



# There is a trade-off between forest productivity and animal biodiversity in Europe

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## Abstract

While forest productivity and biodiversity are expected to be correlated, prioritizing either forest productivity or biodiversity can result in different management. Spatial quantification of the congruence between areas suitable for either one can inform planning. Here we quantify the relationship between net primary productivity of European forests and biodiversity of mammals, birds, reptiles, amphibians, and butterflies both separately and in combination, and map their spatial congruence. We used richness maps obtained by stacking species distribution models for these animal species, and average net primary production from 2000 to 2012 using moderate resolution imaging spectroradiometer (MODIS) data. We tested how biodiversity and primary productivity are correlated and quantified the spatial congruence of these two sources. We show the areas where high or low productivity co-occur with high or low biodiversity using a quantile-based overlay analysis. Productivity was positively correlated to overall biodiversity and mammal, herptile and butterfly biodiversity, but biodiversity of birds showed a weak negative correlation. There were no significant differences in the strength of relationship across species groups, while herptiles had stronger relationships with productivity compared to other groups. Overlap analysis revealed significant spatial overlap between productivity and biodiversity in all species groups, except for birds. High value areas for both productivity and biodiversity in all species groups, except birds, co-occurred in the Mediterranean and temperate regions. The areas with high biodiversity of birds are mainly found in the boreal areas of Europe, while for all other species groups these areas are mostly located on the Iberian Peninsula and the Balkan ranges. Based on the presented maps, areas where regulating wood production activities to conserve species can be identified. But the maps also help to identify areas where either biodiversity or productivity is high and focusing on just one aspect is more straightforward.

**Keywords** Productivity-biodiversity relationship · Spatial congruence · Species richness · Forest management · Trade-offs · Conservation planning · Habitat value · Net primary production

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## Introduction

Forests in Europe are increasingly viewed by various stakeholders as a natural resource that can be exploited for their specific goals. They represent a potentially important source for biomass as a renewable energy provider (Verkerk et al. 2011), a source for raw materials for various industries (Eyvindson et al. 2018), function as pool that can both sequester and store carbon (FAO 2005; Triviño et al. 2015) and act as repositories to more than half of wild plant and animal species (Eyvindson et al. 2018; Schulze et al. 2019). For some of these goals, estimations of forest productivity give important indications of the potential of forests to contribute to these goals. For example when they are a source for raw materials (Liang et al. 2016a, b; Suttidate et al. 2019; Youngentob et al. 2015). At the same time, biodiversity is valued because it is considered a key aspect needed to maintain the functioning and services of natural ecosystems (Pausas and Hawkins 2004; Gamfeldt et al. 2013; Naeem et al. 2009). For example, plant species diversity generally enhances primary productivity and nutrients uptake (Isbell et al. 2011; Liang, Crowther, et al. 2016). Likewise, animal species diversity of, for example, vertebrates and insects, promote pollination, seed dispersal and control of pests. Hence animal biodiversity is often regarded as an indicator of forest health and productivity. There is a thrust to strengthen biodiversity preservation in forests (Díaz et al. 2015) because species loss may substantially disrupt forest resilience and thereby impair the delivery of ecosystem services (Chaudhary et al. 2016).

Maximizing forest productivity and strengthening biodiversity conservation independently, may lead to potential competing claims over forest resource use. For example, forest productivity may be estimated as Net Primary Productivity (NPP), but for timber production purposes only biomass that is stored in tree trunks of certain diameter classes and of certain tree species is relevant (Verkerk et al. 2015). To make sure a forest system is able to provide these products often intensive management practices are required (Duncker et al. 2012). The high management intensity, however, may negatively affect animal biodiversity (Schulze et al. 2019) as it is considered a primary driver of species loss and extinction (Newbold et al. 2015), and reported as a recurrent threat to red listed forest species (Maxwell et al. 2016). On the other hand, biodiversity preservation may limit the potential of raw material production (Kallio et al. 2006) due to strict regulations on the intensity of management practices and imposing restrictions on wood felling (Verkerk et al. 2014a). So, although NPP as an estimator of productivity may not equate directly to timber production, areas with high NPP do give rise to questions whether this area should be managed to enhance timber production, or to be managed to preserve biodiversity. Productivity and biodiversity goals may thus create conflicting interests (Eyvindson et al. 2018; Verkerk et al. 2014b) that lead to a trade-off in either service.

Management strategies can help to optimize forest resource use for intensified productivity for wood production, carbon storage and biodiversity conservation at the same time. This requires assessing the productivity-biodiversity relationship (PBR; Liang, Crowther, et al. 2016) in forests. Also, it helps to identify areas where primary productivity (productivity hotspots) or biodiversity (biodiversity hotspots) can be optimized. In areas where both services show a high potential value, innovative management is needed to combine the claims on the forest resource (Verkerk et al. 2014b). Alternatively, choices for these areas have to be made, based on requirements in society.

The relationship between productivity and biodiversity is a subject of debate for many years. The species-energy theory suggests a positive correlation between species richness and environmental energy (Wright 1983). More productive landscapes are expected to

harbor more species than less productive landscapes (Hurlbert 2004; Srivastava and Lawton 1998a; Wright 1983). While this theory was validated by some studies (Suttodate et al. 2019; Youngentob et al. 2015) it was not supported in other studies (Bailey et al. 2014; Teodoro et al. 2013). There are studies which have stated that PBR may depend on the scale, type of forest, biodiversity measure (Adler et al. 2011; Lecina-Diaz et al. 2018), the taxon that is studied (Adler et al. 2011; Mittelbach et al. 2001) and environmental energy available (Adler et al. 2011). However, few studies have explicitly explored how these factors determine this relationship. Besides, most of the existing studies have predominantly explored PBR's for plant species (Adler et al. 2011; Liang, Crowther, et al. 2016; Nguyen et al. 2012). This could be because traditionally, conservation sites were designated primarily based on plant species. Similarly, in many cases, terrestrial vertebrates have been used as a surrogate for overall biodiversity. However, due to data constraints for these species (Lamoreux et al. 2006) only a limited sample of species is normally considered. Therefore, studies which assessed PBR using animal species were mostly limited to a few species (Bailey et al. 2014; Luck 2007; Rodríguez et al. 2005; Youngentob et al. 2015). This makes findings from multiple taxa incomparable due to scale differences or inconclusive due to biodiversity underrepresentation. Improved insight into PBR for multiple animal taxa under a consistent spatial scale, and perhaps across different forest types can help in further unravelling how biodiversity is distributed across forests.

Besides the relationship between productivity and biodiversity, little is known on the spatial congruence of productivity and biodiversity. We can call this productivity-biodiversity congruence (PBC) in short. Previous studies have either mapped these areas independently (Lamoreux et al. 2006; Neumann et al. 2016; Orme et al. 2005) or specifically looked at the spatial congruence of carbon storage and biodiversity, with results so far suggesting positive (Labrière et al. 2016; Lecina-Diaz et al. 2018), weak (Anderson et al. 2009) or scale-dependent congruence (Anderson et al. 2009; Di Marco et al. 2018). In this study, we expect to find positive PBR for forest productivity and animal diversity, in line with the general finding of previous studies for PBR on plants species and in line with the species-energy theory. Also, in case a strong positive PBR is found, it makes sense to expect strong spatial congruence for these two aspects. However, when the PBR is less strong, it is logical to expect that congruence between biodiversity hotspots and productivity hotspots is also less strong. That means that locations exist where biodiversity is high while productivity is low and vice versa. These locations would be locations where there is less chance of a conflict between either productivity or conservation goals.

The continent of Europe offers an important study site for improving our understanding of PBR and PBC in forests. In Europe, there are approximately 227 million hectares of forests, out of which approximately 24% is protected for biodiversity conservation purposes (Forest Europe 2020). These forests are impacted by international agreements such as the Paris agreement on climate change which aims to promote intensified forest management, and the convention on biological diversity which through Aichi targets aims to halt the loss of natural resources (CBD 2010; Morales-Hidalgo et al. 2015; Naumov et al. 2018). Forest management practices are likely to change and potential conflicts of interest can be expected as the EU considers forest resources as potential sources of bio-energy that can replace fossil fuel and aims to strengthen biodiversity conservation efforts to halt biodiversity loss (Verkerk et al. 2014a, b). These policies potentially lead to conflicting goals in areas where both biodiversity and productivity are high. As forests have often remained in those areas that were not interesting for agriculture in the past (Roberts et al. 2018), the renewed interest in the production function of forests potentially creates pressures that were so far not experienced.

A number of remote sensing platforms offer data streams that allow consistent mapping vegetation productivity at a continental scale. Moderate Resolution Imaging Spectrometer (MODIS) data provides global primary productivity data, that can be used to assess biomass production by plants—an important habitat property. A regional recalculation of MODIS net primary productivity (NPP) has been used successfully validated with forest inventory data and provides NPP data across European forests at 1-km resolution (Neumann et al. 2016). This data has also been used to predict spatial patterns of mammal, bird and butterfly biodiversity (Luck 2007; Phillips et al. 2008) in Australia.

When studying spatial associations, it is important to capture patterns with the right level of detail. This requires to decide on the cell size of the raster that will be used to discretize the territory under investigation. Too high levels of detail (so very small cell sizes) will capture also noise and most probably contain spurious accuracy, while too coarse approximations (so very large cell sizes) will average patterns out too much and lose meaning. At the extent of a continent like Europe, a reasonable compromise is found at 5 km×5 km (Van der Sluis et al. 2016).

This study investigates the spatial relationship between forest productivity and animal biodiversity, separating species data also across species groups. We test PBR for mammals, birds, herptiles and butterflies separately, and whether separating forests into coniferous and broadleaved changes these relationships. Lastly, we evaluate the spatial congruence between productivity and animal biodiversity hotspots of the different species assemblages to see where PBC causes potential competing claims on forest services.

## Methods

### Spatial extent, data sources and sampling approach

The spatial extent of the study was forests in European member states (EU-28, still including the UK) excluding Cyprus and the Macaronesian Islands. The size of grid cells was 5 km by 5 km. We combine data on forest productivity from Neumann et al. (2016), biodiversity of animal species from van der Sluis et al. (2016) and forest cover from Brus et al. (2011) as depicted in Fig. 1. We provide succinct descriptions on the input data, but refer to the original publications for full details on the methods used to generate these input datasets.

### Forest types and productivity

Apart from forests as a broad land cover category, forests were grouped into three categories: coniferous, broadleaved and mixed forests (Barbati et al. 2014). We used data from Brus et al. (2011) on the tree species types of Europe. This dataset with a spatial resolution of 1 km by 1 km provides information on the spatial distribution of the twenty most dominant tree species of Europe. These tree species were then classified into coniferous or broadleaved species based on the European Atlas of Forest Tree Species (EAFTS; San-Miguel-Ayanz et al. 2018). Following the FAO (2015) definition of monoculture forests. An 80% cover threshold was used to separate monoculture stands (coniferous or broadleaved) from mixed stands. The cells with less than 10% forest cover did not meet the definition of a forest area as outlined by (FAO 2000, 2020) and were eliminated from further analysis.

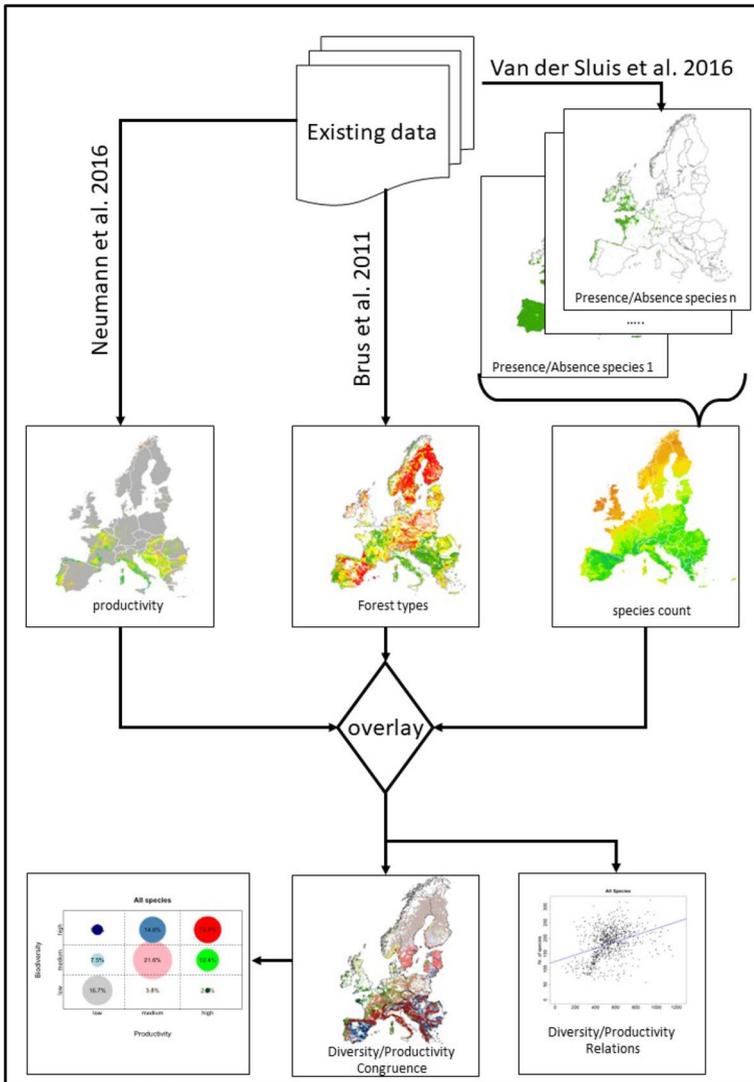


Fig. 1 Simplified overview of the methods used

Net primary productivity (NPP), the difference between gross primary productivity (GPP) and plant autotrophic respiration, denotes the biomass produced by plants through of photosynthesis. NPP is one of the most commonly used ecological metrics to study forest ecosystems and evaluate their potential to supply goods and services (Neumann et al. 2016). NPP derived from MODIS remotely sensed data has particularly received attention in monitoring forest dynamics. MODIS has the capability to capture global land coverage after every one to two days and measures NPP at a continuous scale (Kwon and Baker 2017).

To analyze the NPP at a European regional scale, we used MOD17 product derived from the global MODIS NPP of the Numerical Terradynamic Simulation Group (NTSG). The algorithm behind MOD17 uses climate data, land cover data, leaf area index (LAI) and fraction of photosynthetically active radiation (FPAR) modelled from other MODIS products to estimate GPP and NPP at a spatial resolution of approximately 1 km by 1 km (Neumann et al. 2016; Turner et al. 2006). LAI and FPAR were estimated with MOD15 LAI and FPAR Collection 5. The land cover data was from MOD12Q1 Version 4 Type 2 and the climate data was from E-OBS. Neumann et al. (2016) provides a detailed methodology of a European-wide scale MODIS NPP product that we used in this study. We calculated for each pixel the periodic average from 2000 to 2012 to account for interannual variations in productivity due to drought events or harvesting. Then the grids were resampled to 5 km by 5 km using bilinear resampling to match the species diversity grids.

The MOD17 algorithm incorporates light use efficiency in combination with remotely sensed vegetation data to calculate gross primary productivity (GPP). This in combination with maintenance and growth respiration derives NPP using the following equation:

$$\text{GPP} = \text{LUE}_{\max} \times f_{T_{\min}} \times f_{v_{pd}} \times 0.45 \times \text{SW}_{\text{rad}} \times \text{FPAR}$$

$$\text{NPP} = \text{GPP} - R_M - R_G$$

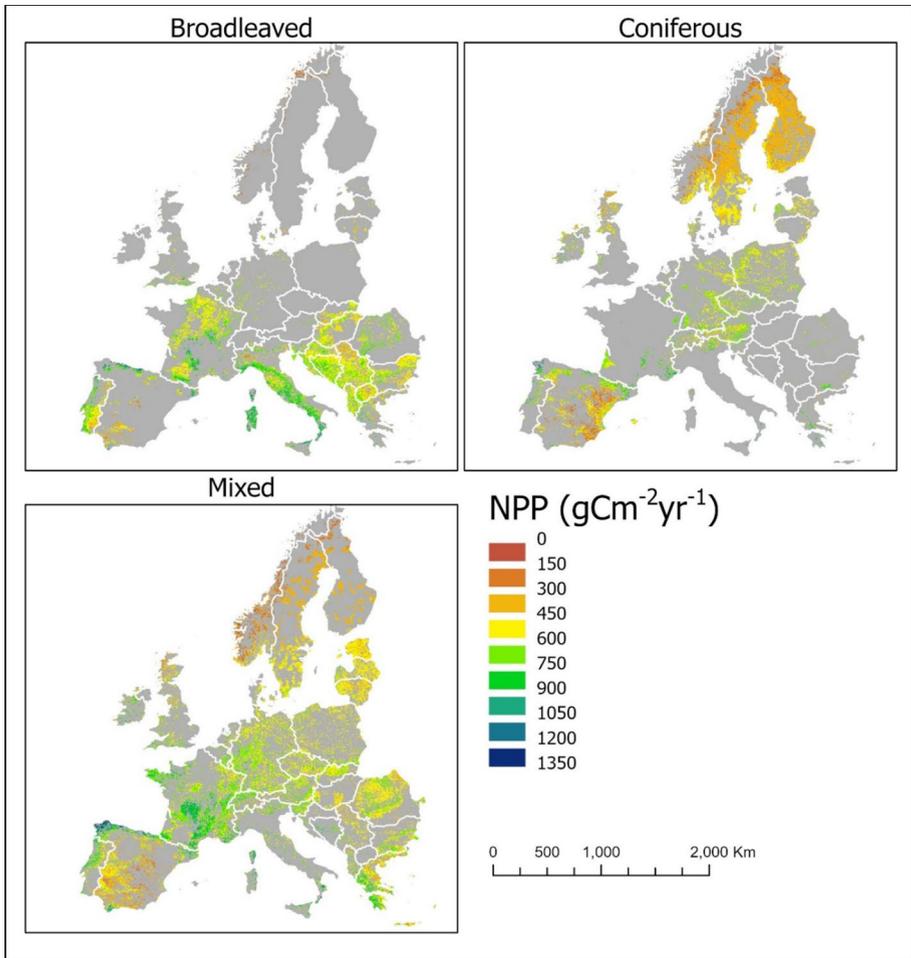
where  $\text{LUE}_{\max}$  is the maximum light use efficiency;  $f_{T_{\min}}$  and  $f_{v_{pd}}$  are fluctuations in light use efficiency from low temperatures that limit the functioning of plants and deficits in high pressure that results to water stress in plants (Coops et al. 2018; Zhao and Running 2010);  $\text{SW}_{\text{rad}}$  is the incident short wave solar radiation, of which 45% is photosynthetically active radiation absorbed by vegetation from MODIS (FPAR);  $R_M$  is the maintenance respiration as measured by leaf area index;  $R_G$  is the fraction of growth respiration and it accounts for about 25% of NPP.

We extracted the NPP for the total forest areas as defined by the areas indicated on the map from Brus et al. (2011). We then parsed the NPP data further by monospecific coniferous forests, monospecific broadleaved forests and mixed forests. Figure 2 shows productivity distribution across the three forest groups that we considered in this study.

## Distribution patterns of biodiversity

Distribution maps of animal species that naturally occur in the territory of the EU28 were compiled by van der Sluis et al. (2016) and a detailed description of the input species, climate data, modelling and validation approaches are provided therein. A brief summary is provided in this article for completeness. The species data was collected from European-wide atlases and predicted range maps. The choice of which source to use was dependent on data reliability. There was variation in terms of data availability and quality among and within taxa influencing the choice of the analytical methods. However, such methods were harmonized to arrive to distribution maps that are as comparable as possible.

In total, there were 169 species of mammals, 294 species of birds, 147 species of herptiles (amphibians and reptiles) and 395 species of butterflies. The dataset excluded invasive and domesticated species of mammals. Sea turtles and herptile species that occur at the fringes of the European continent, but have their dominant ranges in either the African or central European continent, were also excluded. They do not play a relevant role in the PBR and PBC considerations for European mainland forests ecosystems. Endemic birds



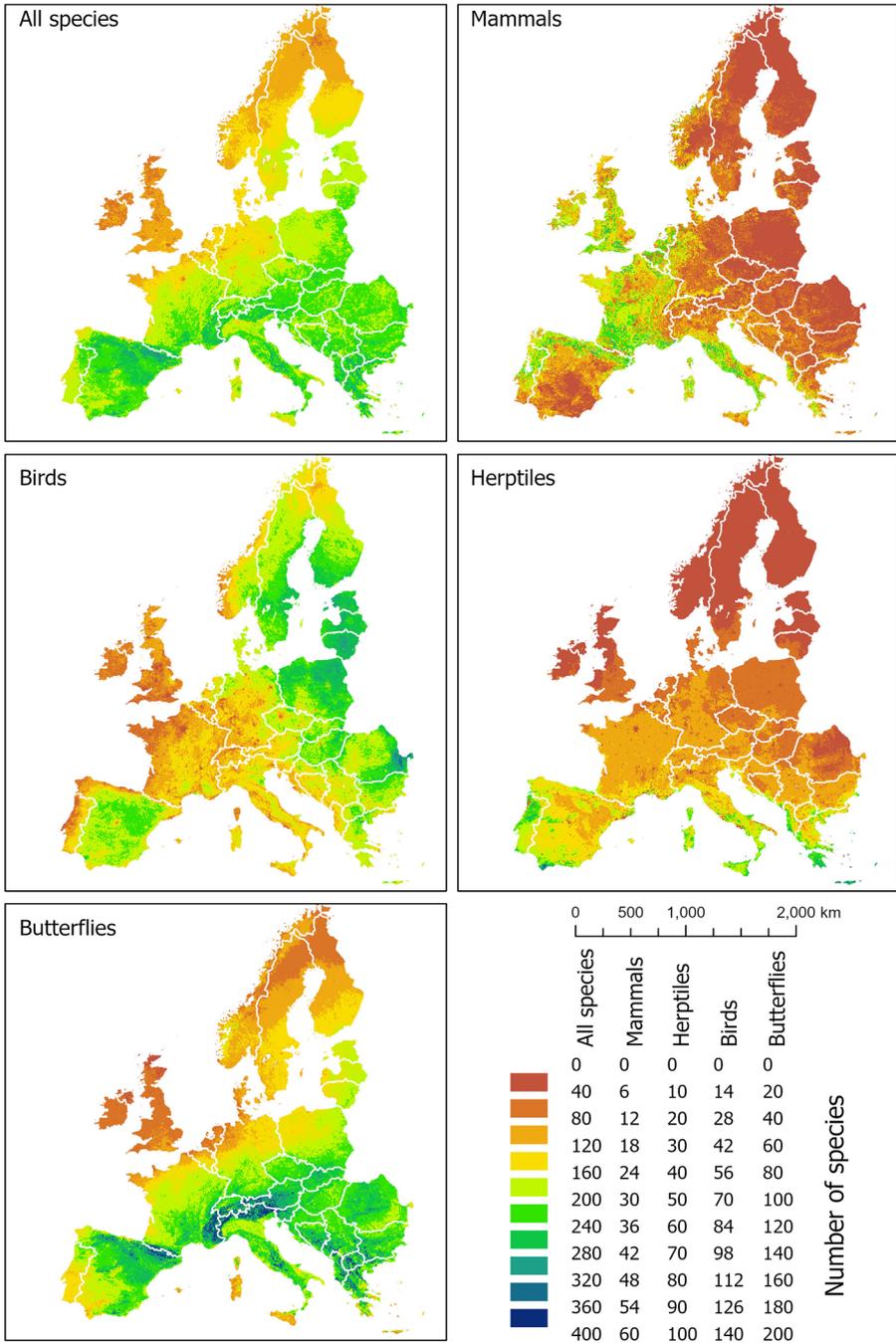
**Fig. 2** Spatial distribution of Net Primary Production (NPP; gCm<sup>-2</sup> yr<sup>-1</sup>) for broadleaved, coniferous and mixed forests

were also excluded because there are very few species in the study region and this might have disproportionately large effects on the fitting of the PBR's. For the same reason rare and very localized species of butterflies were omitted. Hence, biodiversity is characterized in this study by common European animal species (Lennon et al. 2004).

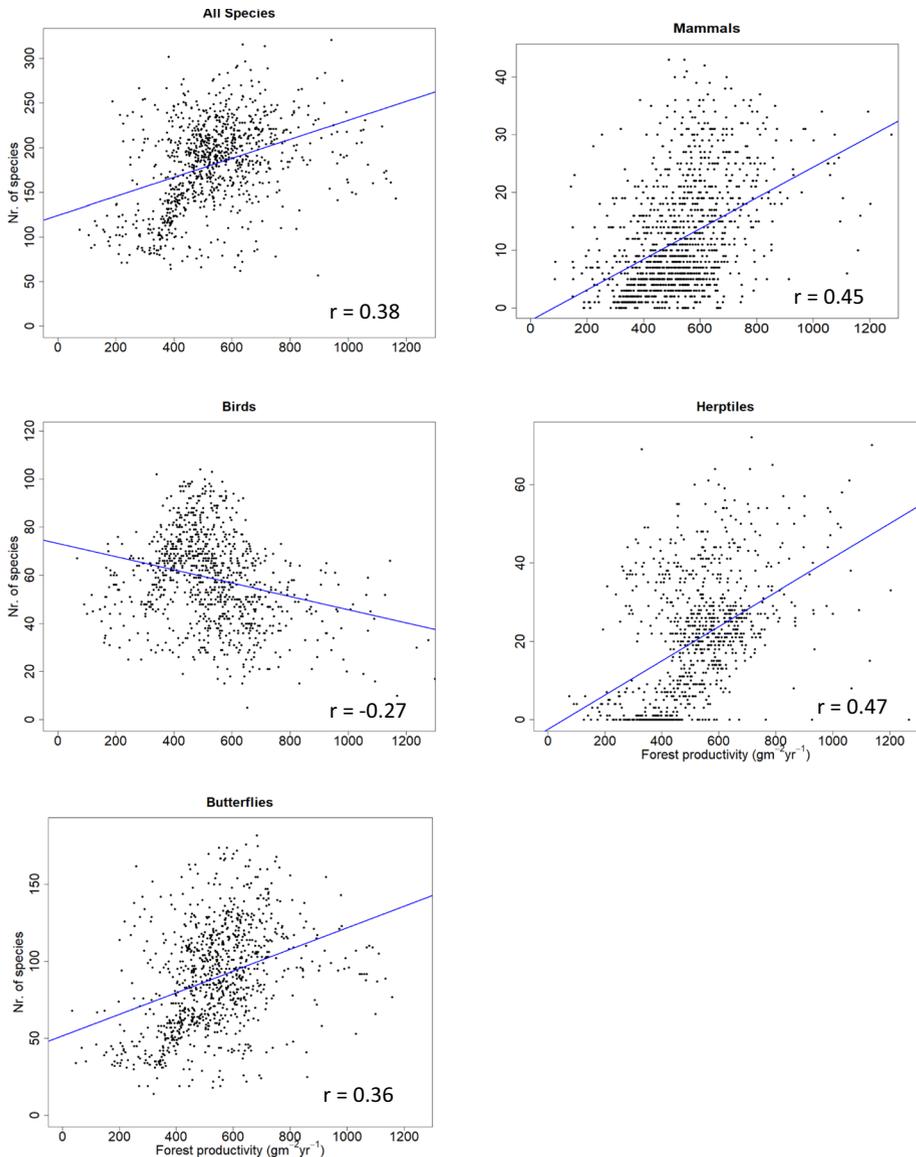
Distribution data for mammal was retrieved from and mammals from from Observado (Observation.org; <http://observation.org>), GBIF ([www.gbif.org/](http://www.gbif.org/)), and the CKmap project (<http://www.faunaitalia.it/ckmap/>). Species data for birds were provided by the European Breeding Bird Atlas (Hagemeijer and Blair 1997), herptiles by Societas Europaea Herpetologica (Sillero et al. 2014) and butterflies by the European Red List of Butterflies (van Swaay et al. 2010). These atlases cover the Pan European distribution (excluding Cyprus and the Macaronesia Islands) at a resolution of 50 km by 50 km resolution. Because of the coarse resolution, the extent of a species range is most likely over-estimated. Besides, the estimation of the presences was not based on

a common standardized method between countries and differed in terms of quality of field work and number of observers per country (van der Sluis et al. 2016). To lessen the effect of these issues, species modeling results (Elith and Leathwick 2009) were validated with several independent datasets. The main approach was to downscale the 50 km by 50 km to 5 km by 5 km using Boosted Regression Trees (BRT). BRT's as implemented in the BIOMOD 2 package in R were used for mammals and herptiles. BRT's as implemented in TRIMmaps (Hallmann et al. 2014) were used for birds and butterflies. As BRT constitutes a generic modelling technique, the possible differences in implementation between the two software packages will constitute only marginal differences in the results. Besides, in a relative sense output maps are comparable, which will be sufficient for the analysis in this study. BRT is used because it can deal with non-linear relationships and accounts for interactions between different explanatory variables (Couce et al. 2013). The species models were fitted with climate, soil, nitrogen and sulfur deposition, forest management and Corine Land cover types 2013 (EEA; for birds, butterflies and herptiles), and Global Land Cover maps 2009 (JRC; for mammals) data. For each species, the models were run ten times on different random subsets. Each subset was made up of 80% training and 20% validation data of presence and absence random allocations. The distributions were then averaged to get the final model predictions. The predicted probability maps were converted into presence-absence maps using a threshold. For the mammals, birds and butterflies, the threshold was based on the value where accuracy for predicted presence and predicted absence would be equal. For the herptiles the threshold was based on the value where the maximum true skill statistic (TSS; Allouche et al. 2006) would be achieved. Although maximum TSS thresholds are not necessarily the same as thresholds based on equal accuracies for absence and presence prediction, the resulting species count maps over the entire extent of Europe will show only marginal differences. Mainly at the outer fringes of a species' range small differences would be expected. These differences might be either increasing or decreasing the total extent of a species range, and across species, this effect should average out. In the original report (van der Sluis et al. 2016) the results of these models were validated at different spatial scales (individual countries and across Europe) with independent data sources. These validations showed a general consistency between species groups in terms of modelling accuracy.

SDMs provide useful information on species richness at a fine scale (Coops et al. 2018; Suttidate et al. 2019) which is more advantageous than would have been if range maps with coarser resolution were used. Biodiversity was predicted by stacking presence absence predictions of individual species from the species distribution models (SDMs). SDMs are used to predict species that co-occur in a region, however, they are likely to overpredict species richness by (1) incorrectly predicting species occurrence in an environment that appears suitable but is outside the species colonizable range (Wisiz et al. 2014), (2) assuming the "species capacity" of the local environment is always reached and (3) excluding biotic interactions that may control species co-occurrence (Anderson et al. 2002). Nevertheless, patterns of relative variations in species richness would still hold, and for the purpose of this study, that should suffice. Biodiversity was thus estimated for the combined taxonomic groups, and for mammals, birds, herptiles and butterflies. All biodiversity metrics, however, gave a similar distribution in biodiversity and we thus chose to report results from only species richness. In Fig. 3, each biodiversity variable is represented as the total number of species in a grid cell (Fig. 4).



**Fig. 3** Spatial distribution of biodiversity (expressed as estimated by species richness for overall or total biodiversity, mammals, birds, herptiles and butterflies



**Fig. 4** Scatterplots and linear regression between forest productivity and biodiversity. All relationships are significant at  $p < 0.001$

### Productivity—biodiversity relationships

The relationships were assessed between mean net primary productivity (NPP) and the five different biodiversity groups that were calculated of all forests and separately for coniferous and broadleaved forests. Because the pixels in the map are contiguous interpolations, spatial autocorrelation can potentially negate the assumption of independent samples when

all pixels from maps are taken into account. Therefore, we first tested for spatial autocorrelation using Moran's I statistics on a randomly selected subset of the data. We found that for each combined variable there was a significant degree of spatial autocorrelation. We accounted for this spatial autocorrelation by using a random selection from the data. In the initial analysis, we fitted regression models on 0.75%, 2%, 5% and 25% of the data to test if sample size had an effect on model performance. The models were fitted on twenty random selections of the data and averaged to get the final correlation coefficient. We did not observe big differences in the correlation coefficient and p-values when fitting on different sized datasets. But when we used very small samples, the statistical significance of the models was lower. The sign of the correlations, or the relative differences between species groups however remained the same. Also, we compared the results with quadratic model fits to our data but there was no difference in the signs and p-values. All models were significant at  $p < 0.0001$ , regardless of the sample size or the model used. Therefore, in our study, we reported on the results from only linear models with a sample size of 0.75% of all pixels for all taxa.

### Spatial congruency analysis

Areas high or low in either productivity or biodiversity were labelled as 'hotspots' or 'coldspots' respectively. Hotspots were delineated by identifying the top 30% quantile of a variable and cold spots by the bottom 30% quantile of a variable (Schröter and Remme 2016). For completeness, we also delineated the remaining areas which were labelled as "medium-spots". Schröter and Remme (2016) and Korpilo et al. (2018) showed that the most common thresholds for quantile ranges to determine hotspots are between 5 and 30%. We also evaluated quantile thresholds of 10% and 5% to assess the impact of setting a threshold influences the results. As the general pattern didn't affect the overall conclusions, we provide them in the supplementary materials (see Figure S3) but do not address them further in the results.

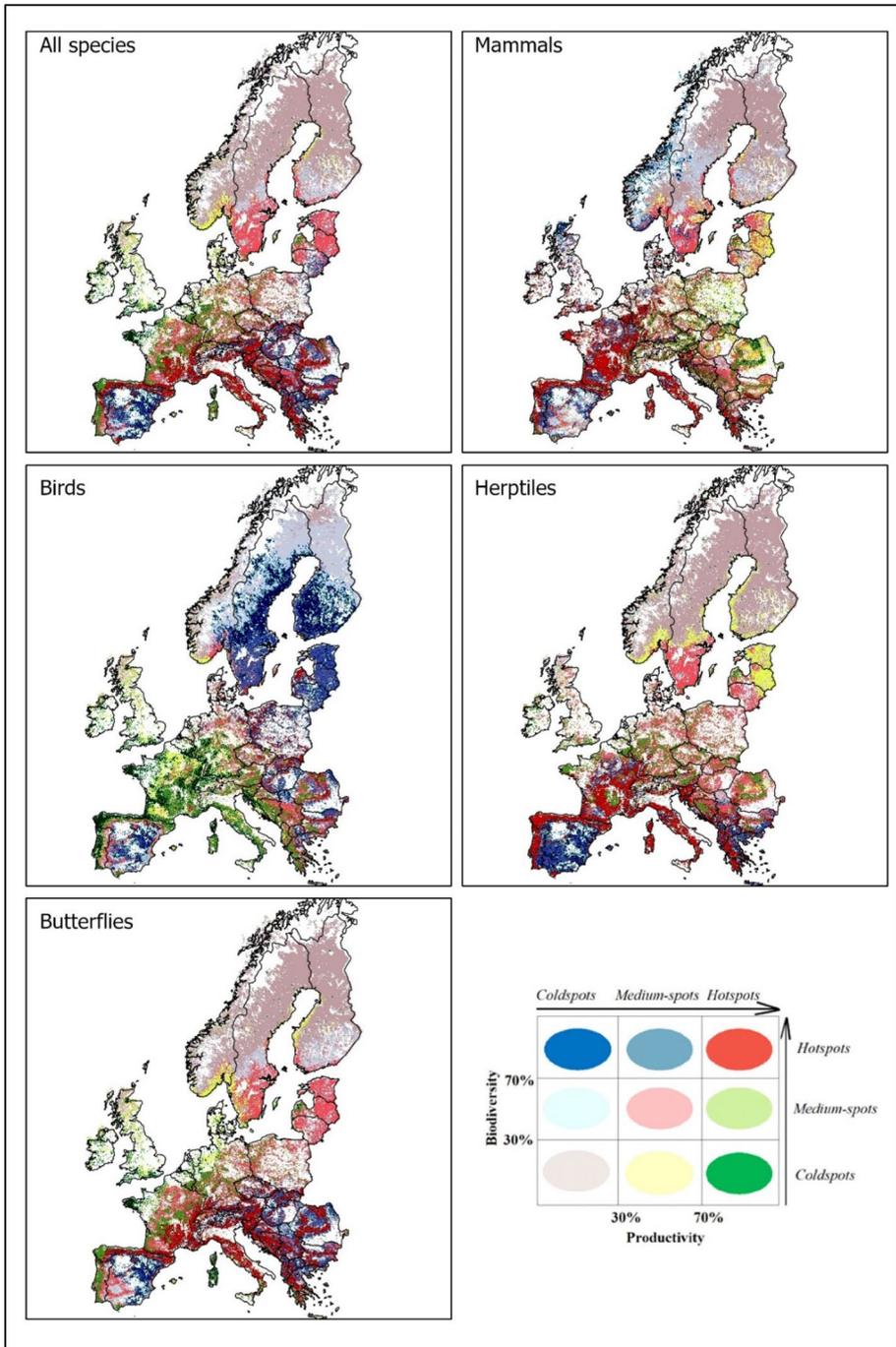
The classified hot-, medium- and coldspot maps of productivity were overlaid with each biodiversity variable and the resulting nine congruence classes of the two variables were tabulated and presented using the color scheme as presented in the legend of Fig. 5.

## Results

Total biodiversity as estimated by species richness metrics varied between 0 and 367 species per cell. Different ranges per taxa were calculated with the highest range for butterflies (between 4 and 222), followed by birds (values between 1 and 127) and lowest for herptiles (values between 0 and 94) and mammals (values between 0 and 49; Fig. 3).

### Productivity-biodiversity relationships

Across all variables, productivity showed positive relationships with all biodiversity groups except for birds which showed a weak negative relationship (Fig. 4). The strongest relationship was observed for herptiles. Although there was a large variation in the number of species per biodiversity group, relationships tended to show only a slight variation in terms of the  $R^2$  values and slope. This is suggesting that the number of species in a group had little effect on the strength of PBR. When there is variation in the number of species



**Fig. 5** Spatial congruence between overall productivity and overall, mammal, bird, herptile and butterfly biodiversity based on a 30% threshold

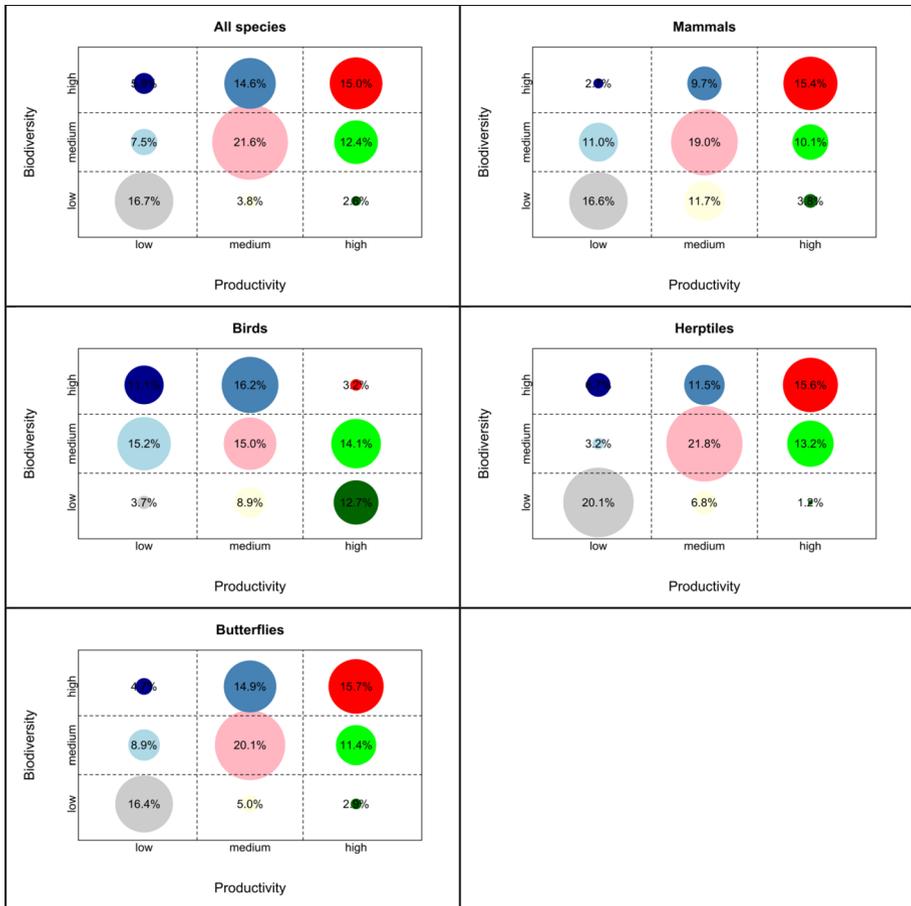
per species group, some authors choose to standardize biodiversity values to correct for these differences. However, the relative differences between our groups will be the main interest in this study, and when we look at differences between quantiles this will become apparent. Also, PBR does not vary with the biodiversity metrics. We noted that relations using species richness were almost similar compared to Margalef and Shannon metrics. The Simpson metric showed relatively lower  $R^2$  values while its p-values were similar to other metrics (Supplementary Figure S1). The Simpson metric measures species evenness and can be very sensitive to the abundance of the most frequently occurring species in a community. In our case we did not have real abundance but used modelled suitability as a surrogate. We assume that there was no species which was dominant in terms of modelled suitability over the other species. But we cannot claim that this is the reason why the Simpson metric was weakly related to productivity.

Separating forests into monoculture coniferous and broadleaved, PBR showed stronger relations in the coniferous forests and weaker relations in the broadleaved forests (Supplementary Figure S2). The extent of coniferous forests was larger than broadleaved forests (see Fig. 2). However we do not consider this as a cause for the difference in the  $R^2$  values because the total forest area was larger than either forest type and also showed lower  $R^2$  values than some PBR's fitted for coniferous forests.

### Biodiversity hotspots and coldspots

The overlap analysis showed that the hotspots of both productivity and biodiversity are mainly found in Temperate and Mediterranean parts of Europe. The coldspots of both productivity and biodiversity are mainly located in the boreal region (Fig. 5). The biodiversity of the four species groups showed a high degree of congruence with productivity in geographical space as shown in Fig. 5. An evaluation at the 30% quantile range revealed significant spatial overlap between productivity and biodiversity hotspots. When diversity and productivity would have been distributed randomly and independently, this overlap would be expected to be around 9% (30% of 30%). But for the cases of all species together, and for the mammals, herptiles and butterflies, overlap areas were covering between 15.2% and 16.9% of the entire forest extent (see the red bubbles in Fig. 6). This is significantly more than expected. Contrastingly, for birds the overlap was significantly lower (3.6%). This indicates that there are considerable areas in Europe where there is a potential trade-off between conservation and forest production goals. A deviation from this observation was found for birds with relatively low spatial overlap between areas with high productivity and high bird diversity.

PBC was also high for the areas where biodiversity and productivity coldspots overlapped. This covered between 16.4% and 10.2% of the European forest extent, again with the notable exception of birds (3.29%; the grey bubbles in Fig. 6). Contrastingly, there was a very low spatial overlap between the biodiversity hotspots and productivity coldspots (blue bubbles in Fig. 6) and biodiversity coldspots and productivity hotspots (green bubbles in Fig. 6). These would intuitively be most suitable for conservation and production goals respectively. Interestingly we noted that such conservation areas for birds were mainly identified in the boreal areas of Europe. For all other species groups their area is mostly located on the Iberian Peninsula and the Balkan ranges (Fig. 5).



**Fig. 6** Bubble charts of the spatial congruence between overall productivity and overall biodiversity and for mammals, birds, herptiles and butterflies based on a 30% threshold

## Discussion

### Relationships between productivity and biodiversity

Our analysis relied on interpolated species data to show the regional distribution of biodiversity of common European animal species, and forest productivity from MODIS. All this data was sampled at a relatively coarse resolution of  $5\text{ km} \times 5\text{ km}$ . This will not match with the exact patterns that will be found on the ground. Especially in highly fragmented landscapes, like for example northwestern Europe, the estimated productivity in a  $5\text{ km} \times 5\text{ km}$  grid cell can represent many different forest conditions. Also, the exact locations that are suitable for certain species and how these add up to diversity metrics at a scale of  $5\text{ km} \times 5\text{ km}$  will constitute an approximation. But a comparison in Van der Sluis et al. (2016) showed that there are good relationships between modelling species distributions at  $5\text{ km} \times 5\text{ km}$  and modelling at  $1\text{ km} \times 1\text{ km}$  for individual countries. Working at the extent of Europe, modelling at a  $1\text{ km} \times 1\text{ km}$  resolution becomes computationally cumbersome,

while it is not expected to lead to qualitatively different results. So we believe that the interpretation we present in this discussion holds for the provided results. The identified productivity-biodiversity relationships in this study may not be exactly comparable with relations based on direct observations. Firstly, because our species distribution models may have likely overestimated species richness. Also, the MODIS product still contains uncertainties for European forests although less than estimates with a global coverage. Nevertheless, our analysis provides general information on the potential trade-offs in these forests. And it is the first to use these datasets to estimate productivity-biodiversity relationships and its congruence in European forests for different species groups at a regional scale.

NPP as a general measure of productivity shows an increasing trend with species biodiversity. This finding corresponds with previous findings (Bailey et al. 2014; Liang et al. 2016a, b; Luck 2007; Rodríguez et al. 2005; Youngentob et al. 2015). Collectively they provide support for prevailing theories in ecology such as the species-energy theory (Wright 1983) and the “more individuals” hypothesis (Srivastava and Lawton 1998b). These suggest that there is a positive association between species richness and available energy. We found significant positive relationships between productivity and overall animal biodiversity, and diversity in mammals, herptiles and butterflies. It seems, however, that the relationships are generally weak as observed from the low  $R^2$  values and is not affected by the type of model fit. We tested also non-linear relationships but found no added value. Also type of biodiversity measure used did not affect this finding (see supplementary materials S1). In a different study, Luck (2007) found different relationships between NPP and species richness of different taxonomic groups in the mainland of Australia. In that study NPP was positively related to butterflies, endemic and geographically restricted species of butterflies, birds, mammals and threatened species of birds. But it was negatively related to threatened mammals and not related to combined threatened taxonomic groups. Although we cannot infer the reasons for these differences from the presented results in this study, potentially the driving factors for animal diversity are very different between the two continents.

The observed negative relationship between productivity and species richness of birds does not concur with previous studies such as Hurlbert (2004) and Phillips et al. (2008) whose study showed that productivity (measured by NDVI and NPP) explained variation in bird richness. Because birds are perceived to be key indicators in monitoring the status of forests and ecosystem services in Europe (Gregory et al. 2008), a positive PBR might seem obvious. But the status of a forest and the services provided by a forest do not rely on productivity alone. Other factors can also shape this relationship. For example, in North America, Hurlbert (2004) found positive PBR for birds and indicated that habitat structure contributed largely to the observed patterns as a measure of productivity. But when the same bird dataset was separated into different functional guilds, Bailey et al. (2014) found that the neotropical migrant birds were correlated with maximum NDVI while no correlation was observed with resident birds. It could well be that in Europe, forest structure, or forest type is much more important for bird diversity than productivity alone. And structure is not necessarily strongly related to productivity.

### **Spatial congruence between productivity and 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 and the ecological requirements of the ecosystem services (Anderson et al. 2009; Gos and Lavorel 2012). However,

irrespective of this degree, the information on spatial overlap is informative for implementing strategies for land management and conservation (Anderson et al. 2009). Based on our literature review, there have been only a few studies on productivity-biodiversity congruence (PBC) particularly for plants and terrestrial animals. Our study found a high degree of congruence between hotspots of productivity and hotspots of biodiversity of all species and biodiversity of mammals, herptiles and butterflies. Especially when this is compared against congruence coldspots in productivity with hotspots in biodiversity. Our results indicated that considerable extents of forest in Europe that are valuable for productivity also support high levels of biodiversity totaling to about 470.000 km<sup>2</sup>. At taxa level these areas covered about 500.000 km<sup>2</sup> for mammals, 430.000 km<sup>2</sup> for herptiles and 490.000 km<sup>2</sup> for butterflies.

Contrary to other taxa, there was a low congruence in hotspots for birds, covering an average area of about 110.000 km<sup>2</sup>. The low spatial overlap is implying that productivity offers minimal support for bird biodiversity. This is true given that the boreal zone of Europe having low productive forests harbor a relatively high number of birds (Sundseth 2005). Possibly other forest characteristics are more important to harbor a wide variety of bird species. For example, nest locations, presence of dead wood and variability in tree species might be more important. These factors are known to be associated with diverse forest structure rather than productivity.

Analysis from previous studies revealed mixed results on the degree of PBC for different species. For example, using carbon as a measure of energy, a high spatial overlap with bird diversity at a 20% quantile range was found in Spain (Lecina-Díaz et al. 2018). On the other hand, results from the UK species of concern (i.e., non-marine feeding birds, terrestrial mammals, herptiles, vascular plants, bryophytes and butterflies) revealed low spatial overlap with carbon storage. And the level of overlap was highly dependent on whether the threshold value used was 10%, 20% or 30% (Anderson et al. 2009). When looking at spatial congruence between species hotspots, studies found that herptiles, mammals and birds show a high degree of congruence at the regional extends of Africa (Lewin et al. 2016) and Australia (Powney et al. 2010). The congruence of herptiles with other taxa is very complex with reference therein showing that lizards are weakly congruent with other species groups compared to other herptile species. If species show high levels of congruence with each other, we expect they will show similar patterns of overlap with productivity.

The concept of hotspot overlap areas offers an independent and objective assessment tool to inform management and conservation planning. However, policies are often developed with a single goal in mind, for example either to enhance productivity or to support biodiversity protection. This may put pressure on areas that are suitable for both activities and, depending on the choices made, may substantially impair one of the ecosystem services offered. Intensification of management practices to promote wood production and subsequently wood removal may negatively affect biodiversity. On the other hand, biodiversity protection and imposing felling restrictions may lower the potential supply of wood. Consistent with Verkerk et al. (2014a, b) these areas are likely to present trade-offs. Therefore, optimizing strategies that can achieve both policy goals should be developed. Although, it is important to assess how these policies impact on each other and other ecosystem services as well, the present study acknowledges that deciding where to impose which policy goals can be critically challenging. We found that large extents of European forests are identified to be suitable for both the goal of wood production and conservation (Sandström et al. 2011; Verkerk, et al. 2014a, b). For these areas it is relevant to develop appropriate management regimes which maintain both wood production and allow for biodiversity protection in the same area. The maps

produced in this study show that land use planning and conservation strategies with an inclusive goal of maintaining productivity and animal biodiversity need to focus on the temperate and Mediterranean parts of Europe. There a significant overlap of hotspots areas was found. On the other hand, significant hotspots of productivity which occurred in coldspots of biodiversity (and vice versa), are revealing areas where a single ecosystem service can be focused on. Hotspots of animal biodiversity with low productivity can be strictly reserved for biodiversity. Highly productive areas with low biodiversity can be maximized for wood production.

## Conclusion

The results of our analysis highlight the potential relationships between productivity and biodiversity among taxa and in various forest types across Europe. The productivity-biodiversity relationships and their spatial congruence across forest ecosystems in Europe concurs well with species energy theory. It also concurs with a number of smaller extent studies across Europe and other parts of the world. Based on our analysis, we can infer that increasing productivity correlates positively with mammal, herptile and butterfly diversity, but (mildly) negatively with bird diversity. We further found that there are large extents of forest where there is high productivity and high biodiversity overlapping. In these areas there is potential conflict between conservation and production priorities. Areas with low productivity and high biodiversity are more suitable for conservation and the ones with low biodiversity and high productivity are more suitable for production purposes. But these areas are much smaller in extent than the areas where hotspots overlap. We assessed the relationships between productivity and biodiversity of common species groups in Europe for the entire forest extent. But we assessed this also for coniferous and broadleaved forest types separately (results in supplementary materials). We found consistent patterns across all our analysis. As such it can serve as a guide to support policy formulation related to sustainable forest management while helping both productivity and animal biodiversity conservation in Europe.

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**Author contributions** CK and TG wrote the main manuscript text. CK, TG, and BT designed the overall approach. MN contributed to the productivity modelling and CS, LS, HS and TG contributed to the SDM modelling of butterflies, mammals, birds and herpetofauna respectively. All authors reviewed the manuscript.

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**Data availability** The used data and modelling results are hosted by the different institutes that collaborated in the earlier project and can be requested at these institutes.

## Declarations

**Competing interest** There are no competing interests to declare for this study.

**Ethical approval** Not applicable.

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