1 Integrating Citizen Science and Multispectral Satellite Data for Multiscale

2 Habitat Management

- 3 Camille Van Eupen^{*,a,b}, Dirk Maes^{c,d}, Stien Heremans^{b,c}, Kristijn R.R. Swinnen^e, Ben Somers^{**,b} and Stijn
- 4 Luca**,a
- 5 * corresponding author; ** joint last authors
- ⁶ ^a Ghent University, Department of Data Analysis and Mathematical Modelling, Coupure Links 653, B-
- 7 9000 Ghent, Belgium; camille.van.eupen@hotmail.com (ORCID 0000-0002-0924-8892);
- 8 <u>stijn.luca@ugent.be (ORCID 0000-0002-6781-7870)</u>
- 9 ^b KU Leuven, Department of Earth and Environmental Sciences, Division Forest Nature and Landscape,
- 10 Celestijnenlaan 200E, B-3001 Heverlee, Belgium; ben.somers@kuleuven.be (ORCID 0000-0002-7875-
- 11 107X); stien.heremans@kuleuven.be (ORCID 0000-0002-5356-1093)
- ^c Research Institute for Nature and Forest (INBO), Herman Teirlinckgebouw, Havenlaan 88 box 73, B-
- 13 1000 Brussels, Belgium; <u>dirk.maes@inbo.be</u> (ORCID 0000-0002-7947-3788); <u>stien.heremans@inbo.be</u>
- ^d Radboud Institute for Biological and Environmental Sciences (RIBES), Radboud University, PO Box
- 15 9010, NL-6500 GL Nijmegen, The Netherlands; <u>dirk.maes@ru.nl</u>
- ^e Natuurpunt Studie, Coxiestraat 11, 2800 Mechelen, Belgium; <u>kristijn.swinnen@natuurpunt.be</u>
- 17 <u>(</u>ORICD 0000-0002-1910-9247)

Acknowledgements: We foremost thank the thousands of volunteers for collecting the thousands of records that supported this study and Natuurpunt Studie for making the data available for this research. This work was supported by the Flemish Research Foundation FWO–SB [grant number 1S92118N].

22 Abstract

Habitat management is necessary for the conservation of threatened species, yet best practices in
fragmented human-dominated landscapes have remained difficult to generalise. We show that multiscale vegetation management decisions in heathlands can be supported by integrating opportunistic
citizen science data and multispectral satellite data.

27 Opportunistic observations were gathered from ten typical, mostly threatened animal species of dry 28 heathlands in Flanders as point records with specified precision. We considered vegetation structure 29 at the local scale, quantified by image texture within 0.25 hectares derived from multispectral satellite 30 data, and heathland heterogeneity at the habitat scale, quantified by the diversity in heathland 31 vegetation communities within 50 hectares. Additionally, locations inside heathlands were attributed 32 to an open, closed or anthropogenic landscape context. Point process models were used to test the 33 impact of heathland size, vegetation structure and heathland heterogeneity on the habitat suitability of the studied species. 34

We found that (1) heathland vegetation management can benefit habitat suitability in fragmented heathlands, but with a different approach for local management of vegetation structure in small versus large heathlands (e.g. due to micro-fragmentation effects), (2) the landscape induces positive and negative edge effects (e.g. due to a high versus low resource availability), especially in small heathlands and (3) habitat suitability is driven by both vegetation structure and heathland heterogeneity but with different relative importance for birds, butterflies and grasshoppers (e.g. due to differences in mobility).

42 Keywords: habitat suitability, image texture, point process models, remote sensing

43 **1. Introduction**

Dry heathlands are human-shaped habitats prioritised in Annex I of the European Habitats Directive 44 45 (92/43/EEC). They can provide a variety of ecosystem services, such as food and water supply, 46 landscape and biodiversity conservation, carbon sequestration and aesthetic/recreational value. They 47 are, however, threatened by land conversion, privatisation, recreation and soil eutrophication from 48 intensive agriculture that causes moss, grass and tree encroachment (Fagúndez, 2013; Webb, 1998). 49 These pressures have led to the fragmentation and reduced habitat quality of heathlands, and an ever-50 increasing proportion of heathland fauna appearing on national red lists (Maes et al., 2019a). 51 Conservation of species that rely on habitats under anthropogenic pressures remains challenging and 52 is in strong need of evidence-based action plans (Maes et al., 2022; Olmeda et al., 2020). In European 53 dry heathlands, conservation management is traditionally designed from a flora perspective with a 54 focus on preserving typical successional heathland vegetation (De Blust, 2022; Webb, 1998). Typically, 55 management schemes are designed to prevent nutrient accumulation and natural succession to forest, for example by sod-cutting, burning or grazing (De Blust, 2022; Fagúndez, 2013). It has become 56 57 generally accepted, however, that heathland fauna profits from management that includes exposure 58 of bare soil, diversifies vegetation communities and increases structural complexity (Byriel et al., 2023; 59 De Blust, 2022; de Vries et al., 2021; Schirmel et al., 2011; van den Berg et al., 2001), yet evidence-60 based action plans in conservation policy remain scarce.

The quality of a habitat, in terms of its suitability for animal species of conservation interest, depends on its environmental characteristics and spatial context. First, habitat suitability is usually higher when a broad range of environmental resources is available (for example for taking shelter, nesting and foraging) (MacArthur and Wilson, 1967; Tews et al., 2004). Second, habitat size generally impacts habitat suitability positively (e.g. Fahrig, 2003; Milanesi et al., 2017; Rutten et al., 2019; van den Berg et al., 2001), although the potentially high suitability of small and isolated patches should not be neglected (Wintle et al., 2019). Third, habitat suitability is also impacted by the landscape context, which can provide opportunities for habitat connectivity (Gibson et al., 2004; Haddad and Baum, 1999)
or induce positive or negative edge effects (Dupont and Overgaard Nielsen, 2006; Fagúndez, 2013;
Neilan et al., 2019; Pfeifer et al., 2017). While the impact of edge effects on heathland vegetation is
spatially confined (e.g. eutrophication effects on vegetation and soil were detected up to ca. 8 metres
into heathland patches according to Piessens et al. (2006)), the impact on heathland fauna might reach
further (e.g. Pfeifer et al., 2017).

74 Vegetation management can diversify environmental resources for animal species and thereby 75 increase habitat suitability. Heathland vegetation management can be implemented at different 76 spatial scales, of which we distinguish two in this study. At the larger habitat scale, we define 77 heathland heterogeneity as the horizontal diversity of heathland-associated habitat subtypes (i.e. 78 vegetation communities) such as wet and dry heathlands, peatlands and/or Nardus grasslands. At the 79 smaller local scale, we define vegetation structure as the variation in vegetation height within a 80 heathland (i.e. bare ground, heathland of different age classes, the presence of shrubs and/or trees; 81 Bergen et al., 2009). Both scales are crucial for determining species' habitats (Bergen et al., 2009; 82 Randin et al., 2020) where, firstly, a high habitat heterogeneity leads to higher habitat suitability for 83 species that need complementary resources (see reviews of Stein et al., 2014 and Tews et al., 2004). 84 Secondly, vegetation structure has been shown to impact the habitat suitability of birds in forests 85 (Farrell et al., 2013; Goetz et al., 2010; Graf et al., 2009; Huber et al., 2016; Seavy et al., 2009) and 86 grasslands (Bellis et al., 2008), butterflies in grasslands and woodlands (de Vries et al., 2021) and 87 lizards in a river valley (Sillero and Gonçalves-Seco, 2014).

Measures of heathland heterogeneity and the landscape context can easily be obtained by a landscape analysis, for example by using landscape metrics based on regional land use maps (Gustafson, 1998; Hesselbarth et al., 2019). Measures of vegetation structure in low-stature habitats such as heathlands are commonly obtained through airborne Light Detection and Ranging (LiDAR) sensors, because of the fine-resolution data they can obtain across large spatial extents (de Vries et al., 2021; Moudrý et al.,

2022; Wehr and Lohr, 1999). LiDAR can deliver accurate measures of vegetation height, although
expensive data acquisition and limited temporal coverage reduce its application potential for habitat
suitability modelling (Moudrý et al., 2022). For instance, there can be an undesired temporal mismatch
between LiDAR-derived explanatory variables and species occurrence data (Randin et al., 2020).
Furthermore, when LiDAR images are taken in the leaf-off season, they fail to accurately capture the
vegetation structure of low-stature habitats (e.g. in grasslands; de Vries et al., 2021).

99 For habitat suitability modelling, alternatives are therefore being explored to remotely quantify 100 vegetation structure across large spatial and temporal extents, such as multispectral data from 101 spaceborne sensors. Multispectral Sentinel-2 data are especially interesting for capturing the 102 temporal dynamics of vegetation structure over large areas as they are freely accessible, with four 103 bands (RGB-NIR) at 10-metre resolutions every 5 to 10 days since April 2017. Both the growing 104 availability of multispectral Sentinel-2 data and the increasing quantity and density of species 105 occurrence data through large citizen science initiatives, such as waarnemingen.be in Flanders 106 (https://www.waarnemingen.be) and observation.org (https://observation.org/) or iNaturalist 107 (https://www.inaturalist.org/) worldwide, facilitate the use of fine-grained habitat suitability models 108 (Milanesi et al., 2017; Randin et al., 2020) such as point process models (PPMs) (Renner et al., 2015). 109 The strength of PPMs is that environmental data can be extracted for each point observation of a 110 species' presence at fine spatial resolutions, which allows to assess fine-scaled drivers of habitat 111 suitability (also see Appendix A).

When LiDAR data are not available, a good alternative to measuring vegetation structure across large spatial extents is satellite image texture (Wood et al., 2012). Image texture quantifies the spatial heterogeneity in pixel tone values of a certain image area (Haralick, 1979) and can therefore be used to quantify the spatial heterogeneity in images of vegetation cover (Wood et al., 2012). For applications in habitat suitability modelling, a recent study proposed the use of Sentinel-2-derived

5

image texture based on the Enhanced Vegetation Index (EVI; Liu and Huete, 1995) in low-stature
habitats, i.e. grasslands and shrublands (Farwell et al., 2021).

119 Here, we test the possibility of integrating opportunistic citizen science data and multispectral satellite 120 data to support multiscale management decisions for the conservation of animal species in 121 anthropogenic regions (Maes et al., 2022). More specifically, we will analyse whether the habitat 122 suitability of dry-heathland species across different taxonomic groups is driven by vegetation structure 123 and/or heathland heterogeneity and whether this relationship depends on the heathland size and 124 landscape context. We hypothesize that heathland management can benefit habitat suitability for species of conservation interest, even in small heathlands (Gábor et al., 2022; Wintle et al., 2019), that 125 126 it should consider the landscape matrix due to positive and negative edge effects (Fahrig, 2003) and 127 that it requires an integrated multispecies approach (Bonari et al., 2017; Maes and Van Dyck, 2005).

128 2. Methods

129 **2.1. Study area**

The study region was the Campine region in Flanders in the northeast of Belgium (Fig. 1a), holding about 13,000 hectares of heathland (De Saeger et al., 2020) and characterised by sandy soils (Couvreur et al., 2004). We limited our study area to heathland patches with more than 40 per cent classified heathland on the 2020 Biological Valuation Map (BVM) (De Saeger et al., 2020) which is a database for land cover in Flanders that includes a map of habitat classes (De Saeger et al., 2017). We omitted three military domains (Fig. 1a), because of a strong negative observation bias due to their inaccessibility, and patches with urban elements.



137

138 Fig. 1: a) Study area and studied heathlands (inaccessible military domains were excluded); b) Environmental 139 covariates used to predict the relative habitat suitability of dry-heathland species of conservation interest at an 140 example location. The landscape context was the dominant surrounding land cover class in a one-kilometre 141 radius around points on a regular grid of 50 metres. Heathland size and heathland heterogeneity were calculated 142 as the mean heathland size and the Shannon diversity in heathland subtypes (such as dry and wet heathlands 143 and heathlands with and without trees), respectively, within a 400-metre radius around points on a regular grid of 50 metres. Vegetation structure is the inverse of the homogeneity (a gray-level co-occurrence matrix (GLCM) 144 145 second-order texture metric) in the Enhanced Vegetation Index, calculated at a resolution of 10 metres, 146 supplemented with the average homogeneity in a 50-metre radius around points on a regular grid of 50 metres 147 in the patch edges with missing values; c) Example locations with low and high vegetation structure (i.e. spatial 148 variation in vegetation height). The location with low structure is characterised by more uniform age-classed dry 149 heather vegetation communities (Calluna – Genista) with few or no trees or shrubs. The location with high 150 structure is characterised (from left to right) by plantings of Scots pine (Pinus sylvestris L.) with undergrowth of 151 shrubs and trees, a woody edge of broom thicket (Cytisus scoparius L.) and different age classes of dry heather

vegetation (Calluna vulgaris L.) with shrub or tree stands (vegetation cover as described on the Biological
Valuation Map version 2020 (De Saeger et al., 2020)).

154 **2.2. Species observations**

155 We considered dry-heathland fauna of conservation interest in Flanders, meaning that they are either 156 species of regional conservation interest (Annex II or IV of the Habitats Directive (92/43/EEC) or Annex 157 I of the Birds Directive (79/409/EEC)) (Paelinckx et al., 2009), Flemish Priority Species (De Knijf et al., 158 2014; Herremans et al., 2014) or habitat-specific species (Habitats Directive habitat types 2310, 2330, 4030) (De Knijf and Paelinckx, 2013) (Tables 2 and B.1). Critically endangered species were excluded 159 160 (e.g. Northern wheatear Oenanthe Oenanthe), mostly because of the low number of observations. 161 Observations from eighteen species from four taxonomic groups (i.e. four birds, five butterflies, seven 162 grasshoppers and two reptiles) were extracted from the data portal waarnemingen.be (Herremans et 163 al., 2018; https://www.waarnemingen.be). They were point observations with specified geographical 164 precision for the study region and study period 2017-2021. Only the months from April to August were 165 considered as this period provided a good overlap between the growing season in Flanders and the 166 reproductive seasons for the focal species. The data was cleansed, checking for wrong coordinates, 167 removing incorrect observations and keeping only observations with a precision below 50 metres.

To construct the model training sets, we extracted opportunistic/unstructured records and first applied data quality filtering according to previous recommendations made by Van Eupen et al. (2022). Data verified as correct were retained based on the taxonomic group, range size and relative body size. Second, we applied spatial thinning at 50 metres per observation date to reduce the impact of duplicates (i.e. observations from an individual at a similar location on the same date). Table B.1 shows the number of presences remaining after data cleansing, data quality filtering and spatial thinning.

174 **2.3. Model covariates**

We used existing maps, satellite imagery and species occurrence data from *waarnemingen.be* tocompile the model covariates, i.e. four environmental covariates (landscape context, heathland size,

177 heathland heterogeneity and vegetation structure) and two sampling bias covariates (accessibility and 178 search effort) (Table 1; sections 2.3.1 and 2.3.2). Most model covariates (all except vegetation 179 structure) were rasterised at a resolution of 50 metres by applying calculations (i.e. summary statistics, 180 landscape metrics, vector lengths) in a buffer area with varying radii around each point at a regular 181 grid of 50 x 50 metres, further called 'dummy points'. Per species, all model covariates were tested 182 for multicollinearity by extracting their values at all training presence locations and calculating variance inflation factors (VIFs) and Pearson correlations in the R package 'fuzzySim' version 4.3 183 184 (Barbosa, 2015). All calculations were performed in R version 4.2.1 (R Core Team, 2022) and QGIS 185 version 3.16.9.

Table 1: Methods applied to obtain the model covariates that were used to predict the relative habitat suitability
of dry-heathland species of conservation interest. Dummy points are points at a regular grid of 50 x 50 metres
throughout the study area. BVM = Biological Valuation Map, rasterised at 5 metres; EVI = Enhanced Vegetation
Index; GLCM = gray-level co-occurrence matrix; ¹ De Saeger et al. (2020); ² retrieved from Google Earth Engine; ³
retrieved from https://land.copernicus.eu/pan-european/corine-land-cover/clc2018; ⁴ retrieved from

191 https://www.geopunt.be/; ⁵ Herremans et al. (2018).

Covariate	Source	Calculation (per pixel)	Scale	Res.	min-max	
ENVIRONMENTAL COVARIATES						
Landscape	Flanders:	Formed 3 land use classes:	Dominant class within	50 m	NA	
context	BVM version 2020 ¹	closed (forest)	one kilometre around		(factor)	
	Outside Flanders:	open (other semi-natural)	each dummy point			
	CORINE version 2018	anthropogenic (urban and				
	3	agricultural)				
Heathland size	BVM version 2020 ¹	Percentage of heathland	Mean within 400 metres	50 m	0.22 - 49.85	
(hectares)		(converted to hectares)	(≈ 50 ha) around each			
			dummy point			
Heathland	BVM version 2020 ¹	4 heathland subtypes (each	Shannon diversity index	50 m	0.00 - 1.71	
heterogeneity		with/without trees or shrubs)	within 400 metres (≈ 50			
		- dry heathlands	ha) around each dummy			
		- wet heathlands	point			
		- peatlands				
		- Nardus grasslands				

Covariate	Source	Calculation (per pixel)	Scale	Res.	min-max
Vegetation	Sentinel-2A images ²	Masked clouds, snow/ice and	5 x 5 moving window (≈	10 m	0.06 - 0.97
structure	April to August	unreliable pixels.	0.25 ha) in steps of 10		
	2017-2021	Calculated EVI (kept values	metres		
	Heathlands (> 40%	between 0.1 and 1).			
	heathland) and semi-	Averaged annual median	Pixels with missing		
	natural edges (> 10%	composites.	values in moving		
	heathland)	GLCM 2 nd order texture:	window: average		
		homogeneity (inverse).	homogeneity (inverse)		
			within 50 metres		
SAMPLING BIAS COVARIATES					
Accessibility	Wegenregister	Length of road segments	within 100 metres (≈	50 m	0.00 - 0.05
(km road/km ²)	version 2.0 ⁴		3.14 ha) around each		
			dummy point		
Search effort	waarnemingen.be ⁵	The annual average number of	within 100 metres (≈	50 m	0.0 - 37.4
(n° species)	April to August	species observed within the	3.14 ha) around each		

192

193

2.3.1. Environmental covariates

2017-2021

194 We chose to include only measures of vegetation structure and habitat composition, although we 195 acknowledge that including measures of soil water, such as the topographic wetness index (Besnard 196 et al., 2015; Moore et al., 1993), or soil biochemistry, such as nitrogen and phosphorus content (Vogels 197 et al., 2017), might have led to additional insights. We motivate the choice of our covariates by the 198 objective of the study (i.e. to illustrate how integrating citizen science and multispectral satellite data 199 can support multiscale heathland vegetation management) and the absence of multicollinearity (Table 200 B.2). Soil water, for example, might be correlated with both heathland heterogeneity and vegetation 201 structure, as soil moisture impacts the composition of vegetation communities and the presence and 202 growth of certain plant species (Schellenberg and Bergmeier, 2020).

considered taxonomic group

dummy point

203

a) Landscape context

Landscape context, but also heathland size (section 2.3.1.b) and heathland heterogeneity (section 205 2.3.1.c) were calculated based on the Biological Valuation Map (BVM) as it includes a detailed classification of habitat types and a classification of land cover in Flanders (De Saeger et al., 2017). To
describe the landscape context, we categorised the land cover into three classes: closed (forest), open
(all other semi-natural land covers) and anthropogenic (urban and agricultural) land use. The
dominant class in a one-kilometre buffer around each dummy point was taken as the landscape
context (Fig. 1b). Land cover within the Campine region was taken from the BVM, while at the borders
of Flanders, we used the CORINE land cover map (https://land.copernicus.eu/pan-european/corineland-cover/clc2018).

213

b) Heathland size

214 To quantify heathland size, we attributed the percentage of heathland associated with each 5-metre 215 pixel in the rasterized BVM following the distribution key of the different habitat units per patch (De 216 Saeger et al., 2020). Consequently, we calculated the mean percentage of heathland in a 400-metre 217 radius (≈ 50 hectares) around each dummy point (Fig. 1b). We chose 400 metres as the maximum 218 radius for all species to facilitate comparability among results. Models were run with continuous 219 heathland size as a covariate to assess its impact on habitat suitability. However, we also categorised 220 heathland size into three classes in the results section for the dual purpose of simplifying the presentation of the results and formulating tangible recommendations. We distinguish between (1) 221 222 small patches (\leq 10 hectares), i.e. mostly small and isolated patches with an occasional heathland patch edge largely surrounded by other land use, (2) intermediate patches/patch edges (10-30 223 224 hectares), i.e. mostly edges of large heathland patches with an occasional medium-sized patch, and 225 (3) large patches (> 30 hectares), i.e. core areas of large heathland patches (Fig. 1b).

226

c) Heathland heterogeneity

Heathland heterogeneity was quantified by the Shannon Diversity Index (shdi) in the R package (landscapemetrics' version 1.5.4 (Hesselbarth et al., 2019), applied to four sub-types of heathland as classified in the BVM version 2020 (De Saeger et al., 2020): dry heathland, wet heathland, peat and Nardus grasslands. We also distinguished subtypes with and without trees or shrubs. The BVM was

rasterised at 5 metres and the shdi was calculated in a 400-metre radius (≈ 50 hectares) around each
dummy point (Fig. 1b). The BVM is a vector layer but was rasterized because the 'landscapemetrics'
package takes raster layers as input.

234 **d**

d) Vegetation structure

235 We used Sentinel-2A imagery to quantify vegetation structure as this satellite has been delivering 236 multispectral data across large spatial extents since April 2017 at a high spatial and temporal 237 resolution (10 x 10 metres every 5 to 10 days for Flanders). Vegetation structure was quantified by 238 calculating the homogeneity, a second-order texture measure for image smoothness (Haralick, 1979; 239 Haralick et al., 1973), of a Sentinel-2 EVI (Enhanced Vegetation Index) composite (Liu and Huete, 1995) 240 (Fig. 1b). When calculating second-order texture measures, the spatial configuration of pixel values is 241 taken into account by first constructing a gray-level co-occurrence matrix (GLCM; Haralick et al., 1973). 242 Second-order homogeneity characterizes mainly vertical complexity with ancillary information on 243 horizontal plant diversity and was suggested to sufficiently capture vegetation structure relevant to 244 species' habitat suitability (Farwell et al., 2021). Fig. 1c shows examples of heathland locations with 245 low structure (i.e. a mostly uniform vegetation cover) and high structure (i.e. a high variability in 246 vegetation height).

247 For each 10-metre pixel in the Campine region, annual median EVI composites from April to August in the study period 2017-2021 were obtained from the near-infrared, blue and red band of the image 248 249 collection "Sentinel-2 MSI: MultiSpectral Instrument, Level 2A" in Google Earth Engine. Before 250 calculating the EVI, pixels with scene classification labels 1 to 3 and 8 to 11 were omitted (i.e. 251 unreliable pixels, clouds and snow/ice). The annual EVI values were averaged, excluding values below 252 0.1 and above 1 as they mostly indicated buildings, paved soils or solar panels. Homogeneity was 253 calculated using the R package 'glcm' version 1.6.5 (https://cran.r-project.org/web/packages/glcm/) 254 with a kernel size of 5 (i.e. a moving window of 5 x 5 pixels or 50 x 50 metres). Vegetation structure

was calculated in steps of 10 metres and the inverse of homogeneity was taken as low values indicateda high vegetation structure and vice versa.

257 We adapted our approach to increase the availability of pixels available for modelling despite the large 258 number of edges in our study area. Since the study area was not a spatially continuous patch, edges 259 were abundantly present inducing one or more missing EVI values in the moving windows used to 260 calculate homogeneity. To reduce the impact of these edge effects and hence increase the number of 261 raster pixels with covariate values for vegetation structure, we took three actions. First, for texture 262 calculations, we included the EVI values from semi-natural edges (i.e. connected patches of seminatural habitats of which at least 10% was identified as heathland). Second, we chose a small kernel 263 264 size to reduce the chance of missing values for texture calculations. Third, we calculated the average 265 homogeneity in a 50-metre radius around each dummy point in the patch edges with missing values 266 and added this information to the raster layer for vegetation structure.

267

2.3.2. Sampling bias covariates

268 In a point process setting, it is common to include additional covariates that can accommodate 269 sampling bias instead of modifying the background (i.e. the quadrature scheme) (Renner et al., 2015), 270 as opposed to, for example, a target group background selection in Maxent (Phillips et al., 2009). We 271 added one accessibility covariate: road density (km road per square km); and one search effort 272 covariate: the annual average number of species observed within the considered taxonomic group in 273 the study period (extracted from waarnemingen.be). Both were calculated in a 100-metre radius 274 around each dummy point. Accessibility accounted for the impact of high observation density around 275 roads (both paved and unpaved) while search effort accounted for the impact of observer activity.

276

2.4. Species distribution model

We ran Gibbs point process models with a Geyer saturation process (Baddeley et al., 2015) per species
and per landscape context to study the impact of heathland size, vegetation structure and heathland

heterogeneity on the habitat suitability of dry-heathland fauna in different landscape contexts. Goodness-of-fit was evaluated with a Diggle-Cressie-Loosmore-Ford (DCLF) test (Baddeley et al., 2014) and predictive performance was assessed in a spatial block cross-validation using the R package 'blockCV' version 3.1-1 (Valavi et al., 2019). Appendix A motivates the selection of the SDM method (section A.1), specifies the model parameters and settings used in this study (section A.2) and elaborates on the methods used for assessing model performance (section A.3).

We encountered some model fitting problems in exploratory analyses and set a threshold of 60 presences to avoid poorly fitted or invalid models. Eight species and four models in the anthropogenic landscape context were, therefore, omitted for further analysis (see Table B.1). We finally kept ten species with valid models in at least two landscape contexts (Table 2).

Table 2: List of selected species with their Red List Status in Flanders (LC = Least Concern, NT = Near Threatened,
EN = Endangered) (Devos et al., 2016; Maes et al., 2017a, 2021), Conservation Interest (BD = Birds Directive, FPS
= Flemish Priority Species, HSS = Habitat Specific Species with Habitats Directive Annex I habitat types) (De Knijf
et al., 2014; De Knijf and Paelinckx, 2013; Herremans et al., 2014; Paelinckx et al., 2009), and species occurrence
in the different landscape contexts (number of presences, after data quality filtering and after spatial thinning
per observation date at 50 metres, and average intensity of the point process expressed as the number of
presence points per hectare).

	English name			Number of presences		
Species		Red List	Conservation	and a	and average intensity	
		status in Interest		(n° points per hectare)		
		Flanders		Open	Closed	Anthr.
BIRDS						
Anthus trivialis	Troo Dinit	NT	HSS ²³¹⁰	907	2638	137
Antinus trivialis	Thee Pipit	INT		0.435	0.637	0.100
	Europoon Nightion	NT	BD Annex I	151	462	
Capriniugus europaeus	European Nightjar	INT	HSS 4030	0.072 0.110	0.110	-
Lullula arboroa	Woodlark	NT	BD Annex I	492	1213	80
	WOOuldik		HSS ^{2310, 4030}	0.236	0.288	0.059
Savicola rubicola	European Stopechat		HSS ^{2310, 4030}	935	1542	130
Saxicola lubicola	Luiopean Stonechat			0.448	0.366	0.095
BUTTERFLIES						
Callonbryc rubi	Groon Hairstroak	EN	HSS ^{2310, 4030}	265	321	
callopiniys rubi	Green Hallstreak			0.127	0.076	-
Hipparchia semele	Grayling	EN	FPS	302	330	485

				Number of presences		
Species	English name	Red List Conservation		and average intensity		
		status in	Interest	(n° points per hectare		ectare)
		Flanders		Open	Closed	Anthr.
			HSS ^{2310, 2330, 4030}	0.145	0.078	0.355
	Silver-studded Blue		HSS 4030	621	483	
Piedejus argus		EN		0.298	0.115	-
GRASSHOPPERS						
Grullus compostris	Field Criskat	EN	HSS ^{2310, 2330}	118	324	
Grynus campestris	FIEID CHICKEL	EIN		0.057	0.077	-
Murmalaatattiv maculatus	Mottled Grassbanner	10	HSS ^{2310, 2330}	68	243	82
	Mottled Grasshopper	LC		0.033	0.058	0.060
Oodinada coorulaceana	Blue Winged Grasshopper	LC HSS ^{2310, 4030}	LICC 2310 4030	112	296	189
Oedipoda caerulescens			0.054	0.070	0.138	

296

297 3. Results

298 **3.1. Point process analysis**

Species occurrence sets showed spatial interaction at radii of 50 to 250 metres (Table B.1 and Fig. B.2 to B.11). Model covariates showed no multicollinearity (Table B.2; VIF < 3 and average Pearson correlations $r = -0.007 \pm 0.193$, $r = 0.023 \pm 0.188$ and $r = -0.060 \pm 0.261$ in open, closed and anthropogenic landscape contexts respectively). Models fitted the data reasonably well, with no goodness-of-fit test (DCLF) rejecting the null hypothesis at a 0.01 significance level (Table B.1). Bird models performed better than most butterfly and grasshopper models, with the latter also presenting more variation in model performance (Table C.1).

306 **3.2. Drivers of habitat suitability**

For the general impact of heathland size, we found that larger heathlands were more suitable than intermediate or small heathland patches for all three taxonomic groups, especially in an anthropogenic landscape context (Fig. 2; Fig. 3). For the general impact of the landscape context, results in semi-natural (i.e. open or closed) contexts were mostly different from those in an anthropogenic context. Note that we could not assess the impact of the landscape context on habitat suitability parametrically due to correlations with all other predictors (Fig. B.1).

313 In the next paragraphs, we will demonstrate that the habitat suitability of the species in all three 314 taxonomic groups was impacted by both vegetation structure and heathland heterogeneity, 315 depending on heathland size and the landscape context. It is important to present these results in an 316 integrated manner. Fig. 2 and Fig. 3 therefore show the impact of both vegetation structure and 317 heathland heterogeneity on relative habitat suitability in the three landscape contexts and three 318 classes of heathland size (section 2.3.1.b), yet in slightly different ways. Fig. 2 shows predictions of the 319 relative habitat suitability across the environmental ranges of vegetation structure, heathland 320 heterogeneity and heathland size at constant values of the sampling bias covariates (Warton et al., 321 2013). The figure allows to assess the combined impact of vegetation structure and heathland 322 heterogeneity and is visually more intuitive, with colours representing a low or high relative habitat 323 suitability (also see Fig. D.1 to D.3). Fig. 3 shows the estimates of the model coefficients (betas in 324 Equation 5 in Appendix A.2) and allows to better interpret the relative importance of the impact of 325 vegetation structure, heathland heterogeneity and heathland size on relative habitat suitability (also 326 see Fig. D.4 to D.6). Predictions (Fig. 2) and estimates (Fig. 3) were averaged within the three classes of heathland size, i.e. small (< 10 hectares), intermediate (10-30 hectares) and large patches (> 30 327 328 hectares). We will discuss the aggregated results for all species and per taxonomic group in the main 329 text and refer to Appendix D for the results per species.

330 The impact of vegetation structure and/or heathland heterogeneity on habitat suitability depended 331 on the surrounding heathland size for most species in at least one landscape context (Appendices D 332 and E). A high vegetation structure became more important at larger heathland sizes, but in small 333 patches in a closed or open landscape context also a low vegetation structure could benefit habitat 334 suitability, especially for birds and butterflies (Fig. 3). A high heathland heterogeneity mostly impacted 335 habitat suitability positively (Fig. 2; Fig. 3) and became more important when heathland size increased 336 in an open landscape context while being equally important across heathland sizes in a closed or 337 anthropogenic context (Fig. 3).

Pooling all species (boxplots in Fig. 3), habitat suitability in an open landscape context was highest in large patches with high heathland heterogeneity or small patches with a low vegetation structure. In a closed landscape context, high heathland heterogeneity is beneficial, as are small heathland patches with a low vegetation structure and large patches with a high vegetation structure. In an anthropogenic landscape context, habitat suitability was highest in patches with a high heathland heterogeneity and a high vegetation structure, especially in large patches.

344 Bird habitat suitability was positively impacted by heathland heterogeneity, especially in large patches 345 in a semi-natural landscape context. Habitat suitability further increased in small and intermediate 346 patches/patch edges with a low vegetation structure in a semi-natural context, and in intermediate 347 patches/patch edges and large patches with a high vegetation structure in an anthropogenic context. 348 Butterfly habitat suitability was positively impacted by both a high vegetation structure and a high 349 heathland heterogeneity in large patches in an open or anthropogenic context. In a closed context, a 350 high vegetation structure increased habitat suitability in large patches and a high heathland 351 heterogeneity did so in intermediate patches/patch edges. In small patches, habitat suitability for 352 butterflies increased with a low vegetation structure, combined with low heathland heterogeneity in 353 an open landscape context and high heathland heterogeneity in a closed context. Grasshopper habitat 354 suitability was higher at a high vegetation structure, especially in intermediate patches/patch edges, 355 and at a high heathland heterogeneity in a closed or anthropogenic landscape context.



356

357 Fig. 2: Predictions of relative habitat suitability: - the impact of vegetation structure (x-axis) and heathland 358 heterogeneity (y-axis) on relative habitat suitability in different landscape contexts, summarised in three classes 359 of heathland size. Predicted intensities were first log-transformed to generate a linear output and then scaled 360 and averaged across all considered dry heathland species and according to taxonomy in different landscape 361 contexts (blue = low relative suitability, orange = high relative suitability). These values are the results of different 362 Gibbs point process models with Geyer saturation process per landscape context, including two-way interactions 363 between heathland size and vegetation structure/heathland heterogeneity. For four species (i.e. Caprimulgus 364 europaeus, Callophrys rubi, Plebejus argus and Gryllus campestris), the model in the anthropogenic landscape 365 context was omitted (see section 2.4).



Taxonomic group * BIRDS * BUTTERFLIES * GRASSHOPPERS

366

367 Fig. 3: Estimates of the model coefficients: the positive or negative impact of vegetation structure and heathland 368 heterogeneity on relative habitat suitability (quantified by intensity) in different landscape contexts, summarised 369 in three classes of heathland size. The distribution of the model coefficients is shown for all species (boxplots) 370 and grouped according to taxonomy, with dots and error bars representing mean estimate values and standard 371 deviations. These values are the results of different Gibbs point process models with a Geyer saturation process 372 per landscape context, including two-way interactions between heathland size and vegetation structure/ 373 heathland heterogeneity. For four species (i.e. Caprimulgus europaeus, Callophrys rubi, Plebejus argus and 374 Gryllus campestris), the model in the anthropogenic landscape context was omitted (see section 2.4).

375 4. Discussion

376 By integrating opportunistic citizen science data and multispectral satellite data in point process 377 models, we have substantiated the importance of vegetation structure for heathland fauna (Byriel et 378 al., 2023; Maes et al., 2017b). At the same time, we highlighted some important considerations in human-dominated and fragmented landscapes (Maes et al., 2022), such as the impact of edge effects from the surrounding land use and the ecological needs of the considered taxonomic group. Quantifying vegetation structure and heathland heterogeneity in a standardized and spatially contiguous way through remote sensing enabled us to produce generalisable results, an important asset for biodiversity policy and conservation.

384 Habitat heterogeneity (larger scale) and vegetation structure (smaller scale) have been shown to 385 increase niche availability and diversify environmental resources (e.g., MacArthur and Wilson, 1967). 386 They usually positively affect habitat suitability and species diversity (Ampoorter et al., 2020; Cramer 387 and Willig, 2002) although this relationship can also remain undetected or even be negative, 388 depending on the spatial scale, the type of heterogeneity measure and the taxonomic group 389 considered (Stein et al., 2014; Tews et al., 2004). Our results also demonstrated positive impacts of 390 heathland heterogeneity and of vegetation structure in core areas of large heathland patches. In small 391 and fragmented patches, however, vegetation structure was often negatively associated with habitat 392 suitability for the studied birds and butterflies. This might be explained by the birds' habitat 393 preference and by the effect of micro-fragmentation, which implies that small-scale habitat 394 heterogeneity can cause niche isolation for less mobile species (Laanisto et al., 2013). The four 395 heathland birds prefer open to semi-open heathlands with occasional trees or shrubs as a viewing 396 point for foraging or defending their territories. These relatively large species need large areas with a relatively low vegetation structure, especially in small and fragmented patches. While intuitively birds 397 398 should be less affected by micro-fragmentation at the considered scale (0.25 hectares), lower food 399 availability of species that are negatively affected by micro-fragmentation, such as invertebrates and 400 plants (Laanisto et al., 2013; Tamme et al., 2010), could also explain the negative relationship with 401 vegetation structure for birds.

Habitat edges induce edge effects that become stronger in smaller and more fragmented habitats
(Ewers et al., 2007; Fahrig, 2003). This probably explains why we found the largest differences

404 between landscape contexts in small patches and patch edges. Traditionally, habitat suitability was 405 negatively associated with fragmentation (Hanski, 1998; MacArthur and Wilson, 1967), but the 406 surrounding land cover might also increase habitat suitability for species that can benefit from edge 407 effects (Dupont and Overgaard Nielsen, 2006; Evens et al., 2018; Maes et al., 2014; Pfeifer et al., 2017). 408 Habitat edges in a semi-natural landscape context can provide resources for the inhabiting species 409 such as shelter, nesting spots or foraging opportunities (Dupont and Overgaard Nielsen, 2006; Evens 410 et al., 2018) and deliver specific habitat conditions such as forest ecotones (Maes et al., 2014; Moquet 411 et al., 2018; Pfeifer et al., 2017). Small and isolated patches can thus have high habitat suitability 412 (Wintle et al., 2019) if located in a resourceful landscape. The surrounding semi-natural land cover 413 might even enhance the habitat heterogeneity to the point that maintaining characteristic heathland 414 vegetation (i.e. dwarf shrubs, quantified by a low vegetation structure; Fig. 1c) will become relatively 415 more important, especially for species that rely on them for food and reproduction (Byriel et al., 2023) 416 such as Grayling (Hipparchia semele), European Stonechat (Saxicola rubicola) and Silver-studded Blue 417 (Plebejus argus). In a closed landscape context that consists of forest only, however, maintaining 418 heathland heterogeneity remains essential. This was also noted for large patches in an anthropogenic 419 context, where maintaining a high vegetation structure and heathland heterogeneity appeared 420 relatively more important compared to large patches in a semi-natural landscape context.

421 Butterflies are considered an umbrella taxon for insect conservation (e.g. van Swaay et al., 2006) and 422 birds are often used as indicators of general habitat quality (Maes et al., 2009). Yet, results among 423 taxonomic groups, even among invertebrates, showed dissimilarities (Fig. 2; Fig. 3). Taxonomic groups 424 respond to different components of vegetation structure at different spatial scales (Atauri and De 425 Lucio, 2001; Davies and Asner, 2014; de Vries et al., 2021; Tews et al., 2004). The impact of local 426 vegetation structure on bird habitat suitability, for example, would not have been detected by large-427 scale measures of habitat heterogeneity and certainly not by those derived from coarse categorical 428 land use maps (Coops and Wulder, 2019). Additionally, possible benefits of edges can be higher for 429 taxonomic groups with larger (birds) or more mobile species (birds and butterflies) (Pfeifer et al., 2017) 430 as opposed to taxonomic groups with small and less mobile species (grasshoppers). For grasshoppers, 431 habitat suitability increased in intermediately large patches or patch edges with a high vegetation 432 structure and at a high heathland heterogeneity in a closed or anthropogenic landscape context, as 433 was observed in an earlier study for Blue Winged Grasshopper (Oedipoda caerulescens) and Mottled 434 Grasshopper (Myrmeleotettix maculatus) (Schirmel et al., 2011). The three heathland grasshopper 435 species are mostly found in relatively open habitats but need sufficient high grasses for food and 436 shelter by bushes or small trees during very hot days (Willott, 1997). Additionally, the "enemy-free 437 space hypothesis" states that prey species prefer dense vegetation with a high structure to escape 438 from predators (Price et al., 1980). This was found to be true for large carabid beetles (Brose, 2003) 439 and is probably also the case for grasshoppers in our study.

440 Although pooling species into taxonomic groups revealed some patterns regarding the impact of the 441 environmental variables on habitat suitability, individual species might respond differently to 442 multiscale vegetation management. Conservation planners must, therefore, consider additional knowledge on habitat requirements of dry heathland species, especially those of conservation 443 444 interest. For example, bird habitat suitability was generally impacted positively by a high heathland 445 heterogeneity, although this was less pronounced for European Nightjar (Caprimulgus europaeus) (Fig. 446 D.4). This species requires complementary habitats for foraging (extensive grasslands) and breeding 447 (heathlands) which may be separated by several kilometres (Evens et al., 2018). Habitat size and 448 heterogeneity on a wider landscape scale will likely be more important than the heterogeneity of 449 habitat subtypes within the heathland itself (Evens et al., 2021). Another example is the overall 450 preference for a low vegetation structure in a closed landscape context for the Silver-studded Blue. 451 This preference was also detected in intermediate and large patches, as opposed to the other two 452 butterfly species which preferred a high vegetation structure in larger heathlands (Fig. D.5; Table E.1).

A low vegetation structure can indicate the presence of relatively young and low *Calluna vulgaris* and *Erica tetralix*, the preferred host plants of the Silver-studded Blue (Diemont et al., 2015).

455 Our results support that restoring and maintaining large and structurally complex habitats with patchy 456 vegetation is a good approach for fauna conservation in heathlands (Byriel et al., 2023; De Blust, 2022; 457 de Vries et al., 2021; Schirmel et al., 2011; van den Berg et al., 2001). The positive impact of an 458 increased heathland size for most species is expected as habitat loss threatens biodiversity (Newbold 459 et al., 2015). Furthermore, positive relationships between increased availability of a species' 460 associated land use or habitat type and occurrence are common, especially for habitat specialists 461 (Fahrig, 2003; Milanesi et al., 2017; Rutten et al., 2019; van den Berg et al., 2001). Heathland 462 enlargement becomes especially important in an anthropogenic landscape context (i.e. urban and 463 agriculture land use; Piessens et al., 2005; Worboys et al., 2010), due to negative edge effects and low 464 suitability of the surrounding land use for species of conservation interest (Fletcher et al., 2018; 465 Newbold et al., 2015; Olivier et al., 2016). Increasing heathland area can be achieved by restoring 466 heathland habitat, for example by felling (non-native) coniferous forests. In regions with highly 467 fragmented and isolated patches facing strong anthropogenic pressures, such as nitrogen deposition 468 from agriculture or industry (Vogels et al., 2017), this can be challenging due to policy restrictions, 469 budgetary limitations or land ownership (Diemont et al., 2015; Maes et al., 2022). In this light, it is 470 essential to understand that even small patches can have adequate habitat suitability for typical 471 (threatened) heathland species when habitat heterogeneity and/or vegetation structure are 472 sufficiently high.

Increasing heterogeneity in nitrogen-polluted heathlands is often realised by large-scale removal of above-ground vegetation (e.g. by clearcutting, machine cutting or burning) or of both vegetation and soil top layers (i.e. sod-cutting or choppering) (De Blust, 2022). Those large-scale and intensive management practices homogenise the vegetation cover, lower vegetation structure and deplete nutrients from the soil, which is beneficial for restoring typical heathland vegetation (Jones et al.,

2017; Schellenberg and Bergmeier, 2020), but can also have a detrimental effect on invertebrates and
larger predators, such as birds, that feed on them (Maes et al., 2017b; Vogels et al., 2021, 2017).
Therefore, intensified large-scale management practices should be avoided when possible, especially
in and around (small) areas where species of conservation interest are known to be present.

482 The proxy that was used to quantify vegetation structure characterizes mainly heterogeneity in 483 vegetation height with ancillary information on horizontal plant diversity (Farwell et al., 2021), yet 484 both components are inextricably linked. Increasing the vertical complexity of vegetation cover at 485 smaller scales will automatically allow for more plant diversity and can be achieved relatively fast, for 486 example by removing above-ground vegetation and preventing grass encroachment of bare soil by 487 mosaic mowing, cutting trees or low-intensity grazing, while allowing other patches to reach older 488 successional stages (Byriel et al., 2023). While using a multivariate structural proxy has been shown to 489 outperform single components of vegetation structure for estimating species distributions and 490 diversity (e.g. Brose, 2003; Farwell et al., 2021), it also complicated the interpretation of which 491 component of the proxy (heterogeneity in vegetation height or horizontal plant diversity) impacted 492 habitat suitability. Combining a structural proxy with LiDAR-derived vegetation height, for example, 493 might help to disentangle the individual impact of the components (Bergen et al., 2009; de Vries et 494 al., 2021; Moudrý et al., 2022). Future research can also include microclimate data at fine scales 495 obtained from remote sensing (Zellweger et al., 2019). This can, for example, shed further light on the 496 importance of vegetation structure for invertebrates in heathlands as a regulator under climatic 497 extremes (Maes et al., 2019b; Mantilla-Contreras et al., 2012; Schirmel et al., 2011; Schirmel and 498 Fartmann, 2014).

We remain careful to generalise our definition of multiscale management to a 'small versus large-scale approach'. We did find important indications that heathland size, the landscape context and taxonomy affect the scale at which heathlands are best managed. Additional findings from a sensitivity analysis (where vegetation structure and heathland heterogeneity are quantified at different spatial scales), 503 however, could further support management recommendations and might highlight some keystone 504 structures in heathland ecosystems (Tews et al., 2004). We also assumed that a species responded 505 uniformly to the environmental gradients throughout the Campine region, as it is a region with similar 506 biotic and abiotic conditions (Klijn and de Haes, 1994). We acknowledge, however, that on larger 507 scales, the impact of climatic variables on habitat suitability becomes more prominent or species 508 populations might respond differently to similar local environmental conditions (Chen et al., 2020). 509 For example, heathland butterflies responded similarly to environmental conditions within the 510 Campine region (Vanreusel et al., 2007) but might respond differently to spatial structure in other 511 regions (De Ro et al., 2021; Schirmel and Fartmann, 2014). Although the presented methods are 512 applicable in any region where both species occurrence and remote sensing data are available at high 513 resolutions, they might not be transferable to every habitat type, as quantifying habitat heterogeneity 514 and vegetation structure possibly needs different approaches or considerations. For example, habitat 515 heterogeneity in farmland is not only impacted by variability in habitat subtypes (such as arable land, 516 cultural grassland and orchards) but also by crop configuration and composition (Fahrig et al., 2011) 517 and by the presence of small landscape features such as hedgerows or flower strips (Dochy, 2014).

518 5. Conclusion

519 Integrating fine-scaled opportunistic citizen science data and remote sensing data with point process 520 models is a promising advance in biodiversity conservation monitoring. By including heathlands of 521 different sizes and the landscape context, management recommendations for fauna conservation 522 could be formulated in highly fragmented landscapes. In summary, we recommend restoring and 523 maintaining large and structurally complex heathlands with patchy vegetation. Conservation should 524 also include action plans to connect fragmented heathlands (e.g. by cutting down pine plantations). 525 When sufficient natural resources are available in the direct (semi-natural) environment of smaller heathlands (e.g. for foraging or nesting), heathland management plans should also emphasize the 526 527 importance of maintaining characteristic dry-heathland shrub vegetation. In anthropogenic

528 landscapes, on the other hand, simply increasing the structural complexity of patches without 529 increasing their surface area might not be enough to avoid the local extinction of species of 530 conservation interest. This is probably the largest challenge for conservation management, as enlarging heathlands in human-dominated landscapes will need the field experience of local 531 managers, the sensitisation of citizens and additional actions and funding at the policy level. We 532 further emphasize the importance of using multiple species from different taxa as a conservation 533 534 umbrella, which has become more and more feasible considering the unprecedented quantity of 535 species occurrence data collected on citizen science data platforms.

536

537 **DECLARATIONS**

- 538 **Ethical approval** (not applicable)
- 539 **Competing interests** (not applicable)

540 Authors' contributions

- 541 Camille Van Eupen: conceptualization, methodology, software, validation, formal analysis, writing –
- 542 original draft, visualization; Dirk Maes: conceptualization, writing review & editing, supervision;
- 543 Stien Heremans: conceptualization, writing review & editing; Kristijn Swinnen: data curation,
- 544 writing review & editing; Ben Somers: conceptualization, writing review & editing, supervision;
- 545 Stijn Luca: conceptualization, writing review & editing, supervision. All authors contributed
- 546 critically to the drafts and gave final approval for publication.

547 Funding

548 This work was supported by the Flemish Research Foundation FWO–SB [grant number 1S92118N].

549 Availability of data and materials

- 550 The cleansed datasets of the ten selected species will be made available in Dryad Digital Repository.
- 551 All species data are available on request at Natuurpunt Studie (<u>natuurdata@natuurpunt.be</u>).

552 **REFERENCES**

- Ampoorter, E., Barbaro, L., Jactel, H., Baeten, L., Boberg, J., Carnol, M., Castagneyrol, B., Charbonnier, Y., Dawud, S.M.,
 Deconchat, M., De Smedt, P., De Wandeler, H., Guyot, V., Hättenschwiler, S., Joly, F.-X., Koricheva, J., Milligan, H.,
 Muys, B., Nguyen, D., Ratcliffe, S., Raulund-Rasmussen, K., Scherer-Lorenzen, M., van der Plas, F., Van Keer, J.,
 Verheyen, K., Vesterdal, L., Allan, E., 2020. Tree diversity is key for promoting the diversity and abundance of
 forest-associated taxa in Europe. Oikos 129, 133–146. https://doi.org/10.1111/oik.06290
 Atauri, J.A., De Lucio, J. V., 2001. The role of landscape structure in species richness distribution of birds, amphibians,
- reptiles and lepidopterans in Mediterranean landscapes. Landsc. Ecol. 16, 147–159.
 https://doi.org/10.1023/A:1011115921050
- Baddeley, A., Diggle, P.J., Hardegen, A., Lawrence, T., Milne, R.K., Nair, G., 2014. On tests of spatial pattern based on
 simulation envelopes. Ecol. Monogr. 84, 477–489.
- Baddeley, A., Rubak, E., Turner, R., 2015. Spatial Point Patterns: Methodology and Applications with R. Chapman &
 Hall/CRC.
- Barbosa, A.M., 2015. fuzzySim: applying fuzzy logic to binary similarity indices in ecology. Methods Ecol. Evol. 6, 853–858.
 https://doi.org/10.1111/2041-210X.12372
- Bellis, L.M., Pidgeon, A.M., Radeloff, V.C., St-Louis, V., Navarro, J.L., Martella, M.B., 2008. Modeling Habitat Suitability for
 Greater Rheas Based on Satellite Image Texture. Ecol. Appl. 18, 1956–1966.
- Bergen, K.M., Goetz, S.J., Dubayah, R.O., Henebry, G.M., Hunsaker, C.T., Imhoff, M.L., Nelson, R.F., Parker, G.G., Radeloff,
 V.C., 2009. Remote sensing of vegetation 3-D structure for biodiversity and habitat: Review and implications for
 lidar and radar spaceborne missions. J. Geophys. Res. 114, G00E06. https://doi.org/10.1029/2008JG000883
- Besnard, A.G., Davranche, A., Maugenest, S., Bouzillé, J.B., Vian, A., Secondi, J., 2015. Vegetation maps based on remote
 sensing are informative predictors of habitat selection of grassland birds across a wetness gradient. Ecol. Indic.
 574 58, 47–54. https://doi.org/10.1016/j.ecolind.2015.05.033
- Bonari, G., Fajmon, K., Malenovský, I., Zelený, D., Holuša, J., Jongepierová, I., Kočárek, P., Konvička, O., Uřičář, J., Chytrý, M.,
 2017. Management of semi-natural grasslands benefiting both plant and insect diversity: The importance of
 heterogeneity and tradition. Agric. Ecosyst. Environ. 246, 243–252. https://doi.org/10.1016/j.agee.2017.06.010
- Brose, U., 2003. Bottom-up control of carabid beetle communities in early successional wetlands: Mediated by vegetation
 structure or plant diversity? Oecologia 135, 407–413. https://doi.org/10.1007/s00442-003-1222-7
- Byriel, D.B., Ro-Poulsen, H., Kepfer-Rojas, S., Hansen, A.K., Hansen, R.R., Justesen, M.J., Kristensen, E., Møller, C.B.,
 Schmidt, I.K., 2023. Contrasting responses of multiple insect taxa to common heathland management regimes
 and old-growth successional stages. Biodivers. Conserv. 32, 545–565. https://doi.org/10.1007/s10531-022 02511-9
- Chen, Q., Yin, Y., Zhao, R., Yang, Y., Teixeira da Silva, J.A., Yu, X., 2020. Incorporating Local Adaptation Into Species
 Distribution Modeling of Paeonia mairei, an Endemic Plant to China. Front. Plant Sci. 10, 1717.
 https://doi.org/10.3389/fpls.2019.01717

587 Coops, N.C., Wulder, M.A., 2019. Breaking the Habit(at). Trends Ecol. Evol. 34, 585–587.

588 https://doi.org/10.1016/j.tree.2019.04.013

- Couvreur, M., Menschaert, J., Sevenant, M., Ronse, A., Van Landuyt, W., De Blust, G., Antrop, M., Hermy, M., 2004.
 Ecodistricten en ecoregio's als instrument voor natuurstudie en milieubeleid. Natuur.Focus 3, 51–58.
- 591 Cramer, M.J., Willig, M.R., 2002. HABITAT HETEROGENEITY, HABITAT ASSOCIATIONS, AND RODENT SPECIES DIVERSITY IN A
 592 SAND–SHINNERY-OAK LANDSCAPE. J. Mammal. 83, 743–753. https://doi.org/10.1644/1545-
- 593 1542(2002)083<0743:HHHAAR>2.0.CO;2
- 594Davies, A.B., Asner, G.P., 2014. Advances in animal ecology from 3D-LiDAR ecosystem mapping. Trends Ecol. Evol. 29, 681–595691. https://doi.org/10.1016/j.tree.2014.10.005
- 596 De Blust, G., 2022. Heide en Heidebeheer, in: Van Uytvanck, J., Hermy, M., De Blust, G., Hoffmann, M. (Eds.),
 597 Natuurbeheer. Praktijk En Wetenschap Hand in Hand. Sterck & De Vreese, Gorredijk, Nederland, pp. 255–286.
- De Knijf, G., Paelinckx, D., 2013. Typische faunasoorten van de verschillende Natura 2000 habitattypes, in functie van de
 beoordeling van de staat van instandhouding op niveau Vlaanderen. INBO.A.2013.139. Instituut voor Natuur- en
 Bosonderzoek, Brussel.
- De Knijf, G., Westra, T., Onkelinx, T., Quataert, P., Pollet, M., 2014. Monitoring Natura 2000-soorten en overige soorten
 prioritair voor het Vlaams beleid. Blauwdrukken soortenmonitoring in Vlaanderen. Rapporten van het Instituut
 voor Natuur- en Bosonderzoek 2014 (INBO.R.2014.2319355). Instituut voor Natuur- en Bosonderzoe.
- De Ro, A., Vanden broeck, A., Verschaeve, L., Van Dyck, H., Jacobs, I., T'Jollyn, F., Maes, D., 2021. Occasional long distance
 dispersal does not prevent inbreeding in a threatened butterfly. BMC Ecol. Evol. 21, 224.
 https://doi.org/10.1186/s12862-021-01953-z
- be Saeger, S., Guelinckx, R., Oosterlynck, P., De Bruyn, A., Debusschere, K., Dhaluin, P., Erens, R., Hendrickx, P., Hennebel,
 D., Jacobs, I., Kumpen, M., Opdebeeck, J., Spanhove, T., Tamsyn, W., Van Oost, F., Van Dam, G., Van Hove, M.,
 Wils, C., Paelinckx, D., 2020. Biologische Waarderingskaart en Natura 2000 Habitatkaart, uitgave 2020. Rapporten
 van het Instituut voor Natuur- en Bosonderzoek 2000 (35). Instituut voor Natuur- en Bosonderzoek, Brussel.
 https://doi.org/10.21436/inbor.18840851
- 612 De Saeger, S., Oosterlynck, P., Paelinckx, D., 2017. The Biological Valuation Map (BVM): a field-driven survey of land cover
 613 and vegetation in the Flemish Region of Belgium. Doc. Phytosociologiques 6, 373–382.
- de Vries, J.P.R., Koma, Z., WallisDeVries, M.F., Kissling, W.D., 2021. Identifying fine-scale habitat preferences of threatened
 butterflies using airborne laser scanning. Divers. Distrib. 27, 1251–1264. https://doi.org/10.1111/DDI.13272
- 616 Devos, K., Anselin, A., Driessens, G., Herremans, M., Onkelinx, T., Spanoghe, G., Stienen, E., T'Jollyn, F., Vermeersch, G.,
 617 Maes, D., 2016. De IUCN Rode-Lijst van de broedvogels in Vlaanderen (2016). Rapporten van het Instituut voor
- 618 Natuur- en Bosonderzoek jaar (11485739). Instituut voor Natuur- en Bosonderzoek, Brussel.
- 619 https://doi.org/dx.doi.org/10.21436/inbor.11485739
- Diemont, W.H., Heijman, W.J.M., Siepel, H., Webb, N.R., 2015. Economy and Ecology of Heathlands. KNNV Publishing,
 Zeist, The Netherlands. https://doi.org/10.1163/9789004277946

- Dochy, O., 2014. Verslag van de Frans-Belgische akkervogelinventarisatie 2013. Provincie West-Vlaanderen, Brugge.
 Brussels, Belgium. https://doi.org/10.13140/2.1.2065.4082
- Dupont, Y.L., Overgaard Nielsen, B., 2006. Species composition, feeding specificity and larval trophic level of flower-visiting
 insects in fragmented versus continuous heathlands in Denmark. Biol. Conserv. 131, 475–485.
 https://doi.org/10.1016/j.biocon.2005.12.020
- Evens, R., Beenaerts, N., Neyens, T., Witters, N., Smeets, K., Artois, T., 2018. Proximity of breeding and foraging areas
 affects foraging effort of a crepuscular, insectivorous bird. Sci. Rep. 8, 11. https://doi.org/10.1038/s41598-01821321-0
- Evens, R., Jacot, A., Artois, T., Ulenaers, E., Neyens, T., Rappaz, L., Theux, C., Pradervand, J.-N., 2021. Improved ecological
 insights commission new conservation targets for a crepuscular bird species. Anim. Conserv. 24, 457–469.
 https://doi.org/10.1111/acv.12650
- Ewers, R.M., Thorpe, S., Didham, R.K., 2007. Synergistic interactions between edge and area effects in a heavily fragmented
 landscape. Ecology 88, 96–106. https://doi.org/10.1890/0012-9658(2007)88[96:SIBEAA]2.0.CO;2
- Fagúndez, J., 2013. Heathlands confronting global change: drivers of biodiversity loss from past to future scenarios. Ann.
 Bot. 111, 151–172. https://doi.org/10.1093/aob/mcs257
- Fahrig, L., 2003. Effects of Habitat Fragmentation on Biodiversity. Annu. Rev. Ecol. Evol. Syst. 34, 487–515.
 https://doi.org/10.1146/annurev.ecolsys.34.011802.132419
- Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M., Martin, J.-L., 2011.
 Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecol. Lett. 14, 101–112.
 https://doi.org/10.1111/j.1461-0248.2010.01559.x
- Farrell, S.L., Collier, B.A., Skow, K.L., Long, A.M., Campomizzi, A.J., Morrison, M.L., Hays, K.B., Wilkins, R.N., 2013. Using
 LiDAR-derived vegetation metrics for high-resolution, species distribution models for conservation planning.
 Ecosphere 4, 1–18. https://doi.org/10.1890/ES12-000352.1
- Farwell, L.S., Gudex-Cross, D., Anise, I.E., Bosch, M.J., Olah, A.M., Radeloff, V.C., Razenkova, E., Rogova, N., Silveira, E.M.O.,
 Smith, M.M., Pidgeon, A.M., 2021. Satellite image texture captures vegetation heterogeneity and explains
 patterns of bird richness. Remote Sens. Environ. 253, 112175. https://doi.org/10.1016/j.rse.2020.112175
- Fletcher, R.J., Didham, R.K., Banks-Leite, C., Barlow, J., Ewers, R.M., Rosindell, J., Holt, R.D., Gonzalez, A., Pardini, R.,
 Damschen, E.I., Melo, F.P.L., Ries, L., Prevedello, J.A., Tscharntke, T., Laurance, W.F., Lovejoy, T., Haddad, N.M.,
 2018. Is habitat fragmentation good for biodiversity? Biol. Conserv. 226, 9–15.
- 651 https://doi.org/10.1016/j.biocon.2018.07.022
- Gábor, L., Šímová, P., Keil, P., Zarzo-Arias, A., Marsh, C.J., Rocchini, D., Malavasi, M., Barták, V., Moudrý, V., 2022. Habitats
 as predictors in species distribution models: Shall we use continuous or binary data? Ecography (Cop.). 1–9.
 https://doi.org/10.1111/ecog.06022
- Gibson, L.A., Wilson, B.A., Cahill, D.M., Hill, J., 2004. Spatial prediction of rufous bristlebird habitat in a coastal heathland: A
 GIS-based approach. J. Appl. Ecol. 41, 213–223. https://doi.org/10.1111/j.0021-8901.2004.00896.x

- 657 Goetz, S.J., Steinberg, D., Betts, M.G., Holmes, R.T., Doran, P.J., Dubayah, R., Hofton, M., 2010. Lidar remote sensing
 658 variables predict breeding habitat of a Neotropical migrant bird. Ecology 91, 1569–1576.
 659 https://doi.org/10.1890/09-1670.1
- Graf, R.F., Mathys, L., Bollmann, K., 2009. Habitat assessment for forest dwelling species using LiDAR remote sensing:
 Capercaillie in the Alps. For. Ecol. Manage. 257, 160–167. https://doi.org/10.1016/j.foreco.2008.08.021
- 662 Gustafson, E.J., 1998. Quantifying landscape spatial pattern: what is the state of the art? Ecosystems 1, 143–156.
- Haddad, N.M., Baum, K.A., 1999. An experimental test of corridor effects on butterfly densities. Ecol. Appl. 9, 623–633.
 https://doi.org/10.1890/1051-0761(1999)009[0623:AETOCE]2.0.CO;2
- 665 Hanski, I., 1998. Metapopulation dynamics. Nature 396, 41–49. https://doi.org/10.1038/23876
- 666 Haralick, R.M., 1979. Statistical and structural approaches to texture. Proc. IEEE 67, 786–804.
- Haralick, R.M., Shanmugam, K., Dinstein, I., 1973. Textural Features for Image Classification. IEEE Trans. Syst. Man Cybern.
 SMC-3, 610–621. https://doi.org/10.1109/TSMC.1973.4309314
- Herremans, M., De Knijf, G., Hansen, K., Westra, T., Vanreusel, W., Martens, E., Van Gossum, H., Anselin, A., Vermeersch,
 G., Pollet, M., 2014. Monitoring van beleidsrelevante soorten in Vlaanderen met inzet van vrijwilligers. Rapporten
 van het Instituut voor Natuur- en Bosonderzoek 2014 (rapportnr. INBO.R.2014.1628917). Instituut voor Natuuren Bosonderzoek, Brussel.
- Herremans, M., Swinnen, K., Vanreusel, W., Vercayie, D., Veraghtert, W., Vanormelingen, P., 2018.
- 674 www.waarnemingen.be. Een veelzijdig portaal voor natuurgegevens. Natuur.focus 17, 153–166.
- Hesselbarth, M.H.K., Sciaini, M., With, K.A., Wiegand, K., Nowosad, J., 2019. landscapemetrics: an open-source R tool to
 calculate landscape metrics. Ecography (Cop.). 42, 1648–1657. https://doi.org/10.1111/ecog.04617
- Huber, N., Kienast, F., Ginzler, C., Pasinelli, G., 2016. Using remote-sensing data to assess habitat selection of a declining
 passerine at two spatial scales. Landsc. Ecol. 31, 1919–1937. https://doi.org/10.1007/s10980-016-0370-1
- Jacobs, C., Zipf, A., 2017. Completeness of citizen science biodiversity data from a volunteered geographic information
 perspective. Geo-spatial Inf. Sci. 20, 3–13. https://doi.org/10.1080/10095020.2017.1288424
- Jones, L., Stevens, C., Rowe, E.C., Payne, R., Caporn, S.J.M., Evans, C.D., Field, C., Dale, S., 2017. Can on-site management
 mitigate nitrogen deposition impacts in non-wooded habitats? Biol. Conserv. 212, 464–475.
 https://doi.org/10.1016/j.biocon.2016.06.012
- Klijn, F., de Haes, H.A.U., 1994. A hierarchical approach to ecosystems and its implications for ecological land classification.
 Landsc. Ecol. 9, 89–104. https://doi.org/10.1007/BF00124376
- Laanisto, L., Tamme, R., Hiiesalu, I., Szava-Kovats, R., Gazol, A., Pärtel, M., 2013. Microfragmentation concept explains non positive environmental heterogeneity-diversity relationships. Oecologia 171, 217–226.
 https://doi.org/10.1007/s00442-012-2398-5
- Liu, H.Q., Huete, A., 1995. Feedback based modification of the NDVI to minimize canopy background and atmospheric
 noise. IEEE Trans. Geosci. Remote Sens. 33, 457–465. https://doi.org/10.1109/36.377946

691 MacArthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press, Princeton.

- Maes, D., Adriaens, T., Decleer, K., Foquet, B., Foquet, R., Lambrechts, J., Lock, K., Piesschaert, F., 2017a. IUCN Rode Lijst
 van de sprinkhanen en krekels in Vlaanderen. Rapporten van het Instituut voor Natuur- en Bosonderzoek 2017
 (29). Instituut voor Natuur- en Bosonderzoek, Brussel.
- Maes, D., Anselin, A., van Swaay, C., Sierdsema, H., De Bruyn, L., Vermeersch, G., Van Dyck, H., 2009. Can we predict the
 distribution of heathland butterflies with heathland bird data? Anim. Biol. 59, 335–349.
 https://doi.org/10.1163/157075609X454962
- 057 Inteps.//doi.org/10.1105/157075009x454902
- Maes, D., Brosens, D., T'Jollyn, F., Desmet, P., Piesschaert, F., Van Hoey, S., Adriaens, T., Dekoninck, W., Devos, K., Lock, K.,
 Onkelinx, T., Packet, J., Speybroeck, J., Thomaes, A., Van Den Berge, K., Van Landuyt, W., Verreycken, H., 2019a.
 Validated red lists of Flanders, Belgium. Research Institute for Nature and Forest (INBO), Brussels.
 https://doi.org/https://doi.org/10.15468/8tk3tk
- Maes, D., Decleer, K., De Keersmaeker, L., Van Uytvanck, J., Louette, G., 2017b. Intensified habitat management to mitigate
 negative effects of nitrogen pollution can be detrimental for faunal diversity: A comment on Jones et al. (2017).
 Biol. Conserv. 212, 493–494. https://doi.org/10.1016/j.biocon.2017.03.001
- Maes, D., Ellis, S., Goffart, P., Cruickshanks, K.L., van Swaay, C.A.M., Cors, R., Herremans, M., Swinnen, K.R.R., Wils, C.,
 Verhulst, S., De Bruyn, L., Matthysen, E., O'Riordan, S., Hoare, D.J., Bourn, N.A.D., 2019b. The potential of species
 distribution modelling for reintroduction projects: the case study of the Chequered Skipper in England. J. Insect
 Conserv. 23, 419–431. https://doi.org/10.1007/s10841-019-00154-w
- Maes, D., Herremans, M., Vantieghem, P., Veraghtert, W., Jacobs, I., Fajgenblat, M., Dyck, H. Van, 2021. IUCN Rode Lijst
 van de dagvlinders in Vlaanderen 2021. Rapporten van het Instituut voor Natuur- en Bosonderzoek 2021 (10).
 Instituut voor Natuur- en Bosonderzoek, Brussel. https://doi.org/10.21436/inbor.34052968
- Maes, D., Jacobs, I., Segers, N., Vanreusel, W., Van Daele, T., Laurijssens, G., Van Dyck, H., 2014. A resource-based
 conservation approach for an endangered ecotone species: the Ilex Hairstreak (Satyrium ilicis) in Flanders (north
 Belgium). J. Insect Conserv. 18, 939–950. https://doi.org/10.1007/s10841-014-9702-0
- Maes, D., Van Calster, H., Herremans, M., Van Dyck, H., 2022. Challenges and bottlenecks for butterfly conservation in a
 highly anthropogenic region: Europe's worst case scenario revisited. Biol. Conserv. 274.
 https://doi.org/10.1016/j.biocon.2022.109732
- Maes, D., Van Dyck, H., 2005. Habitat quality and biodiversity indicator performances of a threatened butterfly versus a
 multispecies group for wet heathlands in Belgium. Biol. Conserv. 123, 177–187.
 https://doi.org/10.1016/j.biocon.2004.11.005
- Mantilla-Contreras, J., Schirmel, J., Zerbe, S., 2012. Influence of soil and microclimate on species composition and grass
 encroachment in heath succession. J. Plant Ecol. 5, 249–259. https://doi.org/10.1093/jpe/rtr031
- Milanesi, P., Herrando, S., Pla, M., Villero, D., Keller, V., 2017. Towards continental bird distribution models: environmental
 variables for the second European breeding bird atlas and identification of priorities for further surveys.
 Vogelwelt 60, 53–60.

- Moore, I.D., Gessler, P.E., Nielsen, G., Peterson, G.A., 1993. Soil Attribute Prediction Using Terrain Analysis. Soil Sci. Soc.
 Am. J. 57, 443–452. https://doi.org/10.2136/sssaj1993.572npb
- Moquet, L., Laurent, E., Bacchetta, R., Jacquemart, A.L., 2018. Conservation of hoverflies (Diptera, Syrphidae) requires
 complementary resources at the landscape and local scales. Insect Conserv. Divers. 11, 72–87.
 https://doi.org/10.1111/icad.12245
- Moudrý, V., Cord, A.F., Gábor, L., Laurin, G. V., Barták, V., Gdulová, K., Malavasi, M., Rocchini, D., Stereńczak, K., Prošek, J.,
 Klápště, P., Wild, J., 2022. Vegetation structure derived from airborne laser scanning to assess species distribution
 and habitat suitability: The way forward. Divers. Distrib. 29, 39–50. https://doi.org/10.1111/ddi.13644
- Neilan, W.L., Barton, P.S., Mcalpine, C.A., Wood, J.T., Lindenmayer, D.B., 2019. Contrasting effects of mosaic structure on
 alpha and beta diversity of bird assemblages in a human-modified landscape. Ecography (Cop.). 42, 173–186.
 https://doi.org/10.1111/ecog.02981
- Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J., Choimes, A., Collen, B.,
 Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K.,
 Alhusseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Laginha, D., Correia, P.,
 Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L.,
 Weiher, E., White, H.J., Ewers, R.M., Mace, G.M., Scharlemann, J.P.W., Purvis, A., 2015. Global effects of land use
 on local terrestrial biodiversity. Nature 520, 45–50. https://doi.org/10.1038/nature14324
- Olivier, T., Schmucki, R., Fontaine, B., Villemey, A., Archaux, F., 2016. Butterfly assemblages in residential gardens are
 driven by species' habitat preference and mobility. Landsc. Ecol. 31, 865–876. https://doi.org/10.1007/s10980 015-0299-9
- Olmeda, C., Šefferová, V., Underwood, E., Millan, L., Gil, T., Naumann, S., 2020. Action plan to maintain and restore to
 favourable conservation status the habitat type 4030 European dry heaths. European Commission, Brussel.
- Paelinckx, D., Sannen, K., Goethals, V., Louette, G., Rutten, J., Hoffmann, M., 2009. Methode voor het opstellen van
 gewestelijke doelstellingen voor de habitats van de Europese Habitatrichtlijn. In: Paelinckx D., et al. (red.),
 Gewestelijke doelstellingen voor de habitats en soorten van de Europese Habitat- en Vogelrichtlijn voor
 Vlaanderen. Mededelingen van het Instituut voor Natuur- en Bosonderzoek INBO.M.2009.6, Brussel, 16-45.
- Pfeifer, M., Lefebvre, V., Peres, C.A., Banks-Leite, C., Wearn, O.R., Marsh, C.J., Butchart, S.H.M., Arroyo-Rodríguez, V.,
 Barlow, J., Cerezo, A., Cisneros, L., D'Cruze, N., Faria, D., Hadley, A., Harris, S.M., Klingbeil, B.T., Kormann, U.,
 Lens, L., Medina-Rangel, G.F., Morante-Filho, J.C., Olivier, P., Peters, S.L., Pidgeon, A., Ribeiro, D.B., Scherber, C.,
 Schneider-Maunoury, L., Struebig, M., Urbina-Cardona, N., Watling, J.I., Willig, M.R., Wood, E.M., Ewers, R.M.,
 2017. Creation of forest edges has a global impact on forest vertebrates. Nature 551, 187–191.
 https://doi.org/10.1038/nature24457
- Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., Ferrier, S., 2009. Sample selection bias and
 presence-only distribution models: implications for background and pseudo-absence data. Ecol. Appl. 19, 181–
 197. https://doi.org/10.1890/07-2153.1

- Piessens, K., Honnay, O., Devlaeminck, R., Hermy, M., 2006. Biotic and abiotic edge effects in highly fragmented heathlands
 adjacent to cropland and forest. Agric. Ecosyst. Environ. 114, 335–342.
 https://doi.org/10.1016/j.agee.2005.11.016
- Piessens, K., Honnay, O., Hermy, M., 2005. The role of fragment area and isolation in the conservation of heathland
 species. Biol. Conserv. 122, 61–69. https://doi.org/10.1016/j.biocon.2004.05.023
- Price, P.W., Bouton, C.E., Gross, P., McPheron, B.A., Thompson, J.N., Weis, A.E., 1980. Interactions Among Three Throphic
 Levels: Influence of Plants on Interactions Between Insect Herbivores and Natural Enemies. Annu. Rev. Ecol. Syst.
 11, 41–65. https://doi.org/10.1146/annurev.es.11.110180.000353
- 769 R Core Team, 2022. R: A language and environment for statistical computing.
- Randin, C.F., Ashcroft, M.B., Bolliger, J., Cavender-Bares, J., Coops, N.C., Dullinger, S., Dirnböck, T., Eckert, S., Ellis, E.,
 Fernández, N., Giuliani, G., Guisan, A., Jetz, W., Joost, S., Karger, D., Lembrechts, J., Lenoir, J., Luoto, M., Morin, X.,
 Price, B., Rocchini, D., Schaepman, M., Schmid, B., Verburg, P., Wilson, A., Woodcock, P., Yoccoz, N., Payne, D.,
 2020. Monitoring biodiversity in the Anthropocene using remote sensing in species distribution models. Remote
 Sens. Environ. 239, 111626. https://doi.org/10.1016/j.rse.2019.111626
- Renner, I.W., Elith, J., Baddeley, A., Fithian, W., Hastie, T., Phillips, S.J., Popovic, G., Warton, D.I., 2015. Point process
 models for presence-only analysis. Methods Ecol. Evol. 6, 366–379. https://doi.org/10.1111/2041-210X.12352
- Rutten, A., Casaer, J., Swinnen, K.R.R., Herremans, M., Leirs, H., 2019. Future distribution of wild boar in a highly
 anthropogenic landscape: Models combining hunting bag and citizen science data. Ecol. Modell. 411, 108804.
 https://doi.org/10.1016/j.ecolmodel.2019.108804
- Schellenberg, J., Bergmeier, E., 2020. Heathland plant species composition and vegetation structures reflect soil-related
 paths of development and site history. Appl. Veg. Sci. 23, 386–405. https://doi.org/10.1111/avsc.12489
- Schirmel, J., Fartmann, T., 2014. Coastal heathland succession influences butterfly community composition and threatens
 endangered butterfly species. J. Insect Conserv. 18, 111–120. https://doi.org/10.1007/s10841-014-9619-7
- Schirmel, J., Mantilla-Contreras, J., Blindow, I., Fartmann, T., 2011. Impacts of succession and grass encroachment on
 heathland Orthoptera. J. Insect Conserv. 15, 633–642. https://doi.org/10.1007/s10841-010-9362-7
- Seavy, N.E., Viers, J.H., Wood, J.K., 2009. Riparian Bird Response to Vegetation Structure: A Multiscale Analysis Using LiDAR
 Measurements of Canopy Height. Ecol. Appl. 19, 1848–1857.
- Sillero, N., Gonçalves-Seco, L., 2014. Spatial structure analysis of a reptile community with airborne LiDAR data. Int. J.
 Geogr. Inf. Sci. 28, 1709–1722. https://doi.org/10.1080/13658816.2014.902062
- Stein, A., Gerstner, K., Kreft, H., 2014. Environmental heterogeneity as a universal driver of species richness across taxa,
 biomes and spatial scales. Ecol. Lett. 17, 866–880. https://doi.org/10.1111/ele.12277
- Tamme, R., Hiiesalu, I., Laanisto, L., Szava-Kovats, R., Pärtel, M., 2010. Environmental heterogeneity, species diversity and
 co-existence at different spatial scales. J. Veg. Sci. 21, 796–801. https://doi.org/10.1111/j.1654 1103.2010.01185.x

- Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M., Jeltsch, F., 2004. Animal species diversity
 driven by habitat heterogeneity/diversity: The importance of keystone structures. J. Biogeogr. 31, 79–92.
 https://doi.org/10.1046/j.0305-0270.2003.00994.x
- Valavi, R., Elith, J., Lahoz-Monfort, J.J., Guillera-Arroita, G., 2019. blockCV: An r package for generating spatially or
 environmentally separated folds for k-fold cross-validation of species distribution models. Methods Ecol. Evol. 10,
 225–232. https://doi.org/10.1111/2041-210X.13107
- van den Berg, L.J.L., Bullock, J.M., Clarke, R.T., Langston, R.H.W., Rose, R.J., 2001. Territory selection by the Dartford
 warbler (Sylvia undata) in Dorset, England: The role of vegetation type, habitat fragmentation and population
 size. Biol. Conserv. 101, 217–228. https://doi.org/10.1016/S0006-3207(01)00069-6
- Van Eupen, C., Maes, D., Herremans, M., Swinnen, K.R.R., Somers, B., Luca, S., 2022. Species profiles support
 recommendations for quality filtering of opportunistic citizen science data. Ecol. Modell. 467, 109910.
 https://doi.org/10.1016/j.ecolmodel.2022.109910
- van Swaay, C., Warren, M., Loïs, G., 2006. Biotope use and trends of European butterflies. J. Insect Conserv. 10, 189–209.
 https://doi.org/10.1007/s10841-006-6293-4
- Vanreusel, W., Maes, D., Van Dyck, H., 2007. Transferability of species distribution models: A functional habitat approach
 for two regionally threatened butterflies. Conserv. Biol. 21, 201–212. https://doi.org/10.1111/j.1523 1739.2006.00577.x
- Vogels, J.J., Verberk, W., Lamers, L., Siepel, H., 2017. Can changes in soil biochemistry and plant stoichiometry explain loss
 of animal diversity of heathlands? Biol. Conserv. 212, 432–447. https://doi.org/10.1016/j.biocon.2016.08.039
- Vogels, J.J., Verberk, W.C.E.P., Kuper, J.T., Weijters, M.J., Bobbink, R., Siepel, H., 2021. How to Restore Invertebrate
 Diversity of Degraded Heathlands? A Case Study on the Reproductive Performance of the Field Cricket Gryllus
 campestris (L.). Front. Ecol. Evol. 9, 1–12. https://doi.org/10.3389/fevo.2021.659363
- Warton, D.I., Renner, I.W., Ramp, D., 2013. Model-based control of observer bias for the analysis of presence-only data in
 ecology. PLoS One 8. https://doi.org/10.1371/journal.pone.0079168
- 819 Webb, N.R., 1998. The traditional management of European heathlands. J. Appl. Ecol. 35, 987–990.
 820 https://doi.org/10.1111/j.1365-2664.1998.tb00020.x
- Wehr, A., Lohr, U., 1999. Airborne laser scanning An introduction and overview. ISPRS J. Photogramm. Remote Sens. 54,
 68–82. https://doi.org/10.1016/S0924-2716(99)00011-8
- Willott, S.J., 1997. Thermoregulation in four species of British grasshoppers (Orthoptera: Acrididae). Funct. Ecol. 11, 705–
 713. https://doi.org/10.1046/j.1365-2435.1997.00135.x
- Wintle, B.A., Kujala, H., Whitehead, A., Cameron, A., Veloz, S., Kukkala, A., Moilanen, A., Gordon, A., Lentini, P.E.,
 Cadenhead, N.C.R., Bekessy, S.A., 2019. Global synthesis of conservation studies reveals the importance of small
 habitat patches for biodiversity. Proc. Natl. Acad. Sci. U. S. A. 116, 909–914.
- 828 https://doi.org/10.1073/pnas.1813051115
- Wood, E.M., Pidgeon, A.M., Radeloff, V.C., Keuler, N.S., 2012. Image texture as a remotely sensed measure of vegetation
 structure. Remote Sens. Environ. 121, 516–526. https://doi.org/10.1016/j.rse.2012.01.003

- Worboys, G.L., Francis, W.L., Lockwood, M., 2010. Connectivity conservation management: A global guide. Earthscan,
 London, United Kingdom. https://doi.org/10.4324/9781849774727
- Zellweger, F., De Frenne, P., Lenoir, J., Rocchini, D., Coomes, D., 2019. Advances in Microclimate Ecology Arising from
 Remote Sensing. Trends Ecol. Evol. 34, 327–341. https://doi.org/10.1016/j.tree.2018.12.012