



UNIVERSITY OF LEEDS

This is a repository copy of *Land-use simplification weakens the association between terrestrial producer and consumer diversity in Europe*.

White Rose Research Online URL for this paper:  
<http://eprints.whiterose.ac.uk/108853/>

Version: Accepted Version

---

**Article:**

Dainese, M, Isaac, NJB, Powney, GD et al. (11 more authors) (2017) Land-use simplification weakens the association between terrestrial producer and consumer diversity in Europe. *Global Change Biology*, 23 (8). pp. 3040-3051. ISSN 1354-1013

<https://doi.org/10.1111/gcb.13601>

---

This article is protected by copyright. All rights reserved. This is the peer reviewed version of the following article: Dainese, M., Isaac, N. J. B., Powney, G. D., Bommarco, R., Öckinger, E., Kuussaari, M., Pöyry, J., Benton, T. G., Gabriel, D., Hodgson, J. A., Kunin, W. E., Lindborg, R., Sait, S. M. and Marini, L. (2016), Landscape simplification weakens the association between terrestrial producer and consumer diversity in Europe. *Glob Change Biol.*, which has been published in final form at <https://doi.org/10.1111/gcb.13601>. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving.

**Reuse**

Items deposited in White Rose Research Online are protected by copyright, with all rights reserved unless indicated otherwise. They may be downloaded and/or printed for private study, or other acts as permitted by national copyright laws. The publisher or other rights holders may allow further reproduction and re-use of the full text version. This is indicated by the licence information on the White Rose Research Online record for the item.

**Takedown**

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing [eprints@whiterose.ac.uk](mailto:eprints@whiterose.ac.uk) including the URL of the record and the reason for the withdrawal request.



[eprints@whiterose.ac.uk](mailto:eprints@whiterose.ac.uk)  
<https://eprints.whiterose.ac.uk/>

1 **Land-use simplification weakens the association between terrestrial producer**  
2 **and consumer diversity in Europe**

3  
4 **Running head:** Diversity associations and land-use change  
5

6 Matteo Dainese<sup>1,2,\*</sup>, Nick J. B. Isaac<sup>3</sup>, Gary D. Powney<sup>3</sup>, Riccardo Bommarco<sup>4</sup>, Erik Öckinger<sup>4</sup>,  
7 Mikko Kuussaari<sup>5</sup>, Juha Pöyry<sup>5</sup>, Tim G. Benton<sup>6</sup>, Doreen Gabriel<sup>7</sup>, Jenny A. Hodgson<sup>8</sup>, William  
8 E. Kunin<sup>6</sup>, Regina Lindborg<sup>9</sup>, Steven M. Sait<sup>6</sup>, Lorenzo Marini<sup>1</sup>  
9

10 <sup>1</sup>DAFNAE, University of Padova, Viale dell'Università 16, 35020 Legnaro, Padova, Italy

11 <sup>2</sup>Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg,  
12 Am Hubland, 97074 Würzburg, Germany

13 <sup>3</sup>Natural Environment Research Council (NERC) Centre for Ecology and Hydrology, Benson  
14 Lane, Crowmarsh Gifford, Oxfordshire, OX10 8BB, UK

15 <sup>4</sup>Department of Ecology, Swedish University of Agricultural Sciences, SE-750 07 Uppsala,  
16 Sweden

17 <sup>5</sup>Natural Environment Centre, Finnish Environment Institute, PO Box 140, FI-00251 Helsinki,  
18 Finland

19 <sup>6</sup>School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds, LS2 9JT, UK

20 <sup>7</sup>Institute of Crop and Soil Science, Julius Kühn-Institut (JKI), Federal Research Centre for  
21 Cultivated Plants, Bundesallee 50, D-38116 Braunschweig, Germany

22 <sup>8</sup>Department of Evolution, Ecology and Behaviour, Biosciences Building, Crown Street,  
23 University of Liverpool, UK

24 <sup>9</sup>Department of Physical Geography and Quaternary Geology, Stockholm University, SE-106 91  
25 Stockholm, Sweden

26 **\*Corresponding author:** Matteo Dainese, Tel.: +49 (0)931 31-88733, E-mail:  
27 [matteo.dainese@uni-wuerzburg.de](mailto:matteo.dainese@uni-wuerzburg.de)

28

29 **Keywords:** biodiversity loss, co-evolution, herbivory, ecosystem resilience, functional and  
30 phylogenetic diversity, habitat loss, host specialization, land-use change, plant-insect diversity,  
31 trophic associations.

32

33 **Paper type:** Primary Research Articles

34 **Abstract**

35 Land-use change is one of the primary drivers of species loss, yet little is known about its effect  
36 on other components of biodiversity that may be at risk, such as local associations between  
37 trophic levels. Here, we ask whether, and to what extent, landscape simplification, measured as  
38 the percentage of arable land in the landscape, disrupts the functional and phylogenetic  
39 association between plants and primary consumers. Across seven European regions, we inferred  
40 the potential associations (functional and phylogenetic) between host plants and butterflies in  
41 561 semi-natural grasslands. Local plant diversity showed a strong bottom-up effect on butterfly  
42 diversity in the most complex landscapes, but this effect disappeared in simple landscapes. The  
43 functional associations between plant and butterflies are, therefore, the results of processes that  
44 act not only locally but are also dependent on the surrounding landscape context. Similarly,  
45 landscape simplification reduced the phylogenetic congruence among host plants and butterflies  
46 indicating that closely related butterfly species are more generalist in the potential resource  
47 lineages used. These processes occurred without any detectable change in species richness of  
48 plants or butterflies along the gradient of arable land. The structural properties of ecosystems are  
49 experiencing substantial erosion, with potentially pervasive effects on ecosystem functions and  
50 future evolutionary trajectories. Loss of interacting species might trigger cascading extinction  
51 events and reduce the stability of trophic interactions, as well as influence the longer-term  
52 resilience of ecosystem functions. This underscores a growing realization that species richness is  
53 a crude and insensitive metric and that both functional and phylogenetic associations, measured  
54 across multiple trophic levels, are likely to provide far deeper insights into the resilience of  
55 ecosystems, and the functions they provide.

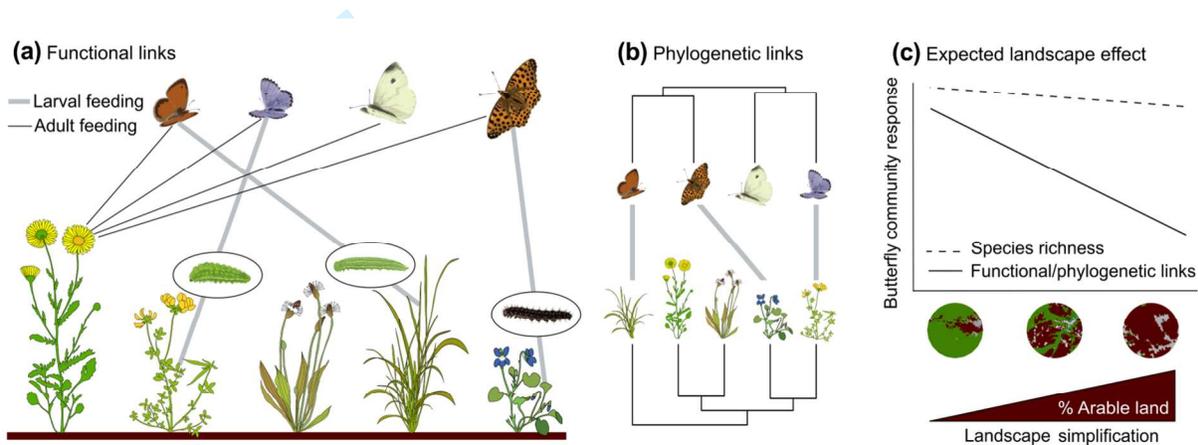
56 **Introduction**

57 Land-use simplification has emerged as one of the fundamental components of global change  
58 (Foley *et al.*, 2005; Turner II *et al.*, 2007; Verburg *et al.*, 2011; Allan *et al.*, 2015; Newbold *et*  
59 *al.*, 2015). Ecology has provided ample scientific evidence that decreasing habitat heterogeneity  
60 and increasing fragmentation, e.g. through agricultural expansion and intensification (a process  
61 often termed “landscape simplification”) (Meehan *et al.*, 2011), are main anthropogenic drivers  
62 of biodiversity loss (Tscharntke *et al.*, 2012). However, biodiversity science has largely focused  
63 on species richness loss, underplaying other components of biodiversity that may be at risk of  
64 landscape simplification (Valiente-Banuet *et al.*, 2015). Traditionally, studies have focused on a  
65 single trophic level, when instead the biodiversity loss at a given trophic level may also affect  
66 other levels, and, hence the associated diversity relationships (Duffy *et al.*, 2007; Scherber *et al.*,  
67 2010). Associations between trophic levels can have a large impact on community responses to  
68 global change (Duffy, 2002; Cardinale *et al.*, 2012; Oliver *et al.*, 2015). Loss of interacting  
69 species can trigger cascading extinction events and reduce the stability of trophic interactions  
70 (Dunne *et al.*, 2002; Haddad *et al.*, 2011), as well as influence the longer-term resilience of  
71 ecosystem functions (Oliver *et al.*, 2015).

72 In many human-managed landscapes that are characterized by fragmented habitats, the  
73 resource base for consumers is often scattered across space (Tscharntke & Brandl, 2004; Winfree  
74 *et al.*, 2011). Because consumer insects are generally highly mobile and affected by land use  
75 change, landscape simplification can also alter relationships between the diversity of different  
76 taxa (Tscharntke *et al.*, 2012; Weiner *et al.*, 2014). Our understanding of these associations is  
77 mainly based on analyses of manipulative experiments (e.g. Haddad *et al.*, 2009; Scherber *et al.*,  
78 2010) or studies at the local scale (e.g. Manning *et al.*, 2015), while empirical data considering

79 the effect of land-use change at larger spatial scales are largely missing. For instance, it remains  
 80 less clear how local associations between producer and consumer diversity are affected by  
 81 landscape simplification. Nevertheless, focusing on the conservation status of local scale trophic  
 82 associations can provide early diagnosis of the functional consequences of biodiversity loss due  
 83 to global scale change (Valiente-Banuet *et al.*, 2015; Harvey *et al.*, 2016).

84



85  
 86 **Figure 1.** Schematic representation of potential associations between plants and butterflies and the  
 87 expected landscape effect on these associations. (a) Butterflies have distinctive functional links with  
 88 plants: they feed on plant tissues as larvae and on nectar as adults. As adult butterflies show low  
 89 specialization with flower resources (Rosas-Guerrero *et al.*, 2014) we hypothesized that butterfly  
 90 abundance depends on the species richness of flowering plants and their functional trait composition. The  
 91 diet breadth of butterfly larvae is more restricted than that of adults due to (b) co-evolution between host  
 92 and consumer (phylogenetically closely related butterflies often prefer to feed on phylogenetically closely  
 93 related host plants). Such functional and phylogenetic associations determine the bottom-up effect of host  
 94 plant diversity on butterfly evenness and species richness. (c) As losses of producer-consumer diversity  
 95 associations may frequently precede the loss of species, we hypothesize a stronger negative effect of  
 96 landscape simplification on producer-consumer diversity associations than on species richness loss.  
 97

98 The potential functional associations between host plants and consumers (functional  
 99 links; Fig. 1a) can be combined with phylogenetic information in order to indicate the degree of  
 100 phylogenetic congruence (Ferrer-Paris *et al.*, 2013; Pellissier *et al.*, 2013). We expected that  
 101 consumers that are phylogenetically related feed on host plant species that are also  
 102 phylogenetically related (phylogenetic links; Fig. 1b)(Ødegaard *et al.*, 2005; Weiblen *et al.*,

103 2006). Although congruent phylogenies are often considered as a signal of tight co-evolutionary  
104 associations between plants and insects, this pattern alone is not sufficient to demonstrate co-  
105 speciation (the matching of speciation events in two or more interacting taxa). There can be other  
106 non-coevolutionary processes that can produce congruent patterns (de Vienne *et al.*, 2013;  
107 Althoff *et al.*, 2014). For instance, some species-specific ecological traits and their geographical  
108 variation can influence such outcome. Host specificity, in particular, is expected to affect the  
109 extent of plant-insect interactions (Clayton *et al.*, 2004).

110         Here, we ask whether, and to what extent, landscape simplification, measured as the  
111 percentage of arable land in the landscape, has disrupted functional and phylogenetic  
112 associations between plants and butterflies. This landscape metric has been used as a relevant  
113 proxy for characterizing landscape simplification (Tscharntke *et al.*, 2005) and agricultural  
114 intensification (Meehan *et al.*, 2011). Depending on the degree of specialization, butterflies are  
115 functionally linked to one or more host plant species, both as herbivores at the larval stage and as  
116 flower-visitors as adults (Fig. 1a). First, we hypothesized that variation in host plant diversity  
117 would mediate the abundance distribution and species richness of butterfly communities (Fig.  
118 1a) and that landscape simplification can disrupt these relationships (Fig. 1 c). The loss of  
119 functional associations might occur in the absence of local species loss. For instance, a  
120 substantial decline in abundance can lead to the loss of interactions with other species without  
121 causing local extinction (Estes *et al.*, 1989; McConkey & O’Farrill, 2015). This loss of  
122 functional relationships is likely to be more evident in human-altered ecosystems, where human  
123 activities affect the abundances of species more frequently than they do their presence or absence  
124 (Chapin III *et al.*, 2000). Second, we determined whether landscape simplification undermined  
125 the degree of phylogenetic congruence in the potential host plant-butterfly linkages. We

126 estimated the degree of phylogenetic congruence for each site and tested the probability of  
127 observing significant signals in relation to landscape simplification. Then, using a randomization  
128 approach, we investigate whether the observed signal was likely to be due to specialization rather  
129 than deeper co-evolutionary history (Clayton *et al.*, 2004; Althoff *et al.*, 2014). We predicted that  
130 the loss of specialist species due to landscape simplification (Öckinger *et al.*, 2010; Weiner *et al.*,  
131 2014) weakens the signal of phylogenetic congruence.

## 133 **Materials and methods**

### 134 *Studies*

135 We used primary data from seven independent regions across four European countries (Finland,  
136 Italy, Sweden, and UK) where data on butterfly and plant composition were available for the  
137 same sites (Marini *et al.*, 2009, 2014; Pöyry *et al.*, 2009; Gabriel *et al.*, 2010; Hambäck *et al.*,  
138 2010; Öckinger *et al.*, 2010, 2012; Dainese *et al.*, 2015) (Appendix S1, Table S1 in Supporting  
139 Information). Observations were conducted in different types of semi-natural grasslands, such as  
140 field margins, meadows, and pastures. All data sets were collected over one season, except for  
141 the UK study where two sampling years were available. Overall, 561 sites in eight datasets were  
142 included (area ranged from 50 m<sup>2</sup> to 26.6 ha). Vascular plants and butterflies were sampled  
143 by plot counts or transect walks with the transect length and search time proportional to  
144 habitat area. A summary of the data sources and sampling methods is provided in Appendix S1  
145 (Table S1). The percentage of arable land surrounding each study site was used as a measure of  
146 landscape simplification (LS) and was calculated on three spatial scales (0.5, 1, 2 km). For the  
147 studies where this information was not available, we calculated the percentage of arable land  
148 using a detailed vector-based land-cover map (specific for each region). The range of arable

149 cover in the landscape was usually large, and there was a good overlap in the different regions  
150 (Appendix S1, Table S1).

151

### 152 *Matrix calculation*

153 Data on species composition deriving from each dataset were merged into two matrices: a  
154 butterfly species-by-site matrix (**B**) and a plant species-by-site matrix (**P**) (Appendix S1, Fig.  
155 S1). For each country, we compiled a list of butterfly-host plant associations derived from  
156 scientific literature and validated by experts (Appendix S1, Table S2). In this way, we accounted  
157 for the potential geographical variation in host plant use. Only the butterfly species that feed on  
158 herbaceous species were used in the butterfly-host plant association. When a butterfly species  
159 feeds on multiple species of an entire family (e.g., *Coenonympha pamphilus* feeding on  
160 numerous *Poaceae* spp. or *Colias crocea* feeding on numerous *Fabaceae* spp.), we used the  
161 family taxonomic level in the list. The same approach was adopted for a butterfly species feeding  
162 on several species of a genus (e.g., *Argynnis aglaja* or *Boloria selene* feeding on *Viola* spp.), i.e.  
163 in these cases we used the genus taxonomic level in the list. In these cases, we assumed that the  
164 occurrence of a butterfly depended on the presence of host family or genus in the plant  
165 community and not by the number of species belonging to that family or genus. As a result, the  
166 host plant list included different taxonomical levels, such as species, genus, or family. Since  
167 many butterfly species are polyphagous (species feeding on plants belonging to different  
168 families), we could have multiple hosts associated with a single butterfly. We converted the  
169 association list into an interaction matrix (**HB**) between host plants (rows) and butterfly species  
170 (columns) occurring in the datasets and based on a binary association index (0 = absence and 1 =  
171 presence) (Appendix S1, Fig. S1). From the plant species-by-site matrix (**P**), we built two sub-

172 matrices: a host plant-by-site matrix (**H**) and a flowering forb species-by-site matrix (**F**)  
173 (Appendix S1, Fig. S1). The host plant species-by-site matrix (**H**) was built using the host plant  
174 list derived from the association matrix **HB**. When a family or genus characterized the host plant,  
175 the weight of all species belonging to the same family or genus and occurring in the community  
176 was equal to one (e.g., if a generalist butterfly fed on numerous *Poaceae* spp. and there were five  
177 plant species related to this family in the community, we scored each species as 0.2 when we  
178 calculated host plant richness). Similarly, when multiple butterflies were associated with a single  
179 host plant, this host plant had a weight equal to one in the community. In this way, we avoided  
180 bias created by overweighing the number of host plants belonging to the same family/genus or  
181 associated to various butterflies. As butterflies show low specialization during adult feeding  
182 (Rosas-Guerrero *et al.*, 2014), we considered all the nectar plants occurring in the communities  
183 to build the flowering forb species-by-site matrix (**F**) (Appendix S1, Fig. S1).

184

### 185 *Traits and phylogeny*

186 For flowering forb species, we selected traits that captured key aspects of floral display and  
187 phenology and for which data were available. The selected traits were as follows: (i) flower size,  
188 (ii) flower colour, (iii) flower morphology, and (iv) flowering period. As a result, a species-by-  
189 trait matrix was built (**T**) (Appendix S1, Fig. S1). For flower size, we considered the flower  
190 diameter in mm. In the absence of more adequate colour classification (e.g. spectral reflectance  
191 data), we classified flower colour in classes as seen by humans, since previous studies found a  
192 significant relationship to visitation patterns of pollinators (Eklöf *et al.*, 2013; Carneiro *et al.*,  
193 2014). We classified the plant species in four classes of flower colour: white, yellow, warm  
194 colours (pink – red – purple), and cold colours (violet – blue). For flower morphology, we

195 classified the plant species into five main categories according to blossom type (Pellissier *et al.*,  
196 2010): disk (plane- or bowl-shaped actinomorphic blossoms with easily attainable pollen and  
197 nectar), funnel (open stereo- and actinomorphic blossoms with a wide opening and a typical  
198 ‘bell-shape’ with easily attainable pollen and nectar), bilabiate (zygomorphic blossoms in which  
199 pollen is placed dorsally or ventrally on the pollinator), tube (actinomorphic blossoms forming a  
200 long tube with nectar hidden at the bottom), and head (flat or globular blossoms composed of  
201 tightly arranged small actinomorphic or zygomorphic flowers). Flowering period was defined as  
202 the number of months over which a plant species usually blossoms. Trait data were derived from  
203 different sources (Klotz *et al.*, 2002; Aeschmann *et al.*, 2004; Royal Botanic Gardens Kew,  
204 2014).

205 For butterflies, host plant specialization (larval feeding niche diet breadth) was  
206 measured using the number of larval host plants species and derived from the butterfly-host plant  
207 association list. Species whose larval feeding niche consisted of a single plant genus were  
208 classified as food specialists whereas species feeding on more than one genus were classified as  
209 generalists (Öckinger *et al.*, 2010). For each site, we calculated the proportion of specialist  
210 species on the total species richness.

211 For the host plants (**H<sub>P</sub>**) (Appendix S1, Fig. S1 and Appendix S2), we calculated a  
212 phylogenetic tree using Phylomatic version 3 (<http://phylodiversity.net/phyloomatic/>) and derived  
213 from the Phylomatic megatree (R20120829) based on the APG III classification (Bremer *et al.*,  
214 2009). For butterflies, we built an updated molecular phylogeny for 115 species (**B**), using  
215 cytochrome oxidase subunit I (COI) gene sequences that were extracted from GenBank (Benson  
216 *et al.*, 2011) (Appendix S2). Both phylogenetic trees were built considering the whole dataset.

217

218 *Butterfly and plant community components*

219 For each site, three community components were calculated for butterflies (calculated using  
220 matrix **B**): total abundance (**B<sub>AB</sub>**), evenness (**B<sub>EV</sub>**), and species richness (**B<sub>SR</sub>**) (Appendix S1, Fig.  
221 S1). Evenness (**B<sub>EV</sub>**) was calculated using the  $E_{var}$  index (Smith & Wilson, 1996):

$$E_{var} = 1 - \frac{2}{\pi} \arctan \left\{ \frac{1}{S} \sum (\ln(p_i) - \mu_{\ln})^2 \right\}$$

222 where  $\mu_{\ln} = \frac{1}{S} \sum \ln(p_i)$  and  $p_i$  is the relative abundance of species. The formula is based on the  
223 variance of log abundances (centered on the mean of log abundances) then appropriately scaled  
224 to cover 0-1 (0 = maximally uneven and 1 = perfectly even). This index is mathematically  
225 independent from species richness (Appendix S1, Fig. S2 and S3).

226 For plants, we considered five community components: species richness, evenness,  
227 functional diversity, functional trait composition, and phylogenetic diversity. Species richness  
228 and evenness were estimated for both host plants (matrix **H** → **H<sub>SP</sub>** and **H<sub>EV</sub>**) and flowering forbs  
229 (matrix **F** → **F<sub>SP</sub>** and **F<sub>EV</sub>**), functional diversity and functional trait composition only for  
230 flowering plants (matrix **F** → **F<sub>FD</sub>** and **F<sub>FC</sub>**), and phylogenetic diversity only for host plants  
231 (matrix **H** → **H<sub>PD</sub>**) (Appendix S1, Fig. S1). Evenness was calculated using the  $E_{var}$  index as for  
232 butterflies. Functional diversity (**F<sub>FD</sub>**), based on multiple traits in matrix **T**, was measured using  
233 the standardized effect size (SES) of the abundance-weighted mean pairwise distance (MPD)  
234 among species in a site (Swenson, 2014), as implemented in the ‘picante’ R package. The MPD  
235 index is equivalent to Rao Quadratic Entropy Index of Diversity (Rao, 1982), as demonstrated in  
236 simulated (Mouchet *et al.*, 2010) and empirical data (Ricotta & Moretti, 2011). The trait matrix  
237 was converted into a Gower distance matrix, which allows mixing different types of variables.  
238 This in turn was converted into a functional dendrogram by a UPGM clustering analysis and

239 used to calculate the MPD. Flower size (continuous trait) was log-transformed before  
240 calculation. Since the variance of MPD strongly depends on local species richness (Swenson,  
241 2014), the observed values of MPD were standardized. To calculate the SES, MPD was centered  
242 and scaled using the mean and standard deviation estimates based on the distribution of the  
243 corresponding indices calculated for 999 null communities as follows:

$$SES = \frac{MPD_{obs} - mean(MPD_{null})}{\sigma(MPD_{null})}$$

244 The null communities were generated with species richness equal to each of the observed  
245 assemblages and species selected at random from the regional species pool of the observed  
246 community. Functional trait composition ( $\mathbf{F}_{FC}$ ) of local plant community was estimated using the  
247 community-weighted mean (CWM) for each plant trait separately ( $\mathbf{F} \times \mathbf{T} \rightarrow \mathbf{F}_{FC}$ ) (Appendix S1,  
248 Fig. S1). CWM represents the average trait value in a community weighted by the relative  
249 abundance of the species carrying each value (Garnier *et al.*, 2004):

$$CWM = \sum_{i=1}^S p_i x_i$$

250 where  $x_i$  is the mean trait value of the  $i$ -th species (the average over all trait measures for a given  
251 species; for binary traits  $x_i$  can be either 0 or 1 and the index reflects the relative abundance of  
252 each category), and  $p_i$  is the proportion of that species. A principal component analysis (PCA)  
253 was then used to reduce traits' redundancy and to produce orthogonal axes of functional trait  
254 composition (Appendix S1, Fig. S4). We ran the PCA on the CWM trait matrix ( $\mathbf{F}_{FC}$ ),  
255 standardized to mean 0 and unit variance. The PCA site-score data in two-dimensional trait-space  
256 ( $\mathbf{F}_{FC1}$  and  $\mathbf{F}_{FC2}$ ) was then used in the statistical modeling (Appendix S1, Fig. S1). The first two  
257 axes of PCA explained about 37% of total variation. The first principal component ( $\mathbf{F}_{FC1}$ ) that

258 accounted for 22% of the functional trait composition variation had high positive loadings for  
259 flower size, warm colour flowers, and head blossoms, as well as high negative loadings for white  
260 colour flowers and disk blossoms (Appendix S1, Fig. S4). The second principal component  
261 ( $F_{FC2}$ ) explained 15% of functional trait composition variation. This axis had high positive  
262 loadings for yellow colour flowers and negative loadings for cold colour flowers (Appendix S1,  
263 Fig. S4). Phylogenetic diversity ( $H_{PD}$ ) was calculated using the standardized effect size (SES) of  
264 the mean pairwise phylogenetic distance (MPD) among species in a site. In this case, the null  
265 communities were generated by randomly reshuffling the tip labels on the host plant phylogeny,  
266 while preserving community composition and related patterns (species richness, species  
267 frequency and co-occurrence patterns across communities).

#### 269 *Phylogenetic congruence of butterfly-host plant associations*

270 For each site, phylogeny trees were pruned from the reference host plant ( $H_P \rightarrow H_{Pi}$ ) and  
271 butterfly ( $B_P \rightarrow B_{Pi}$ ) phylogenies to include only species (family, genus and/or species for host  
272 plants) occurring in the site. The same procedure was repeated for the association matrix ( $HB \rightarrow$   
273  $HB_i$ ). At each site, we tested the congruence between butterfly and host plant phylogenies using  
274 the ParaFit test, implemented in the 'ape' R package, a method originally developed for the co-  
275 evolutionary analyses of hosts and parasites (Legendre *et al.*, 2002). ParaFit is a matrix  
276 permutation test of co-speciation, which aims to test whether interactions between trophic levels  
277 are phylogenetically correlated. The null hypothesis is that butterflies utilize resources randomly  
278 with respect to the phylogenetic tree of the host plants while the alternative hypothesis is that  
279 butterflies and their host plants occupy corresponding positions in their phylogenetic trees. This  
280 method is advantageous because it can accommodate cases where multiple butterflies are

281 associated with a single host plant, or when multiple hosts are associated with single butterfly  
282 species, and it can be used to assess the contribution of each individual butterfly–host plant link  
283 to the total congruence statistics (de Vienne *et al.*, 2013). Distance matrices for butterflies ( $\mathbf{B}_{P_i} \rightarrow$   
284  $\mathbf{dB}_{P_i}$ ) and host plants ( $\mathbf{H}_{P_i} \rightarrow \mathbf{dH}_{P_i}$ ) were derived from the phylogenies using the ‘cophenetic’  
285 function in the ‘ape’ R package. The test was performed for each site (local scale) separately and  
286 included a phylogeny for both the trophic levels ( $\mathbf{dB}_{P_i}$  and  $\mathbf{dH}_{P_i}$ ) and a consumer (butterfly)  $\times$   
287 resource (host plant) species interaction matrix ( $\mathbf{HB}_i$ ) (Fig. S1). A global statistic was then  
288 derived from each site (ParaFit test with 999 permutations). We also performed the test for each  
289 data set (regional scale) separately (Appendix S1, Fig. S5). We converted the  $P$  value derived  
290 from ParaFit test into a binary index, where sites with significant phylogenetic congruence were  
291 coded as 1 and non-significant as 0.

292 To test whether the ParaFit results were not simply a result of specialization but also of  
293 tight co-evolution (Clayton *et al.*, 2004), we repeated the ParaFit test maintaining the same  
294 consumer (butterfly)  $\times$  resource (host plant) species interaction matrix ( $\mathbf{HB}_i$ ) but randomizing the  
295 tips on the butterfly phylogeny (see Jenkins *et al.*, 2012). In this way, we preserved the same  
296 number of associations per butterfly, while randomizing the evolutionary history among them. If  
297 the phylogenetic congruence of butterfly-host plant associations remains intact even after this  
298 randomization approach, butterfly specialization can be considered the process that produces the  
299 congruent patterns.

300 Finally, we conducted an additional analysis to test whether the ParaFit results were  
301 affected by the fact that some butterflies were linked to many host plants, while others to only  
302 one. When a butterfly species feeds on multiple species of an entire family, we used only one  
303 link between a butterfly and a random member of a plant family.

304 *Statistical analysis*

305 All analyses were conducted using R version 3.0.4 (R Foundation for Statistical Computing,  
306 Vienna, Austria, 2014). Before performing the analyses, diversity measures were standardized  
307 using  $z$ -scores  $\left(\frac{y_i - \bar{y}}{SD_y}\right)$  within each study to allow comparisons between studies with contrasting  
308 means  $\bar{y}$  and standard deviations  $SD_y$ , and differences in methodology. We tested the influence  
309 of plant diversity measures on butterfly abundance, evenness, and richness using linear mixed-  
310 effects models (LMMs) with Gaussian error distribution. To account for differences in methods  
311 between the studies, we included study identity as a random factor (i.e., the model estimated  
312 different intercepts  $\alpha_i$  for each study  $i$ ). Model residuals were approximately normally distributed  
313 and exhibited homogeneity of variance. All the LMMs were estimated using the 'lme4' package  
314 in R. We built three models that tested the interactive effect of plant diversity measures and  
315 landscape simplification on butterfly (i) abundance, (ii) evenness, and (iii) richness. Different  
316 components of plant diversity were used in the three models considering the potential  
317 associations between plants and butterflies described in Figure 1. In a fourth model (iv), we  
318 related the phylogenetic congruence signal to landscape simplification.

319 *(i) Influence of local habitat quality and landscape simplification on butterfly abundance*

320 *(hypothesis i)*. Due to a low specialization between adult butterflies and flower resources, we  
321 hypothesize that local habitat quality (i.e. diversity of flower resources) is strongly correlated  
322 with butterfly abundance. In this model, we tested the interactive effect of landscape  
323 simplification and local habitat quality, measured by flowering forb specie richness, functional  
324 diversity, and functional trait composition (the two orthogonal axes derived from the PCA on the  
325 CWM trait matrix) on butterfly abundance.

326 As butterflies are more specialized to host plants at the larval stage, we hypothesize in  
327 models *ii* and *iii* that variation in host plant diversity has instead the main influence on the  
328 evenness and species richness of butterfly communities. We assessed the robustness of  
329 hypotheses *ii* and *iii* including flowering forb evenness or richness in the models.

330 *(ii) Influence of host plant evenness and landscape simplification on butterfly evenness*  
331 *(hypothesis ii)*. We tested the interactive effect of landscape simplification and local host plant  
332 evenness on butterfly evenness. Flowering forb evenness was also included in the model.

333 *(iii) Influence of host plant diversity and landscape simplification on butterfly richness*  
334 *(hypothesis iii)*. We verified the interactive effect of landscape simplification and host plant  
335 diversity (richness and phylogenetic diversity) on butterfly species richness. It was not possible  
336 to include both measures of host plant diversity in the same model, due to problems of  
337 convergence. Similarly, flowering forb diversity was collinear with host plant richness.

338 Therefore, we estimated the effects of these variables by fitting three separate models and using  
339 the Akaike information criterion (AIC) to determine the best model.

340 *(iv) Influence of landscape simplification on phylogenetic congruence among host plants and*  
341 *butterflies (hypothesis iv)*. We verified whether landscape simplification negatively affected the  
342 congruence between butterfly and host plant phylogenies, measured as the proportion of sites  
343 with significant phylogenetic congruence. The proportion of sites with significant congruence  
344 was analysed using a generalized linear mixed-effects model with binomial error distribution.

345 Then, we tested the relationship between butterfly specialization (i.e. the proportion of specialist  
346 species) and the proportion of sites with significant congruence. Finally, to verify whether the  
347 changes in butterfly specialization drove the shifts in phylogenetic association with landscape  
348 simplification or a tight co-evolution signal was also involved, we repeated the analysis

349 considering the proportion of sites with significant congruence derived from the ParaFit analysis  
350 with the randomized butterfly tips. The significance of landscape simplification was determined  
351 with parametric bootstrapping with 1000 bootstrap replicates.

352

353 *Model selection.* As for the UK study, two sampling years were available, we compared the  
354 models considering both years and only one year at a time. The results were qualitatively equal  
355 between the models. In all the models we present results considering both years for the UK  
356 study. For each model (*i-iv*), we tested the effect of landscape simplification (i.e. the percentage  
357 of arable land in the landscape) using the three landscape scales (0.5, 1, 2 km) separately. We  
358 selected the radius that had the strongest effect on model results, that is, with the lowest AIC  
359 value (Appendix S1, Table S3). Models including landscape simplification measured with a  
360 radius of 2 km had the lowest AIC in almost all the cases, even though the magnitude of the  
361 differences were quite similar among the landscape scales (Appendix S1, Table S3). The radius  
362 of 2 km has been previously found to be an appropriate scale for modeling butterfly species  
363 diversity (Krauss *et al.*, 2010; Bommarco *et al.*, 2014). Therefore, we present the results using  
364 the same scale with a 2 km landscape buffer for all the models. In the models relating to  
365 hypotheses *i-iii*, we applied an information-theoretic model selection procedure to evaluate  
366 alternative competing models (Burnham & Anderson, 2002). We compared the fit of all possible  
367 candidate models obtained by the combination of the predictors using second-order Akaike's  
368 information criterion (AICc). Then, we ranked the models according to their AICc, identified top  
369 models (i.e.  $\Delta AICc$  from the best model  $< 7$ ) for each hypothesis, and calculated associated  
370 Akaike weights ( $w_i$ ) for each parameter, we used model averaging based on the 95% confidence  
371 set to incorporate model selection uncertainty into our parameter estimates (Burnham &

372 Anderson, 2002). We also report 95% confidence intervals (CIs) around model-averaged partial  
373 slope coefficients. Akaike weights ( $w_i$ ) were used to measure the relative importance of each  
374 covariate, summing  $w_i$  across the models ( $\sum w_i$ ) in which the covariate occurred. Covariates were  
375 considered important if they appeared in top models ( $\Delta AICc < 7$ ) and had a sum of model  
376 weights  $> 0.6$ . Unconditional CIs that did not include 0 indicated a significant effect. Model  
377 comparison was implemented using the ‘MuMIn’ package in R.

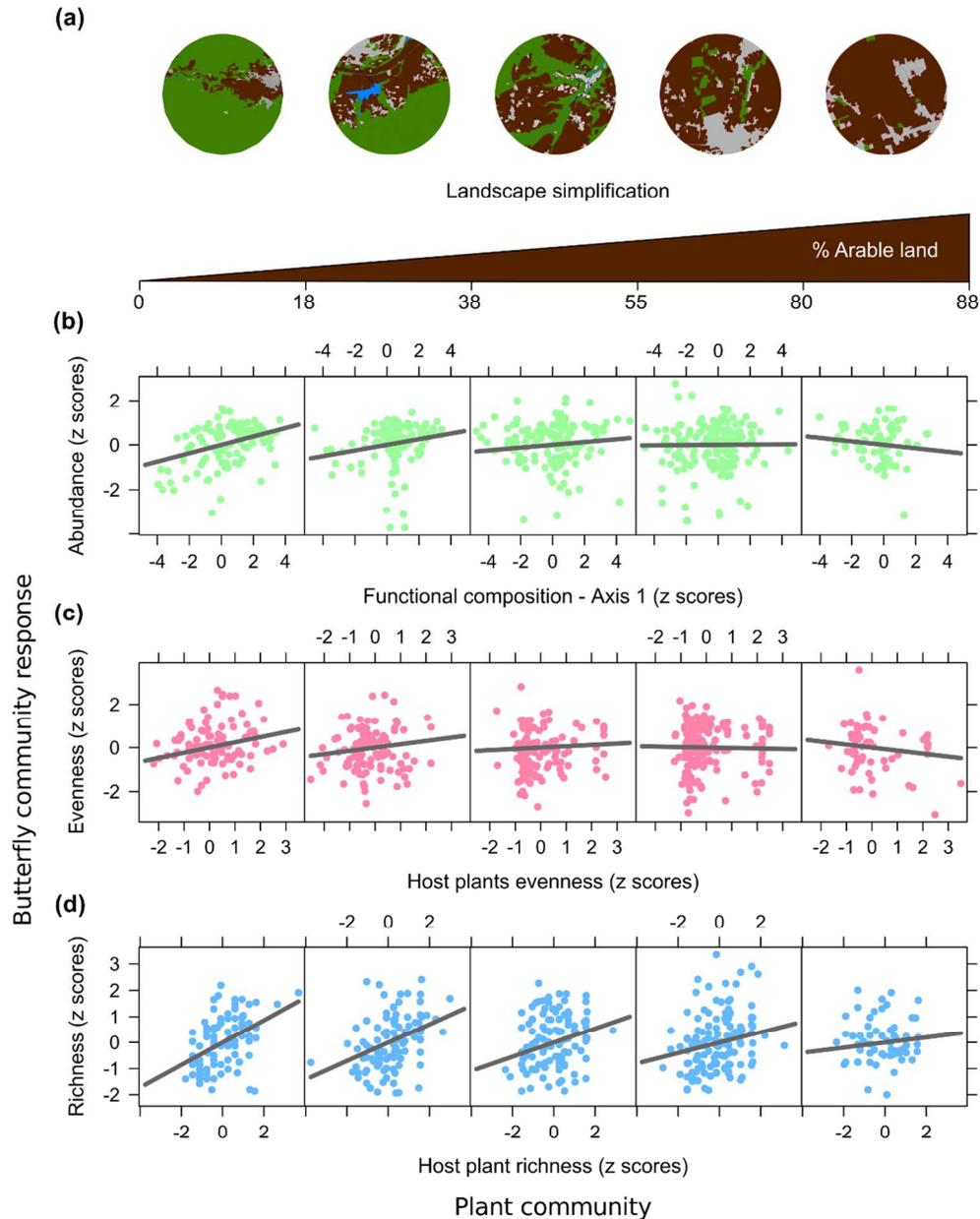
For Review Only

378 **Results**

379 *Effect of landscape simplification on functional associations*

380 We found a positive effect of flowering plant species richness ( $\sum w_i = 1.00; \beta = 0.242$ ) and plant  
381 functional trait composition ( $\sum w_i = 0.99; \beta = 0.067$ ) on butterfly abundance (Appendix S1, Table  
382 S4). Specifically, butterfly abundance was highest on sites with many large warm-coloured  
383 flowers, head blossoms and flowers aggregated into flower heads. Second, host plant  
384 communities with high evenness supported butterfly communities with high evenness ( $\sum w_i =$   
385  $0.83; \beta = 0.067$ ) (Appendix S1, Table S4). Third, we detected a positive effect of both host plant  
386 richness ( $\sum w_i = 1.00; \beta = 0.278$ ) and flowering plant species richness ( $\sum w_i = 1.00; \beta = 0.326$ ),  
387 but not of host plant phylogenetic diversity ( $\sum w_i = 0.35; \beta = 0.012$ ), on butterfly species richness  
388 (Appendix S1, Table S4). Models performed using Chao 1 abundance-based species richness  
389 estimator for butterflies confirmed the same results ( $\sum w_i = 1.00; \beta = 0.212$  and  $0.219$  with host  
390 plant richness or flowering species richness, respectively) (Appendix S1, Table S4).

391 Analyzing the effects of the surrounding landscape on local communities of plants and  
392 butterflies, we found that all the potential functional associations described above were disrupted  
393 by landscape simplification (Fig. 2). The effect of local plant functional trait composition on  
394 butterfly abundance was positive only in the least simplified landscapes, but this effect  
395 disappeared in simple landscapes (Fig. 2b). A similar pattern was observed for the relationship  
396 between host plant and butterfly evenness (Fig. 2c). In the case of butterfly species richness, the  
397 positive effect of host plant richness disappeared at high levels of landscape simplification and  
398 was weak at intermediate levels (Fig. 2d).

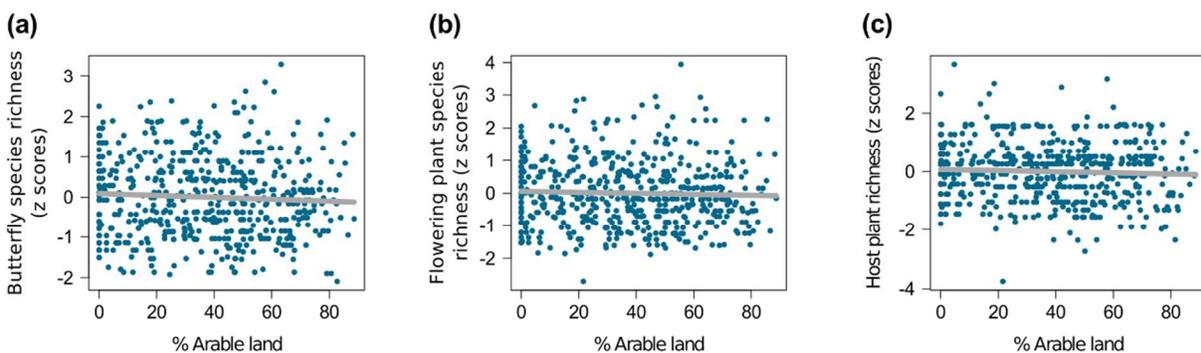


399 **Figure 2.** Interaction between plant diversity and landscape simplification as a function of butterfly  
 400 diversity. (a) Panels are ranked from left to right according to increasing proportion of arable land cover  
 401 in a radius of 2 km surrounding each site. (b) The interaction between plant functional trait composition  
 402 and landscape simplification on butterfly abundance ( $\sum w_i = 0.93; \beta = -0.0033$ ). Functional trait  
 403 composition is a measure of the extent to which plant communities contain large flowers with warm  
 404 colors and head blossoms (Fig. S4). (c) The interaction between host plant evenness and landscape  
 405 simplification on butterfly evenness ( $\sum w_i = 0.63; \beta = -0.0043$ ). (d) The interaction between host plant  
 406 richness and landscape simplification on butterfly species richness ( $\sum w_i = 0.75; \beta = -0.0041$ ). The fitted  
 407 lines (b-d) are general linear mixed model estimates calculated from the best plausible model (Table S4).  
 408 The points represent the 561 study sites and show the partial residuals from the best plausible model.  
 409 Diversity measures from each study were standardized to z scores prior the analysis.  
 410

411 Models with host plant diversity showed a higher AIC (AIC = 1537.8 for host plant richness and  
412 AIC = 1585.7 for host plant phylogenetic diversity) than with flowering plant richness (AIC =  
413 1521.1). However, the model with host plant richness was the most robust maintaining the  
414 significant interaction with landscape simplification when we repeated the analysis using the  
415 Chao 1 abundance-based species richness estimator for butterflies. Instead, for flowering plant  
416 species richness such interaction was no longer significant ( $\sum w_i = 0.25$ ;  $\beta = -0.002$ ) (Appendix  
417 S1, Table S4). There was also no interactive effect in the model including host plant  
418 phylogenetic diversity as a predictor ( $\sum w_i = 0.09$ ;  $\beta = -0.003$ ).

419 Despite the strong effect of landscape simplification on functional associations, we found  
420 no impact of cover of arable land in the landscape on butterfly species richness ( $\beta = -0.002$   $P =$   
421  $0.170$ , Fig. 3a), abundance ( $\beta = -0.0005$ ,  $P = 0.746$ , Fig. 3a) and evenness ( $\beta = -0.0004$ ,  $P =$   
422  $0.815$ , Fig. 3a) or plant species richness (flowering plants:  $\beta = -0.001$ ,  $P = 0.383$ , Fig. 3b; host  
423 plants:  $\beta = -0.002$ ,  $P = 0.258$ , Fig. 3c).

424



425

426 **Figure 3.** (a) Relationship between butterfly species richness and landscape simplification. (b) The  
427 relationship between flowering plant species richness and landscape simplification. (c) The relationship  
428 between host plant richness and landscape simplification. The fitted lines (a-c) are general linear mixed  
429 model estimates.

430

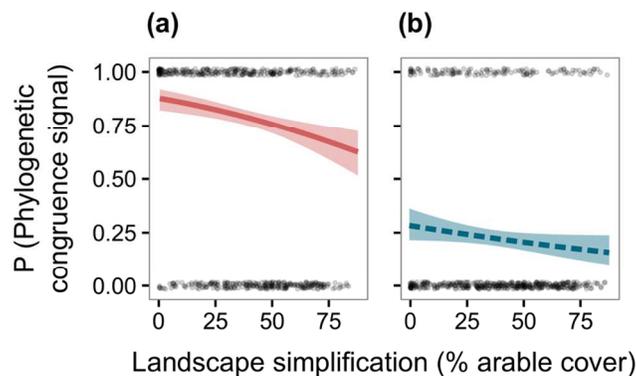
431

432

433 *Effect of landscape simplification on phylogenetic congruence*

434 We found a significant phylogenetic congruence among host plants and butterflies for all the data  
435 sets ( $P < 0.001$ ; Appendix S1, Fig. S5). At the local scale, a phylogenetic congruence was found  
436 in 51.0% of the sites (286 out of 561 sites, median  $P = 0.010$ ). Reducing the number of  
437 associations to one host plant per butterfly gave similar results (42.2% of the sites had a  
438 significant associations, median  $P = 0.012$ ). Testing for butterfly specialization by randomizing  
439 the butterfly tips, although maintaining the same host trees and association matrix showed  
440 weaker evidence of phylogenetic congruence (24.2% of the sites had a significant associations,  
441 median  $P = 0.200$ ).

442



443

444 **Figure 4.** Relationship between phylogenetic congruence signal and landscape simplification. (a) The  
445 proportion of sites with significant phylogenetic congruence signal derived after testing for global  
446 congruence in the local trophic networks. (b) Analysis conducted considering randomized butterfly tips.  
447 Landscape simplification was measured as the proportion of arable land cover in a radius of 2 km  
448 surrounding each site. Fitted line is a generalized linear mixed model estimate.

449

450 Landscape simplification reduced the phylogenetic congruence, as indicated by a negative  
451 relationship between the probability of observing a phylogenetic congruence and the cover of  
452 arable land ( $\beta = -0.014$ ; CIs =  $-0.029, -0.003$ ;  $P = 0.019$ ) (Fig. 4a). The same pattern was  
453 confirmed using the reduced number of associations to one host plant per butterfly ( $\beta = -0.019$ ;  
454 CIs =  $-0.035, -0.003$ ;  $P = 0.018$ ). Phylogenetic congruence was positively related to the

455 proportion of butterfly specialist ( $\beta = 0.024$ ; CIs = 0.008, 0.037;  $P = 0.001$ ) (Appendix S1, Fig.  
456 S6). However, the negative relationship between landscape simplification and phylogenetic  
457 congruence was not confirmed considering the randomized butterfly tips (i.e. no effect of  
458 landscape simplification on phylogenetic congruence;  $\beta = -0.008$ , CIs =  $-0.023$ , 0.008;  $P =$   
459 0.316) (Fig. 4b).

460

## 461 **Discussion**

462 Our results provide clear evidence that landscape simplification through conversion into arable  
463 land weakens the functional and phylogenetic association between terrestrial producer and  
464 consumer diversity. In accordance with our hypotheses, the observed loss of functional and  
465 phylogenetic associations with increased landscape simplification occurred even without  
466 immediate reductions in species richness. The loss of functional associations could be  
467 detrimental for specialized species, in the long term (Tilman *et al.*, 1994; Kuussaari *et al.*, 2009),  
468 suggesting that landscape simplification incurs a substantial extinction debt. The consumer-  
469 mediated losses in host plant species could be less pronounced than those of resource-mediated  
470 losses in consumers, but these effects could be reversed in the long term (Weiner *et al.*, 2014).

471 Local plant diversity showed a strong bottom-up effect on butterfly diversity in the most  
472 complex landscapes, but this effect disappeared in simple landscapes. The functional  
473 associations between plant and butterflies are, therefore, the results of processes that act not only  
474 locally but are also dependent on the surrounding landscape context (Tschardtke *et al.*, 2012).  
475 Landscape simplification can alter such associations through habitat loss and fragmentation.  
476 Probably, the greater habitat diversity and the higher proportion of semi-natural habitats in  
477 complex landscapes positively affect the local persistence of specialist butterfly species

478 (Öckinger *et al.*, 2010). Generalist species are less susceptible to fragmentation because they are  
479 likely capable of finding alternative resources in simplified landscapes (Öckinger *et al.*, 2010).  
480 Hence, the higher degree of butterfly host plant specialization in complex landscapes would  
481 explain the strong relationship between host plant diversity and butterfly diversity (Weiner *et al.*,  
482 2014). Consequently, this could benefit the stability of trophic interactions through resource  
483 diversity, in part by reducing the runaway consumption of plants (Haddad *et al.*, 2011;  
484 Carvalheiro *et al.*, 2014).

485 Another important finding of this study is the importance of plant diversity in  
486 determining the structure of consumer communities in complex landscapes (Scherber *et al.*,  
487 2010). Consequently, positive bottom-up effects of plant diversity to higher trophic levels could  
488 benefit trophic stability by reducing the variability in herbivore abundance and diversity within  
489 sites (Haddad *et al.*, 2011; Borer *et al.*, 2012). Although it has been argued that adult butterflies  
490 are often generalist feeders with low specialization on specific plant traits (Hardy *et al.*, 2007),  
491 our results reflect potential non-random interactions between flowers and adult butterflies. This  
492 would indicate a certain degree of floral specialization among butterfly species to a set of floral  
493 traits such as flower size, color, morphology, and nectar content (Junker *et al.*, 2013; Carvalheiro  
494 *et al.*, 2014; Curtis *et al.*, 2015; Lebeau *et al.*, 2016). Our findings also highlight the limitation of  
495 using plant phylogenetic diversity to predict butterfly diversity. Similar results have been found  
496 in other studies (Whitfeld *et al.*, 2012; Pellissier *et al.*, 2013), suggesting that a global measure of  
497 diversity of plant lineages does not necessarily reflect the associations between hosts and  
498 consumers.

499 Our results revealed that landscape simplification also reduced the phylogenetic  
500 congruence among host plants and butterflies. The weaker congruence among host plant and

501 butterfly phylogenies in highly modified landscapes indicates that closely related butterfly  
502 species are more generalist in the potential resource lineages used (Pellissier *et al.*, 2013).  
503 Although specialization is a necessary precondition for phylogenetic congruence, this is not  
504 necessarily indicative of co-speciation because species can descend from a generalist ancestor  
505 (Clayton *et al.*, 2004; de Vienne *et al.*, 2013; Althoff *et al.*, 2014). However, the change in  
506 butterfly specialization is not the only process underpinning shifts in phylogenetic association  
507 with landscape simplification, suggesting a potential effect of co-evolution (Jenkins *et al.*, 2012).  
508 By randomizing the tips of butterfly trees in the phylogenetic congruence analysis, we first found  
509 that associations between host plant and butterfly strongly decreased, and second, that the effect  
510 of landscape simplification on phylogenetic congruence signal was no longer significant,  
511 consistent with a potential signature of co-evolution. Altering plant-consumer interactions could  
512 impact the fitness of both partners affecting population growth and, in the long term, the co-  
513 evolutionary relationships among species (Agrawal *et al.*, 2006). For instance, given the role of  
514 insect herbivores in the diversification of plant species and their traits, the loss of plant-consumer  
515 associations has potential to alter ecological and evolutionary dynamics in plant populations and  
516 communities (Agrawal *et al.*, 2012). Consequently, herbivore populations could evolve  
517 adaptations to these changes in the plant community, such as host shifts (Singer *et al.*, 1993).  
518 However, there could be a serious risk for insects that become dependent on the perpetuation of  
519 this adaptation to respond to anthropogenic disturbances. Ongoing land use changes are  
520 happening more rapidly than the adaptation that the insects can evidently realize, and thereby  
521 could increase their risk of extinction (Singer *et al.*, 1993; Koh *et al.*, 2004; Krauss *et al.*, 2010;  
522 Scheper *et al.*, 2014). Koh *et al.* (2004) have demonstrated that a large number of butterfly  
523 species are already “co-endangered” as their host species are currently listed as endangered,

524 indicating a need to increase current estimates of extinction risk by taking species co-extinctions  
525 into account. These co-extinctions can lead to the loss of irreplaceable evolutionary and co-  
526 evolutionary history (Purvis *et al.*, 2000) that has contributed to creating a high diversity of plant  
527 and butterfly species (Fordyce, 2010). While land-use change remains the predominant threat to  
528 species persistence and thus to trophic associations, climate change could also dramatically alter  
529 these associations by shifting the geographic distribution of species and driving spatial or  
530 temporal mismatches among previously co-occurring species (Thackeray *et al.*, 2010; Colwell *et*  
531 *al.*, 2012).

532 From an applied perspective, there is a lack of specific reference to species interactions  
533 among conservation initiatives, probably because the importance of such interactions is not well  
534 understood yet (Soulé *et al.*, 2005). Conservation efforts might fail if we do not consider how  
535 landscape simplification affects the cross-trophic-level diversity associations in a local  
536 community (Harvey *et al.*, 2016). For instance, conservation interventions aimed at restoring  
537 consumer diversity by enhancing local plant resources is likely to be more effective in regions  
538 where landscape simplification has been less marked. Therefore, we suggest that monitoring of  
539 the relationships between the diversities of these taxa can serve as an early warning signal of  
540 ecosystem health and conservation status (Valiente-Banuet *et al.*, 2015). In conclusion, although  
541 most of the research on biodiversity loss have largely focused on species richness of individual  
542 taxonomic or functional groups, our novel approach reveals that other components of  
543 biodiversity are lost well before the species richness variation. Our measures of functional and  
544 phylogenetic associations across trophic levels, and how they change in response to landscape  
545 simplification, contribute to a growing understanding of the properties that determine ecosystem  
546 resilience.

547 **Acknowledgments**

548 The authors thank two anonymous reviewers for comments that helped to improve the  
549 manuscript. We are grateful to P. Paolucci for the butterfly and plant images. The research  
550 leading to these results received funding from the European Union Seventh Framework  
551 Programme (FP7) under grant agreement no. 311781, LIBERATION Project  
552 ([www.fp7liberation.eu](http://www.fp7liberation.eu)), to L.M and R.B. E.Ö. received support from the Swedish research  
553 council Formas.

For Review Only

554 **References**

- 555 Aeschimann D, Lauber K, Moser DM, Theurillat JP (2004) *Flora Alpina*. Zanichelli, Bologna.
- 556 Agrawal AA, Lau JA, Hambäck PA (2006) Community heterogeneity and the evolution of  
557 interactions between plants and insect herbivores. *The Quarterly Review of Biology*, **81**,  
558 349–376.
- 559 Agrawal AA, Hastings AP, Johnson MTJ, Maron JL, Salminen J (2012) Insect herbivores drive  
560 real-time ecological and evolutionary change in plant populations. *Science*, **338**, 113–116.
- 561 Allan E, Manning P, Alt F et al. (2015) Land use intensification alters ecosystem  
562 multifunctionality via loss of biodiversity and changes to functional composition. *Ecology*  
563 *Letters*, **18**, 834–843.
- 564 Althoff DM, Segraves KA, Johnson MTJ (2014) Testing for coevolutionary diversification:  
565 linking pattern with process. *Trends in Ecology & Evolution*, **29**, 82–89.
- 566 Benson DA, Karsch-Mizrachi I, Lipman DJ, Ostell J, Sayers EW (2011) GenBank. *Nucleic Acids*  
567 *Research*, **39**, D32–D37.
- 568 Bommarco R, Lindborg R, Marini L, Öckinger E (2014) Extinction debt for plants and flower-  
569 visiting insects in landscapes with contrasting land use history. *Diversity and Distributions*,  
570 **20**, 591–599.
- 571 Borer ET, Seabloom EW, Tilman D, Novotny V (2012) Plant diversity controls arthropod  
572 biomass and temporal stability. *Ecology Letters*, **15**, 1457–1464.
- 573 Bremer B, Bremer K, Chase MW et al. (2009) An update of the Angiosperm Phylogeny Group  
574 classification for the orders and families of flowering plants: APG III. *Botanical Journal of*  
575 *the Linnean Society*, **161**, 105–121.
- 576 Burnham KP, Anderson DR (2002) *Model Selection and Multimodel Inference: a Practical*

577 *Information-theoretic Approach*, 2nd edn. Springer-Verlag, New York.

578 Cardinale BJ, Duffy JE, Gonzalez A et al. (2012) Biodiversity loss and its impact on humanity.  
579 *Nature*, **489**, 326–326.

580 Carvalho LG, Biesmeijer JC, Benadi G et al. (2014) The potential for indirect effects between  
581 co-flowering plants via shared pollinators depends on resource abundance, accessibility and  
582 relatedness. *Ecology Letters*, **17**, 1389–1399.

583 Chapin III FS, Zavaleta ES, Eviner VT et al. (2000) Consequences of changing biodiversity.  
584 *Nature*, **405**, 234–242.

585 Clayton DH, Bush SE, Johnson KP (2004) Ecology of congruence: past meets present.  
586 *Systematic Biology*, **53**, 165–173.

587 Colwell RK, Dunn RR, Harris NC (2012) Coextinction and persistence of dependent species in a  
588 changing world. *Annual Review of Ecology, Evolution, and Systematics*, **43**.

589 Curtis RJ, Brereton TM, Dennis RLH, Carbone C, Isaac NJB (2015) Butterfly abundance is  
590 determined by food availability and is mediated by species traits. *Journal of Applied  
591 Ecology*, **52**, 1676–1684.

592 Dainese M, Inclán Luna D, Sitzia T, Marini L (2015) Testing scale-dependent effects of semi-  
593 natural habitats on farmland biodiversity. *Ecological Applications*, **25**, 1681–1690.

594 Duffy JE (2002) Biodiversity and ecosystem function: the consumer connection. *Oikos*, **99**, 201–  
595 219.

596 Duffy JE, Cardinale BJ, France KE, McIntyre PB, Thébaud E, Loreau M (2007) The functional  
597 role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters*, **10**,  
598 522–538.

599 Dunne JA, Williams RJ, Martinez ND (2002) Network structure and biodiversity loss in food

600 webs : robustness increases with connectance. *Ecology Letters*, **5**, 558–567.

601 Eklöf A, Jacob U, Kopp J et al. (2013) The dimensionality of ecological networks. *Ecology*  
602 *Letters*, **16**, 577–83.

603 Estes JA, Duggins DO, Rathbun GB (1989) The ecology of extinctions in kelp forest  
604 communities. *Conservation Biology*, **3**, 252–264.

605 Ferrer-Paris JR, Sánchez-Mercado A, Vilorio AL, Donaldson J (2013) Congruence and diversity  
606 of butterfly-host plant associations at higher taxonomic levels. *PLoS ONE*, **8**, e63570.

607 Foley JA, Defries R, Asner GP et al. (2005) Global consequences of land use. *Science*, **309**, 570–  
608 574.

609 Fordyce JA (2010) Host shifts and evolutionary radiations of butterflies. *Proceedings of the*  
610 *Royal Society of Biological Sciences*, **277**, 3735–3743.

611 Gabriel D, Sait SM, Hodgson JA, Schmutz U, Kunin WE, Benton TG (2010) Scale matters: the  
612 impact of organic farming on biodiversity at different spatial scales. *Ecology Letters*, **13**,  
613 858–869.

614 Garnier E, Cortez J, Billès G et al. (2004) Plant functional ecology markers capture ecosystems  
615 properties during secondary succession. *Ecology*, **85**, 2630–2637.

616 Haddad NM, Crutsinger GM, Gross K, Haarstad J, Knops JMH, Tilman D (2009) Plant species  
617 loss decreases arthropod diversity and shifts trophic structure. *Ecology Letters*, **12**, 1029–  
618 1039.

619 Haddad NM, Crutsinger GM, Gross K, Haarstad J, Tilman D (2011) Plant diversity and the  
620 stability of foodwebs. *Ecology Letters*, **14**, 42–46.

621 Hambäck PA, Bergman KO, Bommarco R, Krauss J, Kuussaari M, Pöyry J, Öckinger E (2010)  
622 Allometric density responses in butterflies: The response to small and large patches by

623 small and large species. *Ecography*, **33**, 1149–1156.

624 Hardy PB, Sparks TH, Isaac NJB, Dennis RLH (2007) Specialism for larval and adult consumer  
625 resources among British butterflies: Implications for conservation. *Biological Conservation*,  
626 **138**, 440–452.

627 Harvey E, Gounand I, Ward C, Altermatt F (2016) Bridging ecology and conservation: from  
628 ecological networks to ecosystem function. *Journal of Applied Ecology*. doi: 10.1111/1365-  
629 2664.12769

630 Jenkins T, Thomas GH, Hellgren O, Owens IPF (2012) Migratory behavior of birds affects their  
631 coevolutionary relationship with blood parasites. *Evolution*, **66**, 740–751.

632 Junker RR, Blüthgen N, Brehm T, Binkenstein J, Paulus J, Martin Schaefer H, Stang M (2013)  
633 Specialization on traits as basis for the niche-breadth of flower visitors and as structuring  
634 mechanism of ecological networks. *Functional Ecology*, **27**, 329–341.

635 Klotz S, Kühn I, Durka W (2002) *BIOLFLOR – Eine Datenbank zu biologisch-ökologischen*  
636 *Merkmale der Gefäßpflanzen in Deutschland. Schriftenreihe für Vegetationskunde*. Bonn:  
637 Bundesamt für Naturschutz.

638 Koh LP, Dunn RR, Sodhi NS, Colwell RK, Proctor HC, Smith VS (2004) Species coextinctions  
639 and the biodiversity crisis. *Science*, **305**, 1632–1634.

640 Krauss J, Bommarco R, Guardiola M et al. (2010) Habitat fragmentation causes immediate and  
641 time-delayed biodiversity loss at different trophic levels. *Ecology Letters*, **13**, 597–605.

642 Kuussaari M, Bommarco R, Heikkinen RK et al. (2009) Extinction debt: a challenge for  
643 biodiversity conservation. *Trends in Ecology & Evolution*, **24**, 564–571.

644 Lebeau J, Wesselingh RA, Van Dyck H (2016) Floral resource limitation severely reduces  
645 butterfly survival, condition and flight activity in simplified agricultural landscapes.

646 *Oecologia*, **180**, 421–427.

647 Legendre P, Desdevises Y, Bazin E (2002) A statistical test for host-parasite coevolution.  
648 *Systematic Biology*, **51**, 217–234.

649 Manning P, Gossner MM, Bossdorf O et al. (2015) Grassland management intensification  
650 weakens the associations among the diversities of multiple plant and animal taxa. *Ecology*,  
651 **96**, 1492–1501.

652 Marini L, Fontana P, Klimek S, Battisti A, Gaston KJ (2009) Impact of farm size and topography  
653 on plant and insect diversity of managed grasslands in the Alps. *Biological Conservation*,  
654 **142**, 394–403.

655 Marini L, Öckinger E, Bergman K-O et al. (2014) Contrasting effects of habitat area and  
656 connectivity on evenness of pollinator communities. *Ecography*, **37**, 544–551.

657 McConkey KR, O’Farrill G (2015) Cryptic function loss in animal populations. *Trends in*  
658 *Ecology & Evolution*, **30**, 182–189.

659 Meehan TD, Werling BP, Landis DA, Gratton C (2011) Agricultural landscape simplification  
660 and insecticide use in the Midwestern United States. *Proceedings of the National Academy*  
661 *of Sciences of the United States of America*, **108**, 11500–11505.

662 Mouchet MA, Villéger S, Mason NWH, Mouillot D (2010) Functional diversity measures: an  
663 overview of their redundancy and their ability to discriminate community assembly rules.  
664 *Functional Ecology*, **24**, 867–876.

665 Newbold T, Hudson LN, Hill SLL et al. (2015) Global effects of land use on local terrestrial  
666 biodiversity. *Nature*, **520**, 45–50.

667 Öckinger E, Schweiger O, Crist TO et al. (2010) Life-history traits predict species responses to  
668 habitat area and isolation: a cross-continental synthesis. *Ecology Letters*, **13**, 969–979.

669 Öckinger E, Lindborg R, Sjödin NE, Bommarco R (2012) Landscape matrix modifies richness of  
670 plants and insects in grassland fragments. *Ecography*, **35**, 259–267.

671 Ødegaard F, Diserud OH, Østbye K (2005) The importance of plant relatedness for host  
672 utilization among phytophagous insects. *Ecology Letters*, **8**, 612–617.

673 Oliver TH, Heard MS, Isaac NJB et al. (2015) Biodiversity and resilience of ecosystem  
674 functions. *Trends in Ecology & Evolution*, **30**, 673–684.

675 Pellissier L, Pottier J, Vittoz P, Dubuis A, Guisan A (2010) Spatial pattern of floral morphology:  
676 possible insight into the effects of pollinators on plant distributions. *Oikos*, **119**, 1805–1813.

677 Pellissier L, Ndiribe C, Dubuis A, Pradervand J-N, Salamin N, Guisan A, Rasmann S (2013)  
678 Turnover of plant lineages shapes herbivore phylogenetic beta diversity along ecological  
679 gradients. *Ecology Letters*, **16**, 600–608.

680 Pöyry J, Paukkunen J, Heliölä J, Kuussaari M (2009) Relative contributions of local and regional  
681 factors to species richness and total density of butterflies and moths in semi-natural  
682 grasslands. *Oecologia*, **160**, 577–587.

683 Purvis A, Agapow P-M, Gittleman JL, Mace GM (2000) Nonrandom extinction and the loss of  
684 evolutionary history. *Science*, **288**, 328–330.

685 Rao CR (1982) Diversity and dissimilarity coefficients: a unified approach. *Theoretical*  
686 *Population Biology*, **21**, 24–43.

687 Ricotta C, Moretti M (2011) CWM and Rao's quadratic diversity: a unified framework for  
688 functional ecology. *Oecologia*, **167**, 181–8.

689 Rosas-Guerrero V, Aguilar R, Martén-Rodríguez S, Ashworth L, Lopezaraiza-Mikel M, Bastida  
690 JM, Quesada M (2014) A quantitative review of pollination syndromes: do floral traits  
691 predict effective pollinators? *Ecology Letters*, **17**, 388–400.

692 Royal Botanic Gardens Kew (2014) Seed Information Database (SID). Version 7.1. Available  
693 from: <http://data.kew.org/sid/>.

694 Scheper J, Reemer M, van Kats R et al. (2014) Museum specimens reveal loss of pollen host  
695 plants as key factor driving wild bee decline in The Netherlands. *Proceedings of the*  
696 *National Academy of Sciences of the United States of America*, **111**, 17552–17557.

697 Scherber C, Eisenhauer N, Weisser WW et al. (2010) Bottom-up effects of plant diversity on  
698 multitrophic interactions in a biodiversity experiment. *Nature*, **468**, 553–556.

699 Singer MS, Thomas CD, Parmesan C (1993) Rapid human-induced evolution of insect-host  
700 associations. *Nature*, **366**, 681–683.

701 Smith B, Wilson JB (1996) A consumer's guide to evenness indices. *Oikos*, **76**, 70–82.

702 Soulé ME, Esties JA, Miller B, Honnold DL (2005) Strongly interacting species: conservation  
703 policy, management, and ethics. *BioScience*, **55**, 168–176.

704 Swenson NG (2014) *Functional and Phylogenetic Ecology in R*. Springer, New York.

705 Thackeray SJ, Sparks TH, Frederiksen M et al. (2010) Trophic level asynchrony in rates of  
706 phenological change for marine, freshwater and terrestrial environments. *Global Change*  
707 *Biology*, **16**, 3304–3313.

708 Tilman D, May R, Lehman C, Nowak M (1994) Habitat destruction and the extinction debt.  
709 *Nature*, **371**, 65–66.

710 Tschardtke T, Brandl R (2004) Plant-insect interactions in fragmented landscapes. *Annual*  
711 *Review of Entomology*, **49**, 405–430.

712 Tschardtke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C (2005) Landscape perspectives  
713 on agricultural intensification and biodiversity - ecosystem service management. *Ecology*  
714 *Letters*, **8**, 857–874.

715 Tscharrntke T, Tylianakis JM, Rand TA et al. (2012) Landscape moderation of biodiversity  
716 patterns and processes - eight hypotheses. *Biological Reviews*, **87**, 661–685.

717 Turner II BL, Lambin EF, Reenberg A (2007) The emergence of land change science for global  
718 environmental change and sustainability. *Proceedings of the National Academy of Sciences*  
719 *of the United States of America*, **104**, 20666–20671.

720 Valiente-Banuet A, Aizen MA, Alcántara JM et al. (2015) Beyond species loss: the extinction of  
721 ecological interactions in a changing world. *Functional Ecology*, **29**, 299–307.

722 Verburg PH, Neumann K, Nol L (2011) Challenges in using land use and land cover data for  
723 global change studies. *Global Change Biology*, **17**, 974–989.

724 de Vienne DM, Refrégier G, López-Villavicencio M, Tellier A, Hood ME, Giraud T (2013)  
725 Coespeciation vs hos-shift speciation: methodsfor testing, evidence from natural  
726 associations and ralisation to coevolution. *New Phytologist*, **198**, 347–385.

727 Weiblen GD, Webb CO, Novotny V, Basset Y, Miller (2006) Phylogenetic dispersion of host use  
728 in a tropical insect herbivore community. *Ecology*, **87**, S62–S75.

729 Weiner CN, Werner M, Linsenmair KE, Blüthgen N (2014) Land-use impacts on plant-pollinator  
730 networks: interaction strength and specialization predict pollinator declines. *Ecology*, **95**,  
731 466–474.

732 Whitfeld TJS, Novotny V, Miller SE, Hrccek J, Klimes P, Weiblen GD (2012) Predicting tropical  
733 insect herbivore abundance from host plant traits and phylogeny. *Ecology*, **93**, S211–S222.

734 Winfree R, Bartomeus I, Cariveau DP (2011) Native pollinators in anthropogenic habitats.  
735 *Annual Review of Ecology, Evolution, and Systematics*, **42**, 1–22.

736

737 **Supporting Information**

738 Additional Supporting Information may be found in the online version of this article:

739 Appendix S1. Supplementary Tables (S1-S4) and Figures (S1-S7).

740 Appendix S2. Phylogeny.

For Review Only

## Supporting Information

for Dainese et al. “*Land-use simplification weakens the association between terrestrial producer and consumer diversity in Europe*”

### Appendix S1 – Supplementary Tables and Figures

**Table S1.** Description of the datasets included in the study.

Dataset	Habitat type	N sites	Area (ha) (min-max)	N species <sup>1</sup>	Sampling method <sup>2</sup>	Arable (%) (min-max) <sup>3</sup>	Reference
Finland (a)	Dry seminatural grasslands	40	1.1 ± 1.2 (0.1-6.5)	B: 34  H: 19; F: 181	B: Searching time (t) logarithmically related to habitat area (A) $t = \ln(A + 0.75) \times 30$ P: 1 plot of 0.25 ha	33.9 (0.1-74.7)	Unpublished data <sup>4</sup>
Finland (b)	Mesic seminatural grasslands	48	1.3 ± 1.2 (0.3-6.0)	B: 51  H: 20; F: 194	B: Searching time (t) logarithmically related to habitat area (A) $t = \ln(A + 0.75) \times 30$ P: 1 plot of 0.25 ha	31.2 (0.2-60.6)	Pöyry <i>et al.</i> , 2009
Italy (a)	Grassland field margins	90	0.16 ± 0.07 (0.04-0.37)	B: 43  H: 21; F: 92	B: Straight line transects 50 m apart P: 3 plots of 1 × 2 m <sup>2</sup>	61.9 (33.3-88.2)	Dainese <i>et al.</i> , 2015
Italy (b)	Dry seminatural grasslands	27	1.1 ± 1.2 (0.4-8.3)	B: 72  H: 22; F: 68	B: Fixed rectangular area of 50 × 50 m P: 5 plots 1 × 1 m	49.9 (3.2-88.7)	Unpublished data
Italy (c)	Mesic seminatural grasslands	120	3.1 ± 2.2 (0.5-14.3)	B: 81  H: 31; F: 140	B: Fixed rectangular area of 25 × 40 m P: 2 × 16 m <sup>2</sup> quadrats	8.8 (0-62.4)	Marini <i>et al.</i> , 2009
Sweden	Dry to mesic seminatural pastures	45	4.7 ± 2.7 (1.9-16.3)	B: 50  H: 24; F: 137	B: Transects proportional to area (200 m ha <sup>-1</sup> ) P: 10 randomly placed m <sup>2</sup> plots	44.9 (2-86.6)	Ockinger <i>et al.</i> , 2012
UK (2007)	Grassland field margins	95	5.6 ± 8.0 (0.7-26.6)	B: 19  H: 9; F: 135	B: Standardized transect walks of 15 m P: 3 × 1 m <sup>2</sup> quadrats	44.1 (16.6-81.5)	Gabriel <i>et al.</i> , 2010
UK (2008)	Grassland field margins	96	5.6 ± 8.0 (0.7-26.6)	B: 20  H: 8; F: 135	B: Standardized transect walks of 15 m P: 3 × 1 m <sup>2</sup> quadrats	42.1 (8.5-74.2)	Gabriel <i>et al.</i> , 2010

<sup>1</sup>N species: total number of butterflies (B), host plants (H), and flowering forbs (F) in the dataset.

<sup>2</sup>Sampling method: butterflies (B) and plants (P) in the dataset

<sup>3</sup>Arable (%): mean (min-max) arable land cover (%) in a radius of 2 km surrounding each site.

<sup>4</sup>Primary data unpublished but previously included in three synthesis studies (Hambäck *et al.*, 2010; Ockinger *et al.*, 2010; Marini *et al.*, 2014). ‡

## References Table S1

Dainese M, Inclán Luna D, Sitzia T, Marini L (2015) Testing scale-dependent effects of semi-natural habitats on farmland biodiversity.

*Ecological Applications*, **25**, 1681–1690.

Gabriel D, Sait SM, Hodgson JA, Schmutz U, Kunin WE, Benton TG (2010) Scale matters: the impact of organic farming on biodiversity at different spatial scales. *Ecology letters*, **13**, 858–69.

Hambäck PA, Bergman KO, Bommarco R, Krauss J, Kuussaari M, Pöyry J, Öckinger E (2010) Allometric density responses in butterflies: the response to small and large patches by small and large species. *Ecography*, **33**, 1149–1156.

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

Marini L, Öckinger E, Bergman K-O *et al.* (2014) Contrasting effects of habitat area and connectivity on evenness of pollinator communities. *Ecography*, **37**, 544–551.

Ockinger E, Schweiger O, Crist TO *et al.* (2010) Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. *Ecology letters*, **13**, 969–79.

Öckinger E, Lindborg R, Sjödin NE, Bommarco R (2012) Landscape matrix modifies richness of plants and insects in grassland fragments. *Ecography*, **35**, 259–267.

Pöyry J, Paukkunen J, Heliölä J, Kuussaari M (2009) Relative contributions of local and regional factors to species richness and total density of butterflies and moths in semi-natural grasslands. *Oecologia*, **160**, 577–87.

**Table S2.** Butterfly species and larval host plants differentiated for each country. Only butterflies that feed on grassland species are reported.

Butterfly species	Butterfly occurrence								Host plants			
	FIN (a)	FIN (b)	ITA (a)	ITA (b)	ITA (c)	SWE	UK (2007)	UK (2008)	Finland	Italy	Sweden	UK
<i>Aglais io</i>	x	x	x	x	x	x	x	x	<i>Urtica dioica</i>	<i>Urtica dioica</i>	<i>Urtica dioica</i>	<i>Urtica dioica</i>
<i>Aglais urticae</i>	x	x		x	x	x	x	x	<i>Urtica dioica</i>	<i>Urtica dioica</i>	<i>Urtica dioica</i>	<i>Urtica dioica</i>
<i>Agriades optilete</i>	x	x							<i>Vaccinium uliginosum</i>			
<i>Anthocharis cardamines</i>	x	x		x	x	x			<i>Brassicaceae</i>	<i>Alliaria petiolata</i>	<i>Brassicaceae</i>	
<i>Aphantopus hyperantus</i>	x	x		x	x	x	x	x	<i>Poaceae</i>	<i>Poaceae</i>	<i>Poaceae</i>	<i>Poaceae</i>
<i>Araschnia levana</i>		x							<i>Urtica dioica</i>			
<i>Argynnis adippe</i>	x	x			x	x			<i>Viola</i> spp.	<i>Viola</i> spp.	<i>Viola</i> spp.	
<i>Argynnis aglaja</i>	x	x			x	x			<i>Viola</i> spp.	<i>Viola</i> spp.	<i>Viola</i> spp.	
<i>Argynnis niobe</i>		x			x				<i>Viola</i> spp.	<i>Viola</i> spp.		
<i>Argynnis paphia</i>			x	x	x	x				<i>Viola</i> spp.	<i>Viola</i> spp.	
<i>Aricia agestis</i>			x		x					<i>Erodium</i> spp., <i>Geranium</i> spp.		
<i>Aricia artaxerxes</i>		x				x			<i>Geranium</i> spp.		<i>Geranium sanguineum</i> , <i>G. sylvaticum</i>	
<i>Aricia eumedon</i>		x				x			<i>Geranium</i> spp.		<i>Geranium sanguineum</i> , <i>G. sylvaticum</i>	
<i>Boloria dia</i>				x	x					<i>Viola</i> spp.		
<i>Boloria euphrosyne</i>	x				x	x			<i>Viola</i> spp.	<i>Viola</i> spp.	<i>Vaccinium uliginosum</i> , <i>Viola</i> spp.	
<i>Boloria selene</i>	x	x			x	x			<i>Viola</i> spp.	<i>Viola</i> spp.	<i>Viola palustris</i> , <i>V. riviniana</i>	
<i>Boloria thore</i>					x					<i>Viola</i> spp.		
<i>Boloria titania</i>					x					<i>Polygonum</i> spp., <i>Viola</i> spp.		

<i>Brenthis hecate</i>			x	x	x				<i>Filependula</i> spp.
<i>Brenthis ino</i>	x	x			x	x			<i>Viola</i> spp. <i>Filipendula</i> spp., <i>Rubus</i> spp., <i>Sanguisorba</i> spp.
<i>Callophrys rubi</i>	x	x		x	x	x			<i>Ericaceae</i> , <i>Rubus</i> <i>idaeus</i> <i>Anthyllis</i> spp., <i>Hellianthemum</i> spp., <i>Vaccinium</i> spp. <i>Malva</i> spp.
<i>Carcharodus alceae</i>				x					<i>Poaceae</i>
<i>Carterocephalus palaemon</i>				x	x				<i>Poaceae</i>
<i>Carterocephalus silvicola</i>		x							<i>Poaceae</i>
<i>Coenonympha arcania</i>				x	x	x			<i>Poaceae</i>
<i>Coenonympha glycerion</i>	x	x							<i>Poaceae</i>
<i>Coenonympha pamphilus</i>	x	x	x	x	x	x	x		<i>Poaceae</i>
<i>Colias alfacariensis</i>				x	x				<i>Coronilla varia</i> , <i>Hippocrepis</i> <i>comosa</i> <i>Fabaceae</i>
<i>Colias croceus</i>			x	x	x				<i>Fabaceae</i>
<i>Colias hyale</i>				x	x				<i>Fabaceae</i>
<i>Colias palaeno</i>							x		<i>Vaccinium</i> <i>uliginosum</i>
<i>Cupido alcetas</i>					x				<i>Coronilla varia</i> , <i>Galega</i> <i>officinalis</i> <i>Fabaceae</i>
<i>Cupido argiades</i>		x	x	x	x				<i>Fabaceae</i>
<i>Cupido minimus</i>				x	x	x			<i>Anthyllis</i> <i>vulneraria</i> <i>Poaceae</i>
<i>Erebia aethiops</i>					x				<i>Poaceae</i>
<i>Erebia euryale</i>					x				<i>Poaceae</i>
<i>Erebia ligea</i>	x	x			x	x			<i>Poaceae</i>
<i>Erebia medusa</i>					x				<i>Poaceae</i>
<i>Erynnis tages</i>				x	x	x			<i>Hippocrepis</i> <i>comosa</i> , <i>Lotus</i> <i>corniculatus</i>

<i>Euphydryas maturna</i>		x							<i>Melampyrum</i> spp., <i>Veronica</i> <i>longifolia</i>				
<i>Glaucopsyche alexis</i>				x	x	x				<i>Fabaceae</i>	<i>Astragalus</i> <i>glycyphyllus</i> , <i>Lotus</i> <i>corniculatus</i>		
<i>Hamearis lucina</i>						x				<i>Primula veris</i> , <i>P.</i> <i>vulgaris</i>			
<i>Hesperia comma</i>				x	x	x				<i>Festuca ovina</i> , <i>Lolium perenne</i>	<i>Festuca ovina</i>		
<i>Heteropterus morpheus</i>				x						<i>Poaceae</i>			
<i>Hipparchia fagi</i>				x						<i>Poaceae</i>			
<i>Hipparchia semele</i>	x		x	x					<i>Poaceae</i>	<i>Poaceae</i>			
<i>Issoria lathonia</i>	x		x	x	x	x			<i>Viola</i> spp.	<i>Viola</i> spp.	<i>Viola tricolor</i> , <i>V.</i> <i>arvensis</i>		
<i>Lasiommata maera</i>	x	x				x	x		<i>Poaceae</i>	<i>Poaceae</i>	<i>Poaceae</i>		
<i>Lasiommata megera</i>				x	x	x	x			<i>Poaceae</i>	<i>Poaceae</i>		
<i>Lasiommata petropolitana</i>		x						x	<i>Poaceae</i>		<i>Dactylis</i> <i>glomerata</i> , <i>Festuca rubra</i>		
<i>Leptidea sinapis</i>	x	x	x	x	x	x	x	x	<i>Lathyrus</i> spp.	<i>Lathyrus</i> spp., <i>Lotus</i> spp., <i>Vicia</i> <i>cracca</i>	<i>Lathyrus</i> <i>linifolius</i>	<i>Lathyrus</i> spp., <i>Lotus</i> spp., <i>Vicia</i> <i>cracca</i>	
<i>Lycaena alciphron</i>				x	x					<i>Rumex</i> spp.			
<i>Lycaena dispar</i>				x						<i>Rumex</i> spp.			
<i>Lycaena hippothoe</i>								x	<i>Rumex</i> spp.	<i>Rumex</i> spp.	<i>Rumex acetosa</i>		
<i>Lycaena phlaeas</i>	x	x	x	x	x	x	x	x	<i>Rumex</i> spp.	<i>Rumex</i> spp.	<i>Rumex</i> spp.	<i>Rumex</i> spp.	
<i>Lycaena tityrus</i>				x	x	x				<i>Rumex</i> spp.			
<i>Lycaena virgaurea</i>	x	x				x	x		<i>Rumex</i> spp.	<i>Rumex</i> spp.	<i>Rumex</i> spp.		
<i>Maniola jurtina</i>				x	x	x	x	x		<i>Poaceae</i>	<i>Poaceae</i>	<i>Poaceae</i>	
<i>Melanargia galathea</i>				x	x	x		x		<i>Poaceae</i>		<i>Poaceae</i>	
<i>Melitaea athalia</i>	x	x	x	x	x	x			<i>Melampyrum</i> spp., <i>Plantago</i> spp., <i>Veronica</i> spp.	<i>Melampyrum</i> spp., <i>Plantago</i> spp., <i>Veronica</i> spp.	<i>Melampyrum</i> spp.		

<i>Melitaea aurelia</i>				x	x					<i>Plantago lanceolata</i>			
<i>Melitaea cinxia</i>				x	x	x				<i>Centaurea</i> spp., <i>Plantago</i> spp., <i>Veronica</i> spp.	<i>Plantago lanceolata</i> , <i>Veronica spicata</i>		
<i>Melitaea diamina</i>			x	x						<i>Melampyrum</i> spp., <i>Valeriana</i> spp.			
<i>Melitaea didyma</i>			x	x	x					<i>Plantago</i> spp., <i>Stachys</i> spp., <i>Valeriana</i> spp., <i>Veronica</i> spp.			
<i>Melitaea phoebe</i>			x	x						<i>Carduus</i> spp., <i>Centaurea</i> spp., <i>Cirsium</i> spp., <i>Plantago</i> spp.			
<i>Minois dryas</i>			x	x	x					<i>Poaceae</i>			
<i>Ochlodes sylvanus</i>	x	x	x	x		x	x	x	<i>Poaceae</i>	<i>Poaceae</i>	<i>Poaceae</i>		
<i>Papilio machaon</i>		x	x	x	x	x			<i>Apiaceae</i>	<i>Apiaceae</i>	<i>Apiaceae</i>		
<i>Pararge aegeria</i>		x	x	x	x		x	x	<i>Poaceae</i>	<i>Poaceae</i>		<i>Poaceae</i>	
<i>Parnassius apollo</i>					x					<i>Sedum</i> spp., <i>Sempervivum</i> spp.			
<i>Parnassius mnemosyne</i>						x				<i>Corydalis</i> spp.			
<i>Phengaris arion</i>				x	x					<i>Thymus</i> spp.			
<i>Pieris brassicae</i>		x	x		x	x	x	x	<i>Brassicaceae</i>	<i>Brassicaceae</i>	<i>Brassicaceae</i>	<i>Brassicaceae</i>	
<i>Pieris bryoniae</i>					x					<i>Biscutella</i> spp., <i>Cardamine</i> spp., <i>Thlaspi</i> spp.			
<i>Pieris ergane</i>				x						<i>Aethionema saxatile</i>			
<i>Pieris mannii</i>			x	x	x					<i>Alyssoidae</i> spp., <i>Iberis</i> spp.			
<i>Pieris napi</i>	x	x	x	x	x	x	x	x	<i>Brassicaceae</i>	<i>Brassicaceae</i>	<i>Brassicaceae</i>	<i>Brassicaceae</i>	
<i>Pieris rapae</i>	x	x	x	x	x	x	x	x	<i>Brassicaceae</i>	<i>Brassicaceae</i> , <i>Chenopodiaceae</i> ,	<i>Brassicaceae</i> , <i>Reseda lutea</i>	<i>Brassicaceae</i> , <i>Reseda lutea</i>	



<i>Pyronia tithonus</i>			x	x			x	x	<i>Poaceae</i>	<i>Poaceae</i>		
<i>Satyrus ferula</i>				x					<i>Poaceae</i>	<i>Poaceae</i>		
<i>Scolitantides orion</i>		x					x		<i>Sedum telephium</i>	<i>Sedum</i> spp.		
<i>Spialia sertorius</i>				x	x					<i>Potentilla</i> spp., <i>Sanguisorba</i> spp.		
<i>Thymelicus lineola</i>	x	x		x	x	x	x	x	<i>Poaceae</i>	<i>Poaceae</i>	<i>Poaceae</i>	<i>Poaceae</i>
<i>Thymelicus sylvestris</i>								x				<i>Poaceae</i>
<i>Vanessa atalanta</i>	x	x	x	x	x	x	x	x	<i>Urtica dioica</i>	<i>Parietaria</i> spp., <i>Urtica dioica</i>	<i>Urtica dioica</i>	<i>Urtica dioica</i>

For Review Only

**Table S3.** Performance of abundance, evenness, richness, and co-evolution models using proportion of arable land (landscape simplification index) calculated at multiple scales (0.5, 1, 2 km). Table shows the Akaike Information Criterion (AIC). The most explanatory radius was selected based on minimized AIC values.

	Landscape scale		
	0.5 km	1 km	2 km
Abundance	1541.8	1541.8	1539.1
Evenness	1584.9	1584.7	1583.9
Richness	1521.3	1522.8	1521.4
Co-evolution	541.2	543.7	543.5

For Review Only

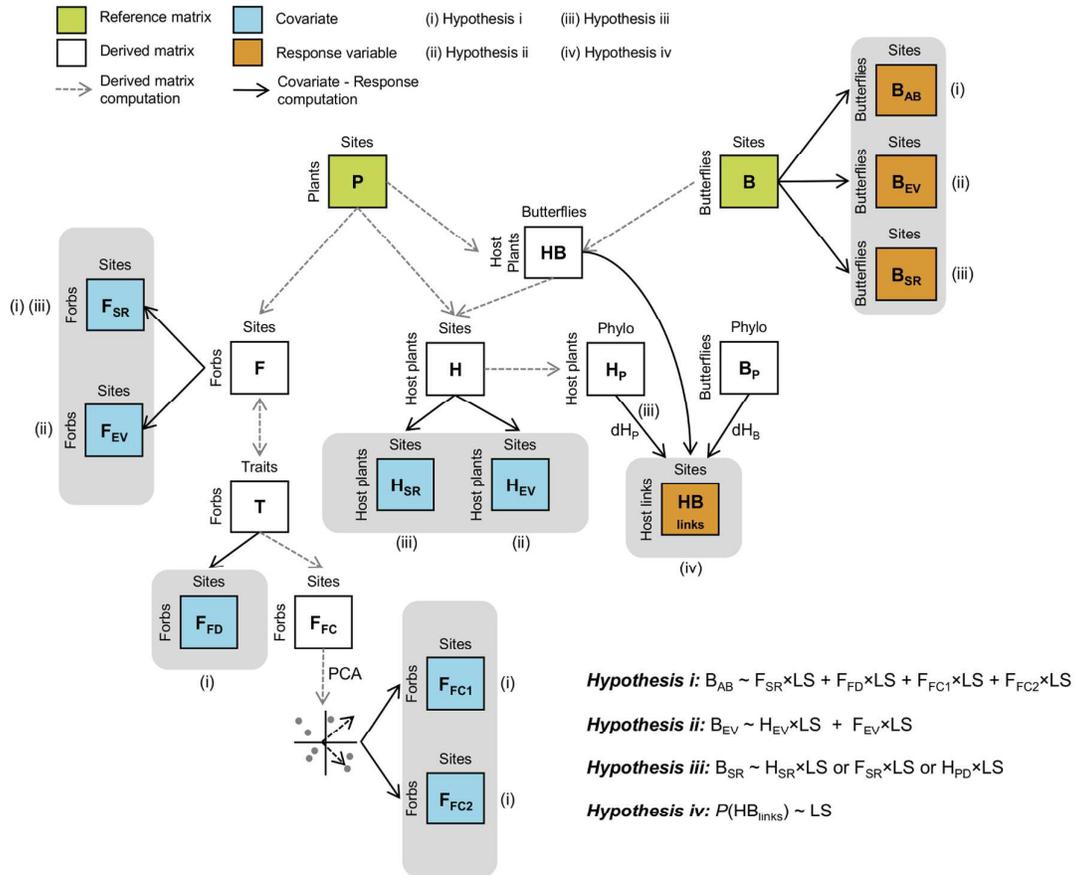
**Table S4.** Model-averaged partial regression coefficients ( $\beta$ ) and unconditional 95% confidence intervals (CIs) from models of butterfly (a) abundance, (b) evenness, (c) species richness, and (d) estimated species richness in relation to local and landscape factors. In bold  $\beta$ s and CIs that do not include 0. Akaike weights ( $w_i$ ) indicate relative importance of covariate  $i$  based on summing weights ( $\sum w_i$ ) across models where covariate  $i$  occurs.  $F_{SR}$  = flowering forb species richness; LS = landscape simplification (proportion of arable land cover in a radius of 2 km surrounding each site);  $F_{FC1}$  = first PCA axis of functional trait composition;  $F_{FC2}$  = second PCA axis of functional trait composition;  $F_{FD}$  = functional diversity;  $F_{EV}$  = flowering forb evenness;  $F_{SR}$  = flowering forb species richness;  $H_{EV}$  = host plant evenness;  $H_{PD}$  = host plant phylogenetic diversity;  $H_{SR}$  = host plant richness.

Covariate	$\sum w_i$	$\beta$	Lower CI	Upper CI
<b>(a) Butterfly abundance (AIC = 1539.1)</b>				
$F_{SR}$	1.00	0.2420	0.1584	0.3257
$F_{FC1}$	0.99	0.0658	0.0170	0.1146
LS	0.98	0.0008	-0.0025	0.0041
$F_{FC1} \times LS$	0.93	-0.0033	-0.0053	-0.0013
$F_{FC2}$	0.48	0.0360	-0.0265	0.0985
$F_{FD}$	0.34	0.0108	-0.0724	0.0941
$F_{SR} \times LS$	0.34	-0.0034	-0.0069	0.0001
$F_{FC2} \times LS$	0.13	0.0003	-0.0024	0.0031
$F_{FD} \times LS$	0.09	0.0001	-0.0032	0.0036
<b>(b) Butterfly evenness (AIC = 1583.9)</b>				
$H_{EV}$	0.83	0.0667	-0.0179	0.1513
LS	0.76	-0.0004	-0.0038	0.0030
$H_{EV} \times LS$	0.63	-0.0043	-0.0077	-0.0009
$F_{EV}$	0.48	0.0208	-0.0626	0.1042
$F_{EV} \times LS$	0.27	0.0030	-0.0006	0.0066
<b>(c) Butterfly species richness</b>				
<i>Host plant richness (AIC = 1537.8)</i>				
$H_{SR}$	1.00	0.2779	0.1980	0.3578
LS	0.85	-0.0018	-0.0051	0.0014
$H_{SR} \times LS$	0.75	-0.0041	-0.0074	-0.0008
<i>Host plant phylogenetic diversity (AIC = 1585.7)</i>				
$H_{PD}$	0.35	0.0014	-0.2447	0.2475
LS	0.54	-0.0013	-0.0098	0.0072
$H_{PD} \times LS$	0.09	-0.0040	-0.0111	0.0033
<i>Flowering plant richness (AIC = 1521.1)</i>				
$F_{SR}$	1.00	0.3255	0.2464	0.4047
LS	0.77	-0.0018	-0.0050	0.0014

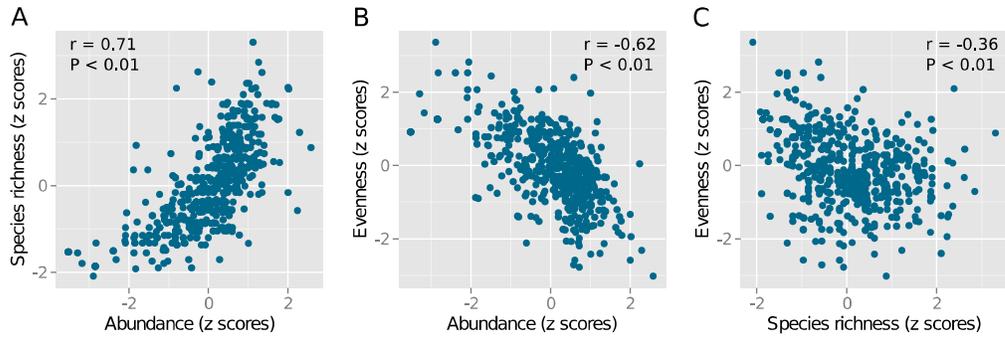
$F_{SR} \times LS$	0.61	-0.0037	-0.0070	-0.0003
<b>(d) Estimated butterfly species richness</b>				
<i>Host plants</i> (AIC = 1546.6)				
$H_{SR}$	1.00	0.2118	0.1311	0.2925
LS	0.84	-0.0027	-0.0060	0.0006
$H_{SR} \times LS$	0.63	-0.0035	-0.0068	-0.0002
<i>Flowering plants</i> (AIC = 1559.5)				
$F_{SR}$	1.00	0.2194	0.1377	0.3011
LS	0.62	-0.0024	-0.0057	0.0009
$F_{SR} \times LS$	0.25	-0.0020	-0.0054	0.0015

---

For Review Only

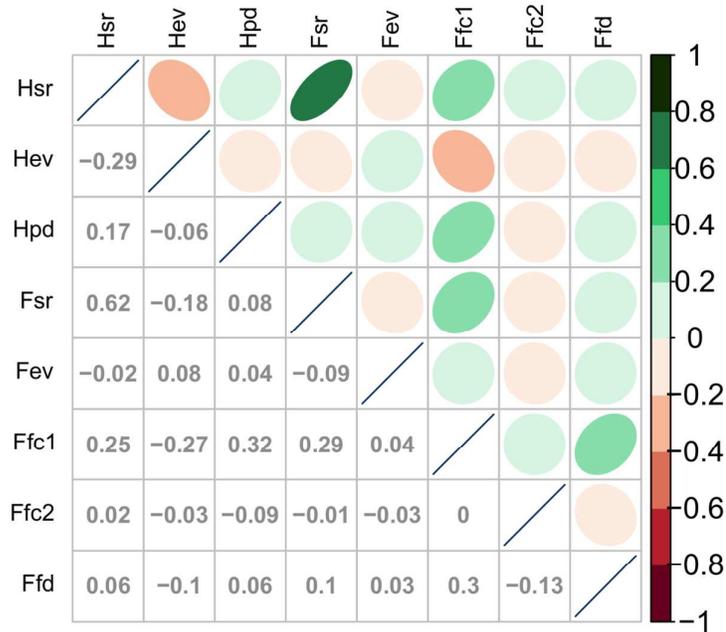


**Figure S1.** Diagram of the matrix computation approach. Sequence of the matrix computation used to derive covariates (light blue) and response variables (orange) from raw data matrices (light green). Matrix abbreviations: B, butterfly species-by-site matrix; F, flowering forb-by-site matrix; H, host plant-by-site matrix; HB, butterfly-host plant association matrix; LS, landscape simplification measured as the proportion of arable land cover in a radius of 2 km surrounding each site; P, plant species-by-site matrix; T, flowering forb-by-trait matrix. Diversity measures abbreviations: AB, abundance; EV, evenness; FC, functional trait composition; FD, functional diversity; P, phylogenetic diversity; SR, species richness. Co-evolution index abbreviation: HBlinks, number of links between butterflies and host plants with co-evolutionary signal. The number in parentheses indicated the hypothesis tested in the paper.

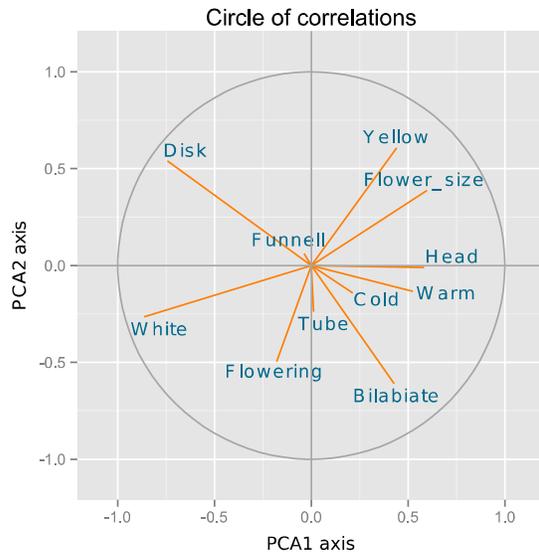


**Figure S2.** Butterfly diversity pairwise relationships. Scatterplots and associated Pearson correlation coefficients between (A) abundance and species richness, (B) abundance and evenness, and (C) species richness and evenness.

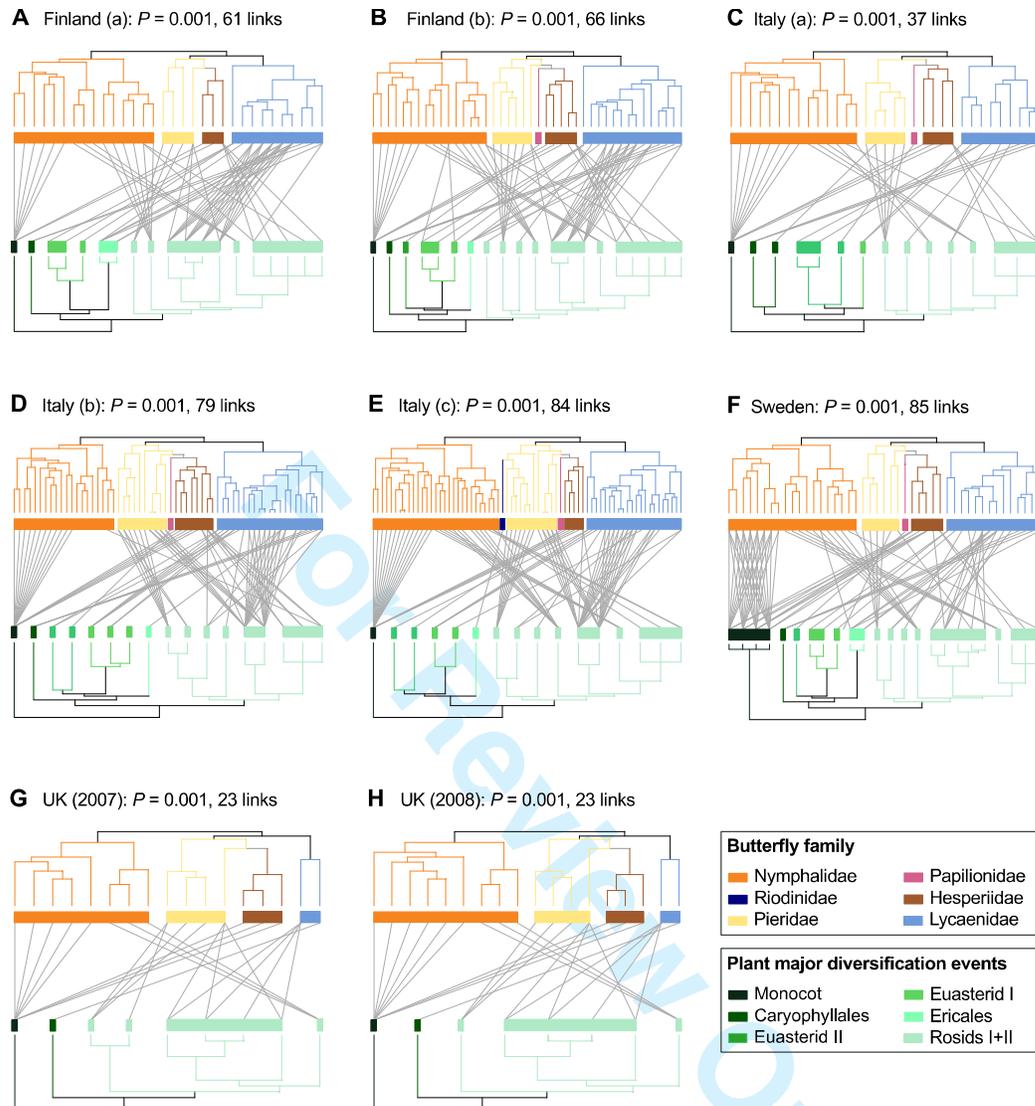
For Review Only



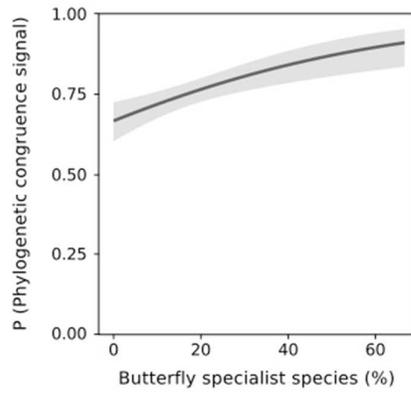
**Figure S3.** Correlation matrix of plant diversity measures. The colour and size of the ellipses in the matrix code for correlation strength and direction; green scale colour represents positive correlation and red scale colour represents negative correlation. Hsr = host plant richness; Hev = evenness of host plants; Hpd = host phylogenetic diversity; Fsr = flowering forb species richness; Fev = evenness of flowering forbs; Ffc1 = first functional trait composition axis derived from the PCA analysis on the CWM trait matrix; Ffc2 = second functional trait composition axis derived from the PCA analysis on the CWM trait matrix; Ffd = functional diversity of flowering forbs.



**Figure S4.** Principal Component Analysis (PCA) on the community-weighted mean (CWM) trait matrix ( $F_{FC}$ ). Circle of correlation was used to illustrate the association between the first two principal components and plant traits.



**Figure S5.** Trophic network and phylogenetic congruence between host plants and butterfly species for each data set separately (A-H). Colours indicate different butterfly families (top part) and plant major diversification events (bottom part), respectively. The host-butterfly trophic networks are highly structured (Parafit test:  $P < 0.001$  in all data sets).



**Figure S6.** Relationship between phylogenetic congruence signal and proportion of butterfly specialist species. The probability of a site having a phylogenetic congruence signal increased with increasing proportion of butterfly specialist species. Fitted line is a generalized linear mixed model estimate (inverse logistic transformation has been applied to the regression line):  $\beta = 0.024$ ,  $P = 0.001$ .

Review Only

## Supporting Information

for Dainese et al. “*Land-use intensification weakens the association between terrestrial producer and consumer diversity in Europe*”

### Appendix S3 – Phylogeny

For the host plants (**H<sub>P</sub>**) (Appendix S1, Fig. S1), we computed a phylogenetic tree using Phylomatic version 3 (<http://phylodiversity.net/phyloomatic/>) and derived from the Phylomatic megatree (R20120829) based on the APG III classification (Bremer *et al.*, 2009). Branch lengths were added to the phylogeny using the branch length adjustment algorithm (BLADJ) in the software Phylocom (Webb *et al.*, 2008). We used the node ages estimated from Wikström *et al.* (2001).

We built an updated molecular phylogeny for 115 butterfly species (**B**), using cytochrome oxidase subunit I (COI) gene sequences that were extracted from GenBank (Benson *et al.*, 2011) *Parnassius apollo* was dropped due to a lack of genetic data. MAFFT (Katoh & Toh, 2008) was used to align the sequences, which were then used to estimate maximum likelihood trees via RAxML (Stamatakis, 2006) with integrated bootstrapped values, based on 1000 bootstraps. Tree estimation was guided with the use of a taxonomy-based constraint tree (Family, Subfamily, Genus). BEAST (Drummond & Rambaut, 2007) was used for rate smoothing, where we implemented the general time reversible (GTR) substitution model with gamma distributed rate variation across sites with a chain length 5,000,000 iterations. All steps of the phylogeny building process were carried out via phyloGenerator (Pearse & Purvis, 2013). Finally, Tracer (<http://beast.bio.ed.ac.uk/Tracer>) was used for model checking and TreeAnnotator (<http://beast.bio.ed.ac.uk/treeannotator>) was used to summarise the trees from phyloGenerator.

### References

- Benson DA, Karsch-Mizrachi I, Lipman DJ, Ostell J, Sayers EW (2011) GenBank. *Nucleic Acids Research*, **39**, D32–D37.
- Bremer B, Bremer K, Chase MW *et al.* (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical*

*Journal of the Linnean Society*, **161**, 105–121.

Drummond AJ, Rambaut A (2007) BEAST: Bayesian evolutionary analysis by sampling trees. *BMC evolutionary biology*, **7**, 214.

Katoh K, Toh H (2008) Recent developments in the MAFFT multiple sequence alignment program. *Briefings in Bioinformatics*, **9**, 286–298.

Pearse WD, Purvis A (2013) phyloGenerator: an automated phylogeny generation tool for ecologists. *Methods in Ecology and Evolution*, **4**, 692–698.

Stamatakis A (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, **22**, 2688–2690.

Webb CO, Ackerly DD, Kembel SW (2008) Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics*, **24**, 2098–2100.

Wikström N, Savolainen V, Chase MW (2001) Evolution of the angiosperms: calibrating the family tree. *Proceedings of the Royal Society of Biological Sciences*, **268**, 2211–2220.