Improving insect conservation in Natura 2000 protected areas using species–habitat networks

Andree Cappellari [Corresp., 1] , **Lorenzo Marini** [1]

[1] Department of Agronomy, Food, Natural resources, Animals and Environment (DAFNAE), University of Padua, Legnaro, Padua, Italy

Corresponding Author: Andree Cappellari
Email address: andree.cappellari@unipd.it

Background. One of the biggest challenges in conservation is to manage multiple habitats for the effective conservation of multiple species, especially when the focal species are mobile and use multiple resources across heterogeneous small protected areas. The application of ecological network tools and the analysis of the resulting species–habitat networks can help to describe such complex spatial interactions and improve the conservation of species at the landscape scale.

Methods. To exemplify the application of species–habitat networks, we present a case study on butterflies inhabiting multiple grassland types across a Natura 2000 area. We sampled adult butterflies in 44 sites in North-East Italy. Each site belonged to one of the five major habitat types in the protected area, i.e. disturbed grassland, continuous grassland, evolved grassland, hay meadow and wet meadow. We first applied traditional diversity analyses and then focused on unipartite and bipartite species–habitat network analyses.

Aims. The aims of this study were: (i) to describe the emerging properties of the species–habitat network (i.e. the whole protected area), and (ii) to identify the key habitats and patches for butterfly conservation

Results. The species–habitat network appeared to have a weak modular structure, i.e. the main habitat types tended to host different species assemblages. However, the habitats also shared a large proportion of species that were able to visit multiple habitats and use resources across the whole study area. Even butterfly species typically considered as habitat specialists were actually observed across multiple habitat patches, suggesting that protecting them only within their focal habitat can be ineffective. Our species–habitat network approach helped identifying both central habitat patches that were able to support the highest number of species and habitat patches that supported rare specialist species, providing key implications for conservation.

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4 Andree Cappellari[1], Lorenzo Marini[1]

5

6 [1] Department of Agronomy, Food, Natural resources, Animals and Environment (DAFNAE),

7 University of Padua, Legnaro, Padua, Italy

8

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10 Email address: andree.cappellari@unipd.it

Abstract

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Introduction

Covering over 18% of the European Union land area, the Natura 2000 network is the largest coordinated system of protected areas in the world. Most of the Natura 2000 areas have relatively small size, with a mean area of 38 km2, and are often composed of a mosaics of small patches of different habitat types (https://ec.europa.eu/environment/nature/natura2000). The conservation of insect diversity across such heterogeneous landscapes may face various problems, in particular when the focal species are mobile and use multiple resources across different habitat patches (Kremen et al. 2007; Marini et al. 2019). For instance, when landscapes are composed of small patches with a large perimeter–to–area ratio, the local communities are heavily impacted by the surrounding landscape (Krauss et al. 2003). Most of the decisions on how to manage single habitats for conservation are usually based on the results of diversity analyses where patches, habitats or interventions are usually ranked according to the number of species and individuals they support (see for example Villemey et al. 2015; Ernst et al. 2017; Denning and Foster 2018). While this approach can help identifying ideal local habitat quality to maximize species diversity, it also overlooks the potential interactions between multiple habitat patches in supporting communities of mobile organisms (Harlio et al. 2019). There have been several

51 attempts to implement landscape-scale approaches to conservation encouraging bigger and larger
52 number of protected areas, enhancing connectivity, and improving habitat quality (Albert et al.
53 2017; Donaldson et al. 2017), but little emphasis has been placed to develop tools to optimize
54 conservation actions within heterogeneous protected areas.
55 Managing multiple habitats for the conservation of multiple species can be challenging.
56 Recently, it has been proposed to adapt network tools to describe such complex spatial
57 interactions (Marini et al. 2019) and to use the resulting species–habitat networks and their
58 metrics to improve conservation of species at the landscape scale (Nardi et al. 2019; Pompozzi et
59 al. 2019; Saunders and Rader 2019). First, topology metrics can inform on the architecture and
60 the emerging properties of the whole species–habitat network. On the one hand, in a protected
61 area with a nested structure species-rich patches host both common and rare species, while
62 species-poor patches are mainly visited by generalist species and so their loss is unlikely to have
63 ripple effects on the entire protected area (Table 1 a). On the other hand, in a protected area with
64 a strong modular structure some species interact more frequently with some habitat types
65 forming modules, so patches belonging to the same module are more tightly connected to each
66 other than to patches belonging to different habitat types (Table 1 b). In this scenario, different
67 modules need to considered as individual management blocks. Second, node-level metrics can
68 describe properties of single habitat patches within the network. For instance, patch centrality
69 can inform about the importance of single habitats and patches in supporting species across the
70 whole protected area. A patch with high centrality hosts many species that also occur in other
71 habitats, playing a fundamental role in supporting generalist species across the whole species–
72 habitat network (Table 1 c).
73 To exemplify the application of species–habitat networks to inform landscape management, we
74 present a case study on the conservation of butterflies across a heterogeneous Natura 2000 area.
75 We selected butterflies as model organisms as they are excellent indicators of habitat quality
76 (Thomas et al. 2004; WallisDeVries and Ens 2010). Moreover, butterfly species largely vary in
77 their life history traits (Dennis et al. 2003). The chosen protected area is composed of five major
78 habitat types intermixed across the area, i.e. three successional stages of dry calcareous
79 grasslands along a natural disturbance gradient, that are usually the focus of conservation plans,
80 and two managed grasslands, hay meadows and wet meadows, that can be seen as potential
81 surrogate habitats to support butterfly diversity. We first applied traditional diversity analyses
82 and then focused on unipartite and bipartite species–habitat network analyses. The aims of this
83 study were: (i) to describe the emerging properties of the species–habitat network at the scale of
84 the whole protected area, and (ii) to identify the key habitat patches for butterfly conservation
85 across the protected areas. The information derived will help to tailor management plan for the
86 protected area.
87
88 **Materials & Methods**
89 **Study area**

90   The study was carried out in the Friuli-Venezia Giulia region (North-East Italy), in the Special
91   Protection Area "Magredi di Pordenone" (SPA-IT 33110011) (46°04'12.5" N 12°45'46.5" E).
92   The size of the protected area is c. 101 km2 and includes four Natura 2000 areas: "Magredi di
93   Tauriano" (SIC-IT3310008), "Magredi del Cellina" (SIC-IT 3310009), "Torbiera di Sequals"
94   (SIC-IT 3310005) and "Risorgive del Vinchiaruzzo" (SIC-IT3310010). The bedrock consists of
95   coarse alluvial calcareous-dolomitic sediments. The area is protected by the Natura 2000
96   network for its high value ecosystems (LIFE10 NAT/IT/000243), and it is characterized by a
97   remarkable diversity of alluvial grassland habitats. We identified five main habitat types: three
98   successional stages of dry semi-natural grasslands on calcareous substrate along a disturbance
99   gradient, i.e. (i) recently disturbed grassland, with a low herbaceous cover (bare ground cover >
100 75%) and mainly composed by pioneer species, (ii) continuous grassland, with intermediate
101 natural disturbance, and a moderate herbaceous cover (10% < bare ground cover < 30%), and
102 (iii) evolved grassland, undisturbed for long time and with a continuous herbaceous cover (bare
103 ground cover < 10%) and presence of isolated shrubs; and two managed grasslands, i.e. (iv) hay
104 meadows, un-improved grassland mown twice a year and (v) wet meadow, mown once every 1-2
105 years (Table S1). The natural disturbance in dry calcareous grasslands is related to periodic
106 floods that destroy the vegetation and the organic layer of the soil, halting the shrub
107 encroachment. The continuous and evolved semi-natural dry grasslands are classified as Natura
108 2000 habitat 62A0 (Eastern sub-Mediterranean dry grasslands, Scorzoneretalia villosae).
109 **Sampling design and butterfly sampling**
110 We selected 44 sites, each belonging to one habitat type (Fig. S1). The number of sites for each
111 habitat type was proportional to their cover in the protected area. We therefore selected 10
112 patches for each successional grassland stage and 7 patches for both hay meadows and wet
113 meadows. Each site covered an area of 2500 m2 (50 x 50 m).
114 Adult butterflies (Papilionoidea) were surveyed five times between March and September 2010.
115 Sampling occurred between 09.00 and 17.00 in days with favorable weather conditions
116 (cloudiness < 25%, low or absent wind, air temperature > 18°C). Each site was sampled for 15
117 minutes for each round. Surveys were always carried out by the same two operators, LM and
118 Paolo Paolucci (University of Padua), which recorded all butterflies in the sampling area by
119 visual sighting. Individuals that could not be identified while in flight were caught, identified and
120 released at the end of the sampling. In each round, the order in which sites were sampled was
121 randomized to avoid bias related to the time of sampling. Butterfly nomenclature follows
122 Karsholt and Nieukerken (2011).
123 **Data analyses**
124 **Diversity analyses**
125 For each habitat patch, we calculated butterfly richness (total number of species) and evenness
126 (E_{var} index) and used linear models to evaluate the effect of the habitat type on diversity indices.
127 Both indices were calculated using the vegan package (Oksanen et al. 2019). All analyses were
128 performed using R version 3.6.1 (R Development Core Team 2019).
129 **Species–habitat network analyses: bipartite network**

130 We built a bipartite weighted network with patches and butterfly species as nodes, and calculated
131 both network- and node-level metrics providing complementary and non-redundant information.
132 At the network-level, we selected three metrics: modularity, weighted NODF, and connectance.
133 Modularity describes how interactions between butterflies and patches are partitioned into
134 separate modules, ranging between 0 (random network) and 1 (complete compartmentalized
135 network) (Newman 2006). Weighted NODF, the weighted Nestedness metric based on Overlap
136 and Decreasing Fill, is the property by which specialist species interact with a subset of the sites
137 that generalist species interact with, ranging between 0 (non-nested network) and 100 (perfectly
138 nested network) (Almeida-Neto and Ulrich 2011). We then checked for both metric significance
139 using z-scores, calculated using 1000 null models obtained with the Patefield algorithm
140 (Dormann and Strauss 2014). The two metrics provide fundamental information about network
141 architecture (Bascompte et al. 2003; Olesen et al. 2007; Bastolla et al. 2009; Thébault and
142 Fontaine 2010; Tylianakis et al. 2010; Carstensen et al. 2016; Grilli et al. 2016). Moreover, we
143 calculated connectance, a measure of network complexity, which specifies the realized
144 proportion of all possible links in a network, ranging between 0 (simple network) and 1 (complex
145 network) (Dunne et al. 2002). To compute network-level metrics, we used the bipartite package
146 (Dormann et al. 2008).
147 **Species–habitat network analyses: unipartite network**
148 Starting from the bipartite species–habitat network, we built a unipartite weighted network, with
149 patches as nodes and shared butterfly species as edges, i.e. links between nodes. For each patch,
150 we calculated weighted degree centrality, which specifies the role played by each patch within
151 the network, highlighting the focal ones. It is based on both the number of connections with other
152 patches and the average weight of these connections, adjusted by an α parameter (Opsahl et al.
153 2010). We set the α parameter to 0.5, so patches with a higher number of connections have a
154 stronger weighted degree centrality value (Rodríguez-Rodríguez et al. 2017). We then used
155 linear models to test the effect of habitat type on the centrality index.
156 Moreover, to further investigate the structure of butterfly communities, we applied community
157 detection techniques. Community detection analysis is similar to modularity analysis in a
158 bipartite network, but it is based on unipartite networks, so the result is a clusterization of
159 patches based on the butterfly species they share. Because of the small network size (44 sites x
160 74 butterfly species) and the high value of the mixing parameter μ calculated using the
161 multimodel algorithm (μ = 0.58), we selected two more algorithms for detecting communities,
162 the spinglass algorithm and the walktrap algorithm (Yang et al. 2016). We used the igraph
163 package (Csardi and Nepusz 2006) for building the unipartite weighted network and for
164 community detection analysis, while weighted degree centrality was calculated using the tnet
165 package (Opsahl 2015).
166
167 # Results
168 In the 44 sites, we sampled 6,273 butterflies belonging to 74 species and 5 families (Table S2).
169 The most abundant species were Coenonympha pamphilus (1022 individuals), Melanargia

170   galathea (711 individuals) and Coenonympha arcania (491 individuals), while the most frequent
171   ones were Pieris rapae (found in 32 sites), Coenonympha pamphilus (found in 31 sites) and
172   Polyommatus icarus (found in 28 sites) (Table S2). We sampled two species included in the
173   Habitats Directive annexes II and IV, Coenonympha oedippus (17 individuals in one site) and
174   Lycaena dispar (11 individuals in one site), one species that is categorized as vulnerable in the
175   Italian Red List for butterflies, Phengaris alcon (1 individual) (Bonelli et al. 2018) and one
176   species that is protected in the Friuli Venezia-Giulia region, Thecla betulae (2 individuals in one
177   site) (Valenti and Renzi 2016) (Table S2). In each site, we found an average of 143 individuals
178   (min = 2, max = 435) and an average of 17 butterfly species (min = 1, max = 32) (Table S3). The
179   poorest habitat in terms of both butterfly abundance and richness was the disturbed grassland,
180   with a total of 68 individuals belonging to 10 species. The richest one was the evolved grassland,
181   with a total of 2655 individuals belonging to 54 species (Table S3).

Whole network

183   The species–habitat network was complex, with highly connected habitat patches and butterfly
184   species (connectance = 0.28), even if its size was relatively small (44 habitat patches x 74
185   butterfly species) (Fig. 1). The network was significantly more modular than expected by chance
186   (modularity = 0.35, modularity z-score = 95), and clusters coarsely matched habitat types, at
187   least for the managed ones (Fig. S2). The modularity value, however, indicated a weak modular
188   structure. On the other hand, the network was less nested than expected from the null models
189   (weighted NODF = 25.04, weighted NODF z-score = -28.8). Community detection analysis
190   confirmed the weighted NODF and modularity results. Both the multilevel and spinglass
191   algorithms identified three communities (Figs. 2 a-b), while the walktrap algorithm identified
192   four communities (Fig. 2 c). In general, the results of the three community detection algorithms
193   converged and identified similar clusters. We can recognize three major communities: one for
194   disturbed dry calcareous grasslands, one for un-managed grasslands (continuous and evolved dry
195   calcareous grasslands) and one for managed grasslands (hay and wet meadows).

Habitat level

197   Species richness and evenness E_{var} and patch weighted degree centrality were strongly related to
198   habitat type (Figs. 3 a-c, Table 2). Disturbed grassland was the habitat with the lower species
199   richness and centrality values, and the higher evenness. The number of butterfly species and the
200   patch centrality values strongly increased along the grassland successional gradient, while
201   evenness exhibited an opposite pattern. All three indices were comparable for evolved grassland
202   and hay meadow, while only species evenness was similar for evolved grassland and continuous
203   grassland.

Patch level

205   Weighted degree centrality for patches was moderately high, with a mean value of 102.38 (min =
206   25, max = 150.39), because of the high number of connections between habitat patches. The
207   ranking of patches based on their centrality values showed that the most central patches did not
208   belong to a single habitat (Figs. 4 a-b). In fact, the ten most central patches belonged to all
209   habitat types except for disturbed grassland: four hay meadow patches, three evolved grassland

210   patches, two continuous grassland patches, and one wet meadow patch. All disturbed grassland
211   patches were peripherals. Species richness and evenness were strongly correlated to weighted
212   degree centrality (Pearson's correlation for patch centrality and species richness = 0.95, p-value
213   < 0.01; Pearson's correlation for patch centrality and species evenness = -0.87, p-value < 0.01),
214   so the most central patches hosted more species and their abundance distribution was more
215   uneven.
216

Discussion

218   Here, we proposed to adapt ecological network tools to describe complex spatial interactions
219   between species and habitats (Marini et al. 2019) and to use the resulting network metrics to
220   improve conservation of butterfly species across a heterogeneous protected area. Despite the
221   small size of the protected area, we found a remarkable diversity of butterflies, with 74 species,
222   more than 25% of the total butterfly richness of Italy (Bonelli et al. 2018). The species–habitat
223   network highlighted a general relaxed specialization of butterflies for habitats, indicating that
224   species were affected by the management of the whole protected areas, beyond the boundaries of
225   their preferred habitat type. The species–habitat network approach helped identifying both
226   central habitat patches that were able to support the highest number of species and also habitat
227   modules that supported rare specialist species.

Whole network

229   Network-level metrics can help to unveil the emergent properties of species–habitat networks.
230   Modularity in bipartite networks plays an important role in network function, often improving
231   community stability (Olesen et al. 2007; Tscharntke et al. 2007; Tylianakis et al. 2010; Grilli et
232   al. 2016). In species–habitat networks, modules are composed of groups of tightly interacting
233   species and patches. In our network, modularity was higher than expected by chance, and
234   modules coarsely matched major habitat types. However, modularity was generally weak,
235   indicating that several modules were still highly connected to each other. In particular, some
236   habitats – the continuous and evolved grasslands – were visited by many species, and those
237   species were mainly generalists. On the other hand, in our modularity analysis based on bipartite
238   networks, four out of seven patches of wet meadow created a single, strong module due to the
239   presence of specialist species such as Coenonympha oedippus and Lycaena dispar (Skórka et al.
240   2007). The removal of the wetland patches can therefore strongly affect the butterfly species
241   pool of the whole protected area, being harmful for the persistence of rare, specialist species.
242   Differences between habitat types were confirmed by the community detection analysis. All
243   detection algorithms yielded similar results and patches belonging to the same habitat almost
244   always clustered together. The first community was roughly composed of only disturbed
245   grassland patches, the second one was composed of calcareous dry habitat patches (continuous
246   and evolved grassland) and the third one was composed of managed habitat patches (hay and wet
247   meadows). It is therefore important to notice that community detection analysis, as all techniques
248   that rely on unipartite networks, is exclusively based on shared species, and does not take into
249   account the unshared ones, while modularity based on bipartite networks can identify key habitat

250   patches for specialist species. For conservation purposes, it is therefore fundamental to apply
251   both approaches to capture different facets of network organization. While modularity allowed to
252   identify groups of patches where specialists are concentrated, centrality helped to identify the
253   habitat patches that supported a larger number of generalists.

Habitat level

255   Species richness, evenness and patch centrality differed among habitats. Disturbed grasslands
256   had the lowest species richness and patch centrality, and the highest species evenness. The low
257   herbaceous cover, low diversity of plant species and low flower availability of disturbed
258   grasslands led to species-poor communities with even abundance distribution. The high evenness
259   in disturbed grasslands was probably driven by the immigration of mobile and generalist species
260   and by the low contribution to density from local recruitment (Marini et al. 2014). As the
261   evolution of grassland ecosystems proceeded, plant cover, plant richness and therefore butterfly
262   species richness and patch centrality increased, with a consequent decrease in species evenness.
263   Evolved grasslands were indeed the most central habitat, due to their considerable diversity of
264   plant species and complex vegetation structure including both herbaceous species and shrubs,
265   and hosted many species (WallisDeVries et al. 2002; Ernst et al. 2017). Hay meadows, despite
266   being impacted by mowing, hosted many species and were as central as evolved grasslands. The
267   positive impact of low-intensity management on plant and butterfly communities has already
268   been investigated (WallisDeVries and Raemakers 2001; Silva et al. 2019), and a mosaic of
269   managed and un-managed patches seems to be the best solution for maintaining biodiversity and
270   network robustness. In fact, managed meadows are located in sites where floods do not occur,
271   safeguarding habitat patches suitable for a large number of butterfly species. The central role of
272   managed meadows also suggests that this habitat can contribute to increase area of suitable
273   habitat for the large majority of butterfly species considered typical of dry calcareous grasslands.

Patch level

275   Planning of conservation actions in protected areas often requires information about the role of
276   single sites in supporting the focal biodiversity groups. The use of centrality measures to rank the
277   importance of single patches has been extensively studied (Estrada and Bodin 2008; Gilarranz et
278   al. 2015; Poodat et al. 2015; Pereira et al. 2017), as central nodes are known to promote stability
279   in habitat networks (Thompson et al. 2017). As explained above, evolved grasslands and hay
280   meadows turned out to be fundamental habitats for butterfly conservation, but the ranking of
281   individual patches based on weighted degree centrality also showed that central patches did not
282   exclusively belong to these habitats. Furthermore, even within the same habitat, not all patches
283   were equally relevant. This indicates that some patches can play an important role in the
284   protected area irrespective of the habitat type. The most peripheral nodes were represented by
285   both disturbed grassland and wet meadow patches, but while disturbed grasslands were always
286   characterized by species-poor communities, wet meadows were rich in specialist species that
287   were not shared with other habitats. As evolved grassland and hay meadow patches had a similar
288   role in supporting butterfly communities within the protected area, several managed meadow
289   patches can be seen as a surrogate habitat for dry semi-natural grasslands in supporting a large

290 number of shared species. Centrality analysis can therefore be a useful tool to highlight the focal
291 patches within a heterogeneous landscape and so to improve conservation planning.
292
293 Conclusions
294 Implications for conservation
295 Developing conservation plans for protected areas across heterogeneous landscapes can be
296 difficult. Here, we highlighted the importance of an integrative approach, combining traditional
297 diversity analysis and network analysis, for the identification of focal habitats and patches in a
298 protected area. The species–habitat network of the protected area appeared to have a weak
299 modular structure where the main habitat types tended to host different species assemblages.
300 However, the habitat modules also shared a large proportion of species that are able to move and
301 use resources across the whole protected area. Even butterfly species typically considered as
302 habitat specialists were actually observed across several habitats, suggesting that protecting them
303 only within their focal habitat can be ineffective. Calcareous dry grasslands are well-known key
304 habitats for butterfly conservation (Silva et al. 2019), but we also pointed out the central role of
305 agriculturally managed meadows across the protected area. Hay meadows, in particular, can act
306 as a surrogate habitat for evolved calcareous grasslands patches, hosting surprisingly similar
307 species assemblages. Although hay meadows are not currently considered priority habitats, more
308 attention should be placed on the maintenance of their extensive management. On the other hand,
309 wet meadows emerged as the only habitats characterized by a distinctive module of wetland
310 specialists. In conclusion, the protected area needs to be considered as a single dynamic unit to
311 plan conservation actions.
312
316

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Figure 1

The bipartite species–habitat network.

Colored nodes represent habitat patches, while black nodes represent butterfly species, with node size reflecting the number of links for each species. Grey links indicate species occurrence.
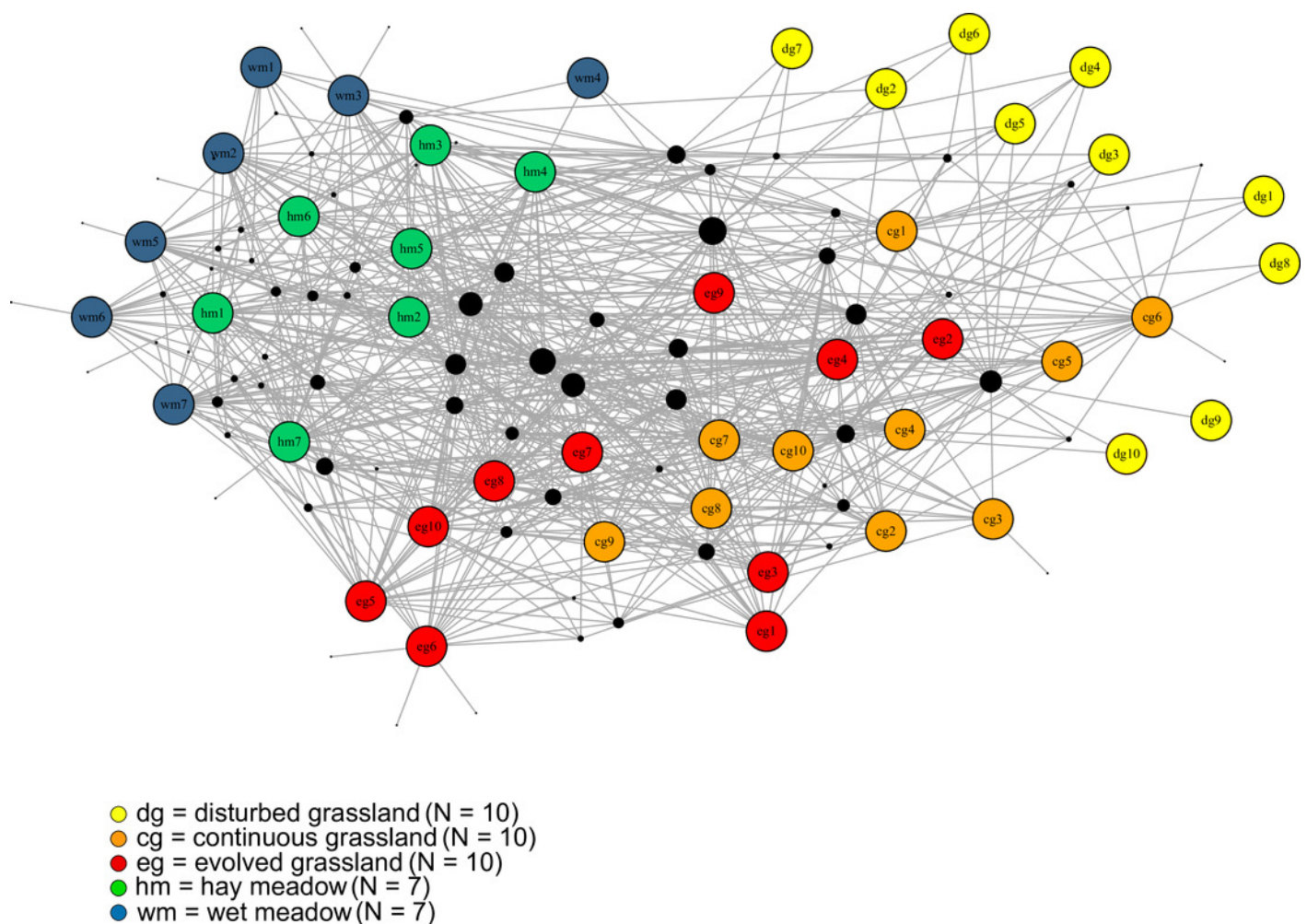

○ dg = disturbed grassland (N = 10)
○ cg = continuous grassland (N = 10)
● eg = evolved grassland (N = 10)
● hm = hay meadow (N = 7)
● wm = wet meadow (N = 7)

Figure 2

Community detection clusterization.

Community detection clusterization with (a) multimodel algorithm, (b) spinglass algorithm, and (c) walktrap algorithm. The different colours indicate the communities detected by the different algorithms based on the shared species, while the numbers represent the a priori habitat classification based on the vegetation physiognomy.
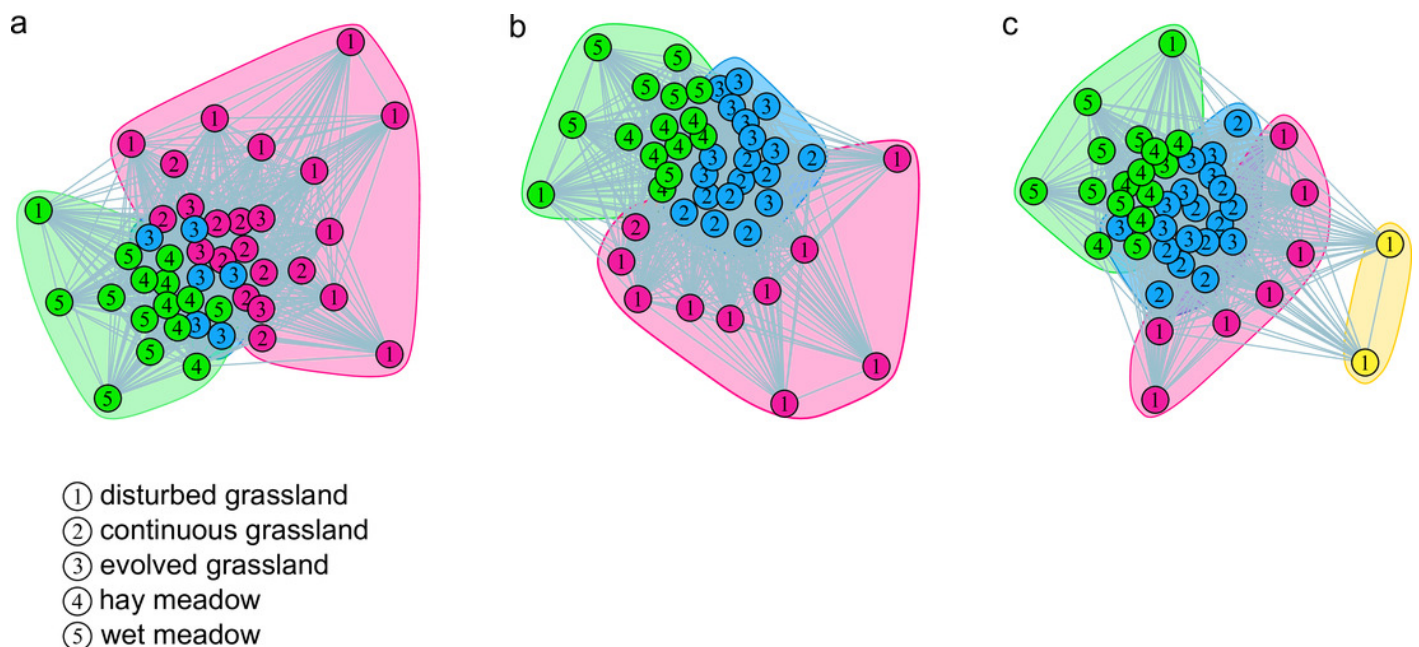

① disturbed grassland
② continuous grassland
③ evolved grassland
④ hay meadow
⑤ wet meadow

Figure 3

Boxplots showing the effect of habitat type on (a) species richness, (b) species evenness E_{var}, and (c) patch weighted degree centrality.
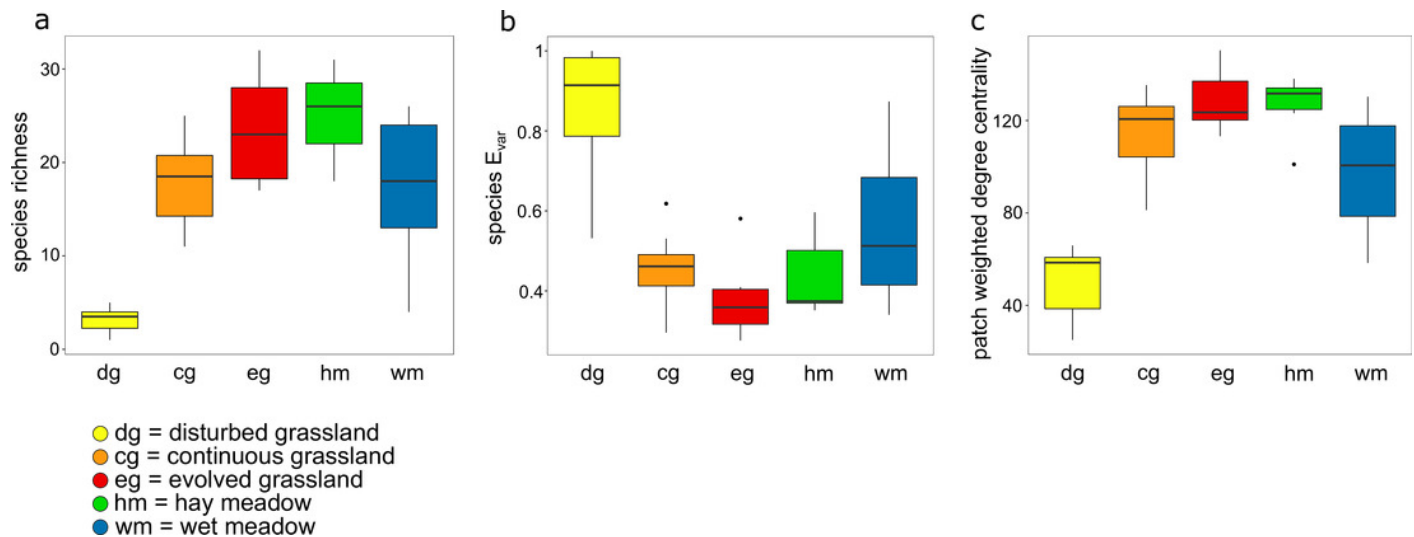
Figure 4

Weighted degree centrality.

(a) Patch ranking based on weighted degree centrality, and (b) map of the 44 sampling sites, with point size reflecting weighted degree centrality.
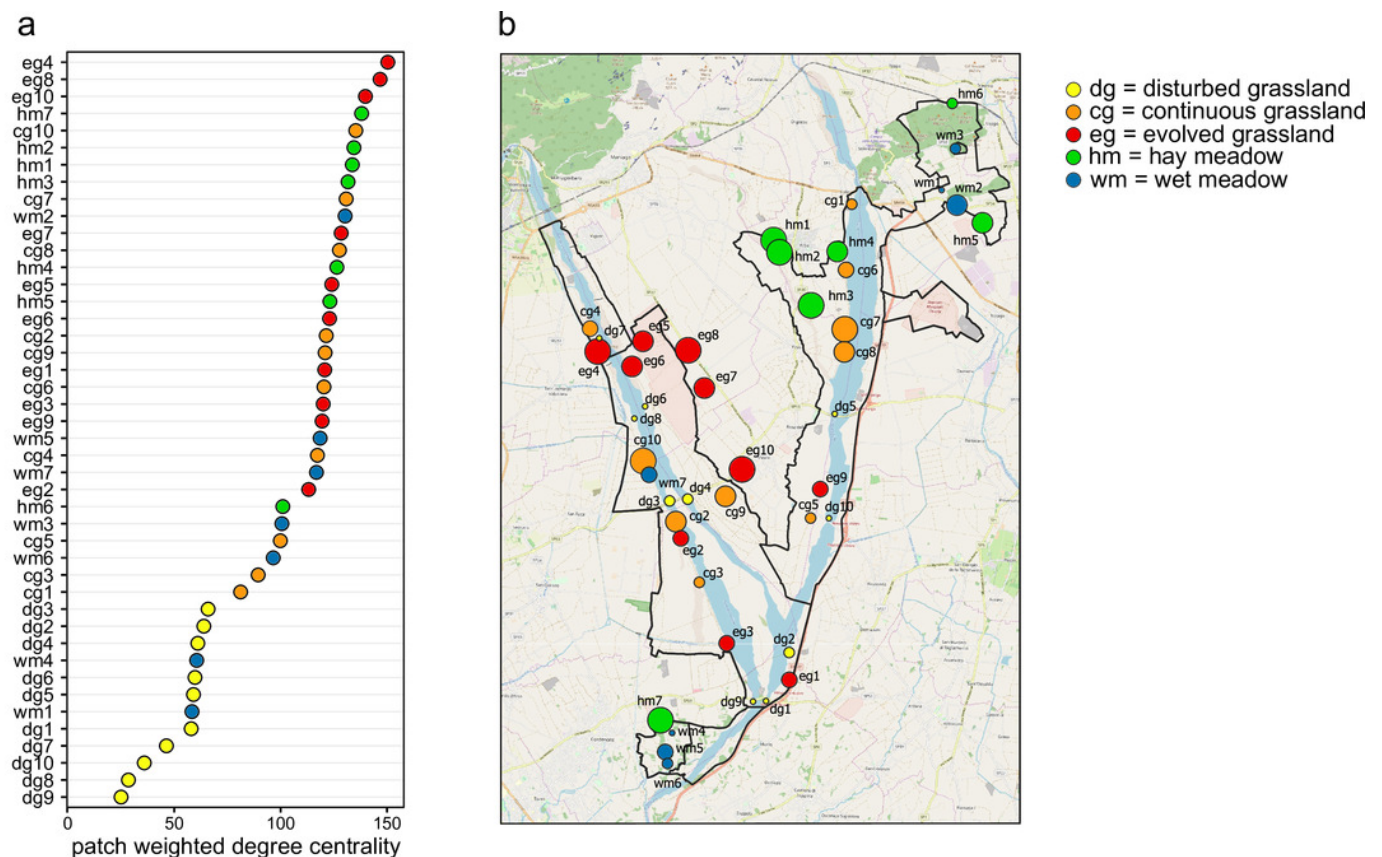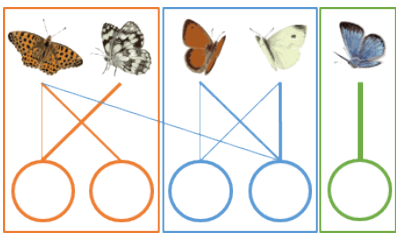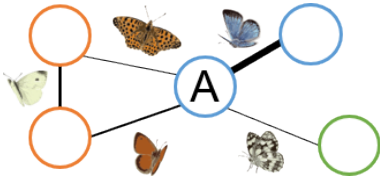
Table 1(on next page)

Species–habitat network metrics.

Explanation and example of conservation implications of the chosen metrics, both at network and node (patch) level.

Network architecture		
Metric	**Explanation**	**Example of conservation implications**
a) Nestedness	Species-rich patches host both common and rare species, while species-poor patches are only visited by generalist species.	A nested structure provides robustness against the loss of species-poor habitats. The management should therefore focus on species-rich sites.
b) Modularity	Some species interact more frequently with some habitat patches, creating modules or compartmentalisations.	A modular structure implies a high level of specialization of species for some habitat patches, and each habitat should be considered as a separate management unit.
Node role		
c) Patch centrality	Central habitat patches are those that share many species with other habitat patches (patch A).	Central habitat patches play a fundamental role in supporting generalist species across the whole species–habitat network.

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Table 2(on next page)

Results of the linear models testing the effect of habitat type on (a) species richness, (b) species evenness E_{var} and (c) patch weighted degree centrality.

		Estimate	SE	t-value	p-value
a) Species richness	Intercept (evolved grassland)	23.60	1.64	14.43	< 0.01
	Hay meadow	1.54	2.55	0.61	0.55
	Continuous grassland	-5.80	2.31	-2.51	0.02
	Disturbed grassland	-20.30	2.31	-8.78	< 0.01
	Wet meadow	-6.17	2.55	-2.42	0.02
b) Species evenness E_{var}	Intercept (evolved grassland)	0.37	0.04	8.81	< 0.01
	Hay meadow	0.07	0.07	1.01	0.32
	Continuous grassland	0.08	0.06	1-34	0.19
	Disturbed grassland	0.49	0.06	8.19	< 0.01
	Wet meadow	0.19	0.07	2.88	< 0.01
c) Patch weighted degree centrality	Intercept (evolved grassland)	128.60	5.60	22.95	< 0.01
	Hay meadow	-1.66	8.73	-0.19	0.85
	Continuous grassland	-14.17	7.93	-1.79	0.08
	Disturbed grassland	-78.27	7.93	-9.88	< 0.01
	Wet meadow	-31.21	8.73	-3.57	< 0.01

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