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Protected habitats of Natura 2000 do not coincide with important diversity hotspots of arthropods in mountain grasslands

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Abstract. 1. Biodiversity assessments for conservation planning are often restricted to a limited set of species. This is also the case in the context of Natura 2000, where surveys focus strongly on vegetation and selected vertebrate species. Without cross-taxon congruence, however, this approach does not guarantee that the relevant aspects of biodiversity are appropriately represented.

2. We here assess the diversity of vascular plants, carabid beetles and spiders in mountain grasslands of the European Alps. We address the questions whether there are distinct species assemblages in different habitats and whether these assemblages show sufficient cross-taxon congruence. Furthermore, we test whether habitats that are protected based on vegetation characteristics also inhabit an arthropod fauna with highest conservation value.

3. We found only weak agreement in assemblage composition and no positive correlation in species richness across the three focal taxa. Furthermore, we found a negative correlation between species richness of plants and carabids, indicating opposing taxon-specific responses to habitat differences and land use intensity. Species richness was higher at protected sites for plants, but not for carabids and spiders. This applied also to the subset of species with highest conservation value.

4. Our results show that prioritisation of sites for conservation based solely on vegetational aspects does not necessarily coincide with important sites for arthropods. This calls for a multi-taxon approach in conservation planning to cover more of the endangered and range-restricted species. Species- and surrogate-based conservation efforts, like the Natura 2000 directive, should therefore be extended to embrace the diversity of arthropods.

Key words. Araneae, biodiversity conservation, Carabidae, cross-taxon congruence, European Alps, land use change, species conservation, subalpine pasture, taxon surrogacy, vascular plants.

Introduction

The world is facing a global loss of biodiversity that is also of societal concern calling for measures to prevent biodiversity loss (Butchart *et al*., 2010). As resources for nature conservation are limited, prioritisation is crucial to maximise conservation efficiency (Myers *et al*., 2000; Davies & Cadotte, 2011). Biodiversity assessments play a major role in conservation planning, to identify areas for conservation, to develop conservation strategies and to evaluate conservation actions (Gaston, 1996; Meine,

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2018). Such assessments are hampered by constraints of funds and time, spatial and temporal complexity, but sometimes also by lack of taxonomic expertise (Gaston, 1996; Sauberer *et al*., 2004; Gioria *et al*., 2011). Efforts can possibly be minimised by the use of taxonomic surrogates that represent a larger range of biodiversity (Gardner *et al*., 2008). Taxon surrogacy is based on the assumption of correlated species richness and concordance in assemblage composition across different taxonomic groups (Noss, 1990; Prendergast *et al*., 1993; Santi *et al*., 2010).

Since surrogates can potentially work as efficient biodiversity indicators, the use of surrogates in biodiversity assessments is hotly debated (e.g. Cabeza *et al*., 2007; Lewandowski *et al*., 2010; Barton *et al*., 2014; de Morais *et al*., 2018). One major criticism is that cross-taxon congruence is often low so that the required representation is not guaranteed (Favreau *et al*., 2006; de Morais *et al*., 2018). Hence, many authors promote multi-taxon approaches (Kotze & Samways, 1999; Finch & Löffler, 2010), while others aim to specify the conditions that justify the use of surrogates (Favreau *et al*., 2006; Westgate *et al*., 2014). The latter includes the question which specific taxa work best as general surrogates or as surrogates for specific other taxa. Vascular plants are often discussed as possible general surrogates, since the group is taxonomically rich and ecologically well described, including a number of specialist species (Prendergast *et al*., 1993; Sætersdal *et al*., 2004; Su *et al*., 2004). Furthermore, vascular plants are comparably easy to be identified in the field, they are persistent at least during the vegetation period, and as primary producers, they structure the habitat for consumers (Anand *et al*. 2005; Vera *et al*. 2011; Santi *et al*., 2010).How far plants can replace surveys of other taxa, in particular those that are more cryptic and taxonomically challenging, is not always clear, however (Santi *et al*., 2010).

Despite the criticism concerning the use of surrogates for conservation decisions, it is common practice to restrict biodiversity assessments to a few taxonomic groups or even a subset of indicator species (Vellend *et al*., 2008). This is also the case in the context of Natura 2000, one of the largest international networks in conservation and a central element in biodiversity conservation in the European Union (Orlikowska *et al*., 2016). The Annexes of the Nature 2000 Directive play a direct role in guiding conservation planning and decision making in the European context, as they list the protected species (Annexes 2 and 4) and the protected habitats (Annex 1), which form the basis for defining the 'Special Areas of Conservation' (Hochkirch *et al*., 2013). These Annexes list mostly rare, endemic or endangered species that themselves are of conservation concern, but they may be of limited value to general biodiversity conservation (see Cardoso, 2012; Rosso *et al*., 2018 for a discussion of limitations and critiques about current species selection).

Invertebrates are significantly underrepresented in Annexes 2 and 4 of the Natura 2000 Directive. Among the about thousand species listed, there are only 122 arthropods (including only 38 species of beetles and a single spider species, Cardoso, 2012), although insects and other invertebrates represent a major portion of total animal biodiversity. Arthropods are ecologically relevant as pollinators and pest control agents, and as primary and secondary consumers, they play a significant role in food webs (Klein *et al*., 2007; Schuldt & Assmann, 2010; Hallmann *et al*., 2017). This diversity is currently at a significant decline, which has recently been convincingly demonstrated for the abundance of flying insects in central Europe (Hallmann *et al*., 2017, 2018). The characterisation of habitats as listed in Annex 1 is mainly based on vegetation. Animals are rarely referred to in the characterisation of habitats, and most animals mentioned in the habitat descriptions are vertebrates in aquatic ecosystems (EC - European Commission DG Environment, 2013). Despite the focus on vascular plants and vertebrate species in the context of Natura 2000, it is not known whether these taxa may efficiently identify areas which are important for invertebrate species (Wolters *et al*., 2006; Lewandowski *et al*., 2010; Schuldt & Assmann, 2010; Westgate *et al*., 2014).

We here assess the diversity, assemblage composition and cross-taxon congruence of vascular plants, carabid beetles and spiders in mountain grasslands of the European Alps in southern Germany. The Alps represent a biodiversity hotspot in Europe and host a large number of endemic species (Tribsch, 2004; Rabitsch, 2009). The Alps have undergone substantial climatic and land use changes over the last decades. This has led to substantial changes in habitats, in particular a decline of grasslands with low land use intensity (Streifeneder & Ruffini, 2007; Marini *et al*., 2009). Alpine grasslands are particularly rich in endemic species, specifically among groups with low dispersal ability, such as many insects. Climate change and land use change may challenge their persistence. Our study was conducted within the frame of an applied conservation project that aimed to assess and evaluate different sites with regard to management in the future.

We used the survey of vascular plants, carabid beetles and spiders to assess cross-taxon patterns of biodiversity. Carabid beetles and spider represent two less often studied groups of arthropods that are not well represented in species- and surrogate-based conservation efforts such as the Natura 2000 directive. We address three specific questions. (i) Do the three groups show similar assemblage composition when compared across different habitats? (ii) Does local species richness correlate across the three groups, such that species richness in one group is predictive for species richness in other groups? We analyse this separately for total species richness and richness of species of conservation concern. (iii) Do protected habitats that were identified based on vegetation characteristics also inhabit the most valuable arthropod fauna? Answers to these questions have implications for the use of surrogates in conservation practice.

Materials and methods

Study area

We studied species diversity of vascular plants, carabid beetles and spiders of the mountain pasture 'Alpe Einödsberg' in the German part of the Alps (47.32°N; 10.28°E). The study area represents a part of the 'Allgäuer Hochalpen', a territory listed as Special Area of Conservation in the European conservation system Natura 2000. The study area ranged in altitude between 1400 and 2000 m above sea level and encompassed pastures with a total area of about 120 ha (Höfer *et al*., 2010). Most of the predominantly west-facing slopes consist of meadows dominated by matgrass (*Nardus stricta*). Woodland belts of Norway spruce (*Picea abies*) and krummholz formed by green alder (*Alnus viridis*) occur throughout the pasture zone. There is a ridge of 2 km length running north–south along the upper section of the pasture.

The pasture has been intensely grazed by sheep during most of the 20th century (up to 15 sheep per hectare). The grazing regime changed markedly in 2001, however. Most parts were from thereon grazed at low intensity by cattle, and in some places, grazing was completely abandoned. Grazing intensity was highly heterogeneous mainly for topographic reasons. The steep parts of the pasture were grazed at low intensity. Grazing intensity, especially at the time of sheep keeping, was highest on the ridge that was preferably used by resting livestock. Deposition of faeces has been especially high at those places, so that vegetation on the ridge differed clearly from the surrounding grasslands. For comparison, we also sampled four ungrazed ridges in other parts of the 'Allgäuer Hochalpen'. In total, we sampled 26 plots (Table S1) that were assigned to four habitat types: montane grassland (five plots), subalpine *Nardus* grassland (nine plots), grazed ridges within the study area (six plots) and ungrazed ridges outside the main study area (three plots). Three plots could not be assigned to any of those habitat types.

Plots were classified as protected/unprotected according to data on protected habitat types (in this case, habitat type 6150 Siliceous alpine and boreal grasslands with the corresponding vegetation) from the Natura 2000 Management Plan of this Special Area of Conservation, which is currently in preparation (RvS - Regierung von Schwaben, 2013). In a few cases, we deviated from the classification in the management plan, since resolution was rather coarse on the local scale. In these cases, we used a more detailed map of vegetation types to identify habitat type 6150 (Urban & Hanak, 2010).

Arthropod sampling

Arthropods were sampled using pitfall traps: plastic cups of 6 cm in diameter, filled with 5% acetic acid, 95% water and a drop of detergent to reduce surface tension, protected against damage by cattle and rain by a metal construction holding a transparent plastic cover (see Fig. 1a in Höfer *et al*., 2010). Traps were installed in two rows of three traps with a distance of 6 m from each other, resulting in a rectangular area of 6 × 12 m. Catches from all six pitfall traps at each plot were pooled in the analyses.

Pitfall traps were opened for 2 weeks in June (just after the first snowmelt at the ridge) and in early July. This sampling scheme was shown to be adequate for carabid beetles in these mountain habitats (Harry *et al*., 2011). All plots were sampled in the context of a conservation project between 2003 and 2008. The complete sampling scheme is described in Höfer *et al*. (2010). For our analysis, arthropod samples were taken from 2008 (16 plots), in 2007 (four plots), 2005 (three plots) and 2004 (three plots). Carabids were identified to species level using Müller-Motzfeld (2004) by I. Harry. Spiders were identified using Heimer and Nentwig (1991), Nentwig *et al*. (2003) and Roberts (1993) by T. Blick, H. Höfer, F. Meyer and C. Muster. Vouchers were deposited at the State Museum of Natural History Karlsruhe. Species nomenclature follows Löbl and Löbl (2015) and World Spider Catalog (2019).

Vegetation surveys

Vegetation survey data were taken from Urban and Hanak (2010) who surveyed the same 26 plots in 2008. All vascular plant species were identified in an area of 5 × 5 m that was centred in the middle of plots used for arthropod sampling. Each species' coverage estimated following the system of Braun-Blanquet (1964). Briefly, the Braun-Blanquet coverage estimates assign each plant species to one of seven cover classes (r = single plants, + = 2–5 plants with coverage < 1%, 1 = 6–50 plants with coverage < 5%, 2 = more than 50 plants and coverage < 5% or coverage 5–25%, 3 = coverage 26–50%, 4 = coverage 51–75%, 5 = coverage 76–100%).

Quantification of cross-taxon congruence

Cross-taxon congruence can be assessed as (i) assemblage concordance that is the covariance in assemblage structure across habitats or as (ii) the correlation in patterns of species richness and/or diversity (Pearson & Carroll, 1999; Gioria *et al*., 2011). Both approaches yield valuable insights. The first is more ecological, since it focuses on how distinct taxon-specific assemblages are in different habitats and how assemblages of different taxa agree in their habitat-specific distinctiveness. This is relevant for habitat classification. The second focuses on agreement in overall biodiversity patterns and is relevant in particular for conservation applications.

Statistical analyses

We used ordination by non-metric multidimensional scaling (NMDS) on each of the three taxonomic groups

for analysing assemblage composition. NMDS is a technique that does not assume multivariate normality and is largely robust to zero values (i.e. shared absences of species). Abundances of carabid beetles and spiders were log-transformed prior to the analysis to avoid that a few highly abundant species dominate the results. Braun-Blanquet plant cover estimates were converted to a scale from 1 to 7 (van der Maarel, 2007). We used the Bray–Curtis measure as dissimilarity index in NMDS, which is well suited for species abundance data because it ignores variables that have zeros for both objects (Dytham, 1999). NMDS was used to reduce complexity to three dimensions that gave acceptable stress values.

Similarity of species composition between the three taxonomic groups was investigated using Procrustes analyses of NMDS outputs (Gower, 1971). Procrustes analysis is a multivariate ordination technique that allows an estimation of the correlation among data matrices using a rotational-fit algorithm by centring, scaling, reflection, rotation and dilation (Jackson, 1995). This technique is considered to be more powerful in detecting congruence between two assemblage matrices than Mantel correlations and offers further options for data examination (Peres-Neto & Jackson, 2001; Gioria *et al*., 2011; Lisboa *et al*., 2014). We used the Procrustean fit parameter m^2 as a measure of matrix concordance. m^2 is the sum of squared residuals between matrices in their optimal superimposition (Gower, 1971). The statistical significance of m^2 for each pair of matrices was assessed using PROTEST (Jackson, 1995; Oksanen *et al*., 2018).

The second aspect of cross-taxon congruence is the comparison of species richness across different taxa and plots. We compared total species richness and species richness of a subset of 'important species', that is species registered either in the national or regional red list of endangered species and/or representing montane and subalpine grasslands specialists. This information was taken from Blick and Scheidler (2003), Lorenz (2003), GAC - Gesellschaft für Angewandte Carabidologie (2009), Schmidt *et al*. (2016) and BfN - Bundesamt für Naturschutz (2017), and the list of species classification is shown in Table S2. We estimated correlations of total and important species richness between taxa.

We also tested whether total or important species richness was higher at protected habitats than at non-protected habitats (see Table S1 for an assignment of plots). This comparison was implemented as taxon-specific independent-sample *t*-tests.

Statistical analyses were conducted using R 3.2.2 (R Core Team 2015), including the packages vegan (Oksanen *et al*., 2018) and MASS (Venables *et al*., 2002).

Results

We collected 4559 carabids (21–542 per plot) and 9941 spiders (53–1048 per plot). We observed 44 species of carabids (8–22 per plot) and 101 species of spiders (9–31 per plot). Vegetation surveys yielded 253 species of vascular plants (11–66 per plot, Table 1).

Ordination of plots

Stress of the NMDS varied between 9 and 10.5 per cent for the three groups. Despite some overlap in the first two dimensions, habitat types formed discrete clusters when assessed in three dimensions (Fig. 1). The lower montane sites were separated most clearly from higher sites in all three taxonomic groups. In plants and spiders, the grazed and ungrazed ridges were separated clearly along the first axis and the subalpine *Nardus* grasslands positioned in-between. In carabids, however, plots on grazed and ungrazed ridges formed closely positioned clusters, separated more strongly from the *Nardus* plots.

Procrustes analyses showed significant pairwise correlations of the ordinations across all three taxa (Table 2). Correlation of ordinations between plants and spiders was strongest ($m^2 = 0.64$; $r = 0.60$), followed by carabids/spiders ($m^2 = 0.66$; $r = 0.58$) and plants/carabids ($m^2 = 0.78$; $r = 0.47$).

Comparison of species richness

In most cases, there was no evidence for correlations among taxonomic groups in species richness (Table 3, Figure S1). The only statistically significant effect was a negative correlation between total species richness in carabids and plants ($r = -0.41$, $P = 0.038$), indicating species richness showed opposing trends in these two groups.

Species richness was higher at plots classified as protected habitats in plants (all species and important species), but not for carabids and spiders (Table 4). For carabids and spiders, we found no differences between plots in protected and unprotected habitats neither in total species richness nor in richness of important species. Linear models showed that the difference between taxa, tested as the interaction between taxon and habitat status, was statistically significant when comparing plants to both arthropods taxa (all species: $F_{2,72} = 9.31$, $P = 0.00025$, important species: $F_{2,72} = 7.55$, $P = 0.0011$), but not between carabids and spiders (all species: $F_{1,48} = 0.08$, $P = 0.78$, important species: $F_{1,48} = 0.35$, $P = 0.56$).

Discussion

We here report on cross-taxon congruence in assemblage composition and species richness across carabid beetles, spiders and vascular plants in mountain grasslands. High cross-taxon congruence is fundamental for taxon surrogacy and so of high relevance to conservation practice. We found overall similarity in species composition of the plots across the three taxa, but also significant differences, in particular a negative correlation between species

Table 1. Summary of species richness and abundance of plants, carabids and spiders at 26 sampling sites. For all three groups, mean, standard deviation (SD), and minimum (min) and maximum (max) of species richness are given.

	Sum individuals				Species richness			
	Mean	SD	Min	Max	Mean	SD	Min	Max
All plants	–	–	–	–	34.9	14.3	11	66
Important plants	–	–	–	–	12.2	7.0	5	31
All carabids	175	133	21	542	14.1	3.4	8	22
Important carabids	131	129	10	472	8.5	2.9	4	14
All spiders	382	255	53	1048	19.0	5.0	9	31
Important spiders	95	126	3	418	4.3	1.8	1	10

richness of plants and carabid beetles, a lack of association between species richness and site's prospective conservation status defined by habitat type (and thus largely by vegetation) and different clustering of habitat-specific assemblages between carabids and the other two taxa. Our results have implications for the use of surrogates in conservation planning in mountain grasslands.

Cross-taxon congruence of species composition

We found significant correlations in species composition between all three taxonomic groups, indicating that patterns of ordinations of the three groups show some similarities. Interestingly, the two functionally more similar groups of epigeic arthropods did not show the strongest correlation. A stronger correlation was found between plants and spiders. Previous studies in montane grasslands have found that carabids assemblages are more strongly influenced by soil parameters, while spiders are primarily influenced by vegetation structure (Luff & Rushton, 1989). Differences in soil properties and vegetation structure are pronounced in our study area, especially between sites on the ridge and on slopes. This dependency on different habitat features (soil, vegetation) might explain the differences between the two arthropod groups. Thus, functional similarity does not imply high cross-taxon congruence in species composition (see also Lovell *et al*., 2007).

Although we found significant correlations of species assemblages in all cases, strength of these correlations was overall weak. Heino (2010) suggests that concordance between multiple organism groups is weak if m^2-values > 0.5. Heino (2010) points out that significant congruence is likely to emerge in analyses where significance testing is based on randomisation tests, which may lead to highly significant results even if the strength of correlations is very low. Consequently, significant congruence is more often reported for species composition than for species richness (Gioria *et al*., 2011). Our results are similar to other studies in grassland ecosystems, where species composition did show no or just few strong correlations and often showed high variability among taxa (Niemela & Baur, 1998; Oertli *et al*., 2005; Lovell *et al*., 2007; compare also Westgate *et al*., 2014).

Cross-taxon congruence of species richness

We found no significant positive correlations in species richness across the three taxa, and correlation coefficients were generally low. This is in agreement with most other studies in grassland ecosystems, where no or at least no strong correlations were found (Niemela & Baur, 1998; Vessby *et al*., 2002; Su *et al*., 2004; Oertli *et al*., 2005; Marini *et al*., 2009; Koch *et al*., 2013). Strong correlations are required when some taxonomic groups are used as surrogates in conservation planning, as only strong correlations lead to mutual informativeness across taxonomic groups, however. Threshold values of $r = 0.7$ (Heino, 2010) or $r = 0.75$ (Lovell *et al*., 2007) have been proposed. Such strong correlations were rarely observed in grassland ecosystems. Sauberer *et al*. (2004) observed strong correlations among several groups, including between spiders and carabids, but not between plants/spiders or plants/carabids. Finch and Löffler (2010) found strong correlations between plants and spiders, but not between carabids/spiders or plants/carabids. Our results add to the heterogeneity in findings, since we found even a negative correlation between plants and carabids. In our case, this negative correlation seems to be driven by low plant species richness at the heavily grazed ridge that coincides with high diversity of carabid species. The ridge carabid fauna comprised many alpine specialists that are usually found at the margins of snowfields and snow pockets at higher altitudes (Holdhaus, 1954; Franz, 1970; Brandmayr *et al*., 2005; Paill & Kahlen, 2009).

Moreover, comparing our results with those from other grassland ecosystems (Vessby *et al*., 2002; Sauberer *et al*., 2004; Finch & Löffler, 2010), we found no consistent pattern for species richness correlation between the same taxa. Pairwise correlations were strong in some studies but absent or weak in others. These equivocal results call for caution in generalising results from individual studies. One difficulty of finding predictive patterns of congruence between different taxa is the spatial scale at which relationships have been investigated (Pearson & Carroll, 1999; Hess *et al*., 2006; Paavola *et al*., 2006; Gioria *et al*., 2011; Schuldt *et al*., 2015). Our study was conducted at a local scale, where correlations are often weaker than at larger scales (Paavola *et al*., 2006; Schuldt & Assmann, 2010;

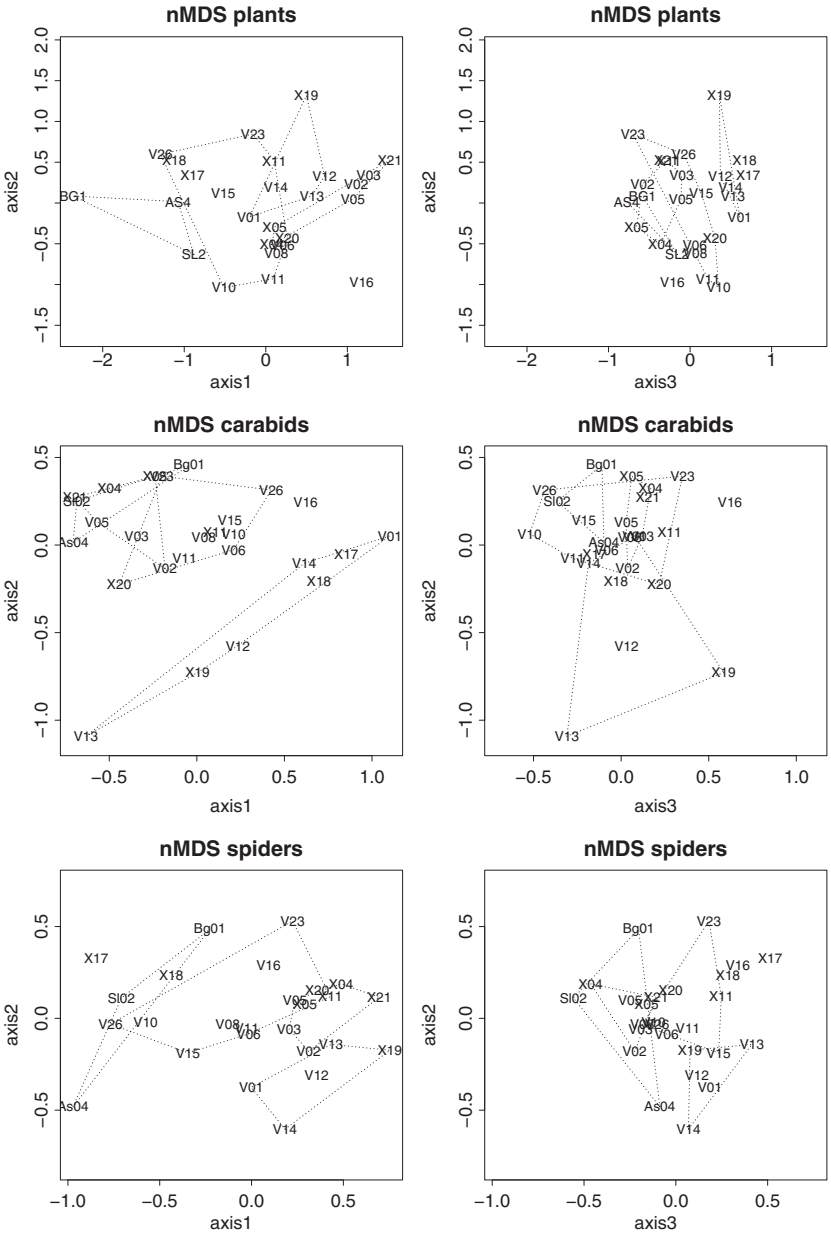

Fig. 1. Results of a three-dimensional NMDS for the three groups: plants, carabids and spiders. The four habitat types (lower montane grasslands, upper montane *Nardus* grasslands, ridges with high grazing intensity, ungrazed ridges) are outlined.

Gioria *et al*., 2011). For many aspects of habitat management, it is the local scale that is most important, and therefore, the scale at which congruence analyses would be of high practical relevance, however.

Comparison of protected and unprotected plots

The designation of protected habitats of the Natura 2000 Special Area of Conservation is mainly based on vegetation characteristics. Not surprisingly, the selection seems appropriate for plants in protecting sites with high species richness and many habitat specialists. The effect does not generalise to carabids and spiders, however. Some of the plots with highest species richness and richness of important species in these taxa were outside protected habitats, especially on the ridge that held no specialised vegetation, but valuable communities of arthropods.

Implications for conservation

Our study shows that an identification of priority sites for conservation basing solely on vegetational aspects will

Table 2. Results of Procrustes analysis of correlations in species composition for every pair of groups tested.

Groups	m^2	Cor (r)	P
Plants spiders	0.64	0.60	0.001
Carabids spiders	0.66	0.58	0.001
Plants carabids	0.78	0.47	0.004

Table 3. Results of species richness correlations. We tested the full data set (all species) as well as a selection of species with high relevance in conservation (important species). Total species richness as well as richness of important species in carabids showed no statistical evidence of deviation from normality (Shapiro–Wilk normality test: all $P > 0.11$), while richness of important species in spiders ($P = 0.002$) and plants ($P = 0.036$) did deviate from normality statistically (see Figure S1).

		Pearson correlation		Spearman correlation	
	Groups	r	p	γ	p
All species	Plants/carabids	−0.41	0.038	−0.43	0.030
	Plants/spiders	0.19	0.359	0.16	0.45
	Carabids/spiders	0.14	0.5	0.11	0.61
Important species	Plants/carabids	−0.1	0.614	−0.20	0.33
	Plants/spiders	0.24	0.246	0.12	0.57
	Carabids/spiders	0.27	0.19	0.22	0.28

Table 4. Results of t-tests for differences in species richness between sites hosting habitat types that are to be protected and sites without such habitats. Data are given for the full data set (all species) as well as a selection of species with high relevance in conservation (important species) of all three taxa.

	Not protected ($n = 10$)	Protected ($n = 16$)	T	df	p
All plants	25	41.1	3.36	20.8	0.003
Important plants	9.6	19.3	3.48	21.6	0.002
All carabids	14.7	13.7	−0.73	18.8	0.48
Important carabids	8.8	8.3	−0.43	14.9	0.67
All spiders	19.2	18.9	−0.15	15.6	0.88
Important spiders	4.1	4.4	0.43	22.4	0.67

not necessarily comprise the important sites for the arthropods. We show that there is no sufficient cross-taxon congruence between the three studied taxa at our study area. Moreover, we found significant negative effects between plant species richness and carabid species richness. Our results suggest that vascular plants are apparently no appropriate surrogates for spiders and carabids – two dominant and species-rich taxa – in mountain grassland ecosystems. We support the notion of other authors who suggest that a range of taxonomic groups has to be used for prioritising locations or actions for conservation (Grand *et al*., 2004; Wolters *et al*., 2006; Westgate *et al*., 2014; Zulka *et al*., 2014; de Morais *et al*., 2018). In case of topographic diverse mountain ecosystem that often exhibits a diverse and specialised fauna with many endemic species, we think an approach covering different taxonomic groups is indispensable for conservation planning (Finch & Löffler, 2010; Viterbi *et al*., 2013).

We are aware that time and money are limited for biodiversity assessments relevant to conservation. A practical solution would be to supplement large-scale vegetational mapping (following Annex 1 of the Natura 2000 Directive) with local sampling at selected plots of all different habitats with an expanded set of taxa. In the Alps, the efforts can be focused on taxa with a large number of endemic species, since these are often of greatest conservation concern. Here, we see the groups of arthropods that we studied as one valuable complement to vascular plants, which is practicable especially as a reduced sampling design gives representative results (Harry *et al*., 2011). A taxonomically broader approach could give us better local knowledge about biodiversity and identification of specific sites that are of particular relevance for the conservation of often neglected taxa.

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Conflict of interest

The authors declare that there is no conflict of interest.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Overview of sampling sites. Habitat type were classified in 4 types, three grassland sites comprising different habitat types were not classified.

Table S2. List of species recorded at any of 25 sampling sites.

Figure S1. Pairwise scatterplots of species richness across plots for the three taxa.

References

Anand, M., Laurence, S. & Rayfield, B. (2005) Diversity Relationships among Taxonomic Groups in Recovering and Restored Forests. *Conservation Biology*, **19**, 955–962.

Barton, P.S., Westgate, M.J., Lane, P.W., MacGregor, C. & Lindenmayer, D.B. (2014) Robustness of habitat-based surrogates of animal diversity: a multitaxa comparison over time. *Journal of Applied Ecology*, **51**, 1434–1443.

BfN - Bundesamt für Naturschutz (2017) FloraWeb: Daten und Informationen zu Wildpflanzen und zur Vegetation Deutschlands. <http://floraweb.de/> 2nd May 2018.

Blick, T. & Scheidler, M. (2003) Rote Liste gefährdeter Spinnen (Arachnida: Araneae) Bayerns. *Schriftenreihe Bayerisches Landesamt für Umweltschutz*, **166**, 308–321.

Brandmayr, P., Pizzolotto, R. & Zetto, T. (2005) *I Coleotteri Carabidi per la Valutazione Ambientale e la Conservazione della Biodiversità: Manuale Operativo*. APAT, Roma, Italy.

Braun-Blanquet, J. (1964) *Pflanzensoziologie: Grundzüge der Vegetationskunde*. Springer, Wien, Austria.

Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W., Almond, R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K.E., Carr, G.M., Chanson, J., Chenery, A.M., Csirke, J., Davidson, N.C., Dentener, F., Foster, M., Galli, A., Galloway, J.N., Genovesi, P., Gregory, R.D., Hockings, M., Kapos, V., Lamarque, J.-F., Leverington, F., Loh, J., McGeoch, M.A., McRae, L., Minasyan, A., Morcillo, M.H., Oldfield, T.E.E., Pauly, D., Quader, S., Revenga, C., Sauer, J.R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S.N., Symes, A., Tierney, M., Tyrrell, T.D., Vie, J.-C. & Watson, R. (2010) Global biodiversity: indicators of recent declines. *Science*, **328**, 1164–1168.

Cabeza, M., Arponen, A. & Van Teeffelen, A. (2007) FORUM: Top predators: hot or not? A call for systematic assessment of biodiversity surrogates: assessing biodiversity surrogates. *Journal of Applied Ecology*, **45**, 976–980.

Cardoso, P. (2012) Habitats Directive species lists: urgent need of revision: habitats Directive species lists. *Insect Conservation and Diversity*, **5**, 169–174.

Davies, T.J. & Cadotte, M.W. (2011) Quantifying biodiversity: does it matter what we measure? *Biodiversity Hotspots: Distribution and Protection of Conservation Priority Areas* (ed. by F.E. Zachos and J.C. Habel), pp. 43–60. Springer, Heidelberg, Germany.

Dytham, C. (1999) *Choosing and Using Statistics. A Biologist's Guide*. Blackwell Science, Oxford, UK.

EC - European Commission DG Environment (2013) *Interpretation Manual of European Union Habitats - EUR28*. European Commission, DG Environment, Brussels, Belgium.

Favreau, J.M., Drew, C.A., Hess, G.R., Rubino, M.J., Koch, F.H. & Eschelbach, K.A. (2006) Recommendations for assessing the effectiveness of surrogate species approaches. *Biodiversity and Conservation*, **15**, 3949–3969.

Finch, O.-D. & Löffler, J. (2010) Indicators of species richness at the local scale in an alpine region: a comparative approach between plant and invertebrate taxa. *Biodiversity and Conservation*, **19**, 1341–1352.

Franz, H. (1970) *Ökologie der Hochgebirge*. Ulmer, Stuttgart, Germany.

GAC - Gesellschaft für Angewandte Carabidologie (2009) Lebensraumpräferenzen der Laufkäfer Deutschlands. Wissensbasierter Katalog. Angewandte Carabidologie, Supplement V, 1–48.

Gardner, T.A., Barlow, J., Araujo, I.S., Ávila-Pires, T.C., Bonaldo, A.B., Costa, J.E., Esposito, M.C., Ferreira, L.V., Hawes, J., Hernandez, M.I.M., Hoogmoed, M.S., Leite, R.N., Lo-Man-Hung, N.F., Malcolm, J.R., Martins, M.B., Mestre, L.A.M., Miranda-Santos, R., Overal, W.L., Parry, L., Peters, S.L., Ribeiro-Junior, M.A., Da Silva, M.N.F., Da Silva Motta, C. & Peres, C.A. (2008) The cost-effectiveness of biodiversity surveys in tropical forests: cost-effectiveness of biodiversity surveys. *Ecology Letters*, **11**, 139–150.

Gaston, K.J. (1996) *Biodiversity: A Biology of Numbers and Difference*. Blackwell Science, Oxford, UK.

Gioria, M., Bacaro, G. & Feehan, J. (2011) Evaluating and interpreting cross-taxon congruence: potential pitfalls and solutions. *Acta Oecologica*, **37**, 187–194.

Gower, J. (1971) Statistical methods of comparing different multivariate analyses of the same data. *Mathematics in the Archaeological and Historical Sciences* (ed. by F.R. Hodson, D.G. Kendall and P. Tautu), pp. 138–149. Edinburgh University Press, Edinburgh, UK.

Grand, J., Buonaccorsi, J., Cushman, S.A., Griffin, C.R. & Neel, M.C. (2004) A multiscale landscape approach to predicting bird and moth rarity hotspots in a threatened pitch pine-scrub oak community. *Conservation Biology*, **18**, 1063–1077.

Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D. & de Kroon, H. (2017) More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS ONE*, **12**, e0185809.

Hallmann, C.A., Zeegers, T., van Klink, R., Vermeulen, R., van Wielink, P., Spijkers, H. & Jongejans, E. (2018) *Analysis of Insect Monitoring Data from De Kaaistoep and Drenthe*. Natuurmonumenten, Nijmegen, the Netherlands.

Harry, I., Drees, C., Höfer, H. & Assmann, T. (2011) When to sample in an inaccessible landscape: a case study with carabids from the Allgäu (northern Alps) (Coleoptera, Carabidae). *ZooKeys*, **100**, 255–271.

Heimer, S. & Nentwig, W. (1991) *Spinnen Mitteleuropas*. Verlag Paul Parey, Berlin und Hamburg, Germany.

Heino, J. (2010) Are indicator groups and cross-taxon congruence useful for predicting biodiversity in aquatic ecosystems? *Ecological Indicators*, **10**, 112–117.

Hess, G.R., Bartel, R.A., Leidner, A.K., Rosenfeld, K.M., Rubino, M.J., Snider, S.B. & Ricketts, T.H. (2006) Effectiveness of biodiversity indicators varies with extent, grain, and region. *Biological Conservation*, **132**, 448–457.

Hochkirch, A., Schmitt, T., Beninde, J., Hiery, M., Kinitz, T., Kirschey, J., Matenaar, D., Rohde, K., Stoefen, A., Wagner, N., Zink, A., Lötters, S., Veith, M. & Proelss, A. (2013) Europe needs a new vision for a Natura 2020 Network: Europe needs an improved reserve network. *Conservation Letters*, **6**, 462–467.

Höfer, H., Harry, I., Hanak, A. & Urban, R. (2010) Biodiversität in der Kulturlandschaft. Das Projekt Einödsberg - Begleituntersuchungen zur geänderten Weidenutzung auf einer Allgäuer Alpe. *Andrias*, **18**, 9–28.

Holdhaus, K. (1954) *Die Spuren der Eiszeit in der Tierwelt Europas*. Universitätsverlag Wagner, Innsbruck, Austria.

Jackson, D.A. (1995) PROTEST: a PROcrustean Randomization TEST of community environment concordance. *Ecoscience*, **2**, 297–303.

Klein, A.-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. & Tscharntke, T. (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 303–313.

Koch, B., Edwards, P.J., Blanckenhorn, W.U., Buholzer, S., Walter, T., Wüest, R.O. & Hofer, G. (2013) Vascular plants as surrogates of butterfly and grasshopper diversity on two Swiss subalpine summer pastures. *Biodiversity and Conservation*, **22**, 1451–1465.

Kotze, D.J. & Samways, M.J. (1999) Support for the multi-taxa approach in biodiversity assessment, as shown by epigaeic invertebrates in an afromontane forest archipelago. *Journal of Insect Conservation*, **3**, 125–143.

Lewandowski, A.S., Noss, R.F. & Parsons, D.R. (2010) The effectiveness of surrogate taxa for the representation of biodiversity. *Conservation Biology*, **24**, 1367–1377.

Lisboa, F.J.G., Peres-Neto, P.R., Chaer, G.M., Jesus, E. da C., Mitchell, R.J., Chapman, S.J. & Berbara, R.L.L. (2014) Much beyond Mantel: bringing Procrustes association metric to the plant and soil ecologist's toolbox. *PLoS ONE*, **9**, e101238.

Löbl, I. & Löbl, D. (eds.) (2015) *Archostemata-Myxophaga-Adephaga. Catalogue of Palearctic Coleoptera*, 2nd edn. Brill, Boston, MA.

Lorenz, W. (2003) Rote Liste gefährdeter Lauf- und Sandlaufkäfer (Coleoptera: Carabidae s. l.) Bayerns. *Rote Liste gefährdeter Tiere Bayerns* (ed. by Landesamt für Umweltschutz), pp. 102–111. Landesamt für Umweltschutz, Augsburg, Germany.

Lovell, S., Hamer, M., Slotow, R. & Herbert, D. (2007) Assessment of congruency across invertebrate taxa and taxonomic levels to identify potential surrogates. *Biological Conservation*, **139**, 113–125.

Luff, M.L. & Rushton, S.P. (1989) The ground beetle and spider fauna of managed and unimproved upland pasture. *Agriculture, Ecosystems & Environment*, **25**, 195–205.

van der Maarel, E. (2007) Transformation of cover-abundance values for appropriate numerical treatment – Alternatives to the proposals by Podani. *Journal of Vegetation Science*, **18**, 767–770.

Marini, L., Fontana, P., Klimek, S., Battisti, A. & Gaston, K.J. (2009) Impact of farm size and topography on plant and insect diversity of managed grasslands in the Alps. *Biological Conservation*, **142**, 394–403.

Meine, C. (2018) Biodiversity Conservation. *The Encyclopedia of the Anthropocene* (ed. by D.A. DellaSala and M.I. Goldstein), pp. 205–214. Elsevier, Oxford, UK.

de Morais, G.F., dos Santos Ribas, L.G., Ortega, J.C.G., Heino, J. & Bini, L.M. (2018) Biological surrogates: a word of caution. *Ecological Indicators*, **88**, 214–218.

Müller-Motzfeld, G. (2004) *Die Käfer Mitteleuropas. Band 2. Adephaga 1: Carabidae (Laufkäfer)*. Spektrum, Heidelberg, Berlin, Germany.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.

Nentwig, W., Hänggi, A., Kropf, C. & Blick, T. (2003). *Central European spiders. An internet identification key*. < http://www.araneae.unibe.ch > October 2008.

Niemela, J. & Baur, B. (1998) Threatened species in a vanishing habitat: plants and invertebrates in calcareous grasslands in the Swiss Jura mountains. *Biodiversity and Conservation*, **7**, 1407–1416.

Noss, R.F. (1990) Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology*, **4**, 355–364.

Oertli, S., Muller, A., Steiner, D., Breitenstein, A. & Dorn, S. (2005) Cross-taxon congruence of species diversity and community similarity among three insect taxa in a mosaic landscape. *Biological Conservation*, **126**, 195–205.

Oksanen, J., DKindt, R., Legendre, P., O'Hara, B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2018) *Vegan: Community Ecology Package*. Version 2.4-6.

Orlikowska, E.H., Roberge, J.-M., Blicharska, M. & Mikusiński, G. (2016) Gaps in ecological research on the world's largest internationally coordinated network of protected areas: a review of Natura 2000. *Biological Conservation*, **200**, 216–227.

Paavola, R., Muotka, T., Virtanen, R., Heino, J., Jackson, D. & Mäki-Petäys, A. (2006) Spatial scale affects community concordance among fishes, benthic macroinvertebrates, and bryophytes in streams. *Ecological Applications*, **16**, 368–379.

Paill, W. & Kahlen, M. (2009) Coleoptera (Käfer). *Endemiten. Kostbarkeiten in Österreichs Pflanzen- und Tierwelt* (ed. by W. Rabitsch and F. Essl), pp. 627–784. Naturwissenschaftlicher Verein für Kärnten, Klagenfurt, Austria.

Pearson, D.L. & Carroll, S.S. (1999) The influence of spatial scale on cross-taxon congruence patterns and prediction accuracy of species richness. *Journal of Biogeography*, **26**, 1079–1090.

Peres-Neto, P.R. & Jackson, D.A. (2001) How well do multivariate data sets match? The advantages of a Procrustean superimposition approach over the Mantel test. *Oecologia*, **129**, 169–178.

Prendergast, J.R., Quinn, R.M., Lawton, J.H., Eversham, B.C. & Gibbons, D.W. (1993) Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature*, **365**, 335–337.

R Core Team (2015) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rabitsch, W. (2009) *Endemiten. Kostbarkeiten in Österreichs Pflanzen- und Tierwelt*. Naturwissenschaftlicher Verein für Kärnten, Klagenfurt, Austria.

Roberts, M.J. (1993) *The spiders of Great Britain and Ireland*, Compact edn. Harley Books, Colchester, UK.

Rosso, A., Aragón, P., Acevedo, F., Doadrio, I., García-Barros, E., Lobo, J.M., Munguira, M.L., Monserrat, V.J., Palomo, J., Pleguezuelos, J.M., Romo, H., Triviño, V. & Sánchez-Fernández, D. (2018) Effectiveness of the Natura 2000 network in protecting Iberian endemic fauna. *Animal Conservation*, **21**, 262–271.

RvS - Regierung von Schwaben (2013) Managementplanung FFH-Gebiet 8528-301 Allgäuer Hochalpen. Karte 2.1: Bestand und Bewertung – Lebensraumtypen. Entwurfsfassung. Regierung von Schwaben, Augsburg.

Sætersdal, M., Gjerde, I., Blom, H.H., Ihlen, P.G., Myrseth, E.W., Pommeresche, R., Skartveit, J., Solhøy, T. & Aas, O. (2004) Vascular plants as a surrogate species group in complementary site selection for bryophytes, macrolichens, spiders, carabids, staphylinids, snails, and wood living polypore fungi in a northern forest. *Biological Conservation*, **115**, 21–31.

Santi, E., Maccherini, S., Rocchini, D., Bonini, I., Brunialti, G., Favilli, L., Perini, C., Pezzo, F., Piazzini, S., Rota, E., Salerni, E. & Chiarucci, A. (2010) Simple to sample: vascular plants as surrogate group in a nature reserve. *Journal for Nature Conservation*, **18**, 2–11.

Sauberer, N., Zulka, K.P., Abensperg-Traun, M., Berg, H.M., Bieringer, G., Milasowszky, N., Moser, D., Plutzar, C., Pollheimer, M., Storch, C., Trostl, R., Zechmeister, H. & Grabherr, G. (2004) Surrogate taxa for biodiversity in agricultural landscapes of eastern Austria. *Biological Conservation*, **117**, 181–190.

Schmidt, J., Trautner, J. & Müller-Motzfeld, G. (2016) Rote Liste und Gesamtartenliste der Laufkäfer (Coleoptera: Carabidae) Deutschlands. *Rote Liste gefährdeter Tiere, Pflanzen und Pilze Deutschlands. Band 4: Wirbellose Tiere (Teil 2)* (ed. by Bundesamt für Naturschutz), pp. 139–204. Landwirtschaftsverlag, Bonn, Germany.

Schuldt, A. & Assmann, T. (2010) Invertebrate diversity and national responsibility for species conservation across Europe – A multi-taxon approach. *Biological Conservation*, **143**, 2747–2756.

Schuldt, A., Wubet, T., Buscot, F., Staab, M., Assmann, T., Böhnke-Kammerlander, M., Both, S., Erfmeier, A., Klein, A.-M., Ma, K., Pietsch, K., Schultze, S., Wirth, C., Zhang, J., Zumstein, P. & Bruelheide, H. (2015) Multitrophic diversity in a biodiverse forest is highly nonlinear across spatial scales. *Nature Communications*, **6**, 10169.

Streifeneder, T. & Ruffini, F.V. (2007) Selected aspects of the agricultural structure change in the Alps - A comparison of harmonised agristructural indicators at municipality level within the Alpine Convention area. *Berichte über Landwirtschaft*, **85**, 406–440.

Su, J.C., Debinski, D.M., Jakubauskas, M.E. & Kindscher, K. (2004) Beyond species richness: community similarity as a measure of cross-taxon congruence for coarse-filter conservation. *Conservation Biology*, **18**, 167–173.

Tribsch, A. (2004) Areas of endemism of vascular plants in the Eastern Alps in relation to Pleistocene glaciation. *Journal of Biogeography*, **31**, 747–760.

Urban, R. & Hanak, A. (2010) Flora und Vegetation der Alpe Einödsberg im Naturschutzgebiet Allgäuer Hochalpen. *Andrias*, **18**, 29–52.

Vellend, M., Lilley, P.L. & Starzomski, B.M. (2008) Using subsets of species in biodiversity surveys. *Journal of Applied Ecology*, **45**, 161–169.

Venables, W.N., Ripley, B.D. & Venables, W.N. (2002) *Modern Applied Statistics with S*, 4th edn. Springer, New York, NY.

Vera, P., Sasa, M., Encabo, S.I., Barba, E., Belda, E.J. & Monrós, J.S. (2011) Land use and biodiversity congruences at local scale: applications to conservation strategies. *Biodiversity and Conservation*, **20**, 1287–1317.

Vessby, K., Soderstrom, B., Glimskar, A. & Svensson, B. (2002) Species-richness correlations of six different taxa in Swedish seminatural grasslands. *Conservation Biology*, **16**, 430–439.

Viterbi, R., Cerrato, C., Bassano, B., Bionda, R., von Hardenberg, A., Provenzale, A. & Bogliani, G. (2013) Patterns of biodiversity in the northwestern Italian Alps: a multi-taxa approach. *Community Ecology*, **14**, 18–30.

Westgate, M.J., Barton, P.S., Lane, P.W. & Lindenmayer, D.B. (2014) Global meta-analysis reveals low consistency of biodiversity congruence relationships. *Nature Communications*, **5**, 3899.

Wolters, V., Bengtsson, J. & Zaitsev, A.S. (2006) Relationship among the species richness of different taxa. *Ecology*, **87**, 1886–1895.

World Spider Catalog (2019). World Spider Catalog. <http://wsc.nmbe.ch> 15.2.2019.

Zulka, K.P., Abensperg-Traun, M., Milasowszky, N., Bieringer, G., Gereben-Krenn, B.-A., Holzinger, W., Hölzler, G., Rabitsch, W., Reischütz, A., Querner, P., Sauberer, N., Schmitzberger, I., Willner, W., Wrbka, T. & Zechmeister, H. (2014) Species richness in dry grassland patches of eastern Austria: a multi-taxon study on the role of local, landscape and habitat quality variables. *Agriculture, Ecosystems & Environment*, **182**, 25–36.

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