ASSESSING THE TRADE-OFF BETWEEN FOREST PRODUCTIVITY AND ANIMAL BIODIVERSITY IN EUROPE

CALYNE NASAMBU KHAMILA
February 2019

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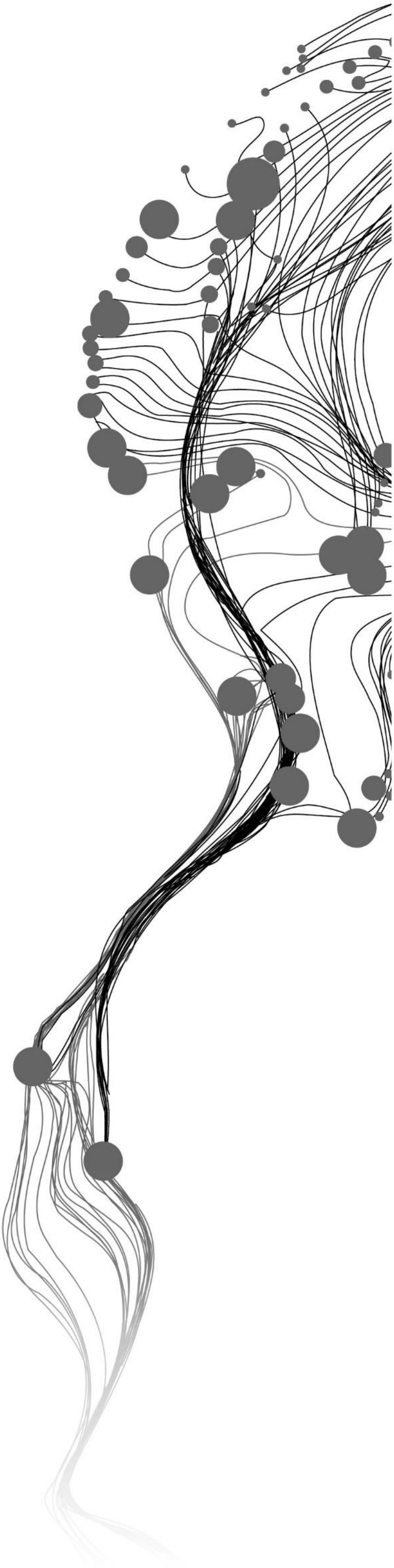

ASSESSING THE TRADE-OFF BETWEEN FOREST PRODUCTIVITY AND ANIMAL BIODIVERSITY IN EUROPE

CALYNE NASAMBU KHAMILA
Enschede, The Netherlands, February 2019

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ABSTRACT

The ability of forests to supply raw materials such as wood to industries, as well as their capacity in maintaining biodiversity and their role to support the functioning and services of natural ecosystems, make forests important terrestrial ecosystems. European forests are particularly valued because they supply wood products that enhance bio-energy consumption across the region. These forests are also important habitats for plants and animal species, and there is a thrust to strengthen biodiversity conservation. The combination of policies for wood production and biodiversity conservation places potentially competing demands on European forests.

To develop viable strategies to maximise productivity from European forests and maintain at the same time biodiversity requires an in-depth understanding of the spatial interaction between productivity and biodiversity. Currently, there is limited knowledge on how productivity is related to animal biodiversity because earlier studies either focused on productivity and diversity exclusively for plants or those which investigated productivity and animals did not consider different biodiversity measures, but mostly relied on species count. Moreover, research on the spatial congruence between productivity and animal biodiversity is currently lacking, although, there are many studies showing the spatial distribution of these two ecosystem services independently. Understanding the spatial relationship between productivity and animal biodiversity along with their spatial congruence can offer an avenue for sustainable management and conservation of forests in Europe.

Remote sensing techniques, in particular, MODIS are widely used to monitor forest productivity. On the other hand, various indices exist to measure ecosystem diversity. Relating MODIS productivity and animal biodiversity can provide insight into the spatial pattern of productivity and animal biodiversity. This study aimed to measure animal biodiversity (mammals, birds, herpetofauna, butterflies and overall animal biodiversity) of European forests using species count, Margalef, Shannon-Wiener and Simpson indices. Since these indices capture different facets of biodiversity, the study also aimed to investigate how they differed regarding the quantity of animal biodiversity they measured by correlating pairs of indices. After that, using the MODIS NPP and animal biodiversity, regression analysis was performed to identify the spatial relationship between productivity and animal biodiversity. Additionally, their upper and lower quantile values were identified, and an overlay analysis made to determine their spatial congruence.

The results revealed that the quantity of biodiversity differed depending on the indices, but Simpson showed the highest biodiversity compared to species count, Margalef or Shannon-Wiener indices. Simpson also showed a lower correlation with either of these indices meaning that it quantified biodiversity differently; hence it may have contained extra information. Meanwhile, productivity was positively related to overall animal biodiversity and biodiversity of mammals, herpetofauna and butterfly, but negatively related to birds. The strength of each relationship, however, varied in respect to forest type and biodiversity index used. At the same time, the level of spatial congruence between productivity and all groups of biodiversity were somehow significant and found in the same range, but a weak congruence was observed with birds. Based on these finding, the study suggests that assessing biodiversity should be done using Simpson and at least species count, Margalef or Shannon-Wiener indices. Similarly, investigating the relationship between productivity and animal biodiversity should consider Simpson and at least one of these indices. The result of this study can serve as a foundation to assist in implementing policies for sustainable planning and using forest resources in Europe.

Keywords: productivity, animal biodiversity, biodiversity index, spatial pattern, synergies and trade-offs, European forests

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Calyne Nasambu Khamila
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EAFTS : European atlas of forest tree species
EC : European Commission
ETRS : European Terrestrial Reference System
EU : European Union
FAO : Food and Agriculture Organisation
FPRA : Fraction of photosynthetically active radiation
GPP : Gross primary production
IPBES : Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services
IUCN : International Union Conservation of Nature
LAI : Leaf Area Index
MODIS : Moderate resolution Imaging Spectroradiometer
NASA : National Aeronautics and Space Administration of the United States
NPP : Net primary production
PA : Presence Absence
UNFCCC : United Nations Framework Convention on Climate Change
WGS : World Geodetic System

1. INTRODUCTION

1.1. Background information

Forests account for approximately 4.03 billion hectares of the earth's land surface and 80% of the plant biomass (Kindermann et al. 2008). Forest ecosystems are important because they are repositories to more than half of the global plant and animal species (Hassan et al. 2005), and are a source of raw materials for bio-energy production (Naumov et al. 2018). Globally, raw materials account for the highest demand placed on forest resources; for example in Europe, out of 1.02 billion ha of the forest area, nearly 83% is used for wood production (UN-ECE 2011). Significant forest areas are also designated for biodiversity conservation, and in Europe for example, at least 11% of the total forest area is set aside for this purpose (UN-ECE 2011; Verkerk et al. 2014). Other values of forest resources include climate change regulation, water supply and purification, and socio-cultural symbols (FAO 2018). Collectively, these benefits are inherently crucial to forest-dependent society and the wellbeing of the environment.

The concept of ecosystem services is highly considered in land use planning, conservation and developing policies for climate change regulation (Lecina-Diaz et al. 2018). Particularly, forest productivity aimed at increasing wood supply is globally recognised as potential sources of renewable energy which can replace fossil fuels. Fossil fuels are considered unsustainable because of their unpredictable high market prices and their threatening impacts of climate change. Biodiversity, on the other hand, is essential in maintaining the functioning and services of the natural ecosystem (Naeem et al. 2012). Specifically, animal biodiversity such as mammals (Jones & Safi 2011), birds (Whelan et al. 2015) herpetofauna (Valencia-Aguilar et al. 2013) and butterflies (Ghazanfar et al. 2016) promote pollination, disperse seeds, control pests and act as indicators of forest health and productivity. There is a thrust to strengthen biodiversity preservation because species loss may substantially impair the inherent values of the natural ecosystems.

The combination of policies related to intensive utilisation of wood products and biodiversity conservation, place potential competing demands on forests, which may lead to trade-offs in resource use. On the one hand, intensive forest management aimed at enhancing wood supply may have negative implications on biodiversity conservation (Pedroli et al. 2013). On the other hand, increased biodiversity protection may impose restrictions on wood removal thereby decreasing the potential of wood supply (Kallio et al. 2006). Whichever path forest use takes, either for wood supply or biodiversity protection; it is likely to lead to a dilemma (Verkerk et al. 2014) once the potential of either service is hampered.

Various international environmental bodies such as the United Nations Framework Convention on Climate Change (UNFCCC), the International Union Conservation of Nature (IUCN) and the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) have differently implemented multilateral agreements and processes (Morales-Hidalgo et al. 2015; Naumov et al. 2018) aimed to help either intensified forest management or biodiversity conservation. For example, there is the Paris Agreement on Climate change which advocates for intensive forest management to regulate climate change. There is also the Convention on Biological Diversity, which through the Aichi Biodiversity Targets aims to halt the loss of natural resources (Naumov et al. 2018). However, for successful efforts, there is a need to reach a reasonable compromise between forest productivity and animal biodiversity conservation. Understanding their relationship could potentially aid in viable strategy development.

Previous studies have been conducted to model the relationship between forest productivity and biodiversity. Different spatial patterns have been encountered. Species-energy theory ("a commonly invoked theory" according to Hurlbert (2004)) suggests that there is a positive relationship between species richness and available energy (Wright 1983). Consistent with this observation is Youngentob et al. (2015). For a unimodal pattern, it is hypothesised that species richness first increases with productivity and then start decelerating (Bailey et al. 2014; Fraser et al. 2015). Other researches have shown that there is no relationship between productivity and biodiversity (Teodoro et al. 2013).

Indeed, the different findings by earlier studies raise a further question on what the actual relationship between productivity and biodiversity is. There are some studies which have stated that it may be dependent on the scale, type of forest, biodiversity measure used (Lecina-Diaz et al. 2018) or taxon under investigation (Mittelbach et al. 2001). However, few studies have explicitly explored how these factors determined this relationship. Many of these studies did not compare biodiversity from different indices but predominantly relied on species count (see references above). Other studies assessed productivity-biodiversity relationship but only for plants (see Liang et al. (2016) for example). Theoretical knowledge, however, states that mixed forests harbour more biodiversity than monoculture forests (Elmer et al. 2004) because they offer a wide range of habitat which results to a variety of resources (Knoke et al. 2008); hence allowing coexistence of diverse species. A more practical study to provide an improved understanding of the relationship between productivity and animal biodiversity measured by different biodiversity indices, across taxa and forest types is thus needed.

In the meantime, ecologists can maximise production from every forest tree and conserve every animal if only they had sufficient financial resources. Ideally, if they know where every tree or animal is found, what its status is, which actions threaten it, then funds can be channelled for its management. However, this is not practical; rather, it calls upon prioritisation on how trees and animal species can sustainably be managed and conserved at least costs. One approach is to identify areas of high potential values, henceforth, referred to as "hotspots" where there is high tree productivity or animal biodiversity or both. Identifying these areas can help to strengthen preservation, in cases of animal biodiversity hotspots, and maximise the potential supply of wood, in cases of productivity hotspots. Therefore, analysing this relationship should extend beyond simply looking at how a unit change in productivity relates to animal biodiversity, to include the spatial congruence of these services.

In earlier studies, patterns of productivity and biodiversity across forests were explored. Neumann et al. (2016) mapped productivity of forests of Europe. The spatial patterns of wood production from forests have also been studied (Hurtt et al. 2006; Verkerk et al. 2015). Geographical patterns of biodiversity have also been mapped based on the hotspots of rare species of plants and animals (Prendergast et al. 1993), terrestrial vertebrate (Myers et al. 2000), species richness and endemism (Orme et al. 2005) and terrestrial vertebrates and endemism (Lamoreux et al. 2006). However, productivity and animal biodiversity have not been spatially compared. This presents a critical missing link regarding their spatial congruence, and perhaps, understanding this congruence may reveal synergies or trade-offs which can aid in sustainable management and conservation strategies.

Recent advances in remote sensing techniques provide an avenue to further examine the interaction between plants and animals at a regional scale. Moderate resolution Imaging Spectroradiometer (MODIS) is widely used to monitor and measure forest productivity (Zhao et al. 2005), hence can be used to derive net primary productivity (NPP). NPP is the net carbon or biomass fixed by vegetation through the process of photosynthesis (Neumann et al. 2016) and is recognised as a potential measure of forest productivity (Phillips et al. 2008). Biodiversity can comprehensively be measured using different indices, given that a measure which can act as a true surrogate for biodiversity, rarely exists (Devictor et al. 2010), partly because of the numerous dimensions of biodiversity (Manhães et al. 2016). The MODIS NPP can then be related to animal biodiversity to reveal their interaction across the forest biome. Understanding this interaction can have a significant implication on biodiversity conservation (Youngentob et al. 2015) and help in sustainable decision making particularly in intensively managed forests (Lindenmayer & Hobbs 2004).

This study sets out to explore the relationship and the spatial congruence between productivity and animal biodiversity. The structured workflow of this paper is organised in the following ways. The remaining part of section 1 will present the underlying research problem, objectives, questions and hypothesis of the study. Section 2 explores the study area and data available. Section 3 will give a general framework on the methods along with data analyses. In section 4, the results of this study will be presented. Section 5 provides an in-depth discussion of the results along with what existing studies have documented. The study will conclude in section 6 with an avenue for future study.

1.2. Problem statement

Despite the ongoing effort to lessen pressure on forests, sustainable use of forest resources and biodiversity conservation are key challenging issues in many countries. Particularly, intensified forest management is affecting ecosystem services such as biodiversity. The current rate of species loss and extinction threatens the functioning and services of forest ecosystems (Isbell et al. 2015). There is pressure on countries to preserve forest resources to prevent further loss of biodiversity (Verkerk et al. 2014).

In Europe, the increasing demand for raw material supply to the industries is putting pressure on forests. Policies (such as EU climate and Energy package) are developed across the region to promote intensification of forest management. Additionally, the international efforts such by UNFCCC which aims to monitor climate change and expects member countries to report the status of carbon "emissions and removals from forest" resources in their countries (Groen et al. 2013), exacerbates intensified forest management at the expense of biodiversity. On the other hand, reinforcing biodiversity conservation efforts restricts the potential production of wood from European forests.

Viable strategies are needed to ensure sustainable use of European forests. Previous studies such as by Lindenmayer & Hobbs (2004) and Youngentob et al. (2015) have shown that understanding the spatial interaction between productivity and biodiversity can be essential in management and conservation actions. However, knowledge on the relationship between productivity and biodiversity particularly for animal species is currently limiting. Moreover, limited studies have been conducted on the spatial congruence between these two ecosystem services. Therefore, it makes it hard to apply any existing knowledge on European forests where research has not been exhaustively established.

The present study mainly aims to investigate the relationship between productivity and animal biodiversity and assess their spatial congruence. Hopefully, it will be useful in the following ways: 1) generate knowledge to ensure forest policy formulation and implementation are scientifically sound and helping both productivity and animal biodiversity conservation; 2) provide insight on areas which may need to be looked into in terms of management; and 3) contribute to the research of the spatial patterns of productivity and biodiversity.

1.3. Research objectives

This study explores the spatial patterns of forest productivity and animal biodiversity of European forests. Net primary productivity will be used as a proxy for productivity and will be related to overall animal biodiversity, and separately to the biodiversity of mammals, birds, herpetofauna (reptiles and amphibians) and butterflies. This objective will be supported by the following sub-objectives:

1) Calculate animal biodiversity using species count, Margalef, Shannon-Wiener and Simpson indices
2) Examine the correlation between the quantity of animal biodiversity calculated by species count, Margalef, Shannon-Wiener and Simpson indices
3) Investigate the spatial relationship between overall productivity and overall animal biodiversity
4) Analyse the spatial relationship between overall productivity and biodiversity of mammals, birds, herpetofauna and butterflies
5) Assess how the relationship between productivity and overall animal biodiversity change across monoculture, mixed, coniferous, broadleaved and coniferous-broadleaved mixed forests
6) Assess how the relationship between productivity and biodiversity of mammals, birds, herpetofauna and butterflies change across monoculture, mixed, coniferous, broadleaved and coniferous-broadleaved mixed forests
7) Evaluate the spatial congruence between the areas of hotspots/medium-spots/coldspots of productivity and overall animal biodiversity, and biodiversity of mammals, birds, herpetofauna and butterflies

1.4. Research questions

1) What is the quantity of animal biodiversity for specific species groups based on species count, Margalef, Shannon-Wiener and Simpson indices?
2) What is the correlation between the quantity of animal biodiversity calculated by species count, Margalef, Shannon-Wiener and Simpson indices?
3) What is the observed spatial relationship between overall productivity and overall animal biodiversity?
4) How is overall productivity related separately to the biodiversity of mammals, birds, herpetofauna and butterflies?
5) How does the spatial relationship between productivity and overall animal biodiversity or biodiversity of specific species groups change across monoculture, mixed, coniferous, broadleaved and coniferous-broadleaved mixed forests?
6) What is the spatial congruence between hotspots/medium-spots/coldspots areas of productivity and overall animal biodiversity or biodiversity of specific species groups?

1.5. Research hypotheses

1) The quantity of animal biodiversity calculated by species count, Margalef, Shannon-Wiener and Simpson indices is positively correlated
2) There is a positive relationship between overall productivity and overall animal biodiversity
3) There is a positive relationship between overall productivity and biodiversity of mammals, birds, herpetofauna and butterflies
4) The relationship between productivity and overall animal biodiversity or biodiversity of specific species groups varies across different forest types, and a stronger positive relationship is expected in the mixed forests than monoculture, and in coniferous-broadleaved mixed forests than in coniferous or broadleaved forests.
5) Sites with high productivity will support high overall animal biodiversity and high biodiversity of specific species groups leading to a strong spatial congruence.

2. STUDY AREA, MATERIALS AND DESCRIPTION

2.1. Study area description, climate and vegetation

The study area covers the EU Member States, Switzerland and Norway as illustrated in Figure 1 below. It is geographically situated approximately between 66^{o}0’0”N to 45^{o}0’0”N and 32^{o}0’0”W to 49^{o}0”0’E. Due to the significant scale under study, this area experiences varied topographic and climatic conditions with heterogeneous landscapes (Lindner et al. 2010).

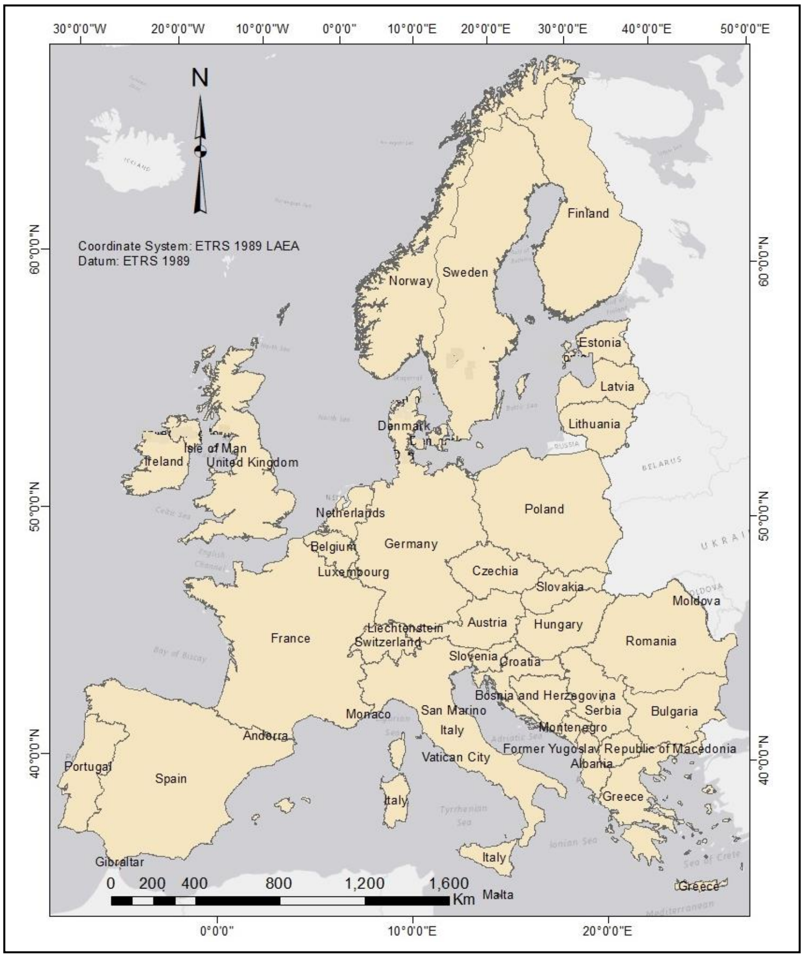


Figure 1: The location of the study area in the region of Europe

The climate in Europe is mainly influenced by the Atlantic Ocean’s Gulf Stream current. The continental landforms such as mountain ranges comprising of the Pyrenees and the Alps also affect the climate in some parts of Europe. Mediterranean condition also exerts some impact on climate in this region. Generally, climatic conditions vary across this region and there are four particular macro-climatic zones including the boreal, temperate oceanic, temperate continental and Mediterranean (Lindner et al. 2010). Each of this region is characterised by a distinct annual temperature and precipitation (refer to Space (2000) and Lindner et al. (2010) for more information).

A wide range of vegetation extending from natural to planted characterises the study area. A vast majority of European forests have been shaped by human activities such as forest clearing for industrial and agricultural purposes, domestic herbivore grazing, and monoculture and exotic species productions (Bengtsson et al. 2000).

There are three broad groups of forests in Europe, and they include coniferous, broadleaved and coniferous-broadleaved mixed forest (Barbati et al. 2014). Coniferous trees are mainly cone-bearing and have needle leaves while broadleaved trees are recognized by their flat leaves and producing seeds inside their fruits. Coniferous forests predominate northern Europe. Broadleaved forests are mainly found in central Europe, but there are few species of coniferous such as Scots pine which also thrive in this region (Leuschner & Ellenberg 2017). Coniferous tree species are important because of their commercial value and they are more productive when they grow in broadleaved habitats than in natural coniferous habitats, hence they are widely planted (Leuschner & Ellenberg 2017). The coniferous and broadleaved forests are each characterised by specific types of tree species. There are twenty types of dominant tree species which are spatially distributed across the study area as shown in Figure 2 below.

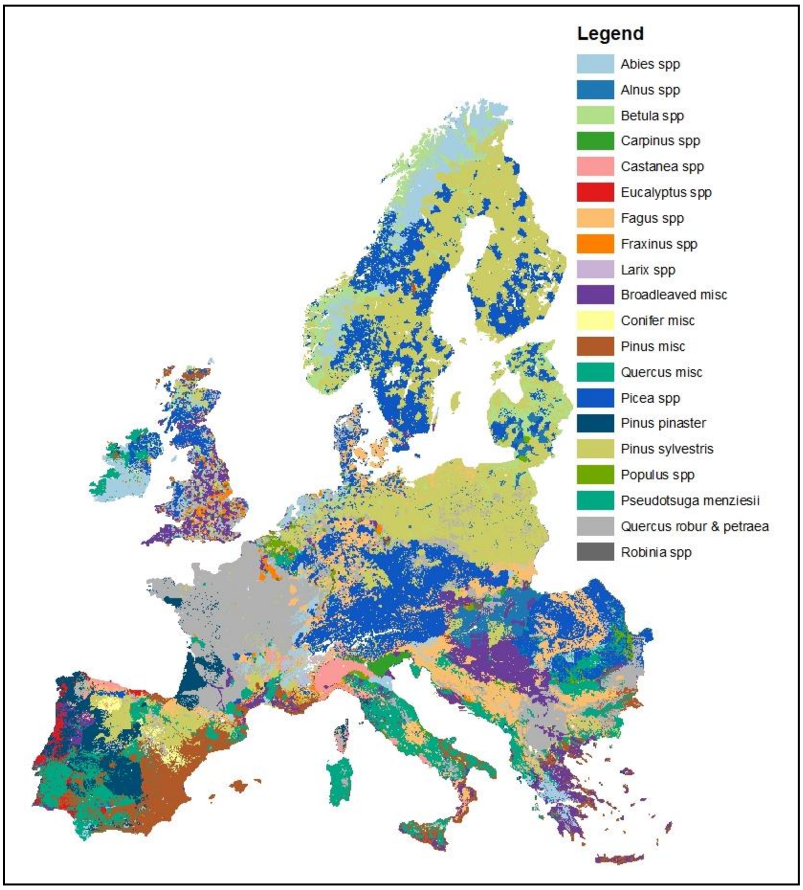


Figure 2: The spatial distribution of 20 dominant tree species across the study area (source: Brus et al (2011))

2.2. A generic summary of the materials, description and analytical methods

An overview of the materials (Table 1) leading to the analytical methods (Figure 3) applied in this study is as follows: In respect to productivity data, the spatial tree distribution data having 20 dorminant tree species was used to classify forests into monoculture, mixed, coniferous, broadleaved and coniferous-broadleaved mixed forests; this was followed by applying an 80% threshold to separate monoculture from mixed forests, and coniferous and broadleaved from coniferous-broadleaved mixed forests (Step 1). After that, forests were only restricted to areas with at least 10% of the forest cover (Step 2). In this same step, the 20 tree species were combined to get the total forest cover. In Step 3, forests types were assigned productivity from MODIS NPP reference data, thereafter, they were validated, and outliers removed (Step 4). Moving onto the animal species data, probability files were first rectified (Step 1), followed by stacking and conversion into binary maps using a predefined threshold method (Step 2). In Step 3, animal biodiversity was calculated, followed by validation and outlier removal (Step 4). From there, productivity was regressed with animal biodiversity and their relationships determined (Step 5). In step 6, a 30 percent quantile was used to delineate hotspot and coldspot areas, and the intermediate areas, assigned as medium-spots (this was done separately for productivity and animal biodiversity). After that, the maps belonging to the two ecosystem services were overlaid and their spatial overlap determined (Step 7).

2.3. Materials

Table 1 below presents materials, their description and the date which they were acquired

Table 1: Materials available for the study, their description and the date which they were acquired

Materials	Description	Acquisition date
Spatial tree distribution	20 rasters each representing the spatial distribution of a single dominant tree species; ETRS 1989 spatial reference; 1km spatial resolution	2011
MODIS NPP	Mean annual NPP; 12 rasters listing annual NPP between years 2000-2012; WGS 1984 spatial reference; 0.0083^{o} spatial resolution; 10*gram carbon meter -2 year -1 units	Annual, 2000 to 2012
Mammals	126 number of species, rasters; ETRS 1989 spatial reference; 5000m spatial resolution	2000 to 2015
Birds	294 number of species, ascii; ETRS 1989 spatial reference; 5000m spatial resolution	2000 to 2015
Herpetofauna	147 number of species, images; ETRS 1989 spatial reference; 5000m spatial resolution	2000 to 2015
Butterfly	381 number of species, ascii; ETRS 1989 spatial reference; 5000m spatial resolution	2000 to 2015
Mask	Reference raster for spatially rectifying all files, ETRS 1989 spatial reference; 5000m spatial resolution	Not applicable

2.4. Data description

2.4.1. Spatial tree distribution

To classify European forests into monoculture, mixed, coniferous, broadleaved and coniferous-broadleaved mixed forests, data from Brus et al. (2011) was used. This dataset with a spatial resolution of 1km by 1km provides information on tree cover (expressed as a percentage) for the entire study area for the 20 most dominant tree species. Meanwhile, the resolution of this data was very high. Therefore, it had to be aggregated to align it with the mask reference raster. This aggregation may have tampered with the original information.

2.4.2. MODIS NPP

Net Primary Productivity (NPP) refers to the net carbon or biomass fixed by vegetation through the process of photosynthesis. To represent NPP across the study area remotely sensed productivity from Neumann et al. (2016) was used. The MODIS NPP was derived from the MOD17 algorithm which uses reflectance data from TERRA and AQUA, the satellites of the National Aeronautics and Space Administration of the United States (NASA). The inputs to MOD17 are climate data, land cover data, leaf area index (LAI) and fraction of photosynthetically active radiation (FPAR) (Neumann et al. 2016). The MOD17 gives estimates of Gross primary production (GPP) and NPP at a spatial resolution of approximately 1km by 1km. MODIS NPP provides detailed information on the annual forest productivity conducted between years 2000 to 2012. Averaging the annual productivity within this time-frame provides an estimate of the average productivity of European forests.

One primary motivation behind the selection of this dataset was that NPP is considered a surrogate for measuring forest biomass and wood (Serra-Diaz et al. 2013), and these are the ecosystem services that are of interest to the present study. Additionally, NPP was preferred over other productivity measures such as Normalized Difference Vegetation Index (NDVI) because it has been found to show consistent measurements of productivity across forest structures (Phillips et al. 2008).

2.4.3. Animal species data

Data consisted of four groups of terrestrial vertebrates, comprising of mammals, birds, herpetofauna (reptiles and amphibians), and one group of terrestrial invertebrates, butterflies. In total, there was data on 948 species. Every species was represented in a single raster, and every pixel of the raster was having a value representing the probability of occurrence of a species. The probability of occurrence values was ranging between 0 and 1, showing low and high chances of finding a species, respectively.

This species data was produced in response to a European Commission call to see how effective the Natura 2000 Network is, in regard to protecting species within its conservation network. Briefly, Natura 2000 is a network of protected areas which conserves the most valuable and threatened species of Europe (EC 2019). The data covers the species with common occurrence and benefiting from Natura 2000 protected sites, and those outside the protected zones as well (van der Sluis et al. 2016).

The choice of this species data for the study was motivated by a study by Lamoreux et al. (2006) which showed that terrestrial vertebrates are widely used to represent animal biodiversity. Additionally, both the vertebrate and invertebrate animals used in this study are recognised as a representative of European animal biodiversity; hence it sufficed the goal of this study.

3. METHOD DESCRIPTION AND DATA ANALYSES

The analytical methods leading to the achievement of the objectives of the present study are presented in Figure 3 below:

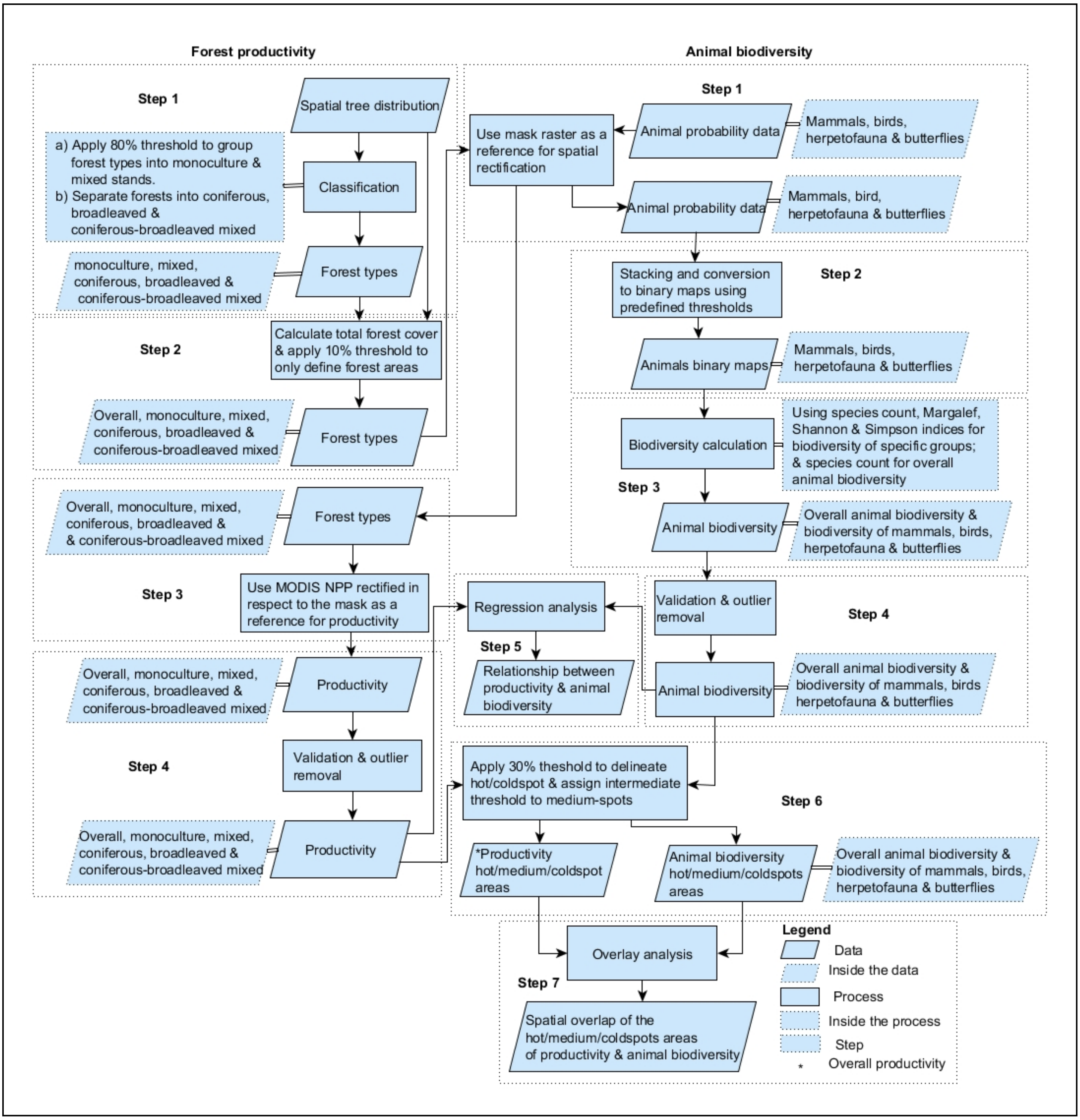


Figure 3: Flow chart of the research methods

3.1. The detailed description of the analytical methods

3.1.1. Overall forest productivity

To calculate overall productivity, spatial tree distribution data was used. The 20 rasters listing dominant tree species were added up using ESRI's Cell statistics tool to get the total value per pixel of forest cover. The totals, however, gave values which were more than the maximum 100%. There were 30 pixels with values above 100%, and the cause of this was due to the projection between different zones (as verified by producers; personal communication). These values above 100% were capped to the maximum 100%. After that, following the definition of forest cover according to FAO (2000), forest area was filtered to only pixels with values above 10%. This resulted in the overall tree species cover data which was then resampled in respect to the mask reference to a 5km by 5km pixel size.

After resampling, the next step was to determine productivity of overall tree species cover based on the MODIS NPP. However, before that, the MODIS NPP needed to be comparable to the mask reference raster. Therefore, the MODIS NPP was first projected to the ETRS 1989, clipped and resampled using the bilinear resampling to a common grid format with 5km by 5km grid cell. The two dataset were then overlaid, and productivity assigned on the basis of pixel by pixel values.

3.1.2. Monoculture and mixed forest productivity

Following Toumeny & Korstian (1947) and Bravo-Oviedo et al. (2013) classification of forests as either monoculture or mixed stand was performed based on the pixels with 80% or more of a single tree species type. Using this threshold, conditional expressions were formulated in raster calculator, and the process was carried out in the model builder, where pixels across all the 20 species-rasters were iterated over, and those with values of at least 80% were added up to get the monoculture forests. The same procedure was repeated for the mixed forests but now considering pixels with less than 80% of the forest cover. A final step for each forest was to select only pixels having at least 10% of the forest values, resample them to the mask grid cell and assign them productivity from MODIS NPP.

3.1.3. Coniferous, broadleaved and coniferous-broadleaved forest productivity

European Atlas of Forest Tree Species (EAFTS) database was used to give information on tree species types belonging to coniferous or broadleaved forests. Briefly, EAFTS is a comprehensive publication of trees where leading scientists and forest professionals channel ground data related to the distribution and type of forest trees species (San-Miguel-Ayanz et al. 2018). The species belonging to coniferous were the *Abies, Larix, Conifer, Pinus, Picea, Pinus pinaster, Pinus sylvestris* and *Pseudotsuga*; and to broadleaved were, the genera *Alnus, Betula, Carpinus, Castenea, Eucalyptus, Fagus, Populus,* and *Quercus*. After classifying species, they were added up in respect to their forest types. Using raster calculator, coniferous pixels whose values occupied 80% or more of the total forest value in a given pixel were classified as monoculture coniferous (or simply coniferous). The same procedure was repeated for broadleaved species. After that, coniferous and broadleaved species with values less than 80% of the total forest values in a given pixel were added to get the coniferous-broadleaved mixed forests. Again, the 10% threshold was applied to identify forests, followed by resampling to the mask reference and then assign them productivity from MODIS NPP.

Finally, productivity data was exported to R (R Core Team 2018) for further analysis. The initial values for productivity ranged from 0 to 6553.5gCm^{-2}y^{-1}. However, the raster contained extremely high values mostly at the edges, and these were associated with the overprediction by the MODIS. The specific causes of this overprediction of NPP in the MODIS product can be traced to the MOD17 algorithm inputs which include maximum light use efficiency, fraction of photosynthetically active radiation and climate data (see Turner et al. (2006) for details on the validation of MODIS NPP across various biomes). The high values at the fringes of the maps were treated collectively as outliers and removed accordingly. This resulted in the final productivity with values up to approximately 1500 g C m^{-2} y^{-1} as shown in Figure 4 below:

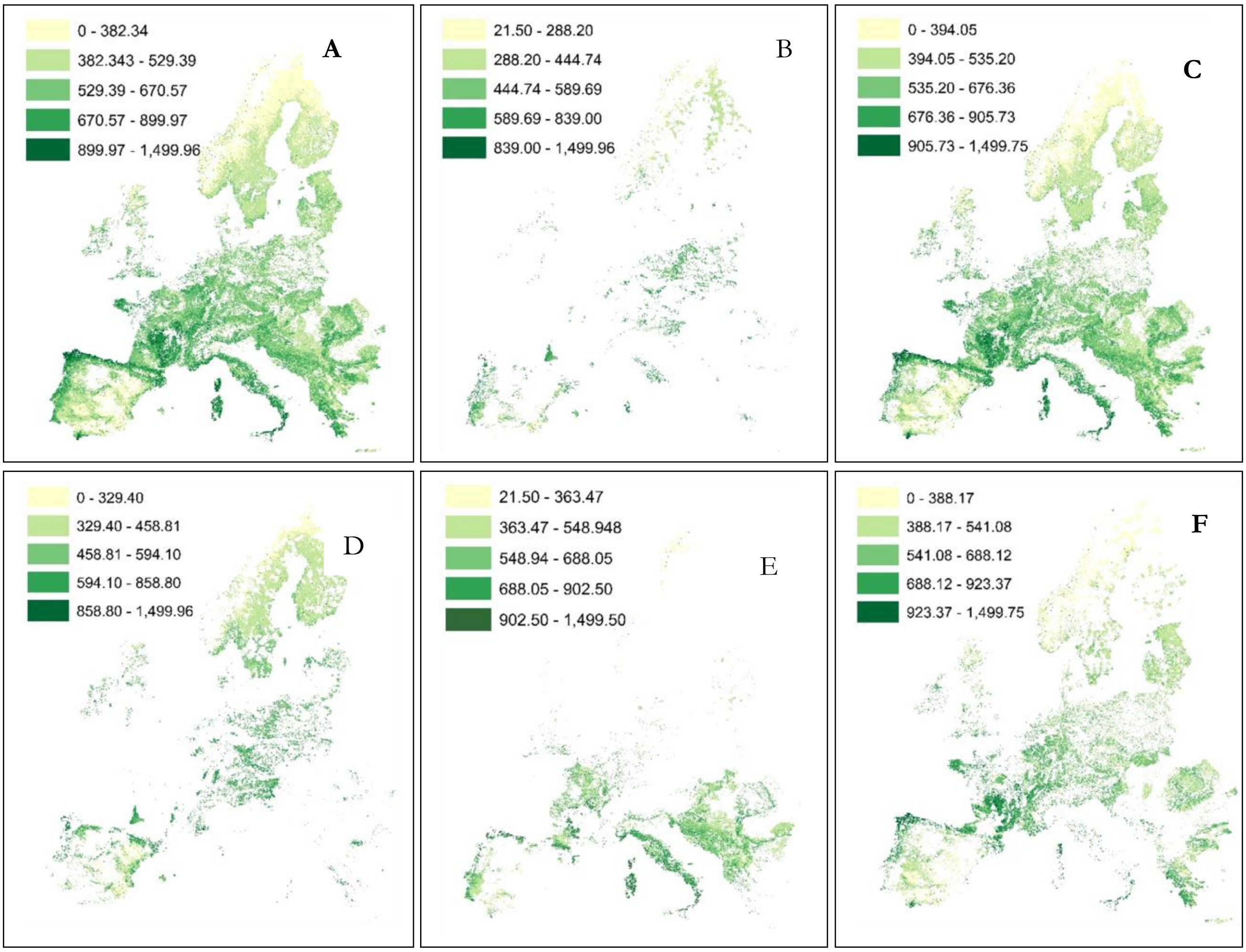


Figure 4: Spatial configuration of productivity of overall (A), monoculture (B), mixed (C), coniferous (D), broadleaved (E) and coniferous-broadleaved mixed (F) forest stands of Europe

3.1.4. Rectification of animal species data

The animal species data was corrected such that it was spatially aligned to the mask reference raster. Additionally, this dataset was standardised such that its information on probabilities was scaled between 0 and 1.

3.1.5. Stacking of animal species data

To get species richness and composition of a given region, the present study applied three steps: (1) selection of biodiversity quantification indices; (2) conversion of each map from a continuous probability of occurrence into presence-absence (PA) using a threshold criteria; and (3) quantification and validation of the PA to produce diversity maps.

3.1.6. Selection of biodiversity quantification indices

The indices that were initially selected to measure biodiversity were: Margalef (Margalef 1958), Shannon-Wiener (Shannon 1948) and Simpson (Simpson 1949). These indices were selected because they are the most common (Kanagaraj et al. 2017) and classic (Kiranya et al. 2018) indices to measure community diversity and have been widely used in various studies (Kanagaraj et al. 2017). For completion, species count was included. These four indices were chosen for comparison given that each measure a specific aspect of biodiversity (as highlighted in the next paragraph) and only one could not have provided adequate statistics or measure of biodiversity. Note that since many indices exist, and they can be used to do similar analyses; the present analyses are not exhaustive, rather illustrative.

- **Species count** is a richness index which computes biodiversity by counting the number of species within a community. The more species, the more biodiverse the community, irrespective of the taxonomic group to which the species belong.
- **Margalef index** considers species richness as a measure of biodiversity allocating a value between 0 and infinity with the highest value representing the most diverse and the lowest representing the least diverse community. Different from species count, it standardises the number of species present in a given sample in relation to the number of observations (Engemann et al. 2015). This index was meant to rectify sampling biases; however, it is sensitive to the number of sampling points (Gamito 2010; Engemann et al. 2015).
- **Shannon-Wiener index** (also known as Shannon-Weaver or simply as Shannon) is a measure of species richness and evenness. It accounts for species equitability and assumes all species to be present and randomly distributed in a community (Stirling & Wilsey 2001). However, it is sensitive to changes in the rare species (Peet 1974; Nagendra 2002). Its biodiversity value ranges from 0 to 5, representing low to high diverse community, respectively.
- **Simpson index** is a measure of species evenness. It is known to be sensitive to the abundance of the most frequently occurring species in a community (Budka et al. 2018); hence it is seen as an index of "dominance of concentration" by Whittaker (1965). It computes biodiversity values ranging between 0 and 1, which represent low to high biodiversity, respectively.

The formulas below show how the four indices compute biodiversity:

Species count (C): $$C = Y1 + Y2 + Y3 \ldots\ldots nth \quad (1)$$

Margalef (R): $$R = \frac{S-1}{ln(N)} \quad (2)$$

Shannon-Wiener (H): $$H = -\sum_{i-1}^{s} Pi\ ln\ Pi \quad (3)$$

Simpson (D): $$D = 1 - \frac{\sum n(n-1)}{N(N-1)} \quad (4)$$

where *P* is relative abundance of species in a sample ; *i* is sample; *N* is total number of individuals in a sample; *n* is actual number of individuals of a single species, *S* is number of species; *ln* is natural logarithm; *Y* is presence or absence

3.1.7. Conversion of probability maps into presence-absence

Most existing studies (such as by Pottier et al. (2013) and Toro et al. (2018)) use presence-absence (PA) data when modelled probabilities are available. Liu et al. (2005) also stated that the use of PA presented more practical information than probability data in the context of environmental conservation and management, and this was indeed useful in regard to the present study's aim. On these bases, PA was used rather than probability, and in the rest of the discussion, animal species data referred to have been derived from PA, not probability.

To convert probability maps into PA maps, predefined thresholds method was used. This method leads to an accurate estimation of species richness and composition (Benito et al. 2013). However, in some cases, it may inevitably lead to errors of omission particularly for species with low prevalence. Consequently, species underestimation could be more costly than overestimation, particularly, when the purpose of estimation is to steer conservation plans (Pineda & Lobo 2009). To remedy these limitations, an effort was made to apply thresholds that were derived from Max TSS criteria (thresholds that were used to produce the probability maps), with every threshold having been fine-tuned in respect to a single species. Pineda & Lobo (2009) recognise using varied thresholds in respect to species types to be effective in reducing overestimation of species richness. Besides, predefined thresholds have proved useful in previous studies (such as by Luck (2002), Benito et al. (2013)). The conversion of continuous probability maps into PA was facilitated by *raster* package (Hijmans 2017) in R (R Core Team 2018).

3.1.8. Quantification of PA data, validation and creation of biodiversity maps

The maps were stacked for combined animal groups and for specific groups. To combine the diversity of multiple species groups into one index, the total number of species considered per group needed to be taken into account. For some species groups (butterflies) more species were considered than for the other species groups (mammals). To correct for these differences, species in each group were added up and divided by the maximum number of species (highest pixel value) of that group to get standardised sum which were eventually added up to get standardised animal biodiversity. To calculate biodiversity for specific species groups, species count, Margalef, Shannon and Simpson indices were used. Standardisation was not required.

After calculating animal biodiversity, data validation was performed by running quantitative tests to identify any pixels whose values deviated markedly from their neighbourhoods. Outliers were found in the mammal data and were removed. No outliers were identified in other species groups.

3.1.9. Delineation of hotspots/medium-spots/coldspots of productivity and animal biodiversity

A review of the existing articles to identify ways in which hotspots are defined was done. Various criteria for definition were found. For example, the top 5% of the total land area with the highest species biodiversity (Prendergast et al. 1993); should contain endemic plant species with at least 0.5% of all plant species worldwide (Myers et al. 2000); richest 2.5% of grid cells of species richness (Orme et al. 2005). While these definitions represent considerable terrestrial biodiversity and the most widely applied according to Orme et al. (2005), their concepts were not in line with the present study, partly because of the possible differences in the size of the area of interest. Moreover, criteria for hotspots definition may serve specific policy goals, thus, the extent of hotspots prioritisation tend to comply with specific conservation goals (Schröter & Remme 2016). In this regard, a 30% quantile method was selected for the present study.

The selection of the 30% threshold was motivated by Schröter & Remme (2016) and Korpilo et al. (2018) whose studies showed that the most common threshold for quantile range was between 5% and 30%. The 30% sufficed because it is neither too narrow nor too broad given the extent of the study area. Therefore, hotspots were defined as 30% pixels with the highest provision of either productivity or animal biodiversity, coldspots as 30% pixels with the lowest provision of either productivity or animal biodiversity, and the intermediate areas between hotspots and coldspots were assigned to medium-spots.

After delineation, productivity and animal biodiversity maps were overlaid, resulting in the areas where the hotspots, medium-spots and coldspots from productivity spatially overlapped those from animal biodiversity. After that, areas for each pixel in a given class was calculated and subsequently summed to get the total area for that class. *Tapply* function was used in R (R Core Team 2018) for that purpose. Maps were produced showing the spatial congruence between the areas of productivity and biodiversity for overall and specific animal groups.

3.1.10. Statistical analysis of animal biodiversity from species count, Margalef, Shannon and Simpson indices

An investigation of how biodiversity values for different indices were spatially distributed was done by means of a symmetry. The symmetry is determined by a measure of skewness which can either be left (also known as negative) or right (also known as positive) or normal (no skewness) (Moore & McCabe 2009). The skewness function of the *e1071* package (Meyer et al. 2018) was used to illustrate this skewness (S). Consistent with Gaedke & Klauschies (2017), the standard of skewness of distribution was interpreted as follows: small values of S, symmetric distribution; large negative or positive values of S, left or right-skewed distribution.

Pairs of indices in the same animal groups were correlated using Pearson's correlation coefficient (R) to show how they differed in the quantity of biodiversity they measured. Although these indices capture different concepts of biodiversity, if they correlated, it means they captured a similar quantity of biodiversity, by contrast, if they uncorrelated, they quantified biodiversity differently (Heino et al. 2005); hence may contain different information.

3.1.11. Statistical analysis of the relationship between productivity and animal biodiversity

For regression analysis, each animal biodiversity data was used separately as a function of each productivity data. For analysis involving combined animal biodiversity, a test was run to compare the results from unstandardised and standardised animal biodiversity dataset. During regression analysis, a sufficient number of pixels were sampled several times, and each time, coefficient of determination (R^2) from the resulting model recorded which were eventually averaged to get the final R^2. Note that sampling, however, did not affect the R^2 that much because even after running the model on the whole dataset, the R^2 remained within the same range. However, using very small samples was avoided because it reduced the statistical significance of the model. This process was conducted using *WVPlots* package (Mount & Zumel 2018) in R (R Core Team 2018).

4. RESULTS

4.1. Quantitative measure of animal biodiversity

4.1.1. Quantitative measure of overall animal biodiversity

The overall animal biodiversity when combining all species groups showed a wide range of variations (Table 2) which can be associated with major differences in the biodiversity across the study area. The distribution of biodiversity values was somehow symmetrically distributed, meaning that the intermediate biodiversity values had the highest frequency of occurrence than the lower or the upper values. The distribution of biodiversity values did not show significant differences when standardised animal biodiversity data was used, although, there was somehow a stronger symmetric distribution and a slight shift in the pattern of biodiversity in the southern parts of Europe as illustrated in Figure 6.

4.1.2. Quantitative measure of biodiversity of mammals, birds, herpetofauna and butterflies

The distribution of biodiversity values, irrespective of the animal species group, showed somehow a symmetric distribution for species count and Margalef indices. This symmetric distribution suggested that the occurrence of the highest frequency of biodiversity was mostly at the intermediate biodiversity values, while the lowest frequency was at the lowest and the highest biodiversity values. Shannon index also showed somehow a symmetric distribution in some cases, and a weak negatively skewed distribution in other cases. Simpson index, on the other hand, showed a negatively skewed distribution with the highest frequency of biodiversity values mostly occurring at the highest biodiversity values. Details are shown in Table 2.

A striking observation from herpetofauna biodiversity calculated by Simpson index was made where this index found very high herpetofauna biodiversity (in the boreal zone), a place where other indices predicted very low biodiversity (see Figure 7). The cause of this high biodiversity prediction by Simpson in that place calls for a further investigation; however, at the moment the present study links it to the inability of the model to allocate an optimum cut-off threshold for determining whether herpetofauna were present or absent in that area. (Refer to Figure 5 for the different zones of Europe).

Table 2: Range of biodiversity values and their skewness

Biodiversity index	**Overall biodiversity**		**a. Mammal biodiversity**		**b. Bird biodiversity**		**c. Herpetofauna biodiversity**		**d. Butterfly biodiversity**	
	range	skew	range	skew	range	skew	range	skew	range	skew
Species count	26-356	-0.17	0-49	0.91	1-127	0.000008	0-94	0.46	4-222	0.21
Standardised animal biodiversity	0.13-2.79	0.051	-	-	-	-	-	-	-	-
Margalef	-	-	1-13.1	0.53	1.44-26.01	-0.17	0-20.47	0.48	2-40.09	0.061
Shannon-Wiener	-	-	0-4.1	-0.55	0-4.84	-1.28	0-4.54	-1.17	1-5.4	-0.72
Simpson	-	-	0-1	-2.46	0.91-0.99	-15.3	0-1	-4.66	0.75-0.99	-2.16

Notes: Skew represents the skewness of biodiversity values; interpretation: positives for low biodiversity; negatives for high biodiversity; close to 0 for normal biodiversity

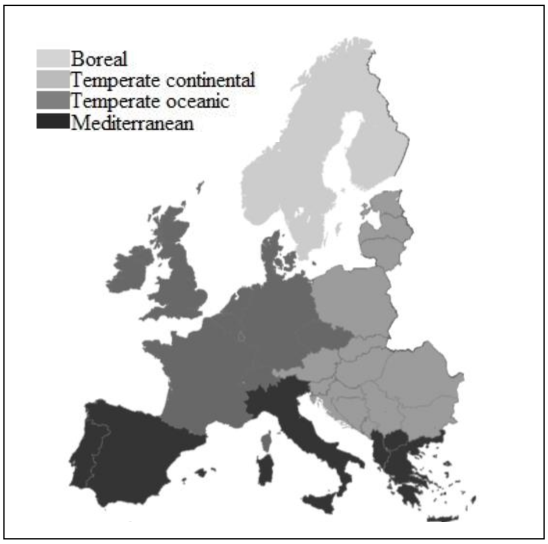


Figure 5: Spatial location of bioclimatic zones of Europe (source: adopted from Lindner et al. (2010))

Notes: The purpose of this Figure 5 is to show the different zones in Europe to help illustrate where the spatial distribution of animal biodiversity for each estimated quantity is found. In the latter sections, the figure will be referred to when explaining the locations of the various delimited areas from the spatial congruence between productivity and animal biodiversity.

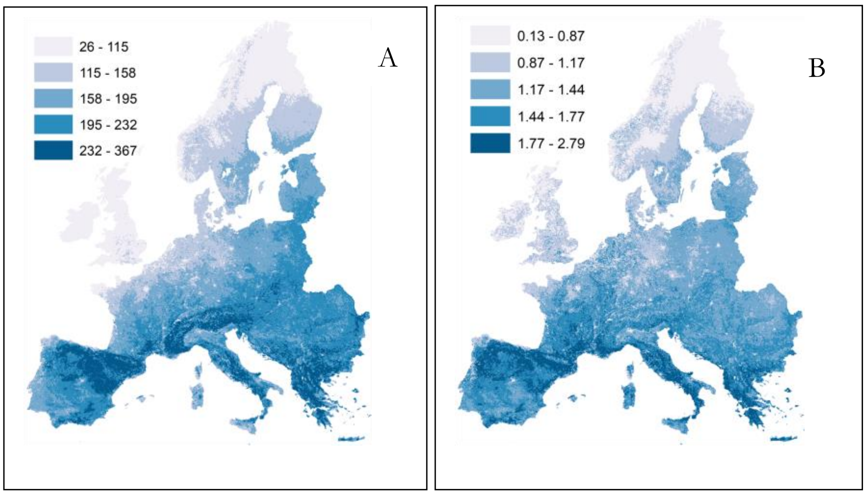


Figure 6: Spatial distribution of overall animal biodiversity (A) and standardised animal biodiversity (B)

Figure 7: Spatial distribution of biodiversity for mammals, birds, herpetofauna and butterflies as measured by species count, Margalef, Shannon and Simpson indices

4.2. Strength of correlation among biodiversity indices

Positive correlations were found for each paired indices in all species groups, but the magnitude tended to vary depending on paired indices and species groups. The highest correlation was found between species count and Margalef indices (R=0.99) in all species group. The correlation between Shannon, and species count, and Margalef were also high. A notable observation was made from the correlation involving Simpson as it showed considerable variation across species groups: the lowest correlation was observed between Simpson and species count, and Simpson and Margalef indices (R=0.36) in the herpetofauna species group; while the highest correlation was found between Simpson and Shannon index (R=0.95) in the butterfly species group. The observed differences in the strength of the correlation justify how mathematically independent the index are regarding how they measure biodiversity (Wilsey et al. 2005).

In the meantime, the magnitude of correlation which generally tended to vary across species groups showed that the indices were more similar when measuring biodiversity for butterfly but showed considerable variation when measuring biodiversity for herpetofauna. More detail is shown in Table 3 below.

Table 3: Strength of correlation between pairs of biodiversity indices

a. Mammal biodiversity				**b. Bird biodiversity**			
Biodiversity index	Margalef	Shannon	Simpson	Biodiversity index	Margalef	Shannon	Simpson
Species count	0.99	0.90	0.57	Species count	0.99	0.96	0.66
Margalef	-	0.91	0.60	Margalef	-	0.96	0.72
Shannon	-	-	0.75	Shannon	-	-	0.82
c. Herpetofauna biodiversity				**d. Butterfly biodiversity**			
Biodiversity index	Margalef	Shannon	Simpson	Biodiversity index	Margalef	Shannon	Simpson
Species count	0.99	0.87	0.36	Species count	0.99	0.96	0.84
Margalef	-	0.93	0.36	Margalef	-	0.97	0.86
Shannon	-	-	0.42	Shannon	-	-	0.95

4.3. Relationships between productivity and animal biodiversity

4.3.1. Relationship between overall productivity and overall animal biodiversity

A significant positive relationship was found between overall productivity and overall animal biodiversity. Analysis undertaken for the purpose of comparison using the same dataset but with standardised animal biodiversity showed a slight increase in the values of R^2. This result as illustrated in Figure 8 below suggests that 16.5% of the variation between overall productivity and overall animal biodiversity, and 24.7% of the variation between overall productivity and standardised animal biodiversity was explained. This result is generally indicating that increasing productivity increases animal biodiversity.

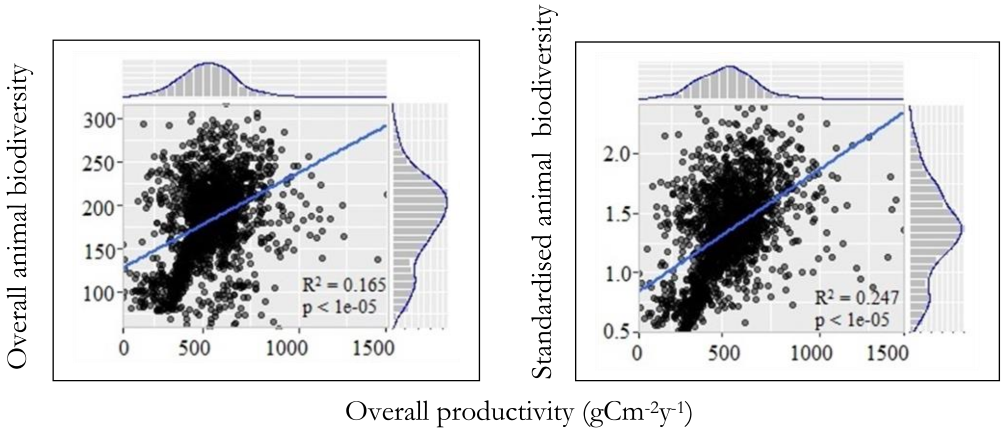


Figure 8: Regression plots of overall animal biodiversity and standardised animal biodiversity each as a function of overall productivity

4.3.2. Relationships between overall productivity and biodiversity of mammals, birds, herpetofauna and butterflies

Separating the animal dataset to account for the strength of the relationship between overall productivity and biodiversity of specific animal groups showed some variations. The most striking observation was made between bird biodiversity because this was the only species group which showed a negative relationship with productivity, when other species groups were showing a positive relationship. The finding (as shown in Figure 9) indicated that productivity explained 21.9%, 8.3%, 22.9% and 15.4% of the variation in biodiversity of mammals, birds, herpetofauna and butterflies, respectively (from species count).

Regressing productivity and species biodiversity from other indices did not yield much differences as can be seen in Figure 9. The strongest relationship was, however, observed between overall productivity and Shannon index, whereas, the weakest was between overall productivity and Simpson index. Interestingly, across all combinations, the overall productivity explained the strongest variation in the herpetofauna biodiversity calculated by Shannon index (31.8%) but explained the weakest variation in the same animal group for the biodiversity calculated by Simpson index (7.1%). In the meantime, the relationship between overall productivity and all biodiversity indices for the mammals, herpetofauna and butterflies were positive, but negative for birds (see the trendlines). Thus, this result highlights that increasing productivity increases biodiversity for all examined species groups but decreases the biodiversity of birds.

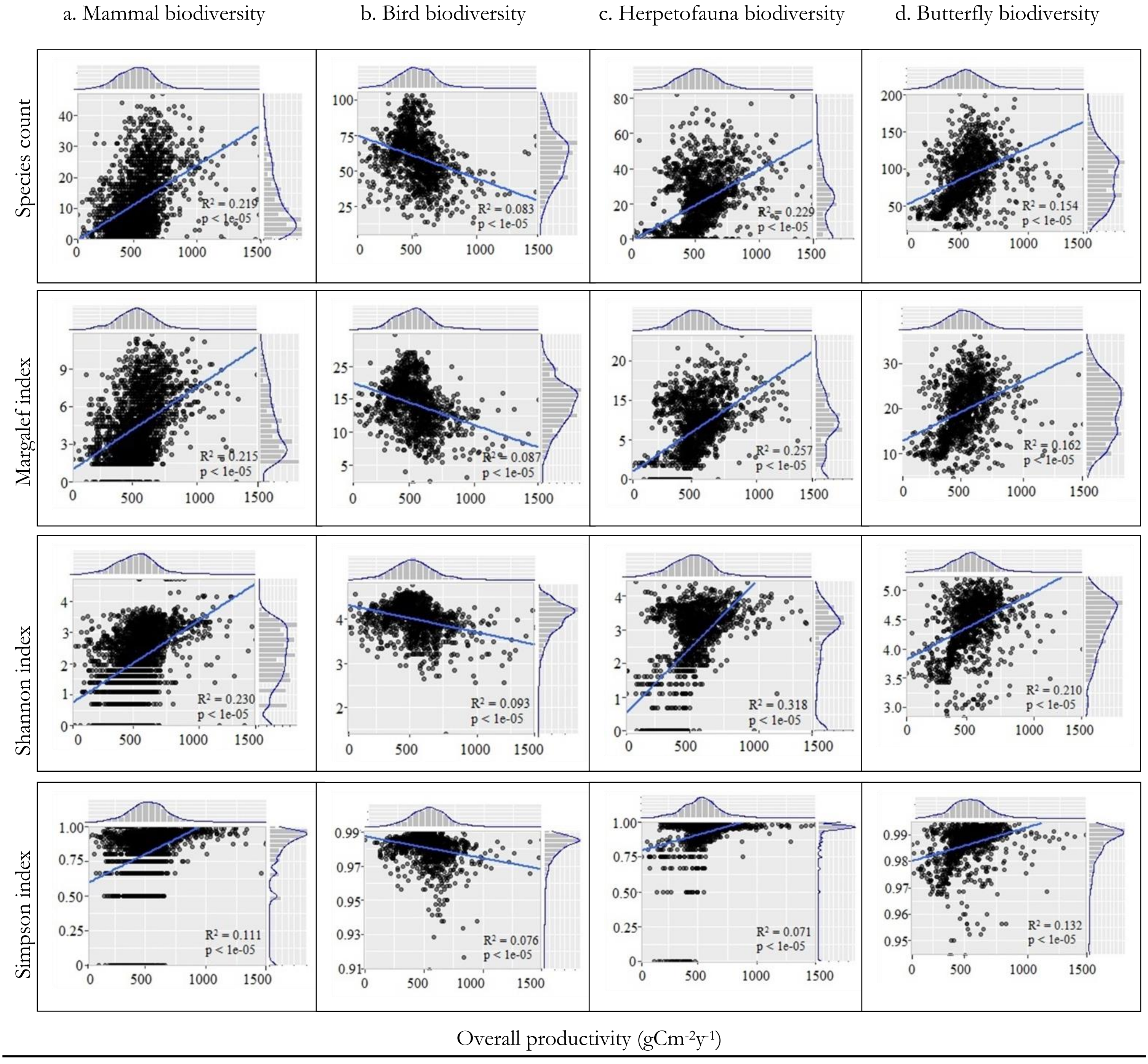


Figure 9: Regression plots of biodiversity of mammals, birds, herpetofauna and butterflies measured by species count, Margalef Shannon and Simpson, each as function of overall productivity

4.3.3. Relationships between productivity and overall animal biodiversity in different forest types

1) Relationships in the monoculture and mixed forests

Contrary to the expectation of the present study, productivity explained more variation in overall animal biodiversity in the monoculture forests (31.2%) than mixed forests (12.4%) (see the R^2 values in Figure 10). This variation increased relatively when standardised biodiversity was used in place of the overall animal biodiversity resulting in the variation of 36.8% in the monoculture and 19.9% in the mixed forests. These findings show that an increase in productivity increases overall animal biodiversity, and this rate is faster in monoculture than in mixed forests of Europe.

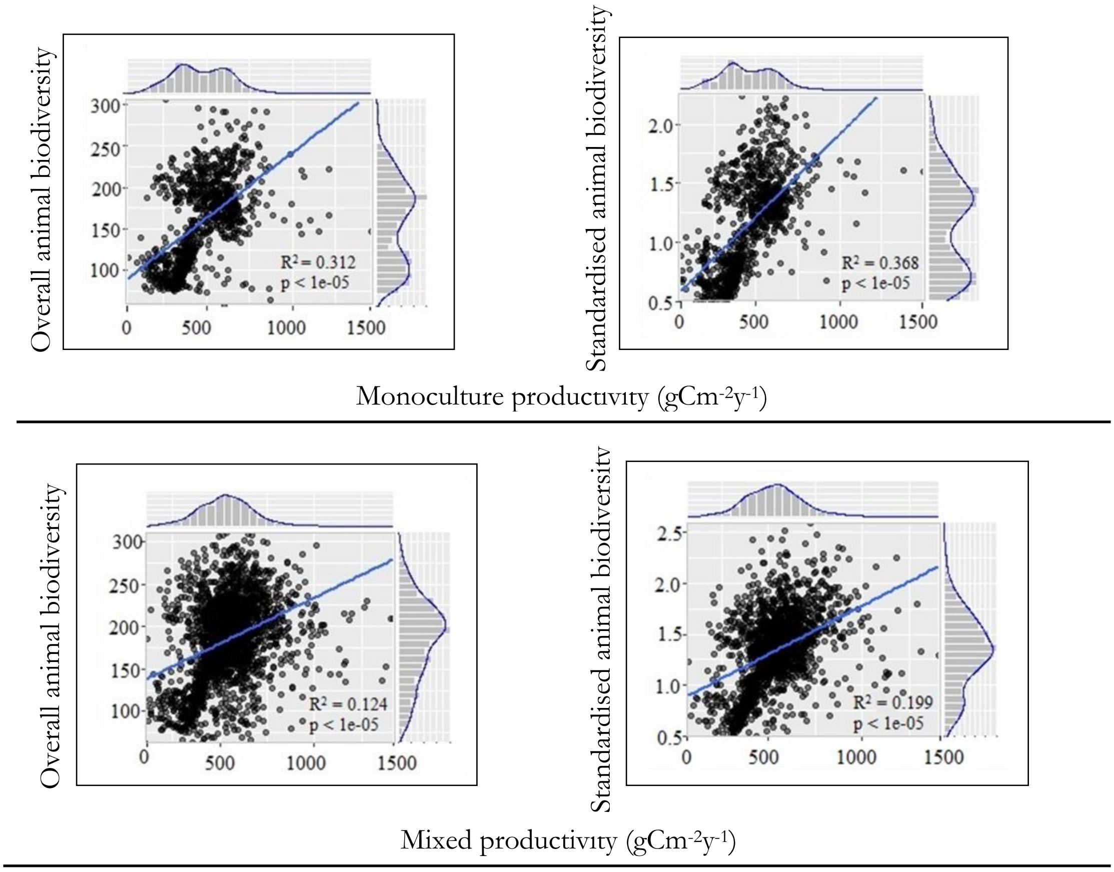


Figure 10: Regression plots of overall animal biodiversity and standardised animal biodiversity each a as a function of monoculture and mixed productivity

2) Relationships in the coniferous, broadleaved and coniferous-broadleaved mixed forests

Generally, productivity had a stronger positive effect on overall animal biodiversity in coniferous than broadleaved or coniferous-broadleaved mixed forests. Approximately, 28.3% of the variation of between productivity and overall animal biodiversity was explained in coniferous forests, while only 6.1% and 8.2% of the variation of the same combination was explained in broadleaved and coniferous-broadleaved mixed forests, respectively. Meanwhile, regressing productivity and animal biodiversity from the standardised dataset increased the variation more in coniferous-broadleaved mixed forests (14.6%) and broadleaved (13.0%) than it did in the coniferous forests (28.9%), although the strongest variation was still found in the latter. Based on the results shown in Figure 11, an increase in productivity increases animal biodiversity more in coniferous than broadleaved or coniferous-broadleaved mixed forests.

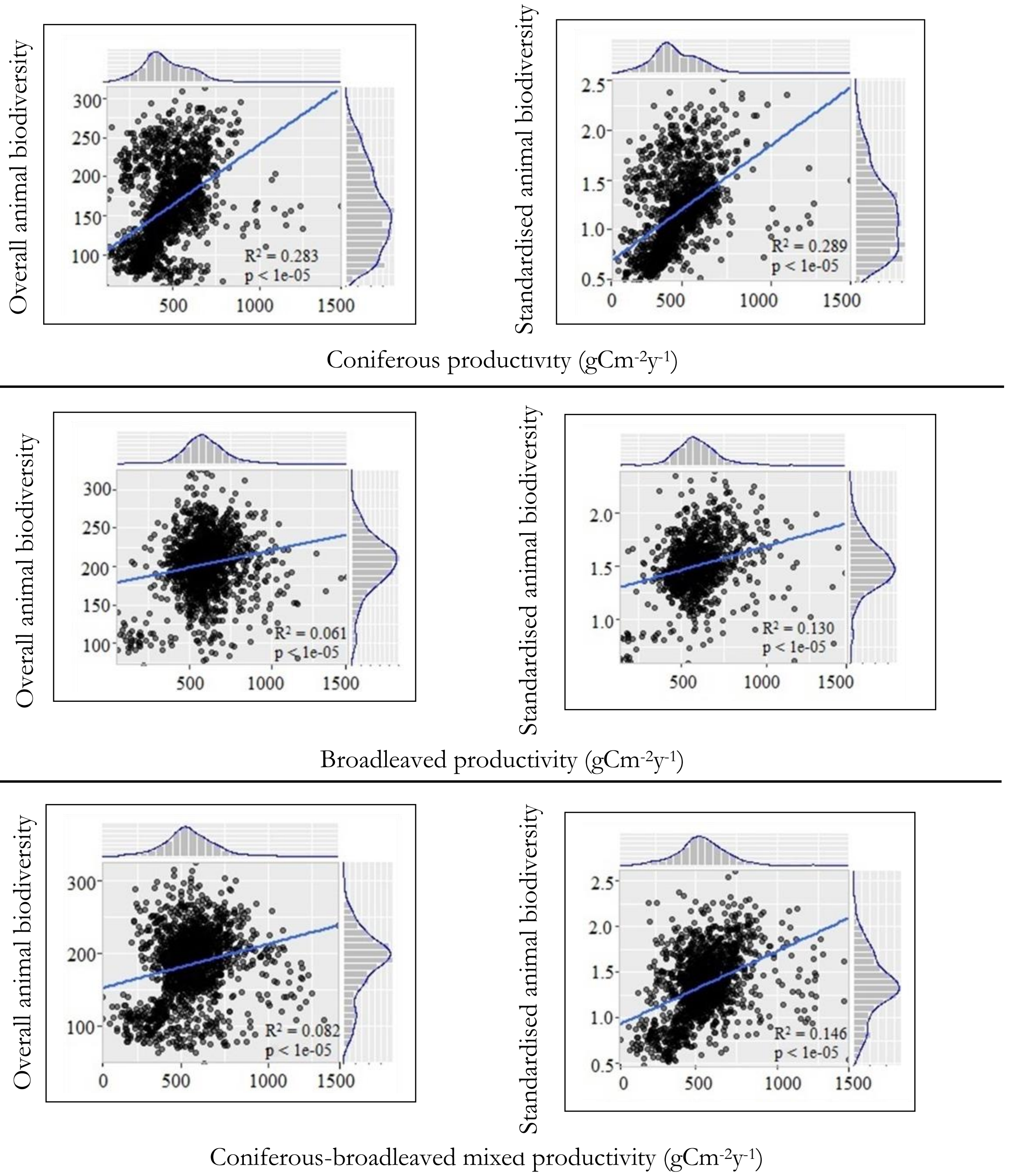


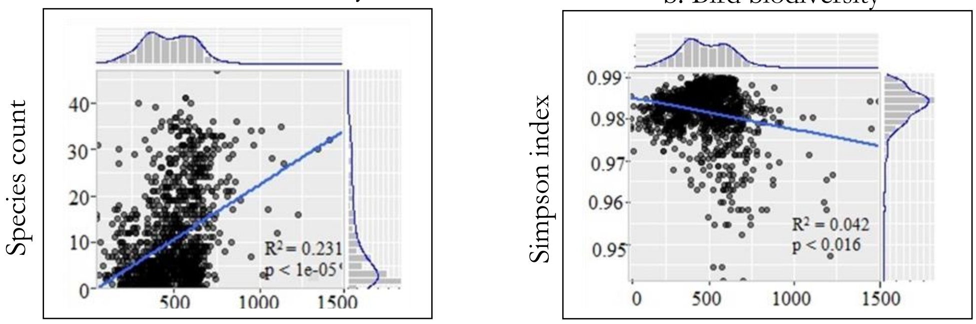
Figure 11: Regression plots of overall animal biodiversity and standardised animal biodiversity each as a function of coniferous, broadleaved and coniferous-broadleaved productivity

4.3.4. Relationships between productivity and biodiversity of mammals, birds, herpetofauna and butterflies in different forest types

In all forest types presented below, there is a consistent pattern as the one discussed in the subsections 4.3.2 and 4.3.3 above. Briefly, productivity exhibited positive relationships with biodiversity of mammals, herpetofauna and butterflies; however, there was a negative relationship with bird biodiversity. Generally, each result suggests that increasing productivity increases the biodiversity of mammals, herpetofauna and butterflies, but decreases biodiversity of birds. In most cases, a stronger relationship was observed in the monoculture than mixed forests, and in the coniferous than broadleaved or coniferous broadleaved mixed forests.

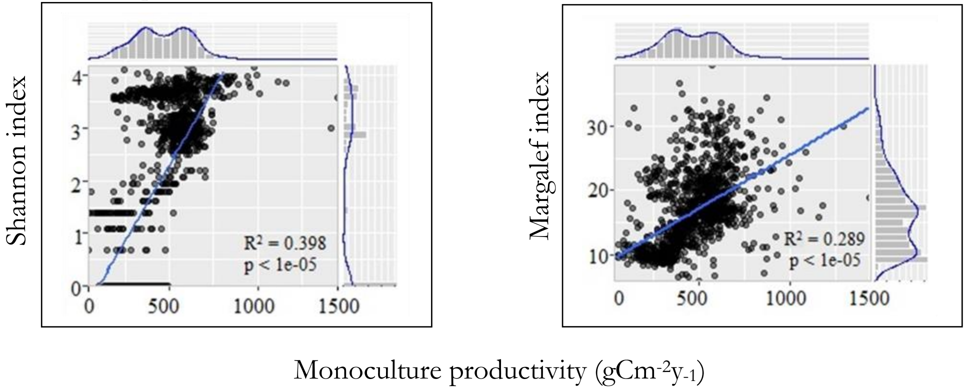
1) Relationships in the monoculture forests

Productivity explained the most variation in herpetofauna biodiversity, particularly, the one calculated by the Shannon index (39.8%). Also, significant variation was observed in the mammal biodiversity with species count recording a slightly stronger variation (23.1%) than other indices. On the other hand, the combination of productivity and Simpson's bird biodiversity showed the most variation (4.2%) than the rest of the indices in that species group, although some relationships were weakly significant. A notable observation was made for the butterfly biodiversity, because irrespective of the index, the variation between productivity and butterfly biodiversity was within the same range (this was indeed contrary to the observed positive relationships from other species groups); however, the strongest variation was explained in Margalef's butterfly biodiversity (28.9%). Figure 12 and Appendix 1 give more details.



a. Mammal biodiversity

b. Bird biodiversity



c. Herpetofauna biodiversity

d. Butterfly biodiversity

Figure 12: Regression plots of biodiversity of mammals, birds, herpetofauna and butterflies, each as a function of monoculture productivity (depicted are the combinations with the strongest R^2 from each species group)

2) Relationships in the mixed forests

Figure 13 below shows that productivity accounted 21.4% of the variation in mammal biodiversity from species count, 12.0% of the variation in bird biodiversity from Shannon, 29.9% of the variation in herpetofauna biodiversity from Shannon and 13.5% of the variation in butterfly biodiversity from Shannon. The combination of productivity and biodiversity from other indices were slightly weaker than the ones presented in the figure therein. Refer to Appendix 2 for specific details.

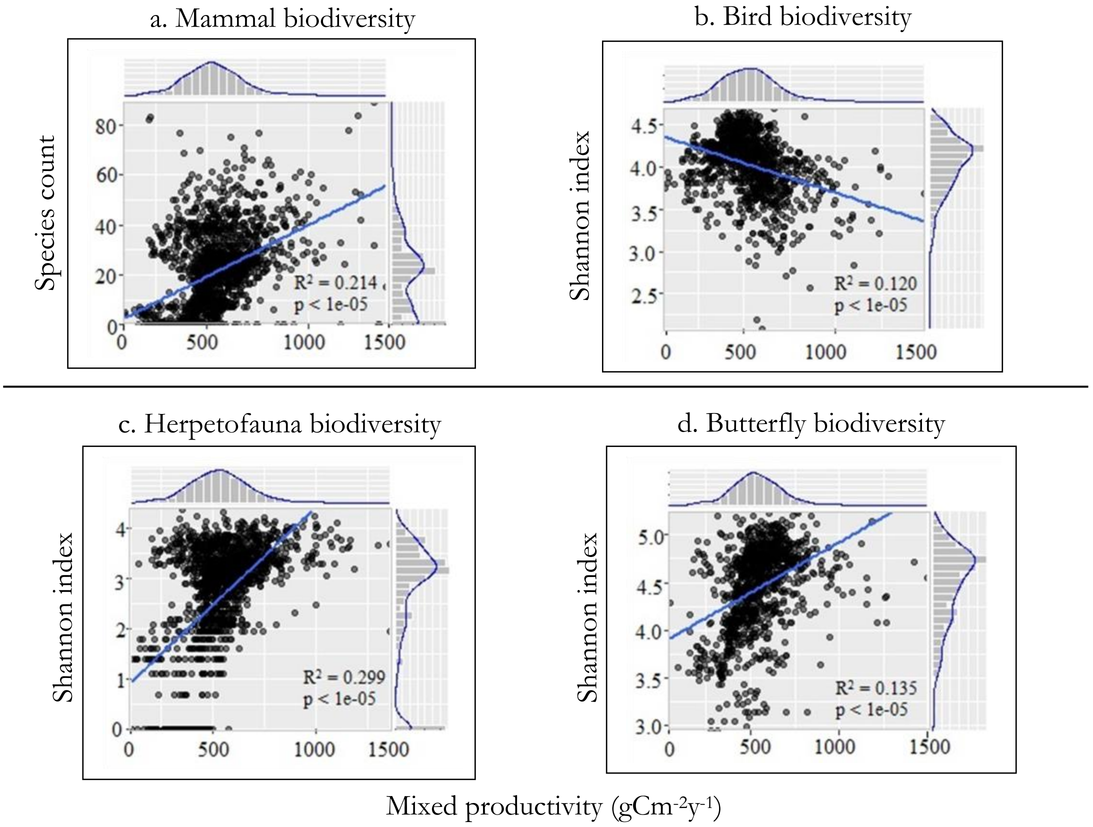
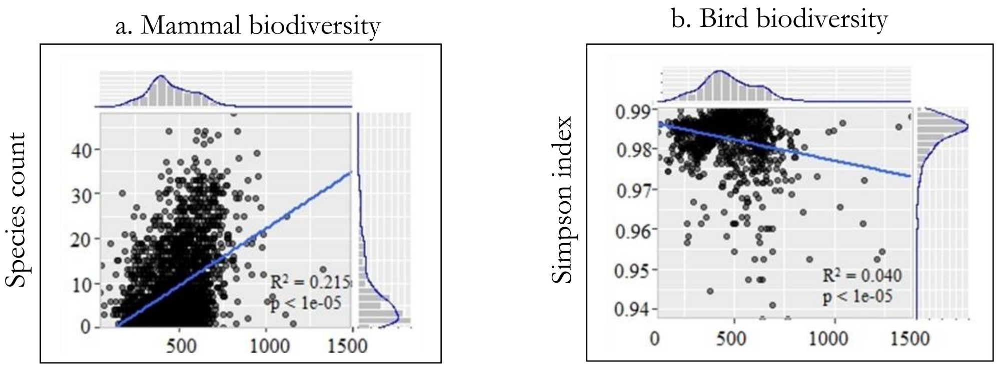
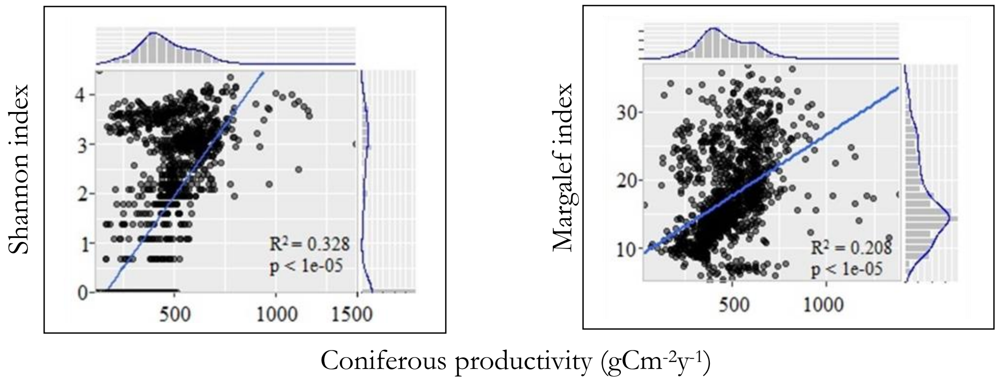


Figure 13: Regression plots of biodiversity of mammals, birds, herpetofauna and butterflies, each as a function of mixed productivity (depicted are the combinations with the strongest R^2 from each species group)

3) Relationships in the coniferous forests

Figure 14 below shows the combinations of productivity and biodiversity from indices which showed the strongest relationship based on R^2 in each species group. Results show that productivity explained 21.5%, 4.0%, 32.8% and 20.8% of the variation in mammal, bird, herpetofauna and butterfly biodiversity, respectively. The remaining combinations, shown in Appendix 3, did not deviate much from the ones presented here, although Simpson index from mammals and herpetofauna recorded the weakest relationship compared to other indices in each group.





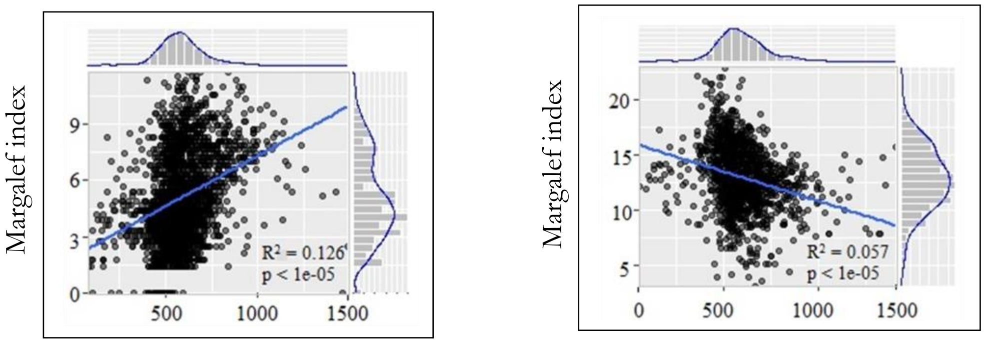
c. Herpetofauna biodiversity

d. Butterfly biodiversity

Figure 14: Regression plots of biodiversity of mammals, birds, herpetofauna and butterflies each as a function of coniferous productivity (depicted are the combinations with the strongest R^2 from each species group)

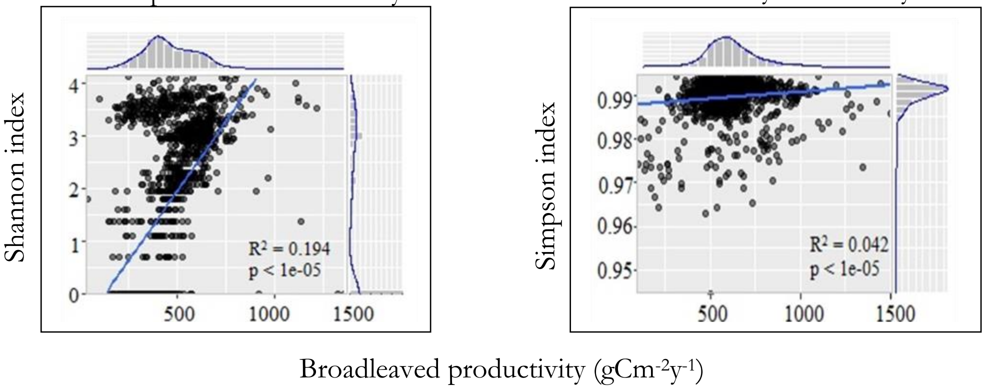
4) Relationships in the broadleaved forests

The combinations which showed the strongest relationship between productivity and animal biodiversity in each species group are presented in Figure 15 below. They show that 12.6%, 5.7%, 19.4% and 4.2% of the variations in biodiversity of mammals, birds, herpetofauna and butterflies, respectively, were explained by productivity. The combinations from other indices (shown in Appendix 4) followed a close pattern like the one presented in the figure therein.



a. Mammal biodiversity

b. Bird biodiversity



c. Herpetofauna biodiversity

d. Butterfly biodiversity

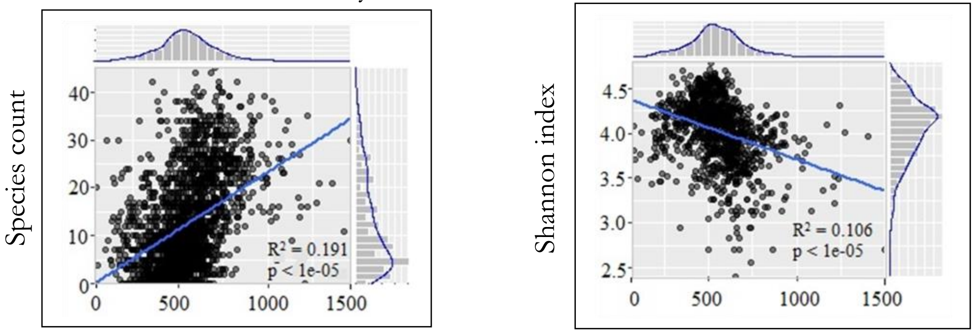
Figure 15: Regression plots of biodiversity of mammals, birds, herpetofauna and butterflies each as a function of broadleaved productivity (depicted are the combinations with the strongest R^2 from each species group)

5) Relationships in the coniferous-broadleaved mixed forests

In Figure 16 below, results show that 19.1% of the variation between productivity and mammal biodiversity, 10.6% of the variation between productivity and bird biodiversity, 22.5% of the variation between productivity and herpetofauna biodiversity, and 13.4% of the variation between productivity and butterfly biodiversity was explained. More information on other combinations is presented in Appendix 5.

a. Mammal biodiversity

b. Bird biodiversity



c. Herpetofauna biodiversity

d. Butterfly biodiversity

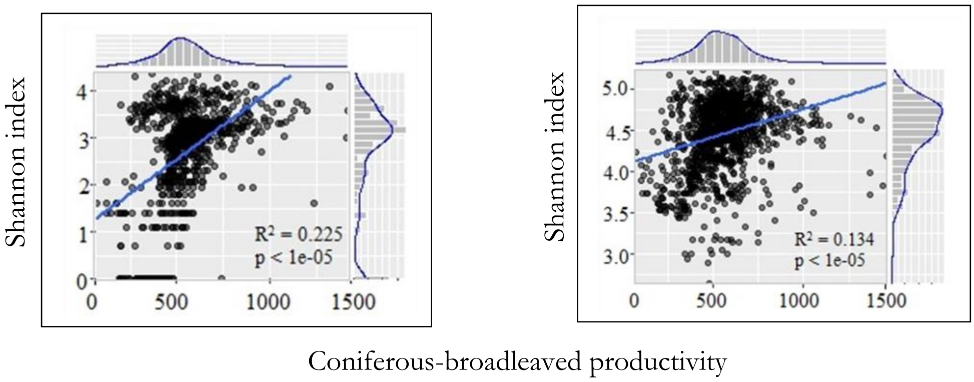


Figure 16: Regression plots of biodiversity of mammals, birds, herpetofauna and butterflies each as a function of coniferous-broadleaved mixed productivity (depicted are the combinations with the strongest R^2 in each species group)

4.4. Spatial congruence between productivity and animal biodiversity

Results show that the spatial overlap between productivity and standardised biodiversity, and biodiversity of mammals, herpetofauna and butterflies did not exhibit much differences. However, the spatial overlap involving bird biodiversity was different from the rest (see Figure 17).

Following the standardised animal biodiversity: relatively significant spatial overlap was observed between areas where the hotspots of productivity overlapped with the hotspots of standardised animal biodiversity (17.16%). At the same time, the areas where the medium-spot from these two ecosystem services overlapped showed a significant degree of spatial overlap (22.06%). However, this degree of spatial overlap is partly attributed to the higher threshold value (40%), that the medium-spots were allocated compared to the low threshold value (30%) that was assigned to the hotspots and the coldspots during delineation (see subsection 3.1.9 for detail). Similarly, the areas where productivity coldspots overlapped with standardised biodiversity coldspots showed a relatively significant degree of overlap (17.99%).

Meanwhile, a low spatial overlap was found between the areas where the hotspots overlapped with the coldspots; in detail, where productivity hotspots overlapped with standardised animal biodiversity coldspots (2.19%) on the one hand, and where productivity coldspots overlapped with standardised animal biodiversity hotspots (5.79%), on the other hand. The areas where the medium-spots overlapped with either the hotspots or the coldspots of productivity and standardised animal biodiversity expectedly showed some considerable spatial overlap as can be observed in Figure 17.

The spatial overlap between productivity and either biodiversity of mammals, herpetofauna or butterflies followed a similar pattern as for the standardised animal biodiversity discussed above. Their percentage overlap as can be seen in Figure 17 did not deviate significantly from the ones presented above. Interestingly, the areas where the hotspots of each of this biodiversity (standardised animal biodiversity, mammal, herpetofauna and butterfly biodiversity) overlapped with the hotspots of productivity were located somehow in the same regions (parts of the temperate and Mediterranean zones of Europe). Similarly, the areas where the coldspots of productivity overlapped with the coldspots of each of this biodiversity were located mostly in the same place (the boreal zone).

A striking observation was made between the spatial overlap of productivity and bird biodiversity, with the findings contrasting observations in other species groups. Specifically, a very low spatial overlap was found between the hotspots areas of both productivity and bird biodiversity (3.60%), on the one hand, and the areas where both coldspots overlapped (3.29%), on the other hand. Significant areas of the hotspots of productivity were found in the coldspots of bird biodiversity (11.92%) (see the temperate oceanic zone). There were also significant areas of the hotspots of bird biodiversity in the coldspots of productivity (12.11%) (see the boreal and parts of Mediterranean zones). More details on other spatial overlap areas are as presented in Figure 17.

Generally, the biodiversity from other indices (Margalef, Shannon and Simpson) for all species groups followed the same pattern as for the species count presented above. However, an exception occurred with Simpson's herpetofauna biodiversity because this index predicted significant herpetofauna hotspot areas in the coldspots of productivity (see the boreal region); other indices predicted that area as a coldspot zone of herpetofauna biodiversity. Consequently, significant hotspot areas of herpetofauna from Simpson were found in the coldspots areas of productivity. Refer to Appendix 6 and Appendix 7 for more details.

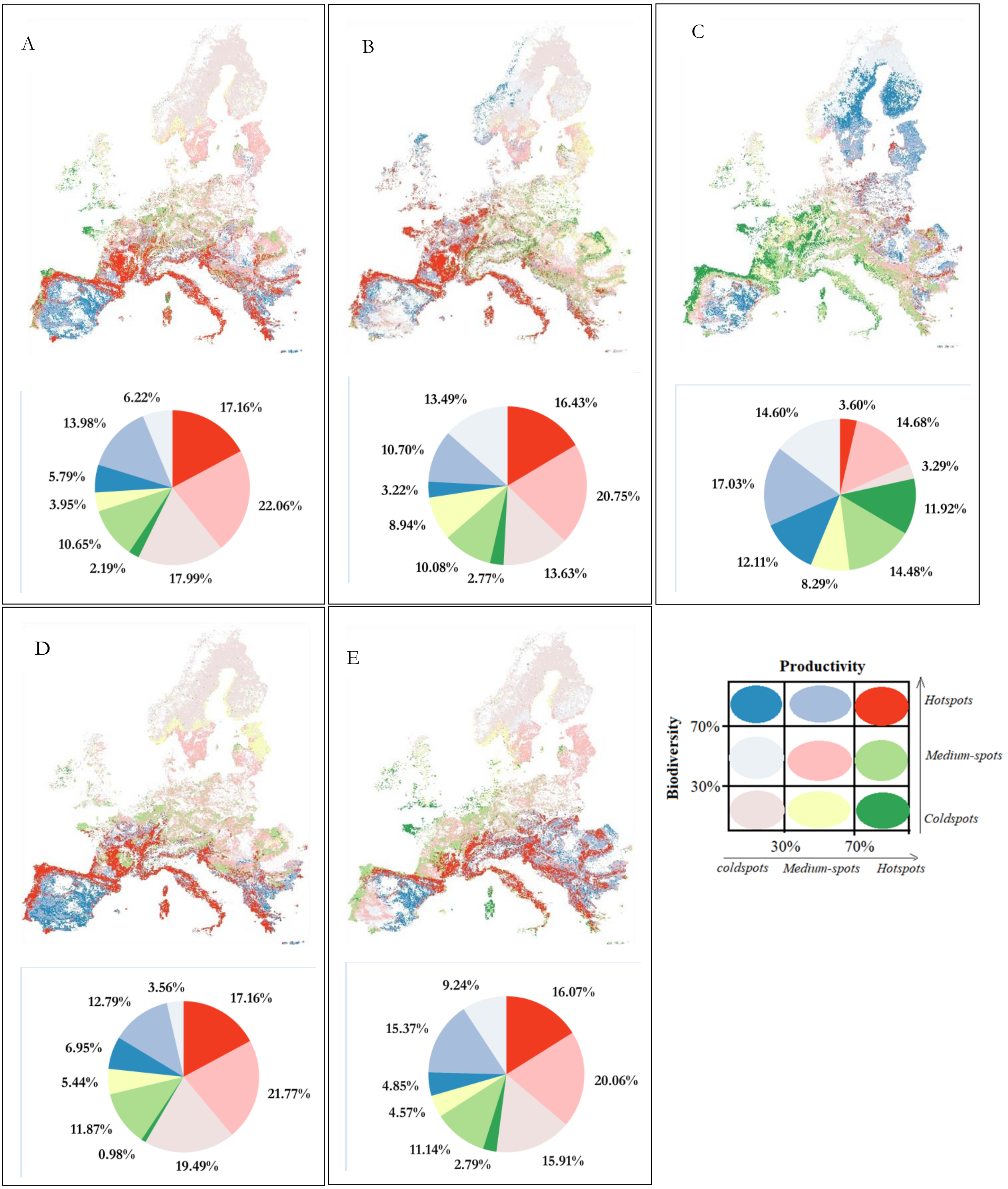


Figure 17: Spatial overlap between overall productivity and standardised animal biodiversity (A), mammal (B), bird (C), herpetofauna (D) and butterfly (E) biodiversity (calculated by species count) across European forests

5. DISCUSSION

5.1. Comparing biodiversity indices

The general observation indicated that, in most cases, Simpson's high values occurred most frequently. These values indicated higher biodiversity estimation by Simpson index compared to species count, Margalef or Shannon indices. Whether an ecosystem is highly biodiverse or not is determined by the species composition, the index used to measure diversity and partly by the number of species present. This is true following a study by Nagendra (2002) which used numeric simulation to vary land cover types in different landscapes; with results demonstrating that Shannon index declares high biodiversity if there are rare landcover types, and Simpson, on the other hand, shows high biodiversity if there are dominant land cover types in a landscape. However, in some cases, the indices find similar biodiversity if a landscape contains many land cover types (Nagendra 2002), this observation, indeed, may justify why the indices were more similar when calculating butterfly biodiversity (with the highest number of species), but showed significant variation for other species group (with the low number of species).

In the meantime, positive correlations were found between pairs of indices, although, their strength tended to vary depending on the correlating indices and species group. A high correlation was observed between species count and Margalef which can be explained by the fact that they are both indices of richness; hence they are inherently positively related. Conversely, Simpson showed a lower correlation with either of these indices while Shannon was intermediately between all indices. This result of the low correlation between richness and evenness indices explains how mathematically independent the indices are in regard to biodiversity measurement (Wilsey et al. 2005), and therefore, disagrees with the notion that all biodiversity indices are strongly correlated (see DeBenedictis (1973)). Similarly, the results of this study are consistent with Stirling & Wilsey (2001) whose study also found positive correlations between richness and evenness indices for both vertebrate and invertebrate groups.

Despite the strength of the correlation, assessing biodiversity using different indices can offer a significant amount of independent information on the variation of biodiversity measure for which each index responds to. Similarly, identifying the hotspots areas where different indices overlapped can provide complementary information on biodiversity. To comprehensively characterise species variation or measure species diversity within European forests, the result of the present study highlights the need for selecting Simpson index with at least Shannon, Margalef or species count. It is also reasonable to assess the goal of conservation.

5.2. Effect of productivity on animal biodiversity

The prevailing theories in ecology such as the species-energy theory (Wright 1983) and the More Individuals Hypothesis (Srivastava & Lawton 1998) state that there is a positive association between species richness and available energy. The present study found considerable support for these theories based on the analysis of the relationship between forest productivity as measured by NPP and overall animal biodiversity of European forests. However, these variables exhibited a weak relationship as illustrated by their low R^2 values; which thus suggests that productivity only explained the variation in biodiversity of animals to a limited extent. Generally, increasing productivity will lead to an increase in animal biodiversity, although, at a relatively slow rate due to their weak positive relationships.

Separating animal dataset to investigate how different animal groups were related to productivity, the study found little variations in the relationship involving biodiversity of mammals, herpetofauna and butterflies. For each of these species groups, the relationship between productivity and biodiversity from species count, Margalef and Shannon were relatively high and were found in the same range. The major differences were observed in Simpson's biodiversity. For mammals and herpetofauna, productivity showed the weakest relationship with Simpson biodiversity compared to its relationship with biodiversity from species count, Margalef and Shannon in these species group. However, for the butterflies, the relationship between productivity and Simpson biodiversity was within the range with other biodiversity indices in this species group. This pattern can be explained by the differences in the number of species in each group (butterfly had the highest number of species compared to mammals or herpetofauna). In that respect, following the discussion presented in subsection 5.1 above, indices seem to measure biodiversity more similarly when there is a high number of species present; hence biodiversity for butterfly from all indices was similar (or highly correlated) leading to little variation in the productivity-butterfly biodiversity relationship across all indices.

Meanwhile, the results illustrated by this study of the positive relationship between productivity and biodiversity of mammals, herpetofauna and butterflies are consistent with previous studies. For example, Youngentob et al. (2015) found out that marsupial mammal species richness and abundance increased with productivity (NDVI) in the eucalypt forests of New South Wales in Australia. In another study, Rodríguez et al. (2005) found out that productivity (NPP) showed a positive relationship with reptiles and amphibians in Europe, with each model explaining 11.0% and 39.8% of the variation in reptiles and amphibians, respectively. In different studies, Luck (2007) found out that productivity (NPP) explained 65.1% of the variation in butterfly richness in the mainland Australia, whereas Bailey et al. (2014) showed that 19.6% of the variation between productivity (maximum NDVI) and butterfly biodiversity was explained in the Great Basin of western North America. Collectively, the results of this study and previous studies are indicating that productivity explained a certain amount of variations in the mammal, herpetofauna and butterfly biodiversity. Specifically for this study, the relationships are relatively weak due to their low values of R^2. However, a general conclusion is that increasing productivity in European forests increases biodiversity of mammals, herpetofauna and butterflies in these forests.

An unexpected negative relationship was found between productivity and bird biodiversity. This finding significantly contradicts earlier studies by Hurlbert (2004) which found out that productivity (NDVI) explained between 45% to 49% of the variation in bird richness in North America, and Phillips et al. (2008) whose study showed that productivity (NDVI and NPP) explained 50% and 51% variation in bird richness, in the same region. This result also did not lend any support to the initial hypothesis where a positive relationship was expected on the ground that birds are used as key indicators in monitoring the status of forests and ecosystem services in Europe (Gregory et al. 2008); hence they should be positively related to productivity. However, it may not always be the case as higher productivity may also be negatively associated with bird biodiversity (see Bailey et al (2014)). Also, Hurlbert (2004), although documented a positive relationship, argued that other mechanisms such as habitat structure contributed largely to the observed patterns; for this particular study, a research can be established to further investigate factors determining productivity and bird biodiversity in Europe.

5.3. Effect of forest composition on productivity-diversity relationship

Contrary to this study's initial expectation, the relationship between productivity and overall animal biodiversity was stronger in monoculture than mixed forests. The biodiversity of mammals, herpetofauna and butterflies generally followed a similar pattern. This observation was, indeed, unexpected because mixed forests are found to be more productive than monoculture forests (see Erskine et al. (2006); Liang et al. (2016)); and since animal biodiversity increases relatively with increasing productivity (as illustrated previously in sub-section 5.2 above), stronger positive association between productivity and animal biodiversity was expected in mixed than monoculture forests. The possible explanation for this finding can be attributed to (1) the differences in the size of the area occupied by each forest stand. In other words, monoculture forests occupied a smaller area than mixed forests, thus making the variation between productivity and animal biodiversity stronger in the monoculture than mixed forests. However, previous studies have documented mixed results on the species-area effect (see Qian (2007); Youngentob et al. (2015), but see Hortal et al. (2008)); therefore, for these specific habitats, it may warrant future research. (2) It is not always the case that mixed forests are more productive than monoculture; higher productivity can also be associated with the latter (see Zeller et al. (2018)). (3) There may be other factors with a higher influence on productivity-animal biodiversity relationship and such factors most probably occurred more frequently in monoculture than mixed forests. Similarly, a stronger relationship was found between productivity and animal biodiversity in coniferous than either broadleaved or coniferous-broadleaved mixed forests, which contradicts the original hypothesis. This finding is suggesting that higher tree productivity can also be associated with coniferous forests (see Romanyà & Vallejo (2004) for the productivity of *Pinus radiata*). Also, there may be other variables which influenced the observed relationship.

5.4. Spatial congruence between productivity and animal biodiversity

The degree of spatial overlap between different ecosystem services is likely to be dependent on the threshold value used to delimit the area of interest (Anderson et al. 2009; Gos & Lavorel 2012) and the ecological requirements of the ecosystem services. However, irrespective of this degree, the information on spatial overlap is essential when implementing strategies for land management and conservation (Anderson et al. 2009).

The result of the present study found a varying degree of congruence between productivity and biodiversity of different animal groups. Relatively significant spatial overlaps were recorded between areas of hotspots of productivity and (1) standardised animal biodiversity (2) mammals (3) herpetofauna and (4) butterflies (overlap range from 15.23% to 17.35%). These results are indicating that some habitats that are valuable to productivity also supported biodiversity of these animals. In previous studies, stronger spatial overlaps than what this study documented, were found between different ecosystem services in various regions: for example, Bai et al. (2011) found spatial overlaps from 23.29% to 45.02% between biodiversity and (1) carbon, (2) water and (3) soil retention in Baiyangdian (China); while Lecina-Diaz et al. (2018) found spatial overlap from 29.5% to 89.5% between carbon stock and biodiversity in Spain (Europe) and Quebec (North America). Collectively, the present results and those from the previous studies suggest that ecosystem services support each other to some extent.

On the other hand, a relatively low spatial overlap was observed between the hotspots of productivity and bird biodiversity (overlap of 3.60% and 3.61%). Similarly, low spatial overlap between ecosystem services have been documented by earlier studies; for example Anderson et al. (2009) found a spatial overlap of up to 4% between biodiversity and (1) agriculture, (2) recreation, and (3) carbon in Britain. The low spatial overlap observed between ecosystem services, or birds and productivity in this case, is implying that productivity offers minimal support for bird biodiversity, and it can be expected for highly productive forests to be less rich in birds. This is true given that the boreal zone of Europe having low productive forests harbour a relatively high number of birds (Sundseth 2005).

Depending on the degree of overlap of the hotspot areas, they offer an environment for management and conservation practices. However, policies developed with a specific goal in mind either to enhance wood production or biodiversity protection may put pressure on these areas which may substantially impair other ecosystem services. In other words, intensification of management practices to promote wood production and subsequently wood removal will negatively affect biodiversity. On the other hand, biodiversity protection and imposing felling restrictions will lower the potential supply of wood. Consistent with Verkerk et al. (2014), these areas are likely to present trade-offs, therefore optimal strategies which can achieve both policy goals should be enforced. Although, it is important to assess how these policies impact on each other and other ecosystem services as well, the present study acknowledges earlier studies which have stated that developing such policy goals can be critically challenging for the ecologist, forest managers and decision makers (Sandström et al. 2011; Verkerk et al. 2014).

However, significant areas where the hotspot of productivity and biodiversity overlapped can be optimised by developing appropriate management regimes which maintain both wood production and biodiversity protection in the same area. This approach can serve as a baseline under which significant hotspots areas (particularly, where productivity overlapped with standardised animal biodiversity and biodiversity of mammals, herpetofauna and butterflies) can be optimised to sustainably conserve the animal biodiversity in intensively managed forests. Therefore, land use planning and conservation strategies with an inclusive goal of maintaining productivity and animal biodiversity need to focus mostly on the temperate and Mediterranean parts of Europe where a significant overlap of hotspots areas was found.

On the other hand, significant hotspots which occurred in non-hotspots areas, particularly in the coldspots, are revealing areas of synergies for a single ecosystem service. In this case, such areas of hotspots of only animal biodiversity can be optimised by zoning protected areas to be strictly for biodiversity and the highly productive areas can be maximised for wood production. Land use planning and conservation strategies should focus mostly in the boreal region if they aimed to conserve birds.

5.5. Reflection on the findings of the present study

The present study measured biodiversity across European forests and investigated its relationship and congruence with productivity. In many aspects, its results may not exactly reflect what is on the ground in terms of number of species and forest productivity because: first, a presence-absence data generated from threshold values were used to discriminate places with species and those without; this approach may have inevitably overestimated or even underestimated the number of species present; second, productivity data was downscaled from approximately 1km to 5km, hence this may have tampered with the original quantity on the ground. However, these limitations are unlikely to change the conclusion of the present study.

The scale of this study was also quite broad which may warrant a follow-up on a narrower scale to ascertain whether the patterns of productivity and animal biodiversity are consistent with broad-scale pattern documented by the present study. In the meantime, previous studies have noted that studies on broad scale provide more robust patterns of the ecosystem services which are essential in management and conservation strategies (Xu et al. 2017) and are more informative than patterns on the local scales (Anderson et al. 2009); therefore, information presented in the present study is useful in influencing strategic forest resource use, planning and decision making across European region.

A key strength of this study is the comprehensive assessment of the spatial patterns across overall animal and specific species groups and forest types which makes the conclusion of this study more relevant than it could have been if only limited biodiversity measure, forest type or taxa were investigated. Conclusively, the present study may serve as a guide to support scientific policy formulation related to sustainable European forest management while helping both raw material production and animal biodiversity conservation.

6. CONCLUSION AND FUTURE STUDY

6.1. Conclusion

1) ***What is the quantity of biodiversity for each species group based on species count, Margalef, Shannon-Wiener and Simpson indices?***

The quantity of biodiversity exhibited by different indices for each species group is as shown in Table 2. This result highlight that the quantity of biodiversity is dependent on the index used to measure biodiversity and the number of species present. Species composition can also be an important determinant factor as illustrated in a study by Nagendra (2002).

2) ***What is the correlation between the quantity of biodiversity measured by species count, Margalef, Shannon-Wiener and Simpson indices?***

The correlation is positive; however, its magnitude varies significantly depending on the paired indices and species group. In all cases, the quantity of biodiversity measured by species count and Margalef were strongly correlated. The lowest correlation was observed between either the quantity of biodiversity measured by species count and Simpson indices or the quantity of biodiversity measured by Margalef and Simpson indices. The quantity of biodiversity from Shannon, on the other hand, was intermediately between all indices. In regard to the species group, the indices were more related when measuring butterfly biodiversity but differed significantly when measuring herpetofauna biodiversity.

3) ***What is the observed spatial relationship between overall productivity and overall animal biodiversity?***
4) ***How is the overall productivity related separately to the biodiversity of mammals, birds, herpetofauna and butterflies?***

All the observed spatial relationships between productivity and mammals, herpetofauna and butterfly biodiversity were significantly positive (R^2 from 0.029 to 0.398, $p<1e-05$) apart from productivity and bird biodiversity whose relationship was negative and, in some cases, weak (R^2 from 0.002 to 0.120, $p = 0.016$ or $p <1e-05$). These observations suggested that increasing productivity increases overall biodiversity, and biodiversity of mammals, herpetofauna and butterflies, but decreases biodiversity of birds.

5) ***How does the spatial relationship between productivity and overall animal biodiversity or biodiversity of mammals, birds, herpetofauna and butterfly change across monoculture, mixed, coniferous, broadleaved and coniferous-broadleaved mixed forests?***

The relationship between productivity and overall biodiversity and biodiversity of mammals, herpetofauna and butterflies was positive and stronger in monoculture than mixed forests. A stronger relationship was also found in coniferous than broadleaved or coniferous-broadleaved mixed forests. Productivity showed a negative relationship with bird biodiversity across all forest types.

6) ***What is the spatial congruence of hotspots/medium-spots/coldspots areas of productivity and overall animal biodiversity or biodiversity of specific species groups?***

Relatively significant spatial overlap was found between productivity and overall biodiversity and biodiversity of mammals, herpetofauna and butterflies. Generally, the level of spatial overlap did not seem to vary significantly across each combined pair. The areas where the hotspot of productivity overlapped with the hotspots of each of these biodiversity groups showed a significant degree of spatial overlap. Also, the areas where their medium-spots and somehow where their coldspots overlapped were relatively significant. However, a low spatial overlap was found between productivity and bird biodiversity, more specifically, between the areas where their hotspots overlapped.

6.2. Future study

1) To improve on the results, the present study needs to follow-up on the species data used in this study to make a robust justification on the different quantities of biodiversity measured by species count, Margalef, Shannon and Simpson indices.

2) The study suggests a further investigation of the factors driving productivity and animal biodiversity, particularly in the various spatial overlap areas. Identifying for example, if factors driving productivity hotspot areas are similar or different from those driving biodiversity can provide an in-depth understanding of the spatial patterns of productivity and animal biodiversity.

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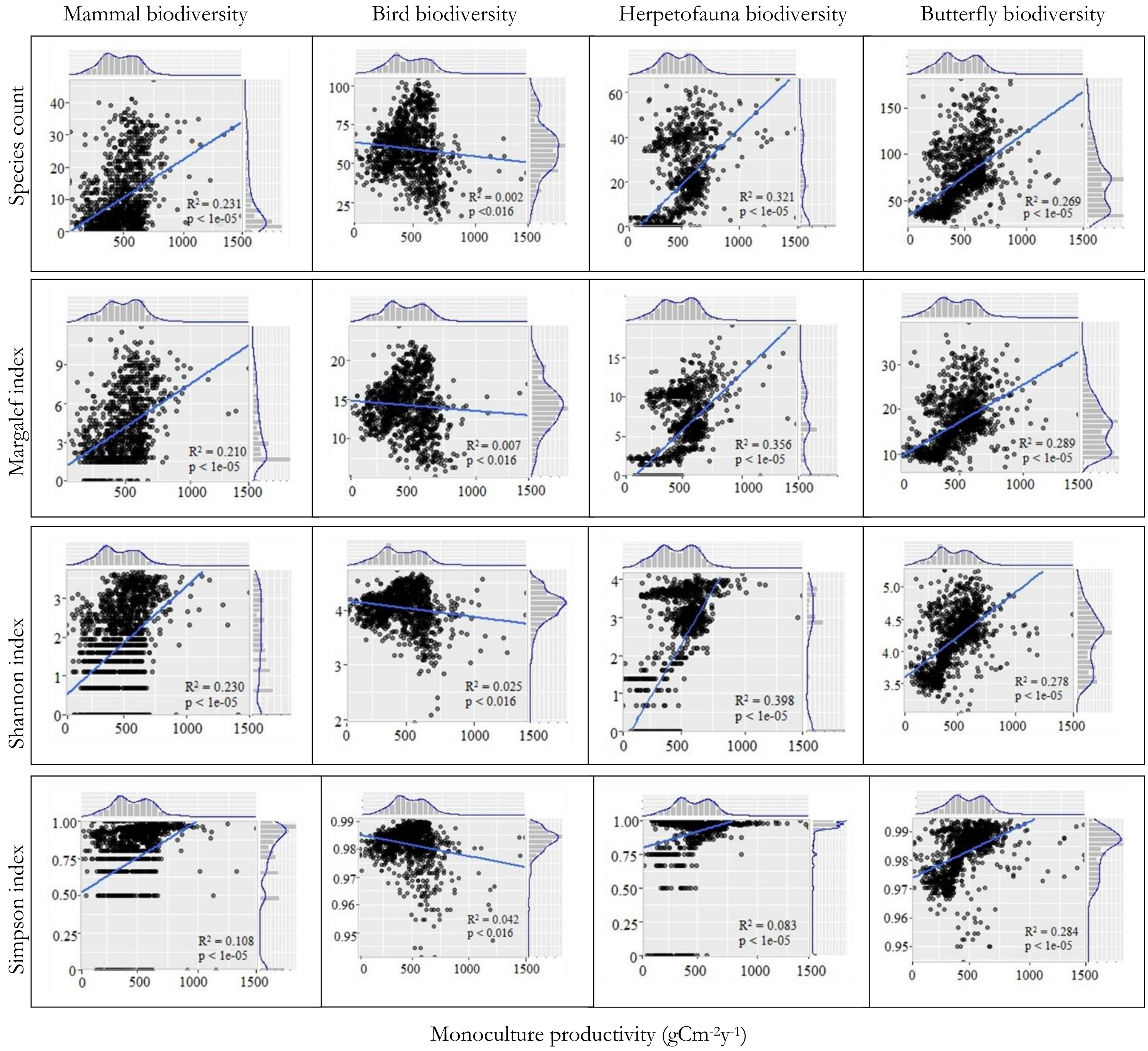
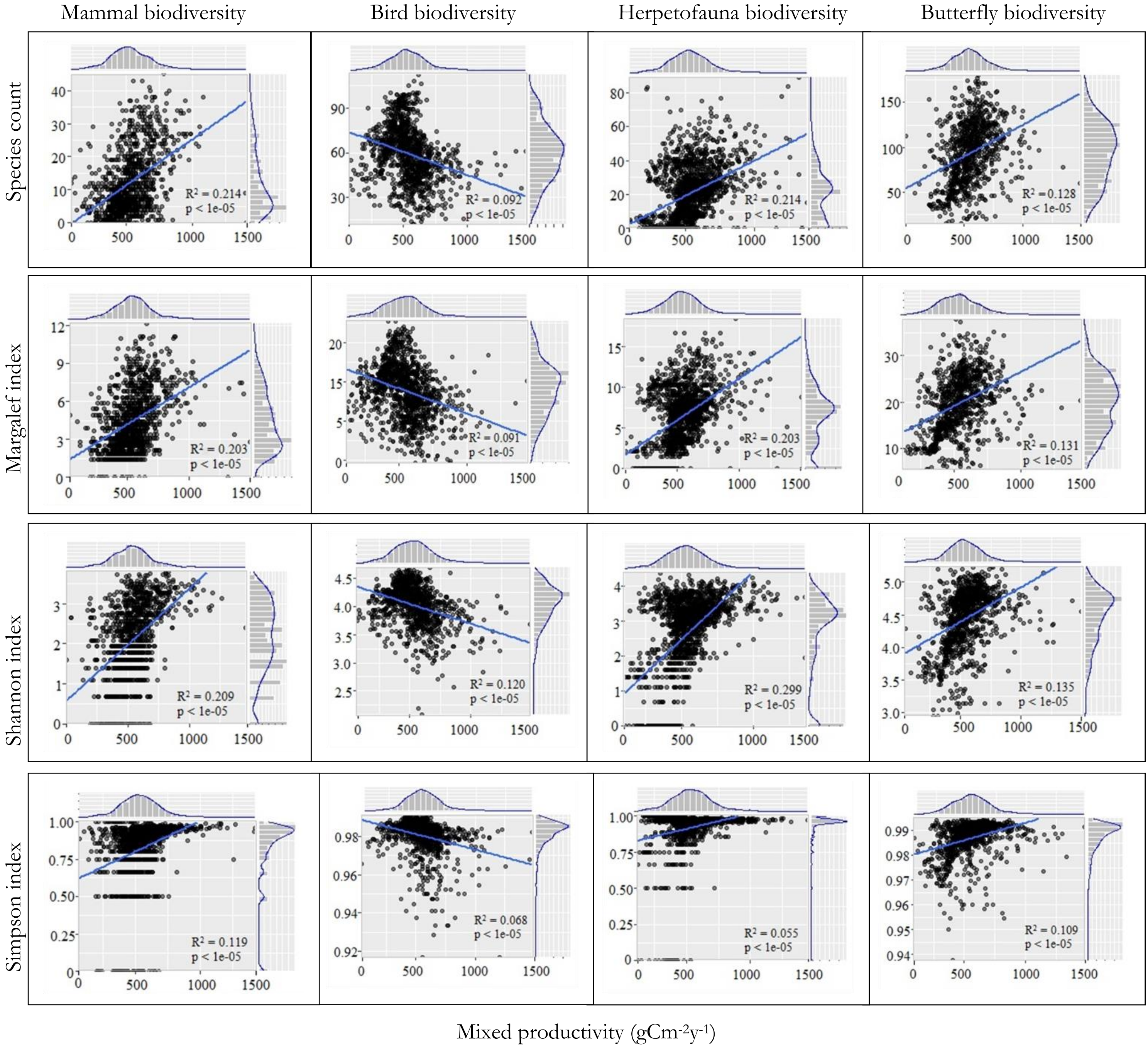
8. APPENDICES

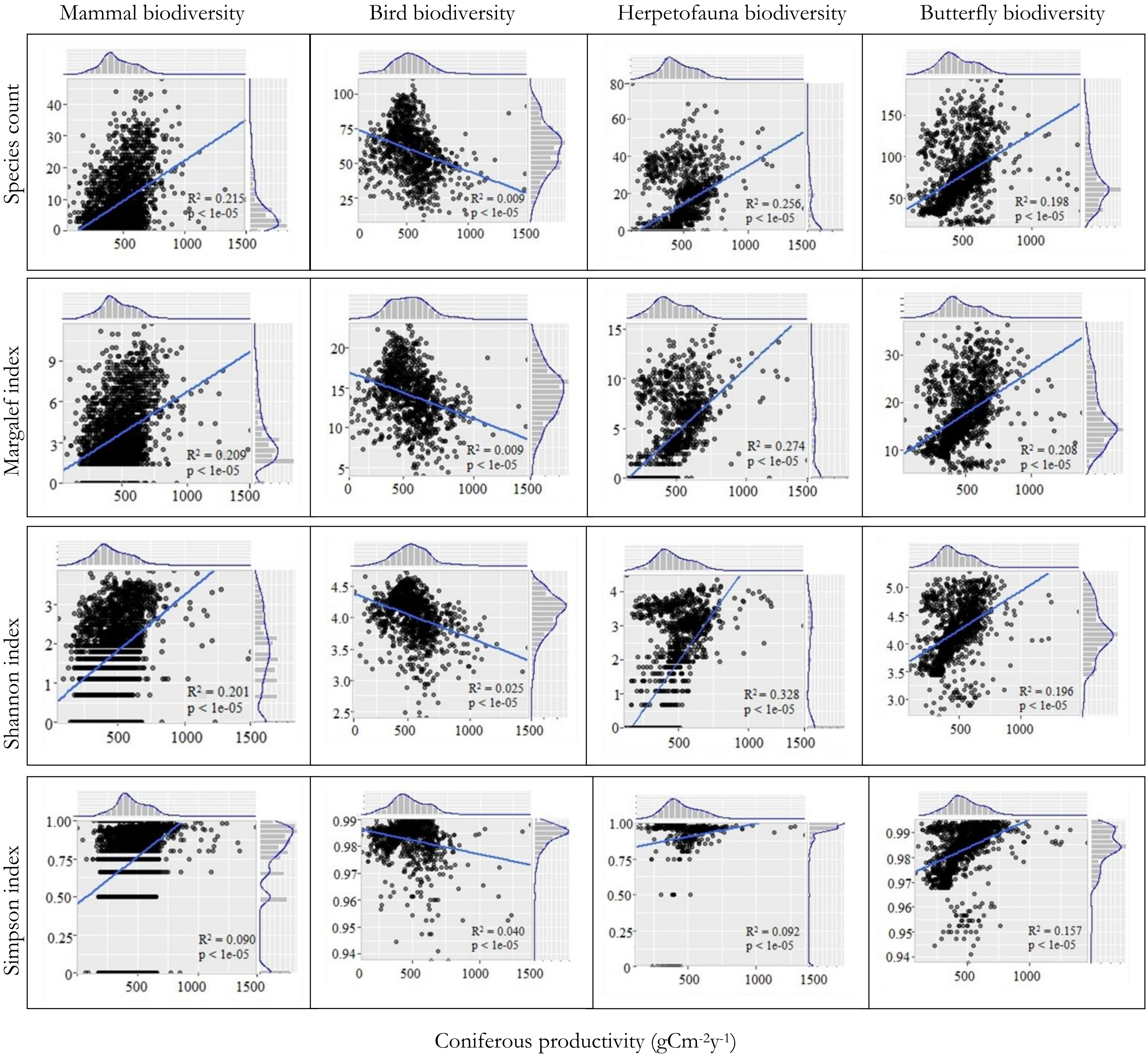
Appendix 1: Regression plots of biodiversity of mammal, birds, herpetofauna and butterfly biodiversity as measured by species count, Margalef, Shannon and Simpson indices, each as a function of monoculture productivity



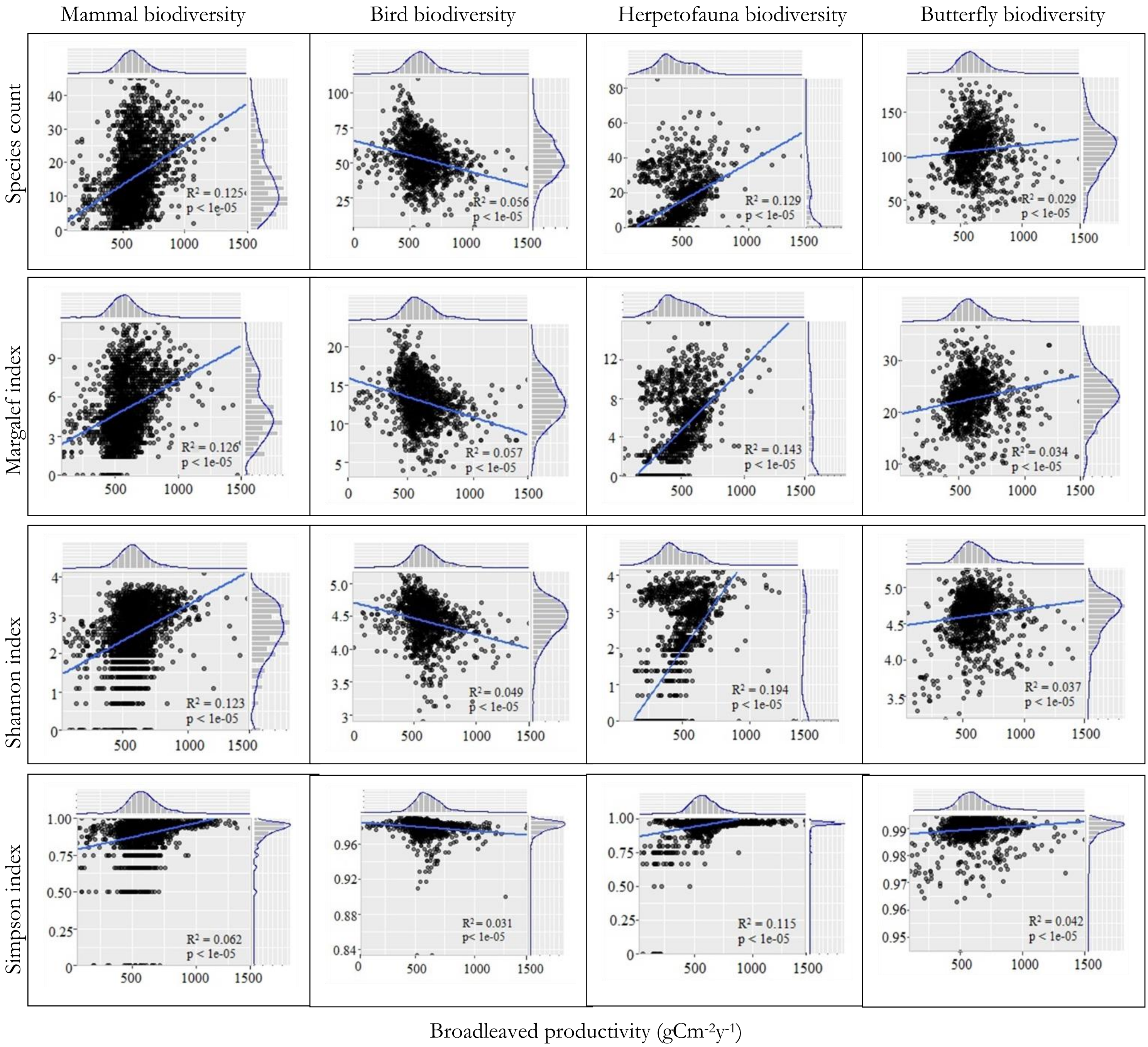
Appendix 2: Regression plots of biodiversity of mammal, birds, herpetofauna and butterfly biodiversity as measured by species count, Margalef, Shannon and Simpson indices, each as a function of mixed productivity



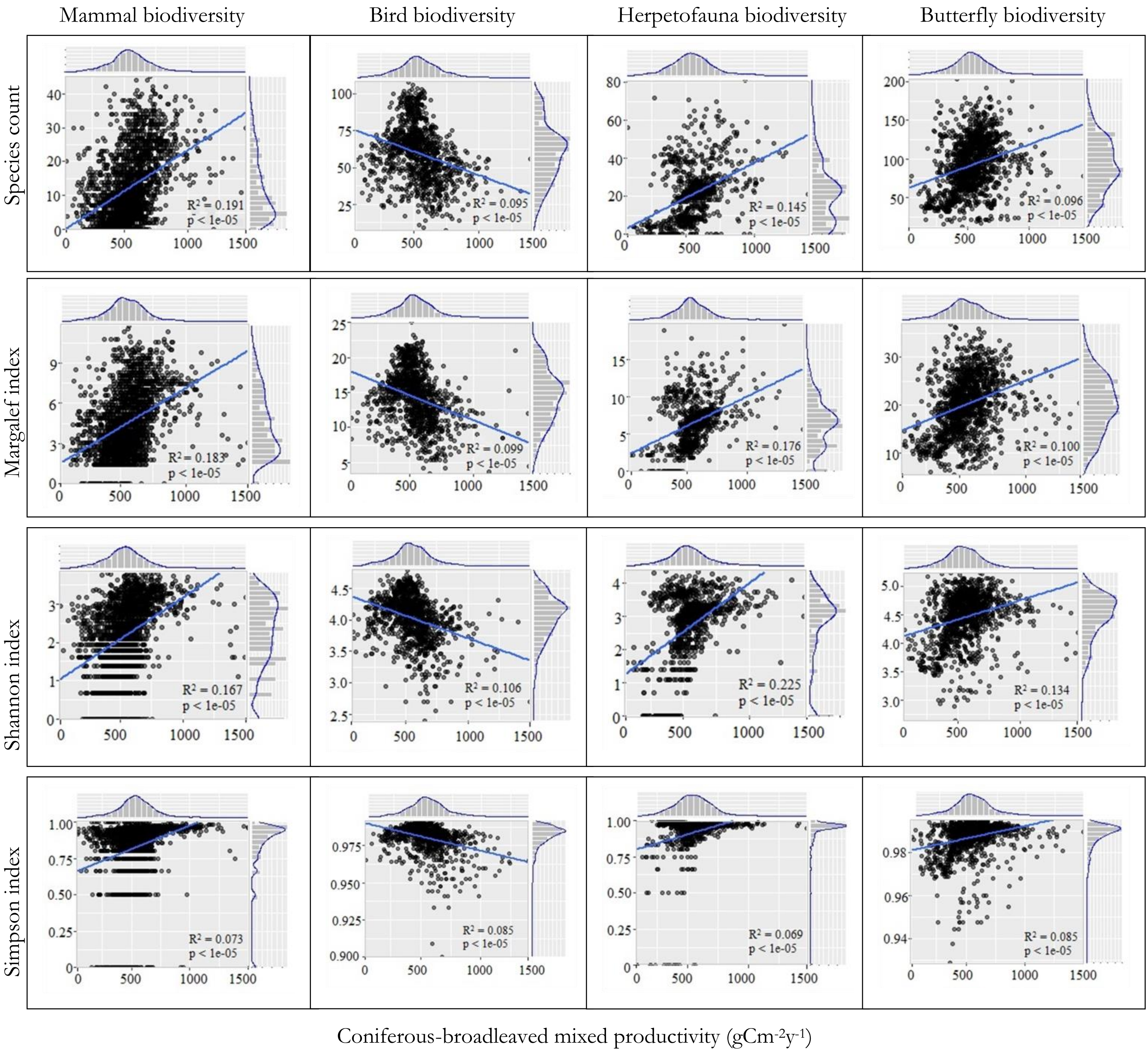
Appendix 3: Regression plots of mammal, bird, herpetofauna and butterfly biodiversity as measured by species count, Margalef, Shannon and Simpson indices, each as a function of coniferous productivity



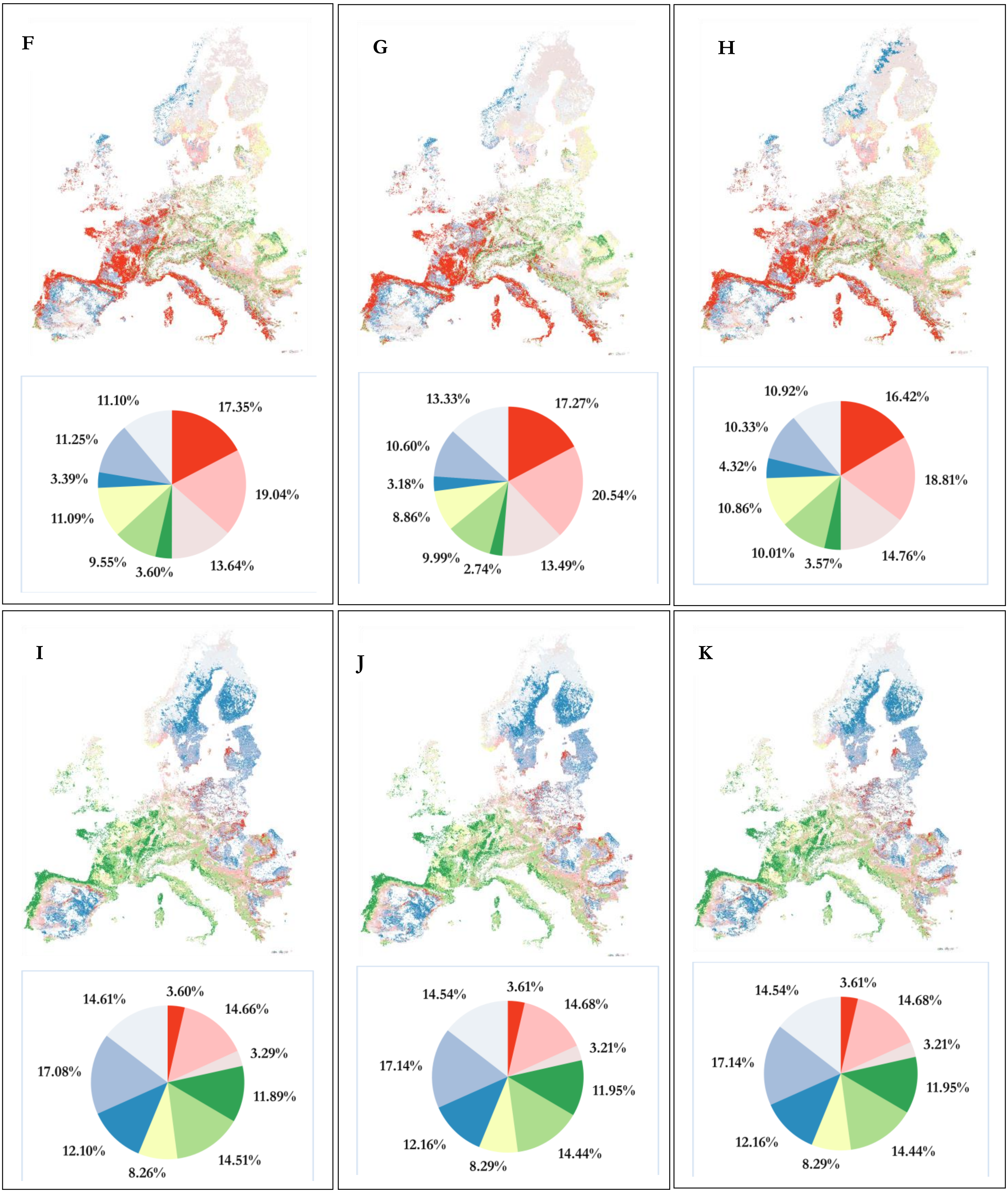
Appendix 4: Regression plots of mammal, bird, herpetofauna and butterfly biodiversity as measured by species count, Margalef, Shannon and Simpson indices, each as a function of broadleaved productivity



Appendix 5: Regression plots of mammal, bird, herpetofauna and butterfly biodiversity as measured by species count, Margalef, Shannon and Simpson indices, each as a function of coniferous-broadleaved mixed productivity



Appendix 6: Spatial overlap of overall productivity and biodiversity of mammal as measured by Margalef (F), Shannon (G) and Simpson (H) indices, and bird as measured by Margalef (I), Shannon (J) and Simpson (K) indices



Appendix 7: Spatial overlap of overall productivity and biodiversity of herpetofauna as measured by Margalef (L), Shannon (M) and Simpson (N); and butterfly as measured by Margalef (O), Shannon (P) and Simpson (Q) indices