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Butterflies show different functional and species diversity in relationship to vegetation structure and land use

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Abstract

Aim: Biodiversity is rapidly disappearing at local and global scales also affecting the functional diversity of ecosystems. We aimed to assess whether functional diversity was correlated with species diversity and whether both were affected by similar land use and vegetation structure drivers. Better understanding of these relationships will allow us to improve our predictions regarding the effects of future changes in land use on ecosystem functions and services.

Location: The Netherlands.

Methods: We compiled a dataset of c. 3 million observations of 66 out of 106 known Dutch butterfly species collected across 6,075 sampling locations during a period of 7 years, together with very high-resolution maps of land use and countrywide vegetation structure data. Using a mixed-effects modelling framework, we investigated the relationship between functional and species diversity and their main land use and vegetation structure drivers.

Results: We found that high species diversity does not translate into high functional diversity, as shown by their different spatial distribution patterns in the landscape. Functional and species diversity are mainly driven by different sets of structural and land use parameters (especially average vegetation height, amount of vegetation between 0.5 and 2 m, natural grassland, sandy soils vegetation, marsh vegetation and urban areas). We showed that it is a combination of both vegetation structural characteristics and land use variables that defines functional and species diversity.

Main conclusions: Functional diversity and species diversity of butterflies are not consistently correlated and must therefore be treated separately. High functional diversity levels occurred even

in areas with low species diversity. Thus, conservation actions may differ depending on whether the focus is on conservation of high functional diversity or high species diversity. A more integrative analysis of biodiversity at both species and trait levels is needed to infer the full effects of environmental change on ecosystem functioning.

1 | INTRODUCTION

It is well known that biodiversity is rapidly disappearing at local and global scales and that this is in great part attributable to human activities, such as deforestation and intensification of land use, which have resulted in land degradation (Tittensor, 2015). In many industrialized countries, extensive areas of the landscape have become more homogeneous in structure, resulting in a reduction in biodiversity levels, owing to their conversion to agriculture and grasslands with high inputs of fertilizers and pesticides (Steffen et al., 2015). This conversion and intensification of land use, among other anthropogenic pressures, pushes species to shift from their present locations, tracking suitable habitats (Lenoir & Svenning, 2015). Species shifts may disrupt community composition and destabilize ecosystem functioning and services (e.g., pollination of crops and wild plants; Thomas, 2005). Different ecosystem functions are often performed by organisms with different sets of traits (i.e., physiological, morphological and genetic characteristics; Díaz et al., 2013). In this way, functional diversity can thus be understood as the variety of traits that allows species to carry out functions in the ecosystem and to move or adapt to new environments (e.g., Aguirre-Gutierrez et al., 2016; Hoffmann & Sgrò, 2011). Hence, species assemblages covering a broader range of traits (i.e., with higher functional diversity) are thought to be more resilient to environmental changes (e.g., change in land use) than functionally more homogeneous assemblages (Cadotte, Carscadden, & Mirotchnick, 2011).

Functional diversity is not always correlated with species diversity, and it is suggested that they refer to different sets of characteristics in an ecosystem (Petchey & Gaston, 2002). In farm ecosystems, it has been shown that certain management approaches may succeed in retaining high species diversity but could in fact fail to maintain high functional diversity (Forrest, Thorp, Kremen, & Williams, 2015). This is worrisome, as recent work has shown that ecosystem services, such as pollination, are strongly mediated by functional diversity in the landscape and not directly by the species diversity per se (Martins, Gonzalez, & Lechowicz, 2015). Moreover, Hoehn, Tscharntke, Tylianakis, and Steffen-Dewenter (2008) have shown that crop yield can be increased by the presence of more functionally diverse pollinators, and Fontaine, Dajoz, Meriguet, and Loreau (2005) demonstrated that in natural systems higher functional diversity of pollinators can also increase plant community diversity. However, given the lack of trait information for most taxa, studies often rely only on species diversity measures when investigating the impacts of environmental changes on biodiversity and

ecosystem services and resilience (Mori, Furukawa, & Sasaki, 2013). Given the mismatch between functional and species diversity, these two may therefore be constrained by different sets of environmental drivers. This makes it of major importance to quantify differences not only between functional and species diversity levels but also in their drivers of change that generate the distribution patterns observed in nature. This may render insights into which areas are more susceptible to on-going and future environmental changes (Jetz et al., 2016).

Changes in land use have been highlighted as a main driver of biodiversity loss and biotic homogenization at local and broad scales (González-Varo et al., 2013). However, changes in land use do not only mean shifting from one type of land use to another but also changes in the structure of the vegetation found at a given location. It is suggested that vegetation structure is highly influential for animal diversity and that different taxonomic groups may respond to different components of habitat structure (Davies & Asner, 2014). Thus, this may be especially important for invertebrates that actively depend on different microclimatic conditions provided by the spatial arrangement of vegetation. Moreover, the vegetation structure could also directly impact the availability of feeding and nesting resources for invertebrates across their different life stages (Berg, Ahrné, Öckinger, Svensson, & Söderström, 2011). Therefore, in addition to the type of land use, the structural characteristics of the local vegetation may be important drivers of functional and species diversity in the ecosystems.

Butterflies (Lepidoptera: Papilionoidea and Hesperioidea) are widely distributed, highly diverse in traits, carry out pollination, are widely used as sensitive indicators of environmental change (Thomas, 2005) and are one of the best-studied invertebrate groups (Merckx, Huertas, Basset, & Thomas, 2013). We use monitoring data of butterflies in The Netherlands collected between 2008 and 2015 to investigate how vegetation structure and land use characteristics drive their functional and species diversity levels. Vegetation structure and land use are characterized using a very high-resolution land cover map of The Netherlands and countrywide remotely sensed LiDAR (light detection and ranging) information. LiDAR-derived proxies of vegetation structure have been successfully applied to infer vegetation species richness, to map species distributions and for conservation planning (Simonson, Allen, & Coomes, 2014). This makes LiDAR data one of the most viable resources for investigating biodiversity distributions and mapping functional diversity across local and broad spatial scales.

We address the following three specific questions in this study. (a) Are land use and vegetation structural parameters correlated with

functional and species diversity? (b) Is functional diversity defined by a different set of parameters from species diversity? (c) From the full set of vegetation structure and land use parameters, which are the most important for defining functional and species diversity? Our hypothesis is that landscapes with heterogeneous vegetation structure and mixed land use types maintain functionally more diverse species sets. This may not be the case for species diverse landscapes, as these could be functionally homogeneous. Given that functional diversity might not be related linearly to species diversity, we expect their drivers to differ in the strength and direction (positive or negative) of their impact.

2 | METHODS

2.1 | Study area and species data

The Netherlands is located in north Western Europe and possesses a temperate Atlantic climate. The average minimal temperature in winter is −1 °C, and maximal temperature averages 24 °C during the summer (Klein Tank, Beersma, Bessembinder, van den Hurk, & Lenderink, 2014). The Netherlands has experienced major changes in land use over the last 100 years and currently shows high levels of habitat fragmentation. Agricultural systems currently account for 55% of the land area, and the forested systems are present in only 11% of the country (http://www.fao.org/countryprofiles).

We selected the butterflies (Lepidoptera: Papilionoidea and Hesperioidea) as our study group given their importance as indicators of ecosystem stability (Thomas, 2005) and the high quality of the data available, surpassing that available for other pollinators (e.g., bees and hoverflies). The butterfly species presence data originate from systematic transect counts from the Dutch Butterfly Monitoring Scheme (van Swaay, Nowicki, Settele, & van Strien, 2008) for the 2008–2015 period (Supporting Information Figure S1). The monitoring transects consist of a series of up to 20 sections of 50 m × 5 m, and only transects with at least 12 counts in a single year were used. We used section-level species data with the total count per species to estimate species abundance. These data have been systematically collected by experts and volunteers, and the quality of species identification and location accuracy of occurrence records has been assessed by the Dutch National Database of Flora and Fauna, NDFF (see http://www.ndff.nl/over-dendff/validatie). For a full description of the species collection methods, see van Swaay, Termaat, and Plate (2011). During the 2008–2015 period, 66 species out of a total of 106 known butterflies species for The Netherlands were collected across 6,075 sampling locations and are used in this study (see Supporting Information Table S1).

2.2 | Species traits, functional diversity and species diversity

We selected eight species functional traits of butterflies that are thought to represent response traits (sensu Díaz et al., 2013) to land use and vegetation structure (Table 1). These traits are related to key aspects of the butterflies' life histories, such as dispersal, reproduction, habitat use and diet. The species traits we selected have also been used as response traits to explain range changes of butterflies given climatic and land use changes (Aguirre-Gutierrez et al., 2016) and to explain species assemblages responses to environmental changes (WallisDeVries, 2014).

We used the above-mentioned traits to calculate functional diversity using the functional dispersion metric, 'FDis' (Laliberté & Legendre, 2010). We selected this metric because it weighs the trait diversity by the relative abundance of each of the species, thereby rendering a robust method to measure functional diversity from a multidimensional trait space. FDis is thus the mean distance, in trait space, of each single species to the centroid of all species (Laliberté & Legendre, 2010). Moreover, as our objective is to compare the drivers of functional diversity with those of species diversity, we also obtained an estimate of species diversity for each sampling location by means of Fisher's α (Fisher, Corbet, & Williams, 1943). Fisher's α is a widely used robust measure of diversity that is relatively unaffected by sample size (Magurran, 2013) and is especially appropriate when species abundance data are available, as in our study.

In order to obtain robust estimates of functional and species diversity, we used only sampling locations where at least 50 individuals were recorded. The FDis analysis was carried out with the 'FD' package and Fisher's α with the 'Vegan' package from R (Development Core Team, http://cran.r-project.org).

2.3 | Vegetation structure and land use data

Countrywide LiDAR data were obtained from the AHN2 project for The Netherlands (http://www.ahn.nl). The AHN2 data were collected throughout 6 years, from 2007 to 2012, by different data suppliers, and thus specific details on scanner type, frequency and average flight elevation are not available. The overall AHN2 point cloud location accuracy is 10 cm, and the systematic height error and SD are 5 cm. The average point density is 10 points/m^2. For full details on the point cloud data from the AHN2 project, see http://www.ahn.nl.

To obtain information on vegetation, we excluded all LiDAR cloud points that fell within built-up areas, defined by the very high accuracy BAG (Basisadministratie Adressen en Gebouwen v.2015) vector dataset (http://www.kadaster.nl), plus a buffer of 250 cm around them. The LiDAR point cloud data were processed to grid cells with a spatial resolution of 100 m × 100 m, which was also used for the land use data (see below). Before data processing, the point cloud was normalized to ground level in order to obtain estimates of vegetation structure in terms of height above the ground. From the resulting point cloud, a total of 12 vegetation structure metrics that are thought to impact the distribution of butterflies and other pollinators were obtained (see brief description in Supporting Information Table S2): average, maximal and minimal vegetation height, average squared height of vegetation, cover gap, percentage vegetation between 0.5 and 2 m, percentage vegetation between 2 and 5 m, percentage vegetation between 5 and 10 m, percentage vegetation between 10 and 20 m, vegetation height skewness, vegetation height kurtosis and vegetation height SD. These metrics represent the variation in vegetation structure across the vertical axis but also render insight about vegetation structure along the

TABLE 1 The characteristics of butterfly traits related to land use and vegetation structure

Trait	Trait category	Units	Description	Reference
Body size	Dispersal	Millimetres	Wing span	(Bink, 1992; WallisDeVries, 2014)
Flight period	Dispersal/ reproduction	Count	Number of weeks flying per year	(Bink, 1992; WallisDeVries, 2014)
Population area	Dispersal/ reproduction	Ordinal with values $1-9$	Area (in hectares) occupied by the population (1: 1; 2: 4; 3: 16; 4: 64; 5: 260; 6: 1,000; 7: 4,000; 8: 16,000; 9: >16,000)	(Bink, 1992; WallisDeVries, 2014)
Larval food preference	Diet	Rank values $1-4$	Diet preference of larvae: Number of host plants (1: monophagous; 2: oligophagous; 3: polyphagous (multiple species, one plant family); 4: polyphagous (multiple species, more than one plant family)	(WallisDeVries, 2014)
Larval food dependence on nitrogen	Diet	Ellenberg nitrogen value	Nitrogen value of host plants: Average Ellenberg nitrogen indicator values of butterflies' larval host plants (describing soil fertility conditions and nitrogen preferences)	(Eliasson, Ryrholm, & Gärdenfors, 2005; Ellenberg et al., 1991; Fujita, van Bodegom, & Witte, 2013; Geraedts, 1986; Heath & Emmet, 1989)
Habitat specialization	Habitat use	Specialist or generalist	Predominant association with anthropogenic CORINE land cover habitat types (agricultural and urban as: generalists) or not (semi-natural habitats: specialists)	(van Swaay, Warren, & Loïs, 2006; WallisDeVries, 2014)
Moisture	Habitat use	Ordinal with values $1-5$	1: dry and warm; 2: dry; 3: average or indifferent; 4: moist; 5: bogs and marshland	(Bink, 1992; WallisDeVries, 2014)
Habitat openness	Habitat use	Ordinal with values $1-10$	Niche breadth relative to the openness of the landscape. Range is from from 1: closed forest; 5: park landscape; to 10: short grassland	(Bink, 1992)

Note. These traits are hypothesized to be 'response' traits (Díaz et al., 2013) to land use and vegetation structure and are grouped in the following four trait categories: dispersal, reproduction, habitat use and diet.

horizontal axis, as for instance, the vegetation height *SD*. The LiDAR point cloud data analysis was carried out with LAStools v.160429 (http://rapidlasso.com/LAStools) and Python v2.7 within ArcGIS v10.2.2.

The land use map (LGN6 dataset) was obtained from the geo-information department of Wageningen University (http://www.wageningenur.nl) for the year 2008 at an original resolution of 25 m × 25 m and with high classification accuracy (*c*. 95%; Hazeu, Schuiling, Dorland, Oldengarm, & Gijsbertse, 2010). This land use map is thought to be representative of the land use available in the period when species were collected. The original land use map, with a thematic resolution of 39 land use classes, was reclassified to 10 aggregate classes (see Supporting Information Table S3). The final reclassified land use classes were as follows: agriculture, sandy soils vegetation, coniferous forest, deciduous forest, mixed forest, managed grasslands, natural grassland, moors/peat, marsh vegetation and urban. Based on the resulting map, to account for the spatial resolution at which the species data were collected and also the spatial resolution of the LiDAR-derived vegetation structure data, we calculated a total of 11 land use metrics at a spatial resolution of 100 m × 100 m. The calculated metrics have been shown to influence the distribution of butterflies and other pollinators (Aguirre-Gutiérrez et al., 2015), the proportion of each land use class

and the number of land use classes in each grid cell. These metrics characterized an important aspect of landscape quality, as well as landscape composition (Tscharntke et al., 2012). All land use calculations were carried out with the Geospatial Modelling Environment (Beyer, 2012).

2.4 | Statistical analysis of drivers of functional and species diversity

We carried out a correlation analysis on land use and vegetation structure variables and included only those with Pearson's correlation coefficients $\leq |.70|$ to avoid distorting model predictions (Dormann et al., 2013). Following this procedure, the following variables were excluded: cover gap, kurtosis, maximal elevation, minimal elevation and percentage of vegetation between 10 and 20 m. All land use variables showed low correlations and were therefore included in the final set of variables used during the modelling step (see Supporting Information Figure S2).

We used mixed-effects models with Gaussian error structure (Zuur, Ieno, Walker, Saveliev, & Smith, 2009) to investigate whether and how land use and vegetation structure drive functional diversity and species diversity at a landscape level. We used grid cell identity as

a random factor to account for the sampling structure, because more than one sampling location may fall within the same 100 m × 100 m grid cell. Moreover, sampling locations closer to each other may be more similar than ones that are further apart. To remove this effect, we first computed the Moran's *I* spatial autocorrelation test, which resulted in significant correlation ($p < .001$). Therefore, we tested different mixed-effects models with and without spatial autocorrelation structures (linear, exponential, Gaussian and spherical), including the grid cell identity as a random factor. The preliminary results showed that the model without the spatial autocorrelation structure but with the grid cell identity as a random factor was the best model based on their Bayesian information criteria (BIC). This suggested that the random factor already accounted for the correlations present in the data. This model structure was used for further analysis.

We constructed two mixed-effects models using the grid cell identity as a random factor, one to investigate the extent to which vegetation structure and land use explained functional diversity and one to explain species diversity as a function of the same variables. As our objective is to investigate the main differences between vegetation structure and land use as drivers of functional and species diversity, we did not include any interaction terms between them. We selected the most parsimonious model based on the BIC. The stepwise backward and forward model selection based on the BIC was chosen because this method penalizes more complex models by excluding terms that explain only little variability (Aho, Derryberry, & Peterson, 2014). For comparison, we also kept all candidate models with ΔBIC lower than two units (see Results section). We also calculated the relative importance of the vegetation structure and land use variables in explaining functional and species diversity. For each of the land use and vegetation structure variables, their importance was calculated as the sum of the Akaike weights over all model combinations (from the model selection explained above) where the variable is present (Burnham & Anderson, 2003). As the number of model combinations where each of the variables is present is the same across variables, their importance values are directly comparable (Burnham & Anderson, 2003). All analyses were carried out in R with the 'ape', 'lme4' and 'MuMIn' packages.

3 | RESULTS

3.1 | Functional diversity

We included 66 species in our functional diversity analysis (FDis) of each community (100 m × 100 m grid cell) of a total of 6,075 sampling locations. After selecting the most parsimonious model based on the BIC, our first best mixed-effects model (BIC −26,005.44) was significantly better than our initial full model (BIC −25,930.57; Table 2). Our first best model (out of three) contained the same or a broader array of explanatory variables as the subsequent models, with the exception of agriculture; we therefore focus on the first best model (see Supporting Information Table S4). According to this model, functional diversity (FDis) of butterflies is mainly driven by a mixed set of structural variables, height of vegetation and distribution of vegetation at different strata, and land use variables, specifically natural grassland, sandy soils

vegetation, marsh vegetation and urban areas (Table 2 and Figure 1). The average height of vegetation and vegetation density in the 0.5–2 m stratum presented positive coefficients with an average FDis of *c*. 0.15, which increased up to just below 0.25 for locations that contain 40% of their vegetation between 0.5 and 2 m (Figure 1 and Supporting Information Table S4). In contrast, an increase in vegetation in the 2–5 m stratum generated a loss of almost one-third of FDis, decreasing from *c*. 0.15 down to 0.10. Overall, as the proportion of only one land use type increased in the landscape the functional diversity decreased without exception from the selected land use variables in the best mixed-effects model (Figure 1 and Table 1). In our prediction of FDis for the entire area of The Netherlands, the FDis estimates ranged from 0.04 to close to 0.31 (see Figure 2a). The communities with higher functional diversity (FDis *c*. 0.31) occupy a great part the centre of the country around forest–heathland complexes with heterogeneous vegetation structure; meanwhile, patches of coastal dune areas in the west showed the lowest functional diversity (*c*. 0.4; Figure 2a).

3.2 | Species diversity

When investigating species diversity, after selecting the most parsimonious model based on the BIC, our first best mixed-effects model (BIC 15,017.83) was significantly better than our initial full model (BIC 15,063.62; Table 2). Our first best model (out of four) contained the same explanatory variables as the subsequent models, with exception of the proportion of coniferous forest and moors/peat. Given the high change in BIC values of the subsequent models (> 1.5), we focus here on the first best model results (see Supporting Information Table S5 for the results of all models).

Species diversity (Fisher's α) increased with the average vegetation height until reaching an optimum (at *c*. 8.6 m) in semi-open conditions when compared with its squared height (Figure 3). Moreover, the amount of vegetation between 0.5 and 2 m and the increase in heterogeneity of vegetation height (vegetation height *SD*), which had almost the same positive effect size, led to increases in Fisher's α of *c*. 1, increasing from *c*. 4 to close to 5 (Figure 3). Our first best mixed-effects model showed a negative relationship between high proportions of any land use type included and species diversity (Table 2 and Supporting Information Table S5). Hence, more homogeneous landscapes in terms of land use tend to be less diverse in butterfly species than other landscapes composed by different land use types in different proportions (Figures 2b and 3). Based on our best model, the predicted species diversity (Fisher's α) for The Netherlands ranged between 0.51 and almost 7.5 (Figure 2b). The areas with higher observed species diversity were found in the east part of The Netherlands, almost across its full latitudinal gradient, in areas with different proportions of forest vegetation as well as in the coastal areas with sandy soils vegetation in the west (Figure 2b).

3.3 | Importance of drivers of functional and species diversity

The analysis of variable importance showed that both land use and vegetation structure parameters drive functional and species diversity.

TABLE 2 Effects of land use and vegetation structure on functional and species diversity of butterflies

Explanatory variables	Functional diversity: Dispersion		Species diversity: Fisher's α	
	Full model	Best model 1	Full model	Best model 1
Vegetation structure				
Average vegetation height	(+)	(+)	(+)	(+)
Percentage of vegetation between 0.5 and 2 m	(+)	(+)	(+)	(+)
Percentage of vegetation between 2 and 5 m	(−)	(−)	(+)	
Percentage of vegetation between 5 and 10 m	(−)		(−)	
Average vegetation squared height	(−)		(−)	(−)
Vegetation skewness	(−)		(+)	
Vegetation height SD	(−)		(+)	(+)
Land use				
Number of land use classes	(+)		(+)	
Proportion of agriculture	(+)		(−)	(−)
Proportion of coniferous forest	(−)		(−)	
Proportion of deciduous forest	(−)		(−)	(−)
Proportion of mixed forest	(−)		(−)	(−)
Proportion of managed grassland	(−)		(−)	(−)
Proportion of natural grassland	(−)	(−)	(−)	(−)
Proportion of moors and peat	(−)		(−)	
Proportion of sandy soils vegetation	(−)	(−)	(−)	(−)
Proportion of marsh vegetation	(−)	(−)	(−)	(−)
Proportion of urban areas	(−)	(−)	(−)	(−)
BIC	−25,930.57	−26,005.44	15,063.62	15,017.83

Note. The most parsimonious model selected by means of the Bayesian information criteria (BIC) is shown together with other models with a $\Delta BIC < 2$. The plus or minus signs within parenthesis represent the direction of the effect (positive or negative) of a given land use and vegetation structure parameter on functional and/or species diversity. Empty spaces indicate that the given parameter was not included in the final best model. For a detailed version of the table, see Supporting Information Tables S4 and S5.

However, the identity of these drivers generally differed between those defining functional diversity levels and species diversity (Figure 2c). The relationship between functional diversity and the species diversity in the landscape, each 100 m × 100 m, was weak (Pearson's correlation = .34; Figure 4a). Standardizing the functional and species diversity and computing their spatially explicit difference shows that in 56% of The Netherlands its functional diversity is lower than its species diversity; this is thus low species trait diversity (Figure 4b). For functional and species diversity, there were six vegetation structure and land use parameters with importance values > 0.90 (range 0–1). Three of these parameters were highly important for both functional and species diversity, namely the average vegetation height, the percentage of vegetation between 0.5 and 2 m and the proportion of marsh vegetation in the landscape, all with the same direction of effect (Figure 2c). Conversely, the amount of vegetation between 5 and 10 m, vegetation skewness and the number of land use classes showed some of the lowest importance (≤ 0.03) in driving both the functional and species diversity of butterflies (Figure 2c). For functional diversity, only one

land use variable, the proportion in urban areas, presented intermediate importance (0.68), with all other parameters showing low importance values (≤ 0.38) in driving functional diversity. In comparison to the drivers of functional diversity, for species diversity we detected a slowly decreasing gradient in variable importance of most vegetation and land use parameters, ranging in importance between 0.71 and 0.01 (Figure 2c).

4 | DISCUSSION

Much attention has been given to the importance of having species-rich communities in comparison to the importance of having a species traits-rich system (but see Martins et al., 2015) and even less to the interrelationship between functional diversity and species diversity and what drives their distribution patterns. Recent studies have emphasized the roles that different land use types play in defining the distribution of biodiversity (Rösch, Tscharntke, Scherber, & Batáry, 2013; Tscharntke et al., 2012). However, little is known about how the
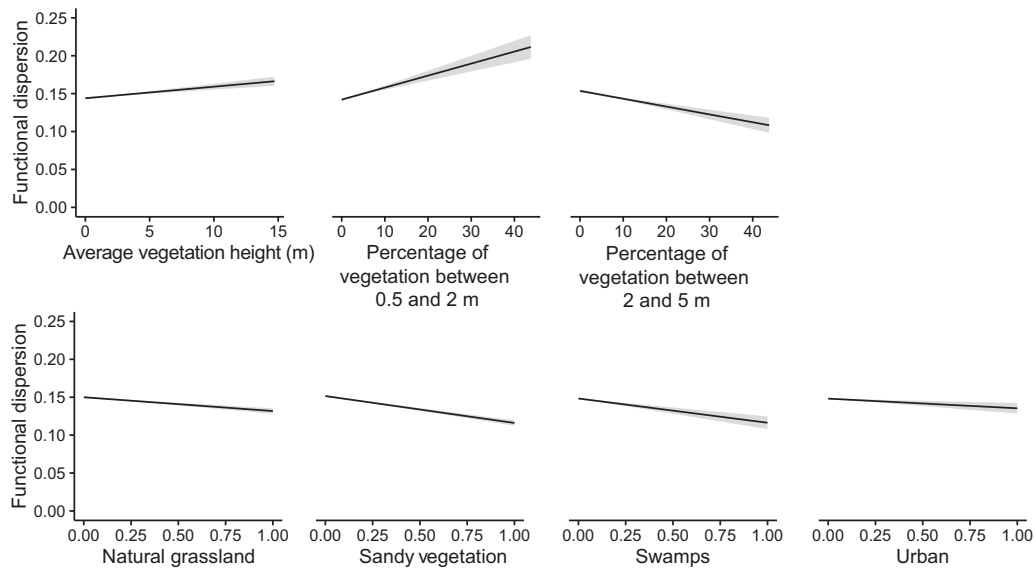
FIGURE 1 Functional diversity of butterflies, represented by the functional dispersion index, explained by land use and vegetation structural parameters. Only the parameters present in the best model are shown. Average predictions ± 95% confidence intervals (grey bands) are shown. The land use parameters are presented as their proportion in the landscape (each 100 m × 100 m grid cell). For statistical details of the best model see Supporting Information Table S4

vertical and horizontal structural arrangement of vegetation influences species distributions, and it is not yet clear what the combined effects of vegetation structure and land use type are, neither on functional diversity nor on species diversity, for most species groups (but see Jankowski et al., 2013; Moretti et al., 2013). One of the reasons for this gap has been the lack of data, especially related to vegetation structural parameters at large spatial scales. Here, we gathered butterfly presence data from a long-term monitoring scheme, land use and LiDAR-derived

vegetation structural parameters to investigate their effect on the functional and species diversity of butterflies at a countrywide scale. Butterflies, like other invertebrates, carry out important ecosystem services and functions (e.g., acting as pollinators and environmental quality indicators) around the world and in natural and managed ecosystems (Fleishman & Murphy, 2009; Scheper et al., 2013), and their distribution is greatly driven by land use patterns at local and landscape-level scales (González-Varo et al., 2013). Our study clearly
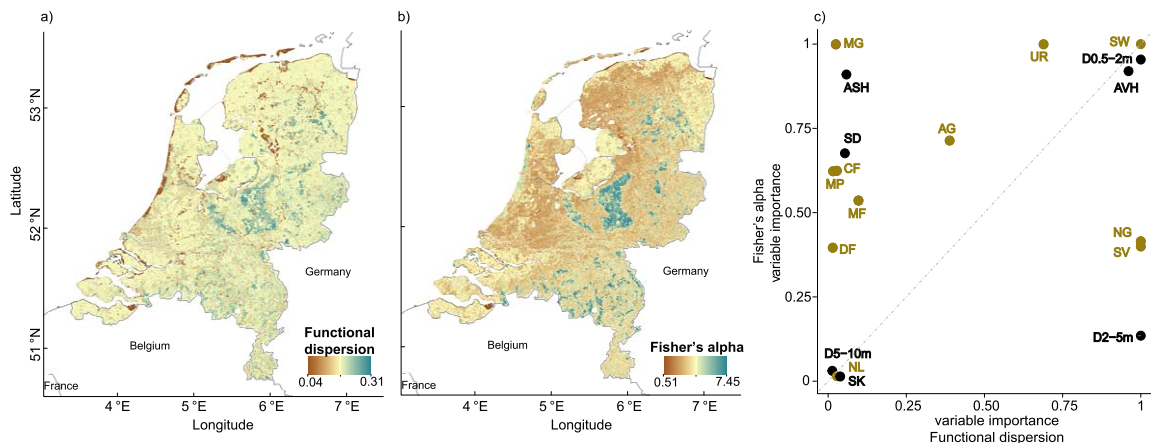

FIGURE 2 Distribution of different facets of butterflies' biodiversity, functional diversity and species diversity, in The Netherlands. (a) Modelled functional diversity (dispersion index) based on butterflies' species presence records from the period 2008–2015, functional traits (see Table 1) and land use and vegetation structure parameters (see Methods). (b) Modelled butterflies' species diversity (Fisher's α), based on species records from the period 2008–2015, as a function of land use and vegetation structure parameters. (c) Comparison of the importance values of each land use (brown) and vegetation structure (black) parameter resulting from the full mixed-effects models (see Methods) for functional diversity (functional dispersion) and species diversity (Fisher's α; see Methods). AG = proportion of agriculture; ASH = average vegetation squared height; AVH = average vegetation height; CF = proportion of coniferous forest; DF = proportion of deciduous forest; D0.5–2m = vegetation between 0.5 and 2 m; D2–5m = vegetation between 2 and 5 m; D0.5–2m = vegetation between 5 and 10 m; MF = proportion of mixed forest; MG = proportion of managed grassland; MP = moors and peat; NG = proportion of natural grassland; NL = number of land use classes; SD = vegetation height standard deviation; SK = vegetation skewness; SV = proportion of sandy soils vegetation; SW = proportion of marsh vegetation; UR = proportion of urban areas
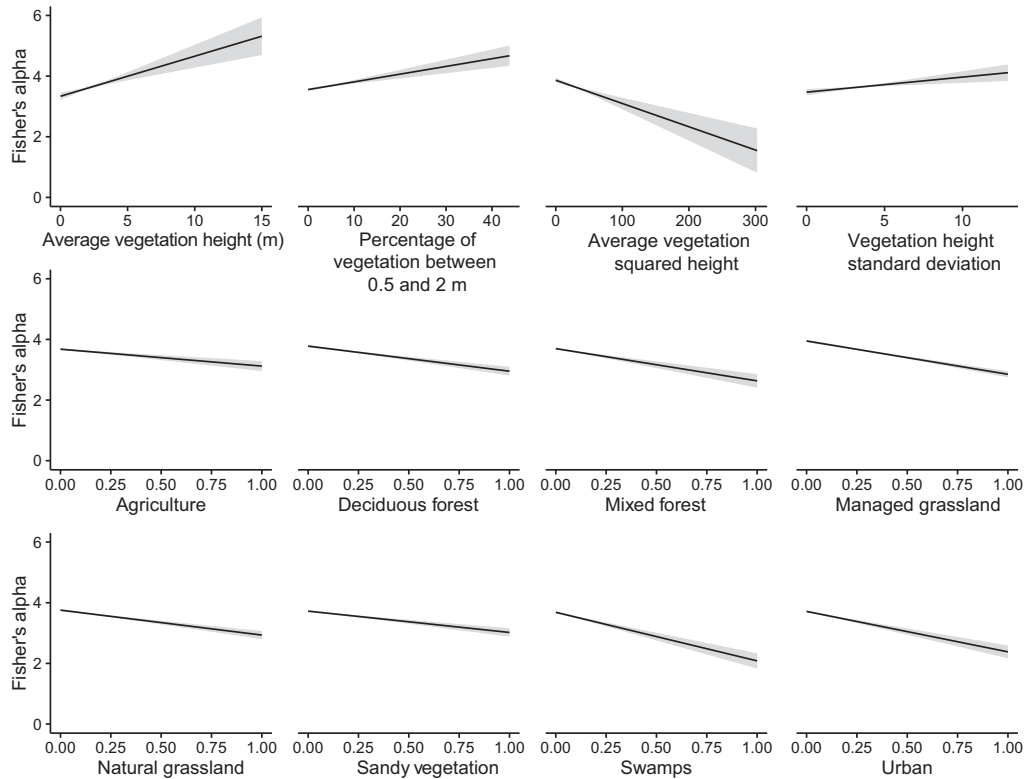
FIGURE 3 Species diversity of butterflies, represented by the Fisher's α, explained by land use and vegetation structural parameters. Only the parameters present in the best model are shown. Average predictions ± 95% confidence intervals (grey bands) are shown. The land use parameters are presented as their proportion in the landscape (each 100 m × 100 m grid cell). For the complete statistical details of the best model see Supporting Information Table S4
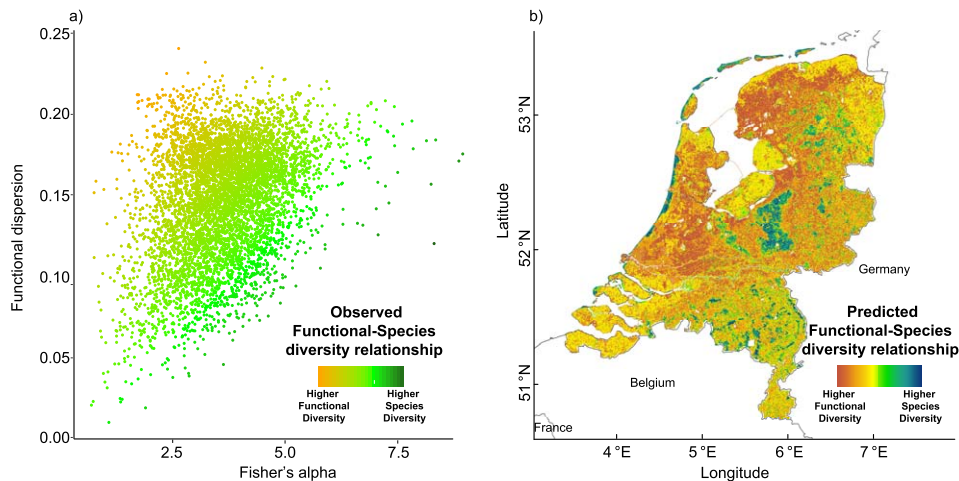

FIGURE 4 Statistical and spatial relationship between functional and species diversity of butterflies in The Netherlands. (a) The relationship between the observed functional and species diversity in the sampling locations (Pearson's correlation= .34). Functionally diverse areas can contain low (brown–light green) to high diversity of species (brown–dark green) showing that high species diversity does not necessarily translate into high fucntional diversity. (b) The predicted spatial relationship between functional and species diversity. This was computed as the 0 to 1 standardized values of functional diversity minus species diversity. Areas with high functional and low species diversity are shown in brown–yellow colours (highest difference was 0.53), highlighting more resilient areas against land use changes. The areas with high species and low functional diversity (strongest difference was −0.49), and thus more fragile against land use changes, are shown in green–blue colours

shows that high species diversity does not translate into high functional diversity and that they are mainly driven by different sets of structural and land use parameters. Moreover, we show that it is a tight combination of both vegetation structural characteristics and land use parameters that defines functional and species diversity of butterflies.

4.1 | Interacting patterns of functional diversity and species diversity

We detected a mismatch between functional diversity and species diversity of butterflies and showed that their relationship is nonlinear. Although high functional diversity is often found with higher species diversity levels, low functional diversity can also be observed with high species diversity. It has been suggested that communities with low functional diversity and low trait redundancy might be more susceptible to environmental changes than functionally richer communities (Oliver et al., 2015). However, whether low functional diversity really implies low resilience may depend on the type of disturbance and on the species response traits analysed (Mori et al., 2013). As shown by our study, it is striking how areas that contain high species diversity do not always maintain high functional diversity (see the western dunes and some forested areas of the study area). This is most probably attributable to biotic homogenization given by the presence of only a set of vegetation-specialized species where more structurally homogeneous vegetation occurs. Moreover, this suggests that the standard community of butterflies already covers most of the functional trait space available, and thus species-rich communities do not substantially increase the functional diversity. However, these species-richer communities might increase trait redundancy and thus resilience (Mori et al., 2013). The low levels of functional and species diversity of butterflies detected for a great part of the study area may well be linked to the fact that land use types such as agriculture and managed grasslands occupy more than half of the country (http://www.fao.org/countryprofiles). These are precisely the areas that contain structurally homogeneous vegetation. The predicted low functional and species diversity for these areas may be the result of historical land use (Hazeu et al., 2010; Knol, Kramer, & Gijsbertse, 2004) and climate (Klein Tank, 2004) changes that have occurred, especially during the last half-century in The Netherlands.

It is striking that more than half of the study area is predicted to have lower levels of functional diversity in comparison to their species diversity, as these areas with low functional diversity may suffer the most from changes in environmental conditions (Oliver et al., 2015). This highlights that conserving only those areas with high species diversity would not necessarily conserve a functionally diverse ecosystem. In the same manner, focusing conservation only in high functional areas may mean disregarding the conservation of functionally redundant species. We show that for butterflies, areas with more structurally complex vegetation in the lower level are functionally more diverse, as shown in some parts around the Veluwe area (central region of the country). Hence, these communities may be more resilient towards environmental changes. Maintaining the areas with high functional diversity is particularly important for The Netherlands, where most of the landscapes are highly managed and dominated by homogeneous land use types at large spatial scales.

4.2 | Functional diversity: Relationship with vegetation structure and land use

We found that there is not an exact match between the drivers of functional diversity and species diversity, especially in those variables related to land use. However, most vegetation structure variables determining functional diversity were also important for determining species diversity (see Table 1). The butterflies' habits of dispersal, reproduction, diet and habitat use given by their functional traits may explain the high importance of vegetation structure. This is because areas with higher habitat heterogeneity may render more varied niches and thus different sets of species adapted to them according to their specific traits (Davies & Asner, 2014; Tews et al., 2004). We expected that the more structurally heterogeneous areas would facilitate the presence of higher functional diversity in comparison to more homogeneous areas. This was the case when most of the vegetation was short, with some large trees (effect of average vegetation height), which can be observed by the high functional diversity around forested areas, but not per se within old tall forest (see the central region in Figure 2a). In particular, the vegetation height and the proportion of vegetation at different height strata can affect the microclimatic conditions, such as moisture, which are related to the response traits we used (see Table 1). Microclimatic conditions are hypothesized to have a great effect on the survival and development of butterflies because they also control for the availability of larval habitats and adult nectar sources in the landscape (Suggitt et al., 2015). Thus, these landscape characteristics can greatly determine the local functional diversity.

The amount of each type of land use in the landscape strongly defined functional diversity. In contrast to analysis of species diversity, the effects that the amount of different land use types have on functional diversity of pollinators, and specifically of butterflies, has not been broadly examined (but see Cariveau, Williams, Benjamin, & Winfree, 2013; Rader, Bartomeus, Tylianakis, & Laliberté, 2014). We showed that three of four land use types that drive functional diversity of butterflies are mostly composed of short vegetation (vegetation in sandy soils, marsh vegetation and natural grasslands), and steep increases in their extent in the landscape led to lower functional diversity. Increases in the proportion of only one land use type reduces the availability of different resources that other land use types may offer. Hence, the decline of functional diversity when any of the above-mentioned land use types increases (e.g., sandy soils vegetation) should not be considered as a negative effect pertaining to the land cover type per se but to the decrease in the variety of available niches that are otherwise rendered by more heterogeneous landscapes. This is especially important for butterflies because they inhabit different vegetation and feed on different sources at different life stages (Rösch et al., 2013).

4.3 | Species diversity: Relationship with vegetation structure and land use

The species diversity patterns we show in this analysis are consistent with other small-scale analyses carried out in The Netherlands that also included information on climate and land use and recently reported on species distributions of butterflies (Aguirre-Gutiérrez et al., 2015; WallisDeVries, 2014). However, those studies did not investigate how the structural arrangement of vegetation drives species distributions. Previous studies suggest that higher diversity can be found in the east in comparison to the west of The Netherlands (Aguirre-Gutierrez et al., 2016), a pattern that we have also found but at much finer spatial resolution, in this way detecting butterfly habitats related to land use type and the arrangement of vegetation. The higher species diversity predicted in the eastern regions could be attributable to the fact that more (semi-) natural areas with different levels of vegetation succession are found there in comparison to the western regions, where agricultural landscapes dominate (see map provided by Hazeu et al., 2010). We show that the spatial arrangement of vegetation in the landscape plays a major role in determining the butterflies' diversity distribution patterns, with more structural and qualitative heterogeneous areas also sustaining higher levels of diversity. Similar findings have been reported for other regions (e.g., north-west U.S.A.; Hess et al., 2013) for which the structural arrangement of vegetation, especially in the lower strata, is considered a main driver of the presence and abundance of different butterfly species. Müller and Brandl (2009) detected that the heterogeneity of vegetation height (as the *SD*) drives the richness and diversity of other arthropods, such as beetles, in a mixed forest in Germany. In addition, similar to our results, Müller, Bae, Röder, Chao, and Didham (2014) showed that the vegetation structural heterogeneity acts as a main driver of arthropod diversity in coniferous forests.

Most types of land use were important for driving the species diversity of butterflies, in contrast to those defining functional diversity, which were related to a few vegetation types. This suggests that areas containing a highly varied landscape of land use types might enhance the diversity of species (Perović et al., 2015). However, in most instances these species may share most of their trait characteristics and thus represent low functional diversity, as shown for some forested and coastal regions in The Netherlands. Furthermore, we show that areas dominated by grasslands are within the landscapes with the lowest predicted species diversity. This could be related to a lack of vegetation structural heterogeneity but also to a lack of feeding resources, as the grasslands in The Netherlands are, for the most part, intensively managed ecosystems with high inputs of fertilizers (Oenema, van Ittersum, & van Keulen, 2012). The high input of fertilizer could mean that only butterflies specialized in diets with a high nitrogen level occupy these areas, reducing the possible species and also, most probably, functional diversity in the landscape.

4.4 | Conclusions

We show that high functional diversity can often be covered by a few species with a varied set of traits. This suggests that ecosystem functioning may often be determined by a few species. Thus, the conservation and management for high levels of species richness may actually require a different focus from the conservation and management for ecosystem functioning (see also Kleijn, Rundlöf, Scheper, Smith, & Tscharntke, 2011). Overall, our results call for a more integrative analysis of biodiversity distributions, accounting not only for the distribution of species but also for the distribution of traits and thus of functional diversity in the landscape. Moreover, these analyses should more directly relate functional diversity to the communities' resilience towards specific environmental changes. We suggest that future studies on biodiversity distributions should incorporate as far as possible information not only on the type of landscape but also on its vegetation structural diversity, because this can define patterns and processes of functional and species distributions.

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BIOSKETCH

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