (a) shifts in magnitude, and (b) shift in trend bins. Colours as in Figure 3.2. Black dots and error bars show the mean \pm one standard deviation. Number of sampled sites per bin are shown above each bin.

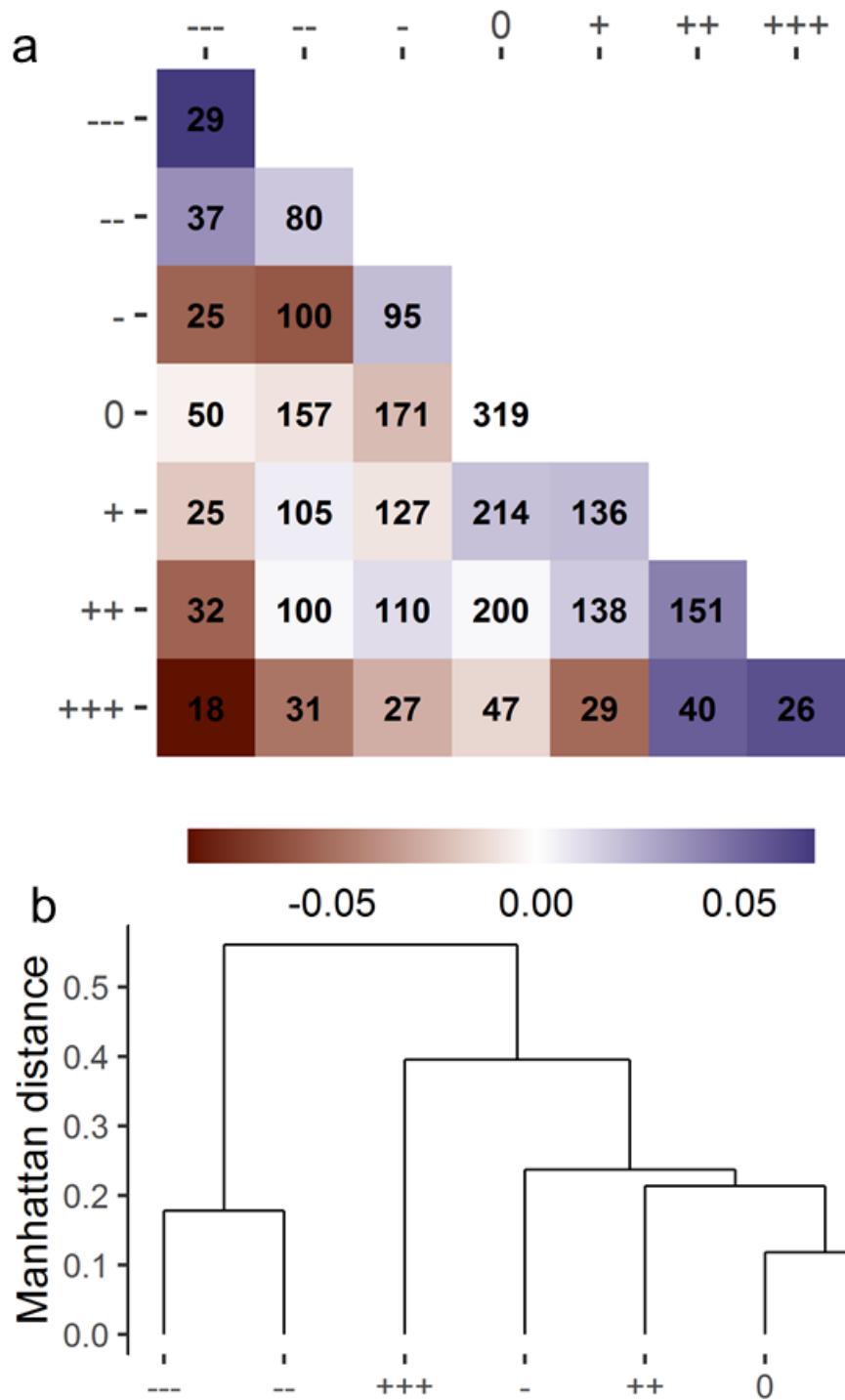


Figure A.3.5: Mean similarity in species assemblage composition (Sørensen similarity index) between pairs of sites with a shift in trend. Calculated as average similarity within the same study and land-use category without (0) and with an abrupt land change with varying shifts in EVI trend (a). Colours indicate whether similarity of species assemblages was on average greater (purple) or smaller (brown) relative to unchanged sites. Symbols indicate positive (+++, ++, +) or negative (---, --, -) shifts in trend of annual EVI (see Methods). Numbers in (a) indicate the total number of studies for which pairwise comparisons between sites could be made. (b) Dendograms show hierarchical clustering of all pairwise similarities based on the average Manhattan distance between pairs of sites; sites with more similar assemblage composition are in branches of closer proximity.

Appendix - Chapter 4

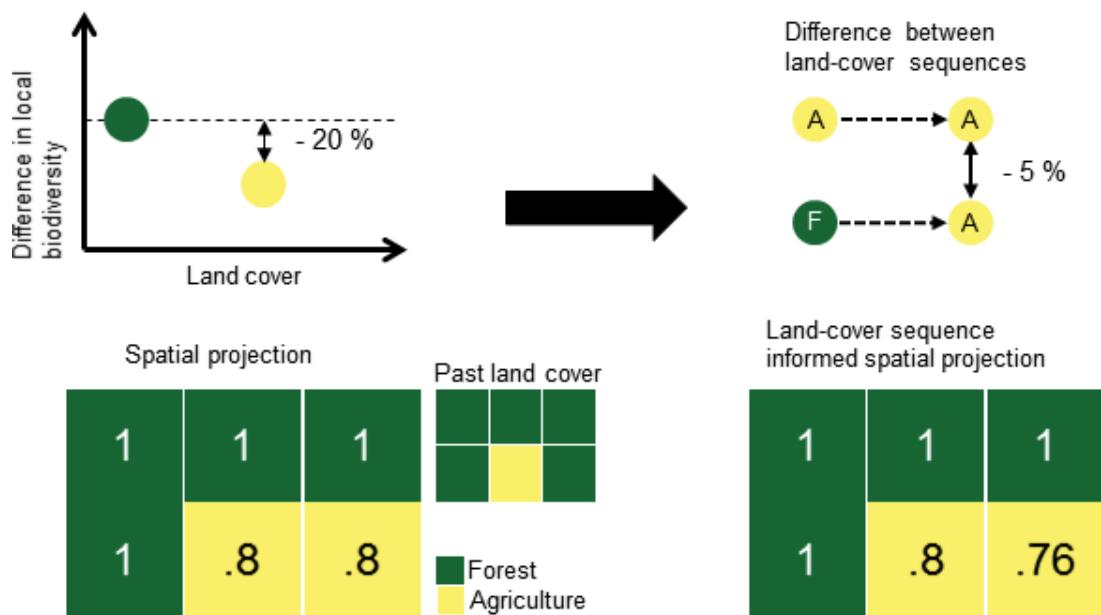


Figure A.4.1: Schematic on how spatial projections of biodiversity difference can be informed by models of past land-cover sequences. First a “baseline” spatial projection is created based on the difference in local biodiversity between forest and agricultural sites. Knowing that past land cover in the bottom-right cell was forest covered, this baseline spatial projection is then updated based on the specific coefficient from the models (Figure 4.3) for each land-cover sequence.

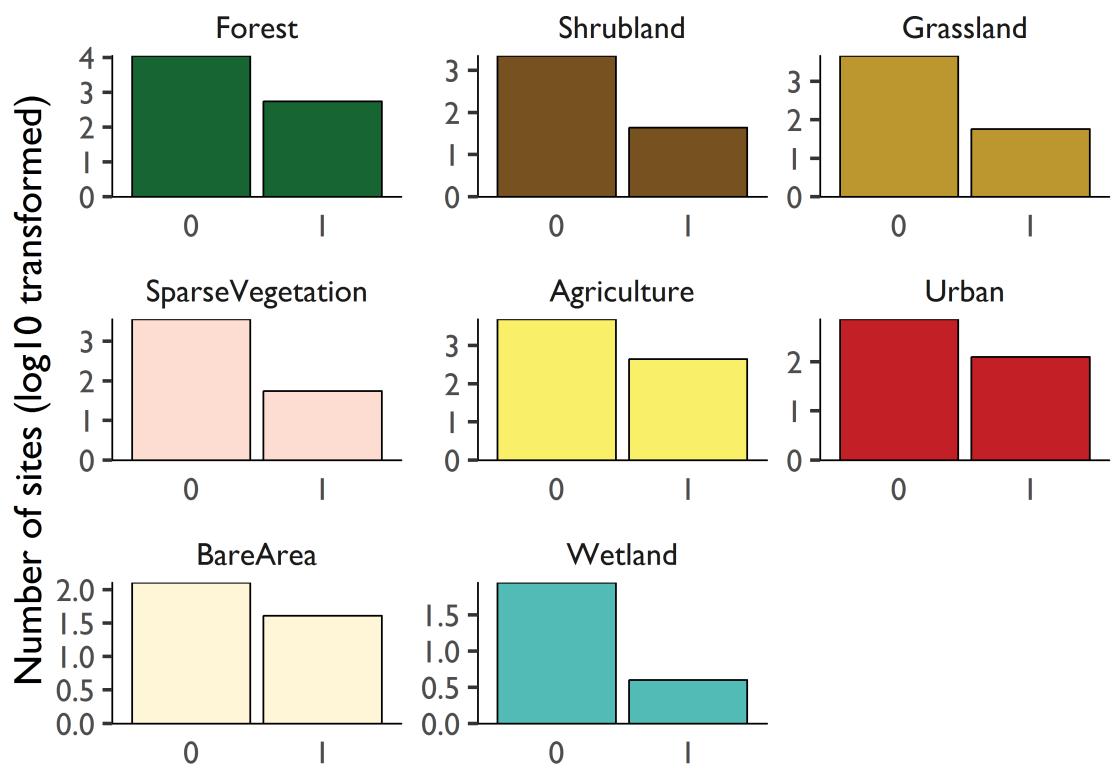


Figure A.4.2: Total number of sites (\log_{10} transformed) without (0) and with (1) a past land-cover change. Colours indicate the land-cover category at the time of biodiversity sampling.

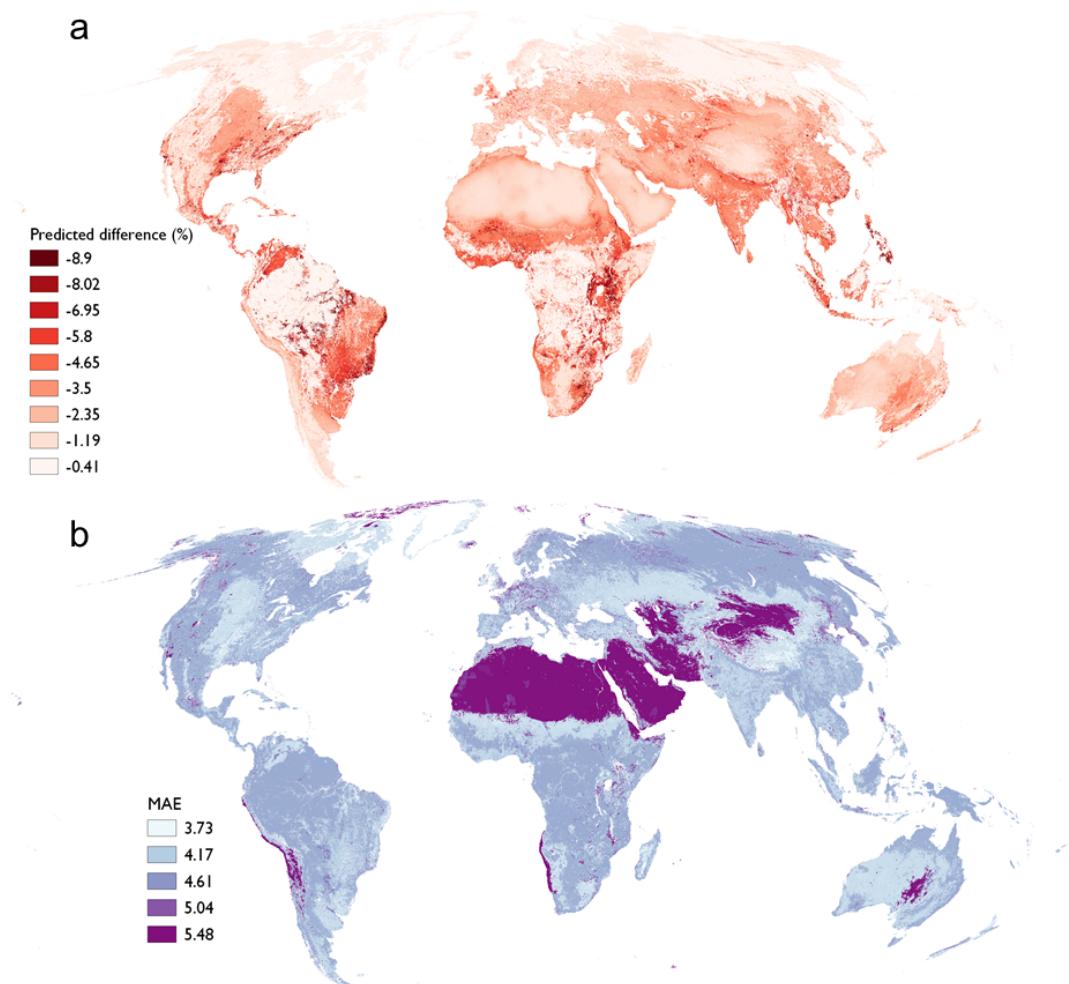


Figure A.4.3: (a) Globally projected difference in species richness (%) – weighted by vertebrate richness, see methods – relative to local species richness in forests with zero human population density. (b) The predicted (unweighted) uncertainty in local species richness shown as mean absolute error (MAE).

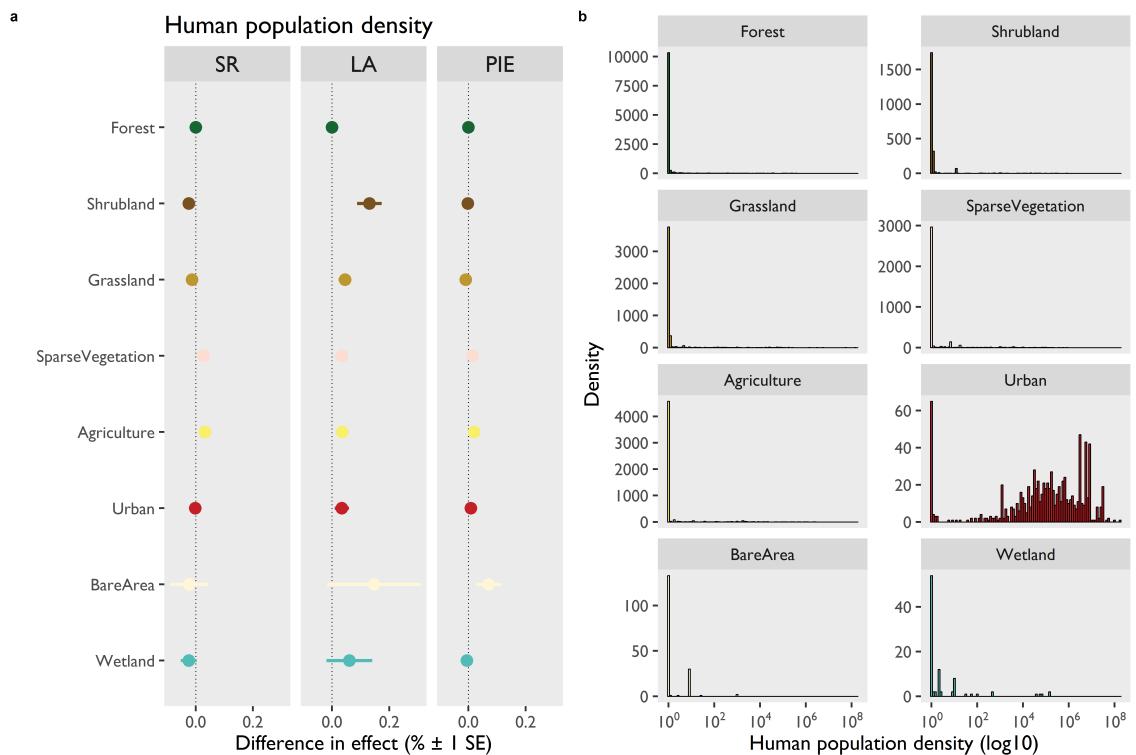


Figure A.4.4: (a) Difference in the effect size (linear slope) of human population density on species richness (SR), total abundance (LA) and assemblage evenness (PIE). All effects shown relative to the effect of forest cover on local biodiversity, with values greater than 0 indicating a linear increase of the response. Error bars show the estimated standard error. (b) Number of PREDICTS sites per land-cover category and human population density (log₁₀-transformed) from the global human settlement product (Pesaresi et al., 2016).

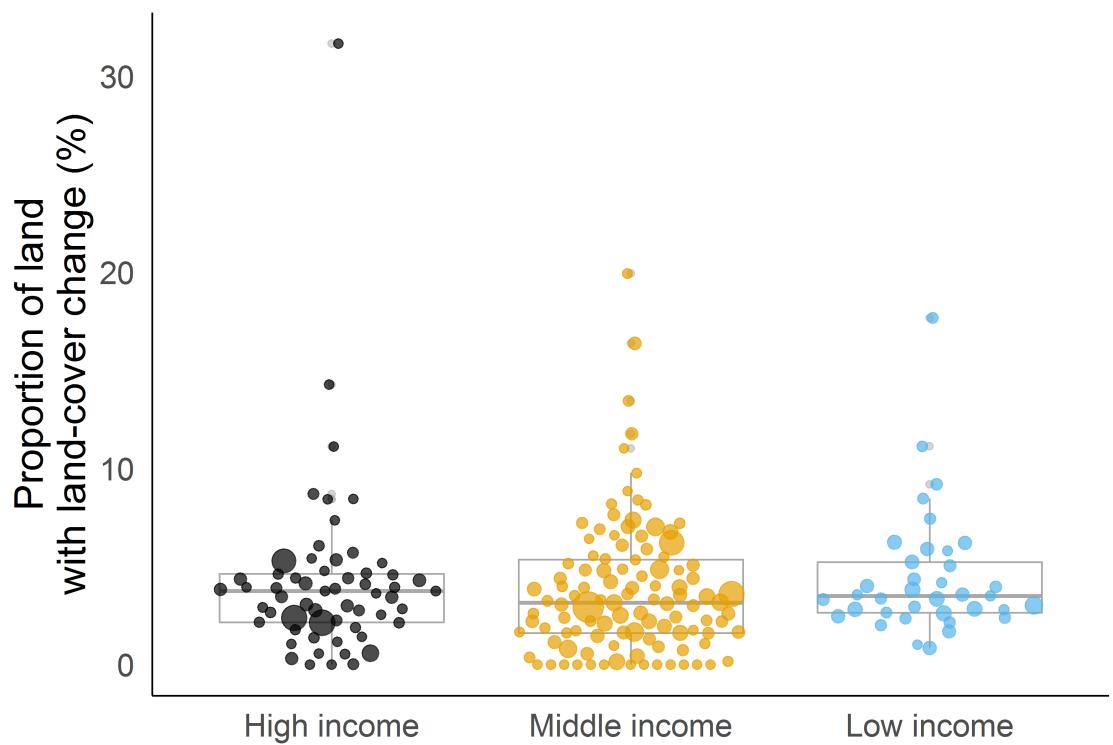


Figure A.4.5: Shows the proportion of land (in %) with a past land-cover change in the period 2000 to 2015 relative to the total land area. Size of the points is scaled with land area (small to large). Colours indicate whether a country (data from [data.un.org](#)) is considered to have high (black), middle (orange) or low (blue) income.

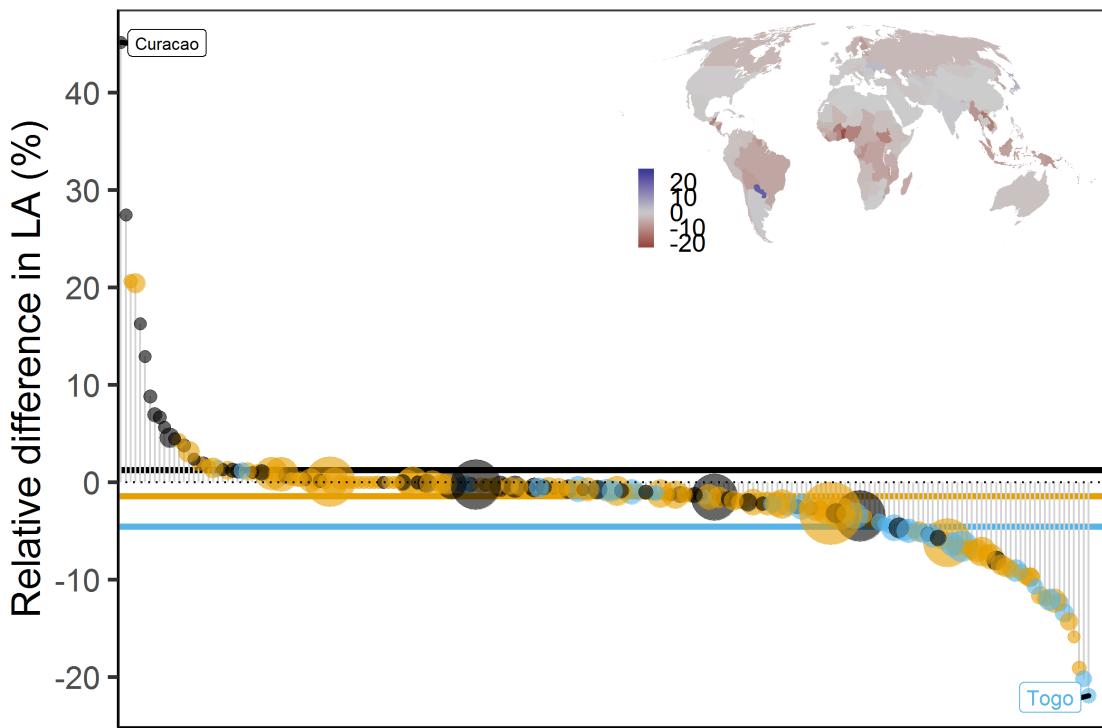


Figure A.4.6: As in Figure 4.5 but for total abundance (LA).

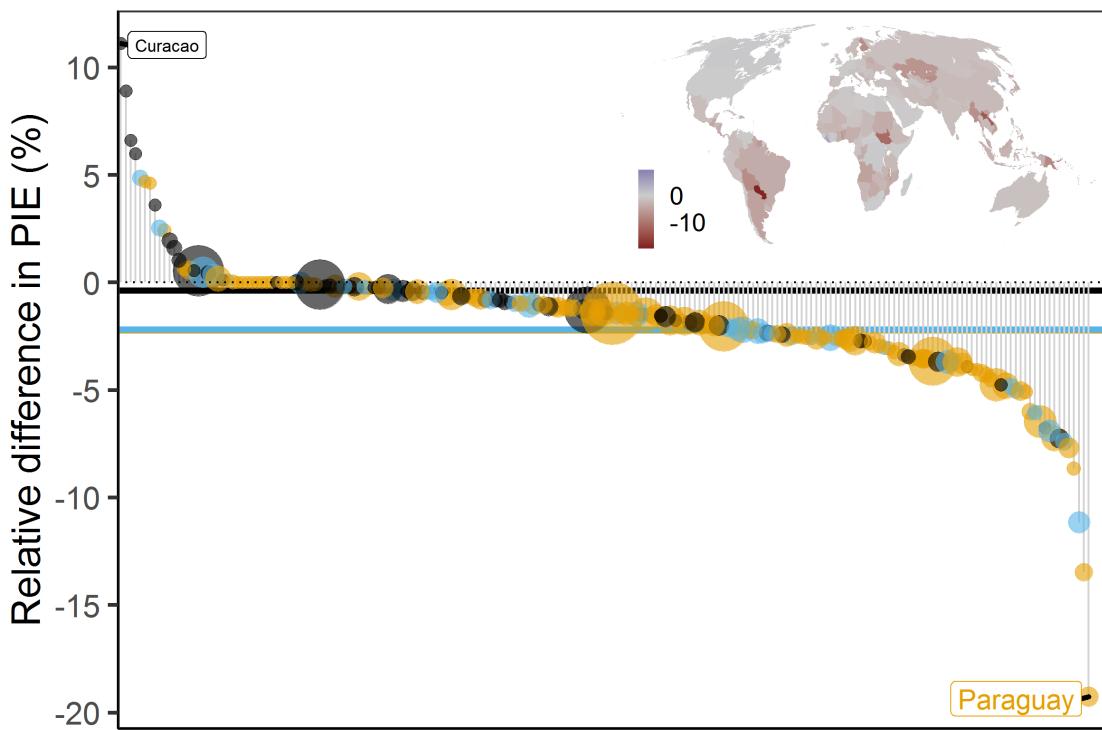


Figure A.4.7: As in Figure 4.5 but for species assemblage evenness (PIE).

Appendix - Chapter 5

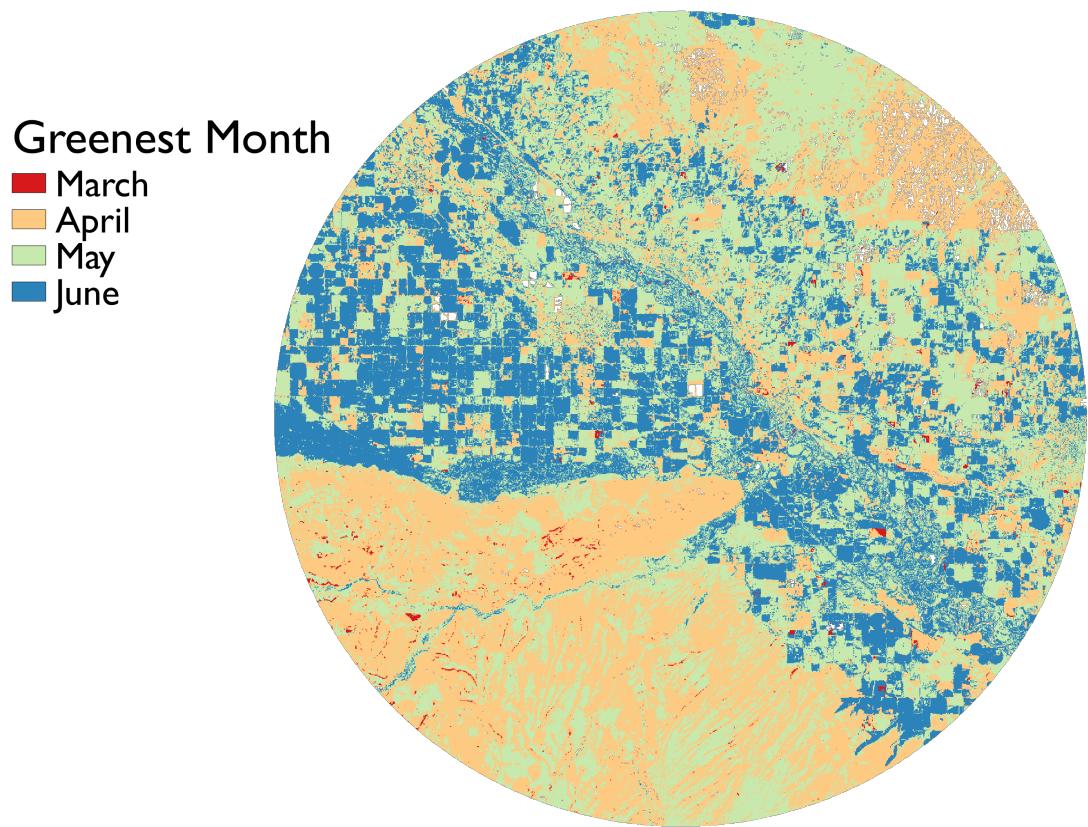


Figure A.5.1: Annual Landsat composite for a single year (2018) and route (RTENO: 89020, Routename: *Wapato* in the State of Washington) showing the month with the greenest EVI value in the period 20th March to 20th June.

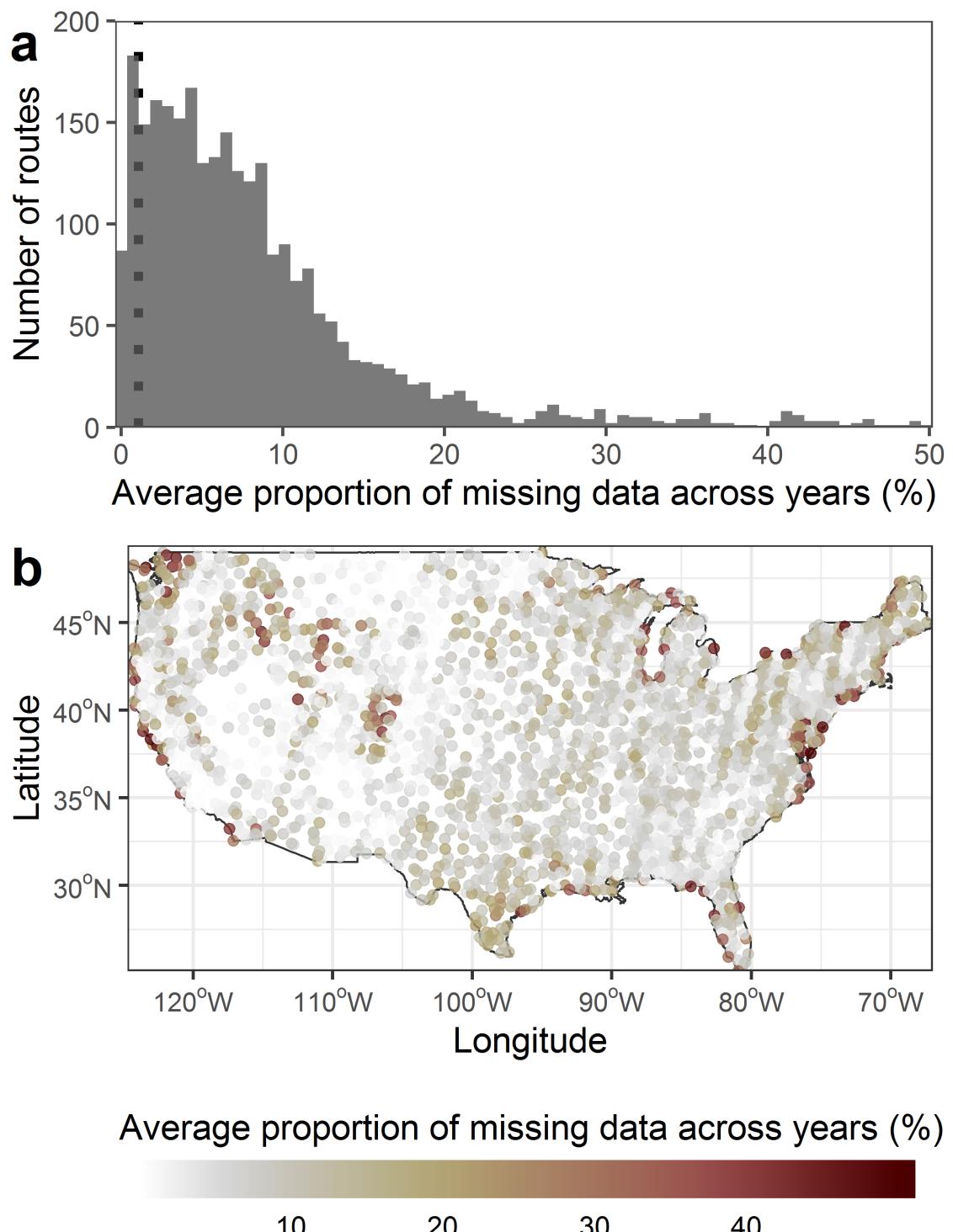


Figure A.5.2: (a) Average proportion of missing Landsat data across years for all routes with the median (1.06%) indicated (dotted line). (b) Map showing each BBS Route coloured by the average proportion (%) of missing data across years.

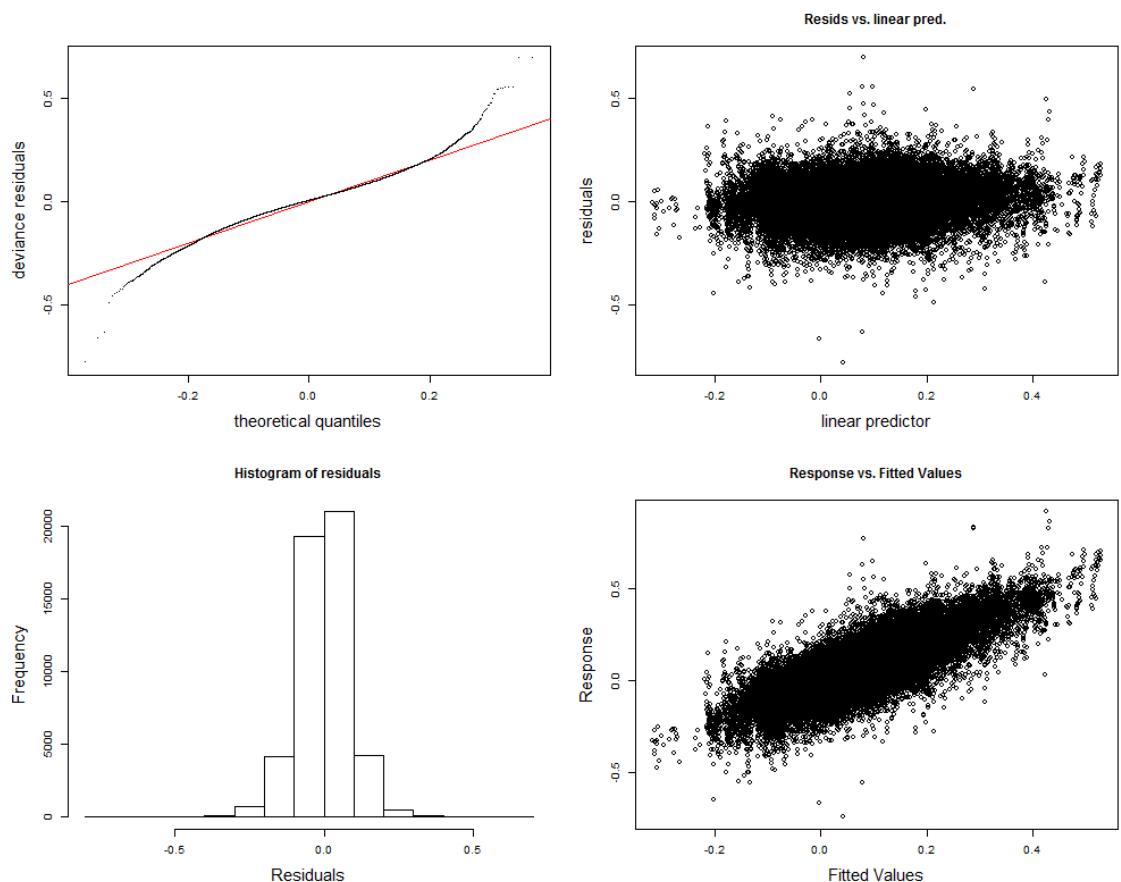


Figure A.5.3: Model diagnostics of the full model (see 5.2.5) for the geometric mean of relative abundances (GM).

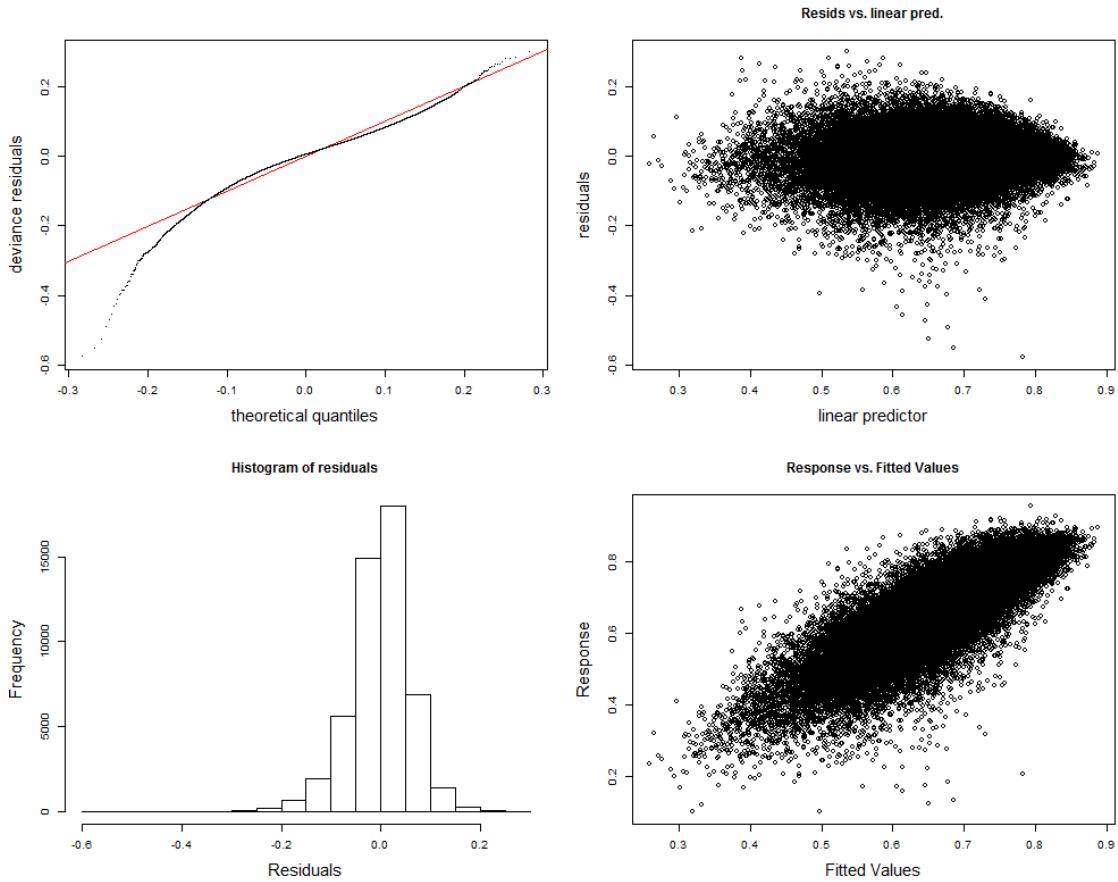


Figure A.5.4: Model diagnostics of the full model (see 5.2.5) for the progressive Bray-Curtis index (pBC).

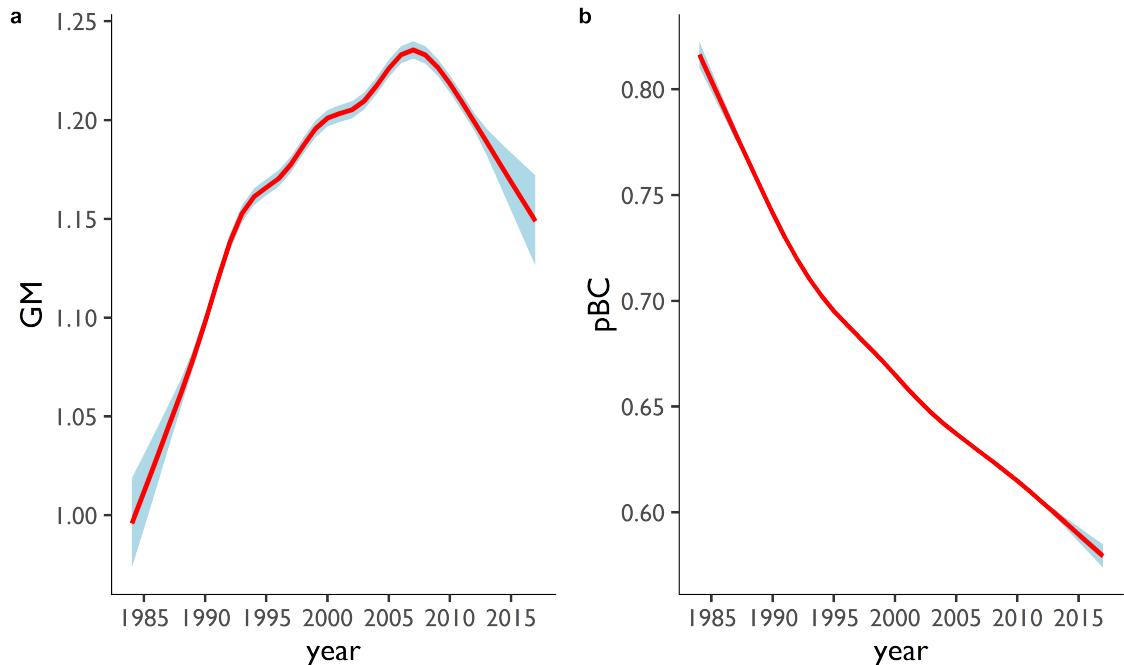


Figure A.5.5: Average trend in the (a) GM and (b) the pBC over the considered monitoring period (1984-2017) and across all 2745 BBS routes. Error margins show ± 1 standard error.

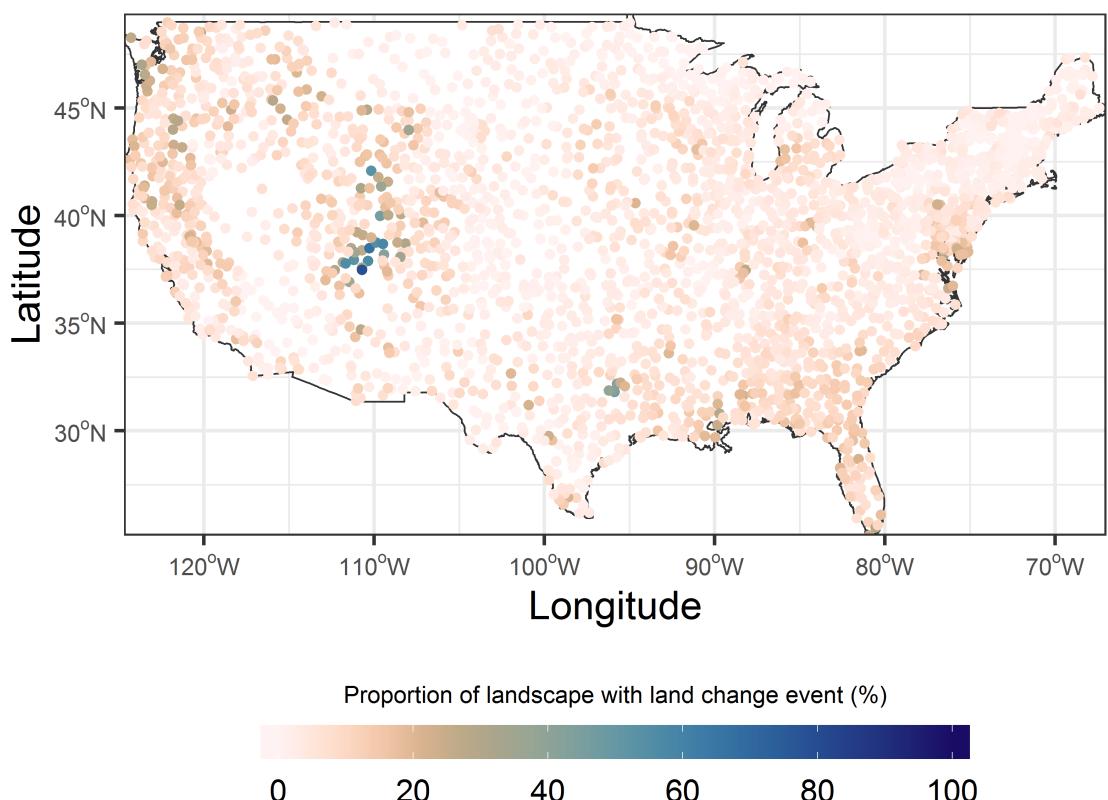


Figure A.5.6: The centroids of all BBS routes (see methods) coloured by the total proportion of the landscape that had at least one land change event in the period 1984 to 2017.

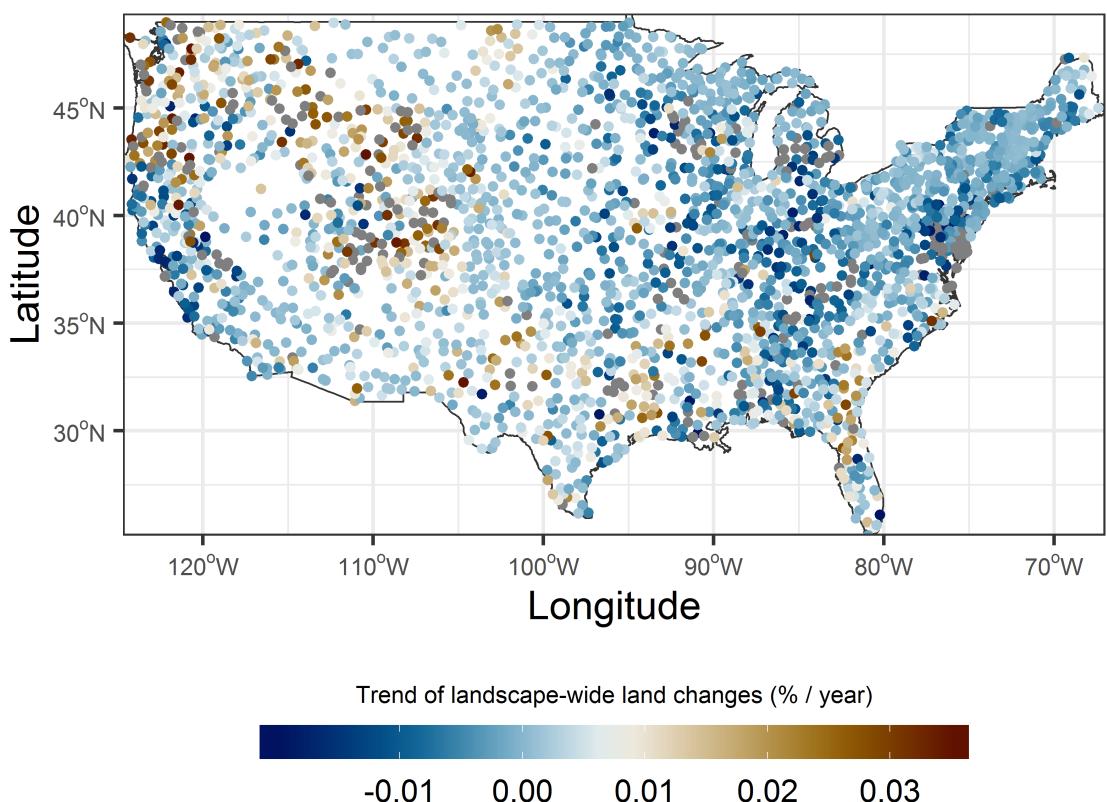


Figure A.5.7: Robust annual linear trends in the proportion of land with an abrupt shift in magnitude (loss + gain) across all landscapes surrounding BBS routes. The most extreme estimate (99% lower and upper limits) were excluded from this visualization ($N = 56$).

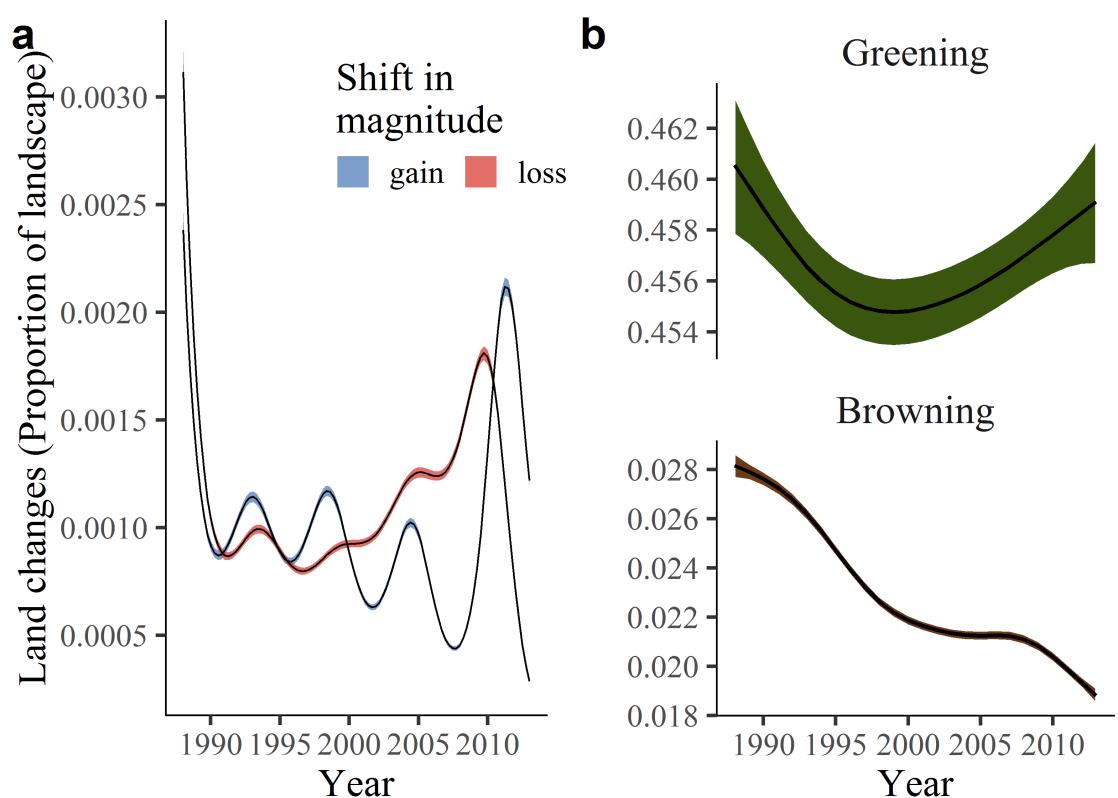


Figure A.5.8: Average trend of land changes with abrupt shift in (a) magnitude or (b) shift in trend as predicted by a GAM that includes a non-linear term for year only. Error bands show the fitted standard error.

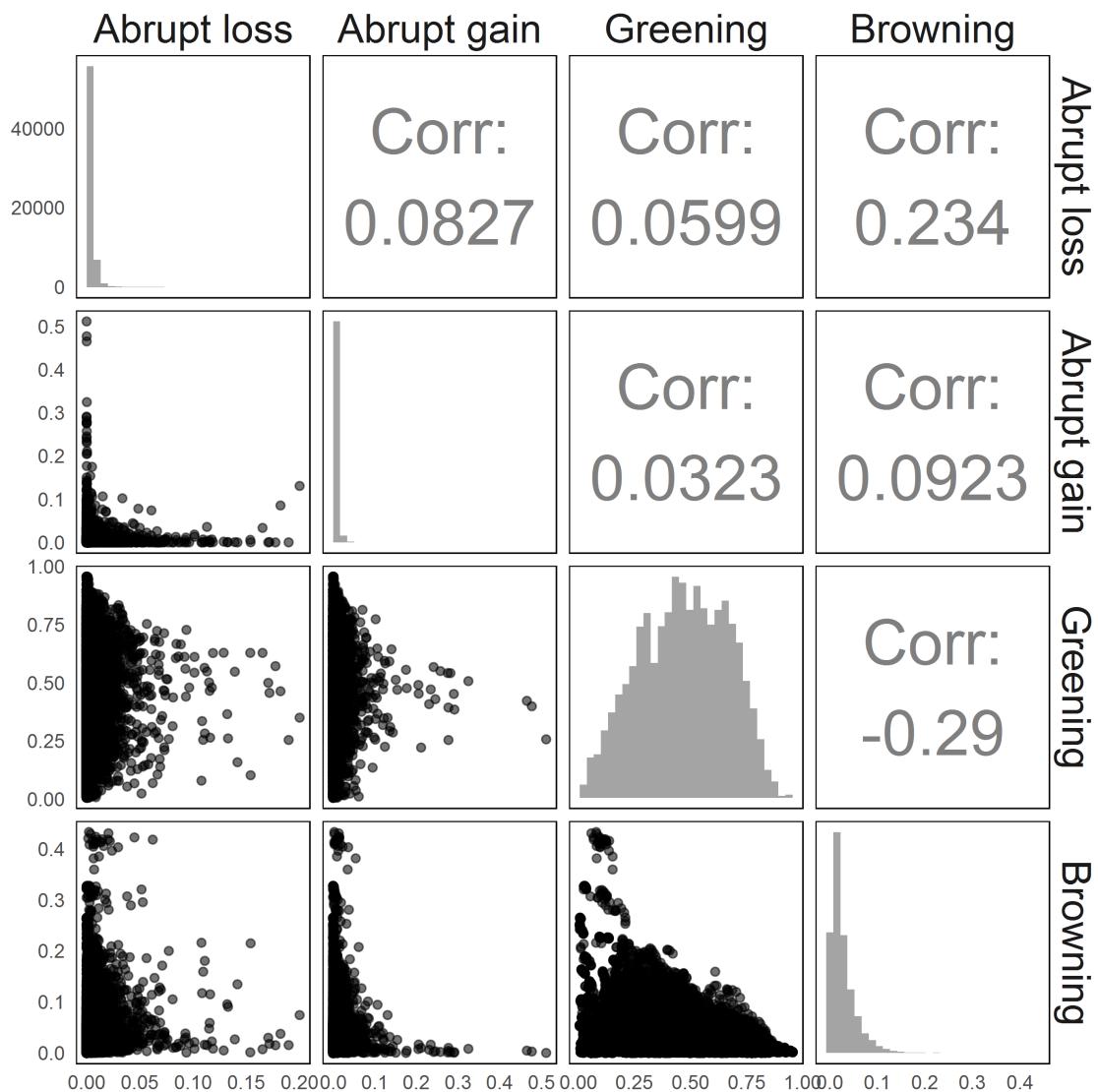


Figure A.5.9: Pairwise correlation plot between the proportion of land changes with abrupt shifts in magnitude (gains and losses in photosynthetic activity) and trend (greening and browning). Text in upper triangle shows the Pearson correlation coefficients.

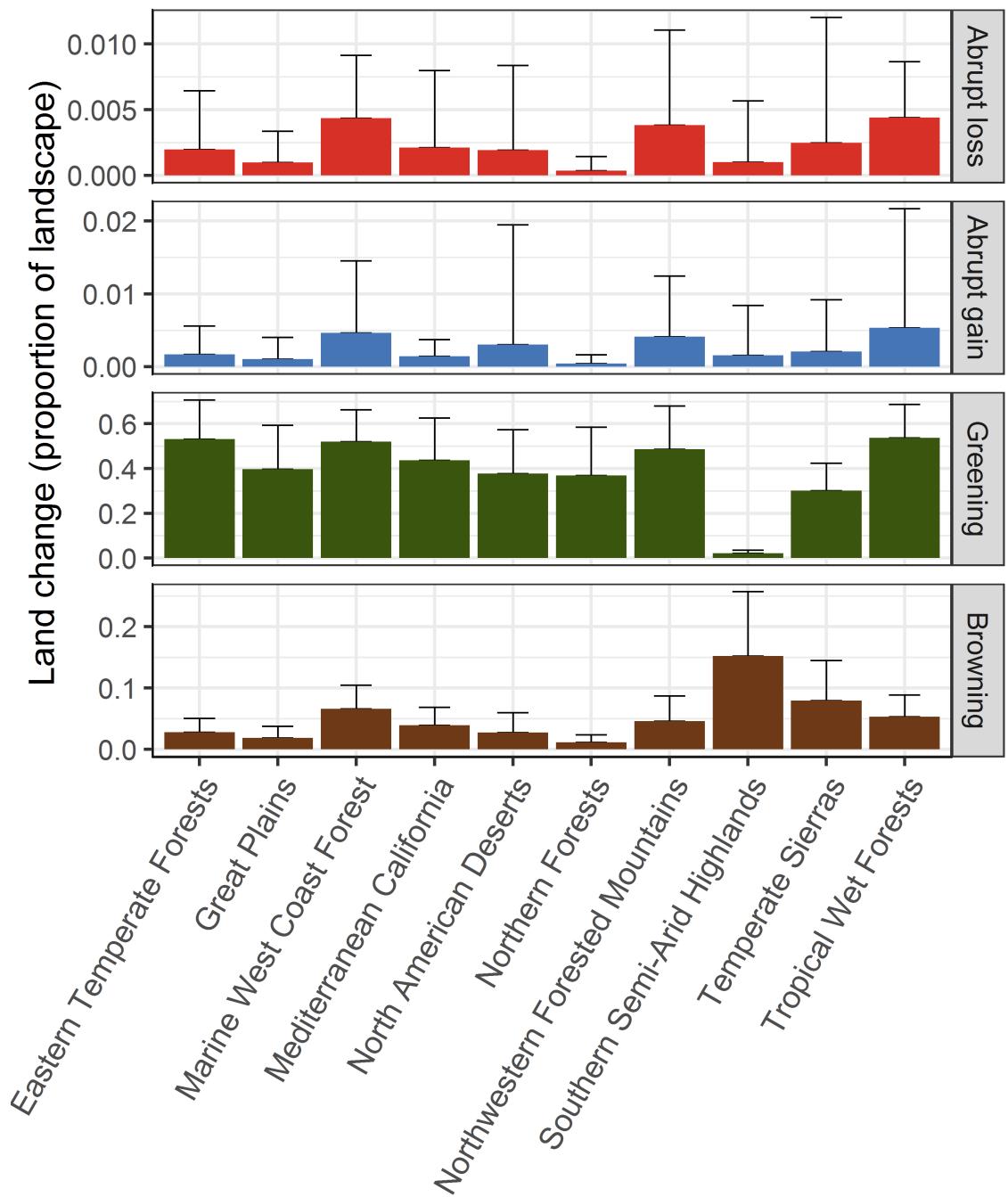


Figure A.5.10: Average proportion of landscape-wide land change – shifts in magnitude, e.g. abrupt losses and gains, and shift in trends, e.g. greening and browning – across 10 US ecoregions. Error bars show the calculated standard deviation. Colours as in Appendix figure A.5.8.

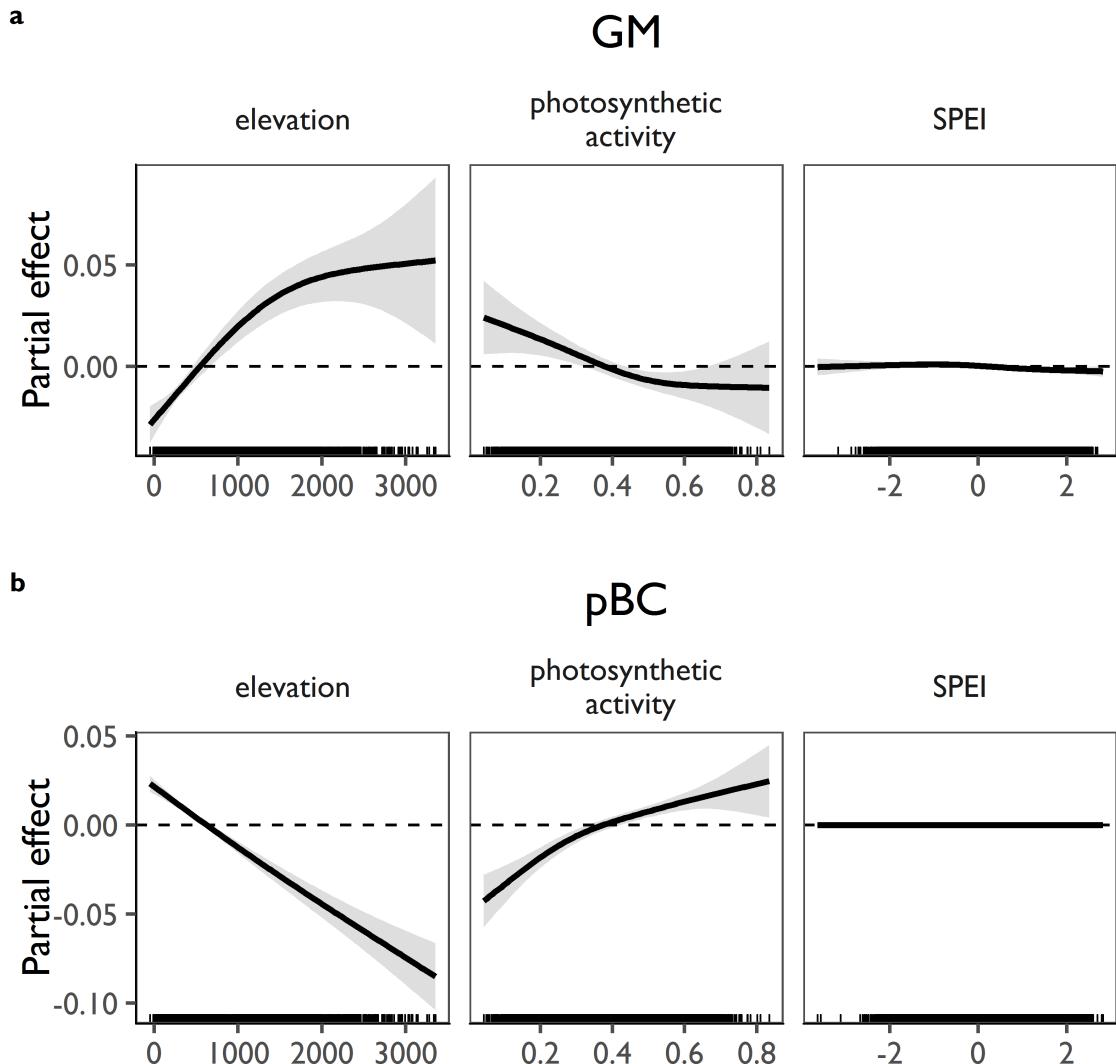


Figure A.5.11: Estimated partial effect of f_{local} variables (see methods 5.2) on (a) GM and (b) pBC. The Y-axis shows the annual change in GM or pBC for each unit of the f_{local} variables. Photosynthetic activity is measured as average EVI across the entire landscape and time period (1984-2017). SPEI stands for the Standardised Precipitation-Evapotranspiration Index (Vicente-Serrano et al., 2010). Flat lines without uncertainty indicate that the term was penalized out during the model fitting and therefore had no additive effect on the biodiversity measure. Error margins show the estimated standard errors of the partial effect.

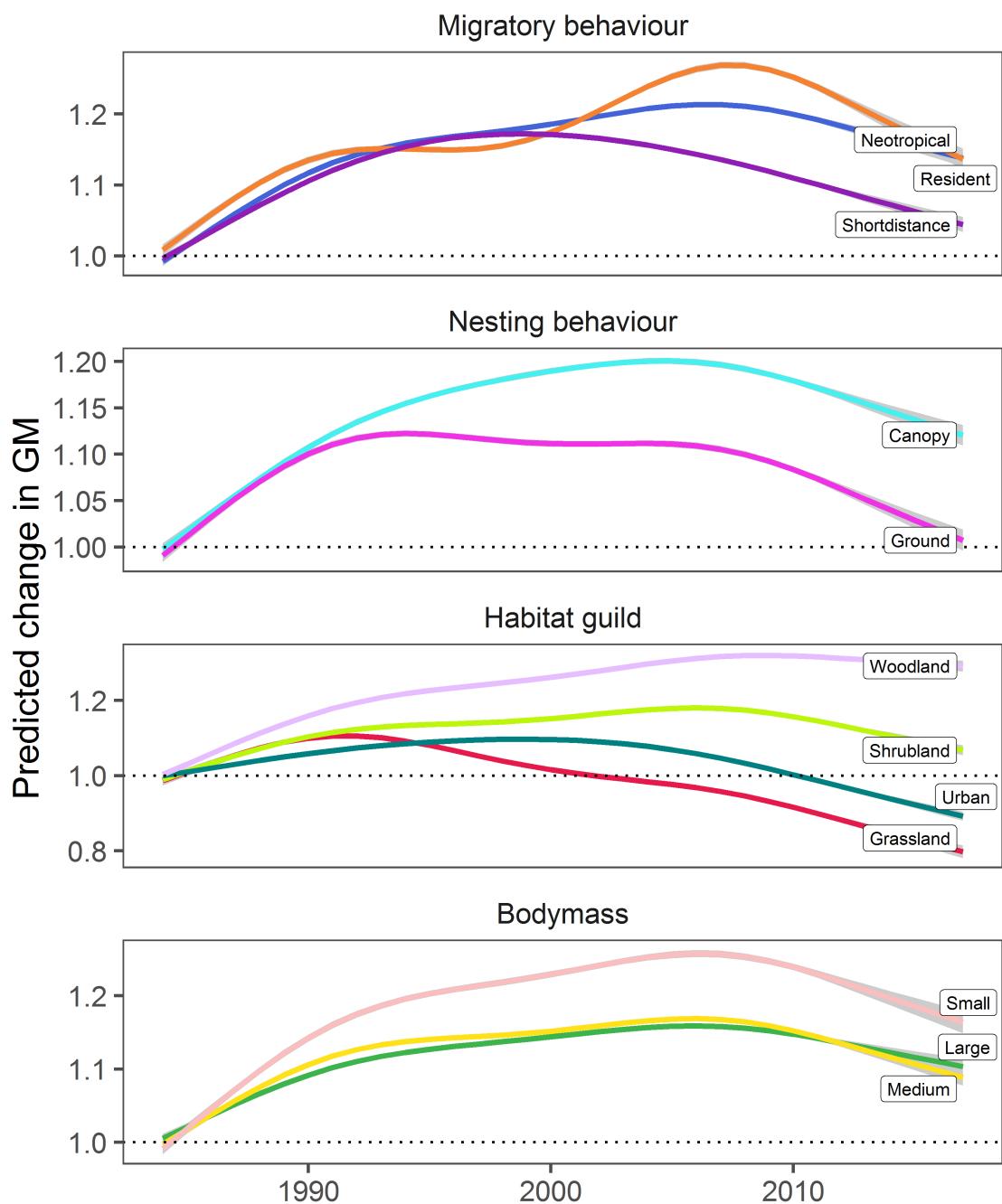


Figure A.5.12: Change in GM for bird species binned by functional groups of traits. Coloured for better visual distinction only. Error ribbons show the predicted standard error.