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# Effect of habitat spatiotemporal structure on collembolan diversity

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## ABSTRACT

Landscape fragmentation is a major threat to biodiversity. It results in the transformation of continuous (hence large) habitat patches into isolated (hence smaller) patches, embedded in a matrix of another habitat type. Many populations are harmed by fragmentation because remnant patches do not fulfil their ecological and demographic requirements. In turn, this leads to a loss of biodiversity, especially if species have poor dispersal abilities. Moreover, landscape fragmentation is a dynamic process in which patches can be converted from one type of habitat to another. A recently created habitat might suffer from a reduced biodiversity because of the absence of adapted species that need a certain amount of time to colonize the new patch (e.g. direct metapopulation effect). Thus landscape dynamics leads to complex habitat spatiotemporal structure, in which each patch is more or less continuous in space and time. In this study, we define habitat spatial structure as the degree to which a habitat is isolated from another habitat of the same kind and temporal structure as the time since the habitat is in place. Patches can also display reduced biodiversity because their spatial or temporal structures are correlated with habitat quality (e.g. indirect effects). We discriminated direct meta-community effects from indirect (habitat quality) effects of the spatiotemporal structure of habitats on biodiversity using Collembola as a model. We tested the relative importance of spatial and temporal

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26 structure of habitats for collembolan diversity, taking soil properties into account. In an agroforested  
27 landscape, we set up a sampling design comprised of two types of habitats (agriculture vs forest), a  
28 gradient of habitat isolation (three isolation classes) and two contrasting ages of habitats. Our results  
29 showed that habitat temporal structure is a key factor shaping collembolan diversity. A reduced  
30 diversity was detected in recent habitats, especially in forests. Interactions between temporal  
31 continuity and habitat quality were also detected by taking into account soil properties: diversity  
32 increased with soil carbon content, especially in old forests. Negative effects of habitat age on  
33 diversity were stronger in isolated patches. We conclude that habitat temporal structure is a key factor  
34 shaping collembolan diversity, while direction and amplitude of its effect depend on landuse type and  
35 spatial isolation.

## 36 **1. Introduction**

37 Habitat fragmentation is well known to be a major threat to biodiversity in many  
38 macroorganisms (Saunders et al., 1991; Tilman, 1994; Tilman et al., 1994; Finlay et al., 1996;  
39 Stratford and Stouffer, 1999; Cushman, 2006; Mapelli and Kittlein, 2009; Krauss et al., 2010).  
40 Biodiversity is not only driven by local environmental conditions, but also by spatial processes  
41 (Hanski, 1994; Ettema and Wardle, 2002; Holyoak et al., 2005). It is now largely recognized that  
42 ecological processes shaping communities occur at least at two distinct organisation levels (Shmida  
43 and Wilson, 1985; Ricklefs, 1987; Wardle, 2006). (1) Regional processes occur since habitats within a  
44 landscape are interconnected by dispersal, which gives birth to meta-community dynamics (Gilpin and  
45 Hanski, 1991; Hubbell, 2001; Leibold et al., 2004). At regional scale, an increase in habitat spatial  
46 connectivity increases the probability of a species to reach an unoccupied habitat and thus may  
47 enhance local diversity (Bailey, 2007; Brückmann et al., 2010). (2) Local factors such as  
48 environmental conditions and competition between organisms act as filters enabling species to  
49 maintain a viable population in a patch of habitat (Decaëns et al., 2011; Petit and Fried, 2012) and thus  
50 reduce local diversity. Within this framework, patches are defined as spatial units of habitat differing  
51 from the surrounding area (Forman and Godron, 1986). Even though patches may display an internal  
52 heterogeneity at finer scale, e.g. microhabitat (Leibold et al., 2004), they contain a single type of

53 habitat defined by relatively homogeneous biotic and abiotic factors such as temperature, humidity or  
54 vegetation cover.

55 In fragmented landscapes, biodiversity can be locally reduced when patches become too small  
56 to sustain a species or when species are not mobile enough to efficiently recolonize patches where they  
57 went extinct. Characteristics of habitat patches (e.g. vegetation cover, configuration, shape and area)  
58 also have various effects on biodiversity (Forman, 1995; Tanner, 2003; Davies et al., 2005) depending  
59 on how the focal group of organisms perceives the surrounding landscape and on its ability to move  
60 from a patch to another (Kotliar and Wiens, 1990; Ettema and Wardle, 2002; Tews et al., 2004). While  
61 the effects of fragmentation are well documented for aboveground animals such as birds or  
62 amphibians (Stratford and Stouffer, 1999; Cushman, 2006) they have hardly been studied in soil  
63 organisms (Decaëns, 2010). However, soil fauna is the most species-rich component of ecosystems  
64 (André et al., 1994), known to provide many ecosystem services (Lavelle et al., 2006) that could be  
65 negatively impacted by habitat fragmentation. Soil invertebrates are known to have a low active  
66 mobility because of their small body size (Finlay et al., 1996; Hillebrand and Blenckner, 2002) and  
67 because it is more difficult to move within the soil than above it. For these reasons they should not  
68 react to habitat fragmentation in the same way as larger aboveground animals. We tackle here these  
69 general issues using Collembola as a model and focussing on the impact of habitat spatiotemporal  
70 structure on their diversity. Collembola constitute a relevant model because (1) they are very abundant  
71 in most soils and ecosystems, (2) many species can be found in a single location and (3) collembolan  
72 species are known to differ in their dispersal abilities and their level of specialisation for different  
73 habitat types (Ponge et al., 2006; da Silva et al., 2012).

74 Recent insights into the influence of landscape structure on collembolan diversity showed that  
75 at patch scale, collembolan (alpha) diversity in forests may respond negatively to habitat diversity at  
76 landscape scale (Ponge et al., 2003; Sousa et al., 2006). In these cases, the decrease in local or alpha  
77 diversity was attributed to habitat fragmentation occurring in diverse landscapes. Indeed, patch  
78 isolation which is most of the time increased in fragmented habitats, may reduce the chances of  
79 colonization by species, especially if these have poor dispersal ability (Hewitt and Kellman, 2002). In  
80 contrast, Querner (2013) showed that landscape heterogeneity may increase local (alpha) collembolan

1 81 diversity in oilseed rape fields (i.e. in agricultural habitats). In this case, species are thought to express  
2 82 preferences for different habitat types so that regional (gamma) diversity is increased by habitat  
3  
4 83 heterogeneity (Vanbergen et al., 2007). Since these preferences are not strict, and species move  
5  
6 84 between patches, habitat heterogeneity in the neighbouring landscape would also increase diversity at  
7  
8 85 patch scale (alpha diversity). These results suggest that it is difficult to predict a priori the impact of  
9  
10 86 habitat isolation on local (alpha) species diversity and that this impact depends on the ecosystem under  
11  
12 87 investigation. Here, we compare the effect of patch isolation in two broad habitat types, open vs.  
13  
14 88 closed vegetation, within the same landscape.

17 89 Most empirical studies on metacommunity dynamics assume that local communities have  
18  
19 90 reached equilibrium at sampling time. However some authors suggested that the time elapsed, since  
20  
21 91 the first species successfully colonized a patch of habitat, is essential for the understanding of  
22  
23 92 observed diversity patterns (Mouquet et al., 2003). These authors assume that communities at the first  
24  
25 93 stages of the assembly process are unsaturated because only a subset of the regional species pool has  
26  
27 94 yet been able to colonize the patch. Besides spatial structure, patch temporal structure may thus also  
28  
29 95 influence collembolan alpha diversity. Ponge et al. (2006) showed that landscape heterogeneity may  
30  
31 96 come with a more dynamic patch temporal structure. They suggest that regions that include more  
32  
33 97 diverse habitat types may also include more patches of habitat that have experienced a recent change  
34  
35 98 in land use (e.g. patches that switched from forest to agriculture or the reverse, and thus are not  
36  
37 99 continuous through time). This may have subsequently reduced collembolan diversity at patch scale  
38  
39 100 (alpha diversity). In this sense, the lack of diversity observed in most heterogeneous landscape might  
40  
41 101 be due to patch history, i.e. to temporal discontinuity, rather than to patch spatial structure, i.e.  
42  
43 102 fragmentation.

48 103 Another source of complexity for understanding the influence of habitat structure on diversity  
49  
50 104 patterns is that patch characteristics (age, spatial isolation, land use type) may influence local  
51  
52 105 communities either directly or indirectly. They directly impact local communities through their effect  
53  
54 106 on meta-community dynamics (Driscoll et al., 2012). Patch characteristics may also impact  
55  
56 107 communities through complex links between landscape dynamics and local environmental properties  
57  
58 108 (Wu and Loucks, 1995). For example, isolation and age of a patch can impact local microclimatic  
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65

109 conditions (Saunders et al., 1991; Magura et al., 2003), and increased edge effects in isolated patches  
110 can be responsible for changes in soil properties. In this case, patch spatial structure would be  
111 responsible for changes in local conditions which would consequently affect local (alpha) diversity  
112 (e.g. indirect effect). Conversely, pre-existing local conditions may impact land use changes (e.g. if the  
113 forest soil is fertile, the forest is more likely to be turned into a field). Such direct and indirect effects  
114 must be disentangled to determine the effects of landscape structure on local communities.

115 In the present study, we intend to disentangle the relative effects of spatial vs. temporal  
116 continuity of habitats on collembolan alpha diversity in both agricultural and forest habitats. We will  
117 assess the effect on diversity of 1) temporal continuity of habitats (temporal structure), 2) spatial  
118 isolation of habitats (spatial structure), 3) interaction of temporal and spatial habitat structures, 4) local  
119 environmental conditions (land use and soil) and whether they depend on habitat spatiotemporal  
120 structure (indirect effect), and 5) forest and agricultural habitats.

121 According to the rationale above (Ponge et al., 2006), we expect (H1) stable habitats (i.e. old  
122 or temporally continuous patches) to support a higher alpha diversity than habitats that have been  
123 disturbed in the past decades (i.e. recent or temporally discontinuous patches). Besides being  
124 considered as stable habitats, forests display a wider variety of niches than agricultural land due to the  
125 quality of their soils and humus: forests have a well-developed humus layer (often including  
126 fragmented OF horizons and sometimes humified OH horizons) that is absent in open or agricultural  
127 habitat (Hågvar, 1983 ; Ponge, 2000). Additionally, soil carbon content and moisture are higher in  
128 forest than in agricultural habitats (Batlle-Aguilar et al., 2011), thereby favouring Collembola given  
129 the well-known requirements of these animals in water and organic matter (Hopkin, 1997). We thus  
130 expect (H2) to find a higher diversity and a higher abundance of Collembola in forested habitats. We  
131 think that vegetation structure in agricultural habitats makes dispersal easier than in forests because  
132 passive dispersal vectors such as wind are more efficient in open than in closed vegetation (Morecroft  
133 et al., 1998). We thus expect (H3) that spatiotemporal continuity will have a lower effect in  
134 agricultural habitats when compared to forests.

## 135 2. Material and methods

### 136 2.1. Study site

137           Sampling took place in the northern part of the Morvan Regional Natural Park (Burgundy,  
 138 Center-East France). The study area is located in the northern part of the Park (523 6000 – 525 2000  
 139 N, 573 800 - 588 800 E ; WGS84, UTM 31N) and represents an area of 16 x 15 km. The climate is  
 140 submontane-atlantic with continental influence (mean annual rainfall 1000 mm and mean temperature  
 141 9°C). The bedrock is made of granite and soils are mostly acidic (Cambisols, IUSS Working Group  
 142 WRB 2006). We selected this region because it displays diverse habitat spatiotemporal structures and  
 143 relatively homogeneous soil conditions among all habitat of the same type. The region is rural, with  
 144 intensive to extensive agriculture (55%) and forestry (45%). From the beginning of the twentieth  
 145 century Douglas fir [*Pseudotsuga menziesii* Mirbel (Franco)] and Norway spruce [*Picea abies* (L.)  
 146 Karst.] have been intensely planted for saw-wood production and coniferous stands have progressively  
 147 replaced the formerly dominant deciduous stands. However, large areas of oak [*Quercus petraea*  
 148 (Matt.) Liebl.] and beech (*Fagus sylvatica* L.) forest still subsist. Nowadays, agricultural areas consist  
 149 of permanent pastures (40%), hay meadows (40%) and crops (20%). Forested areas are comprised of  
 150 planted coniferous stands (45%) and deciduous stands (mostly *Ilici-Fagenion*) (55%). In this region,  
 151 the landscape has experienced a dynamic period (1962 to present) due to agricultural abandonment  
 152 and European subsidies that encouraged farmers to convert meadows into plantation forests. This  
 153 afforestation created many recent forest patches.

### 154 2.2. Sampling design

155           Our sampling design was comprised of 60 sites (28 forested and 32 agricultural) classified in  
 156 12 combinations of three habitat descriptors: habitat type (HT), temporal continuity (TC) and spatial  
 157 isolation (SI). For each spatiotemporal combination we sampled 3 to 9 replicates (Appendix A).

#### 158 2.2.1. Habitat type

159           Collembolan communities are likely to depend on the dichotomy between open and closed  
 160 vegetation (Ponge et al., 2003; Vanbergen et al., 2007). Hence we decided to split the landscape into

161 two major habitat types: forest and agricultural land. Thus, sampled sites can either be meadows,  
162 pastures, crops, or Christmas tree plantations for agricultural habitats and coniferous or deciduous  
163 stands for forest habitats (Appendix A). Christmas tree plantations might at first be thought as forest  
164 habitats. However, they display many characteristics of agricultural habitats: absence of litter and  
165 developed humus profiles (due to low stature and density of Christmas trees), use of ploughing and  
166 pesticides, i.e. same characteristics as agricultural land. They are generally constituted by no more  
167 than five-year-old trees and have been shown to support collembolan communities typical of  
168 agricultural habitats (Ponge et al., 2003). It is well known that the transition from deciduous to  
169 coniferous stands implies an abrupt change in soil physicochemical properties (pH, humus form, etc.)  
170 (Gauquelin et al., 1996; Augusto et al., 2003). However, Ponge et al. (2003) showed that in the  
171 Morvan region, collembolan communities do not differ between coniferous and deciduous stands,  
172 contrary to often-reported detrimental effects of coniferous plantations, mostly ascribed to changes in  
173 humus form and soil acidity (Cassagne et al., 2004; Hasegawa et al., 2009). In any case, collembolan  
174 communities of both forest types differ less from each other than they differ from agricultural  
175 communities. The absence of pronounced reaction of collembolan communities to tree species  
176 composition was also observed in similar acidic soil conditions in Germany (Salamon and Alpei,  
177 2009). This is explained by the fact that on acidic bedrocks of the studied region, similar humus forms  
178 with thick litter layers and strong soil acidity (moder) develop under both stand types (Ponge et al.  
179 1993). It has been shown that *Collembola* mostly feed on microorganisms and animal faeces and  
180 rarely consume directly leaves or needles (Ponge, 1991; Caner et al., 2004). As such, they are most of  
181 all influenced by humus forms whatever the composition of forest canopies (Ponge, 1993).  
182 Additionally, coniferous tree species planted in the Morvan region (Douglas fir, silver fir and more  
183 rarely Norway spruce) have a more nutrient rich litter and do not acidify the soil to the same extent as  
184 pines (Augusto et al., 2003). This allowed us to group both forest types into a single broader category.  
185 We avoided sampling in special habitats such as humid areas or clear-cuts so as to minimize the  
186 influence of particular environmental conditions within forests and agricultural land.

### 2.2.2. Habitat temporal continuity



188 In order to assess the temporal continuity of each habitat within the focus area, we  
1 implemented a dynamic cartography (i.e. picturing both spatial and temporal continuity) using aerial  
2 189 photographs. In total, about two hundred aerial photographs (IGN, France) were required from 1948 to  
3 190  
4 191 2008 with a photograph taken approximately every five year. We categorised each habitat into two age  
5 192  
6 193 classes (Appendix A). Those in place at least since 1948 were classified as old. Recent forests were  
7 194  
8 195 agricultural habitats until conversion to forest 30 to 40 years ago (in our classification, a change from  
9 196  
10 197 deciduous to coniferous stand is not a temporal discontinuity). Recent agricultural habitats were  
11 198  
12 199 forests until conversion to agricultural land 20 to 30 years ago. Studied local collembolan communities  
13 200  
14 201 were thus included in habitats that were homogeneous in type and age. In the context of this study, we  
15 202  
16 203 considered that a patch is not only a continuous block of the same habitat type but also a continuous  
17 204  
18 205 part of the same habitat type over time, meaning that we mapped four types of patch: old forest, recent  
19 206  
20 207 forest, old agricultural and recent agricultural.

### 200 2.2.3. Habitat spatial isolation

201 Using the previously mentioned cartography, we selected sampling points in both habitat types  
202 (agriculture and forest) and habitat temporal continuity classes (recent and old) and then categorized  
203 the landscape mosaic in a buffer zone of 300 m radius around sampling points (Appendix A). Two  
204 parameters were considered to define habitat spatial isolation: edge contrast and dominant age of the  
205 matrix. Edge contrast measures the magnitude of the difference between adjacent habitat types. It is  
206 calculated as the percent edge of the habitat (containing the sampling point) shared with an opposite  
207 habitat within a 300 m radius. Opposite habitat was forest for agricultural land and vice versa. Of  
208 course, edge contrast is nil or close to nil for isolation class 0. The matrix was defined by the  
209 proportion of the dominant habitat type of a given age which occupies the matrix around the sampling  
210 point.

211 Isolation class 0 was comprised of large continuous habitats, i.e. larger than the scale of  
212 observation around the sampling point (the 300 m buffer zone). Thus sampling points of isolation class  
213 0 (whether in recent or old habitat) were entirely included in a matrix made of the same type of habitat  
214 300 m around it (except for one recent forest patch that shared 11% of its edge with an old agricultural

215 patch). The matrix surrounding sampling points of isolation class 0 was mostly old (continuous or  
 216 non-isolated spatial structure).

217 For isolation classes 1, criteria of spatial isolation slightly differed between forest and  
 218 agricultural habitats. Agricultural patches of isolation class 1 shared a single edge with an old forest.  
 219 The matrix surrounding them was mostly comprised of old (and less frequently recent) forest habitats.  
 220 Forest patches of isolation class 1 corresponded to a particular situation that we repeatedly found in  
 221 the studied region, e.g. some remnant forest patches in place since 1948 (i.e. old) that have been  
 222 reconnected by a (recent) forest patch to another old forest patch since the last 30-40 years. Old forests  
 223 of isolation class 1 shared 25 to 83 % of their edge with an old agricultural land and the rest with a  
 224 recent forest. Recent forests of isolation class 1 were the “reconnecting patches”, sharing 19 to 69% of  
 225 their edge with an old agricultural land and the rest with an old forest. The matrix surrounding  
 226 sampling points of isolation class 1 was comprised of old and recent habitats.

227 For isolation class 2, spatial isolation also slightly differed between forest and agricultural  
 228 habitats. Forest patches of isolation class 2 were remnant patches, entirely surrounded by an old  
 229 agricultural matrix. They have been completely isolated since they are in place. Old and recent  
 230 agricultural patches of isolation class 2 shared respectively 60 to 100 % and 45 to 80% of their edge  
 231 with a forest. The matrix surrounding agricultural patches of isolation class 2 was mostly old. Isolation  
 232 class 1 was considered to be less isolated than isolation class 2 because with the appearance of recent  
 233 habitats in the surrounding matrix of isolation class 1, some newly created habitats were of the same  
 234 type as the one located at the sampling point, originating in a less isolated context.

235 In forests as well as in agricultural land, patches of isolation classes 1 and 2 were sampled at  
 236 least 10 m (but no more than 50 m) away from the opposite habitat type edge.

### 237 *2.3. Collection of fauna and soil data*

238 Sampling took place from June 27 to July 9, 2010. Each site was sampled for litter/soil  
 239 mesofauna using a cylindrical soil corer (5 cm diameter x 7 cm depth, one sample at each sampling  
 240 site). We thus sampled exactly the same volume of soil at each site, meaning that values of species  
 241 density, i.e. the number of species per unit area sensu Gotelli and Colwell (2001) here presented

242 correspond to the number of species found over 0.2 dm<sup>2</sup>. Litter/soil were brought back to the  
 1 laboratory within a week and placed in a Berlese dry-funnel extractor for 10 days. Animals were  
 2 243 collected and stored in 70% ethyl alcohol until identification. Collembola were mounted, cleared in  
 3  
 4 244 chloral-lactophenol and identified to species level under a light microscope (400x magnification),  
 5  
 6 245 according to Hopkin (2007), Potapow (2001), Thibaud et al. (2004) and (Bretfeld, 1999). A list of  
 7  
 8 246 species is given in Appendix B.  
 9  
 10 247

11  
 12 248 We also sampled soils (organo mineral horizon, between 0 and 10 cm) in each site in order to  
 13  
 14 249 characterize soil physicochemical properties at each sampling site. Three samples were taken around  
 15  
 16 250 soil fauna samples and were pooled together. Soils were air-dried and sieved to 2 mm before  
 17  
 18 251 measuring total carbon (C<sub>tot</sub>) and total nitrogen (N<sub>tot</sub>) contents (gas chromatography), pH (H<sub>2</sub>O),  
 19  
 20 252 bioavailable phosphorus (Olsen method) and cation exchange capacity (CEC). Additionally, the top  
 21  
 22 253 five soil centimetres were sampled using a Burger cylinder (0.1 L volume) and immediately packed in  
 23  
 24 254 waterproof bags in order to determine soil moisture and bulk density. The humus form was  
 25  
 26 255 characterized according to Brêthes et al. (1995) and the Humus index was calculated according to  
 27  
 28 256 Ponge et al. (2002), and was used as a proxy of litter amount and recalcitrance to decay (Ponge et al.,  
 29  
 30 257 1997; Ponge and Chevalier, 2006).  
 31  
 32  
 33  
 34  
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#### 36 258 *2.4. Statistical analyses*

37  
 38  
 39 259 The following diversity indicators were calculated for each site: species density (sensu Gotelli  
 40  
 41 260 and Colwell, 2001), i.e. the actual number of species found in each sample, species richness (sensu  
 42  
 43 261 Gotelli and Colwell, 2001) i.e. the local number of species estimated to be found in a smaller sample  
 44  
 45 262 containing 25 % of the mean individual density (i.e. 57 individuals), Shannon index, dominance  
 46  
 47 263 (relative frequency of the most abundant species), and abundance (total number of individuals).  
 48  
 49

50 264 These diversity indicators were analysed using linear models (type III sums of squares used  
 51  
 52 265 for unbalanced design and because significant interactions were expected, see Appendix B), testing for  
 53  
 54 266 habitat type (HT), spatial isolation (SI), and temporal continuity (TC) effects as well as effects of all  
 55  
 56 267 interactions between these factors. To fulfil linear model assumptions, dominance had to be log-  
 57  
 58 268 transformed. In order to detect possible effects of habitat spatiotemporal structure (regional factors) on  
 59  
 60  
 61  
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 65

269 its soil quality that could influence diversity indicators, we tested the effect of habitat descriptors on  
1 soil physicochemical properties. Most of natural or log-transformed data fulfilled the assumptions of  
2 270  
3 linear models. When this was not the case, we used generalized linear models with a Gamma link  
4 271  
5 function or a Poisson link function. All possible correlations (Pearson) between diversity indicators  
6 272  
7 and soil properties were calculated and tested. We also calculated and tested these correlations in both  
8 273  
9 habitat types separately.  
10 274

13 275 Finally, we constructed complete linear models, testing the effects of the three habitat  
14 descriptors on diversity indicators and including most important soil parameters as covariates, together  
15 276  
16 with all their interactions. Since there are many combinations of habitat descriptors and many soil  
17 277  
18 parameters it was not possible to include all of them and their interactions in a single model. Therefore  
19 278  
20 we focussed our analysis on the two soil parameters that were the most correlated with diversity and/or  
21 279  
22 that were significantly affected by habitat descriptors, i.e. Ctot and pH. These two variables can be  
23 280  
24 considered as proxies for two main physico-chemical factors which impact collembolan communities  
25 281  
26 at two different scales (species or community): Ctot is a proxy for general habitat and resource  
27 282  
28 availability and thus determines the total abundance; and pH is a proxy for local environmental filter  
29 283  
30 which selects species within communities, since several collembolan species are only adapted to low  
31 284  
32 or high soil acidity (Ponge, 1993; Salmon, 2004). We analysed two models testing separately for the  
33 285  
34 effect of these two variables, the three habitat descriptors and all their interactions (two-, three- and  
35 286  
36 four-way interactions). Simple effects of variables and interactions that were kept in each final model  
37 287  
38 were selected using an automatic selection procedure based on AIC (procedure step, with backward  
39 288  
40 direction, Bodzogan, 1987; Posada and Buckley, 2004). Combinations of habitat descriptors were  
41 289  
42 compared using least square means and associated multiple comparisons of means (Tukey). All  
43 290  
44 statistical analyses were performed using Mass, car, vegan and Lsmeans packages of R software (R  
45 291  
46 Development Core Team, 2010).  
47 292  
48

53 293 Altogether, these analyses enabled us to discriminate between direct and indirect effects. The  
54 first type of models (testing the effect of the three habitat descriptors on diversity indicators) includes  
55 294  
56 both direct and indirect effects of spatiotemporal structure. If the second type of models (testing the  
57 295  
58 effect of the three habitat descriptors on soil properties) reveals significant effects, it means that  
59 296  
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297 indirect effects are likely to occur. Even if they do not, little differences in soil properties between  
298 habitat spatiotemporal structures could still slightly influence collembolan diversity. This is why we  
299 constructed a third type of models, testing for the effect of the three habitat descriptors on diversity  
300 and including an influential soil property in the same model. If simple effects of habitat descriptors are  
301 significant, it means that they have a direct effect on diversity. However, if simple effects of soil  
302 properties are significant, indirect effects are occurring. The comparison of the first and third types of  
303 models enabled us to assess whether direct or indirect effects were occurring or if both effects were  
304 present at the same time (Fig. 1).

### 305 **3. Results**

#### 306 *3.1. Effects of the three habitat descriptors on collembolan diversity*

307 In total, 6339 individuals were identified to 70 species. We found 3639 from 57 species in  
308 forest and 2700 individuals from 39 species in agricultural habitats. In forests, 44 species were found  
309 in old sites and 42 in recent sites. In agricultural land, 36 species were found in old sites and 24  
310 species in recent sites. Thirteen species were present in recent forests but not in old forests and 15  
311 species were present in old forests and not in recent forest. In agricultural sites, 15 species were  
312 present in old but not in recent sites and only 3 species not present in old sites were found in recent  
313 sites. Rarefaction curves (Fig. 2) showed that our sampling was nearly exhaustive for both habitat  
314 types whatever old or recent, and that forests (both recent and old) harbored more species in total  
315 (gamma diversity) than agricultural land (old > recent). Statistical models implemented on diversity  
316 indicators (Model type 1 in Fig. 1, Table 1) showed that habitat type (HT) exerted an effect on species  
317 density, species richness and total abundance. Species density, species richness as well as abundance  
318 of Collembola were higher in forest compared to agricultural habitats (on average respectively 11.4  
319 versus 8.6 for species density and 9.1 versus 7.9 for species richness). However, no effect of HT was  
320 detected either on Shannon index or on dominance. Furthermore, only Shannon index, species richness  
321 and species density responded to habitat temporal continuity (TC), old habitats showing higher values  
322 than recent habitats (on average 10.8 versus 9.3 for species density, 1.8 versus 1.6 for Shannon index,  
323 and 9.1 versus 7.5 for species richness). Multiple comparisons among means (Tukey) showed that this

324 effect was mainly due to differences between old and recent forests (on average respectively 13.1 and  
1 325 9.4 for species density, 1.9 and 1.5 for Shannon index, and 10.2 versus 7.9 for species richness),  
2 326 whereas old and recent agricultural lands showed closer values (on average respectively 9.1 versus 7.7  
3 327 for species density, 1.7 versus 1.5 for Shannon index, and 8.3 versus 7.1 for species richness) (Fig. 3).  
4 328 Both coniferous and deciduous forests displayed significantly lower values for species density, species  
5 329 richness and Shannon index in the recent age class compared to the old one (data not shown). We did  
6 330 not detect any effects of spatial isolation (SI) on diversity indicators, either in forest or in agricultural  
7 331 habitats, and no interaction between habitat descriptors (Fig. 4).  
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### 19 332 *3.2. Effects of the three habitat descriptors on soil characteristics*

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21 333 Most soil properties were significantly different according to HT. Models testing the effect of  
22 334 HT on soil properties showed that CEC, Ctot, C:N and Humus index had significantly higher values in  
23 335 forest than in agricultural habitats, whereas soil density, soil moisture and pH showed opposite trends  
24 336 (Model type 2 in Fig. 1, Tables 2 and 3). On the other hand, only a few of them, i.e. pH, P and C:N,  
25 337 responded to the two other habitat descriptors (SI and TC). Soil pH, bioavailable phosphorus, and  
26 338 carbon to nitrogen ratio (C:N) showed differences between isolation classes. Soil pH was higher in  
27 339 isolation class 1 (on average 4.3) than in isolation classes 0 and 2 (on average respectively 3.7 and  
28 340 3.8), but only in forest patches, resulting in a significant interaction between HT and SI. Bioavailable  
29 341 phosphorus content was higher in isolation class 2 than in isolation classes 0 and 1 (on average  
30 342 respectively 74, 55 and 44 mg/kg). Only C:N was significantly impacted by TC and was higher in old  
31 343 habitats than in recent ones. Moreover, for C:N, many interactions between habitat descriptors were  
32 344 significant (Table 3). Multiple mean comparisons showed that these effects were mostly due to non-  
33 345 isolated old forest habitats (isolation class 0) that showed significantly higher values (on average 20.6)  
34 346 than every other forest habitats whatever their SI or TC (in old habitats: isolation 1, 15.8; isolation 2,  
35 347 16; in recent habitats: isolation 0, 14.5; isolation 1, 14.3; isolation 2, 13.8). In agricultural land, no  
36 348 effect of the spatiotemporal descriptors on C:N was detected.  
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349 *3.3. Effects of the three habitat descriptors and soil characteristics on collembolan diversity*

1  
2 350 When implemented on data from both forest and agricultural habitats, no correlations between  
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4 351 Shannon index and soil properties were significant (Fig 5). On the other hand, many correlations  
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6 352 between species density and soil properties were significant at 5% level. Species density was  
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9 353 positively correlated with CEC, Ctot, C:N and Humus Index (0.37; 0.38; 0.43 and 0.44, respectively)  
10  
11 354 and negatively correlated with bulk density and pH (-0.3 and -0.38, respectively) (Fig 5). Only  
12  
13 355 positive correlations between species richness and Ctot, C:N, CEC and Humus index (respectively  
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15 356 0.30, 0.27, 0.28 and 0.33) were observed. However, most of these correlations reflected the above-  
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18 357 mentioned differences in soil properties between forest and agricultural habitats. When implemented  
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20 358 separately in the two HTs no correlations with species density, species richness or Shannon index were  
21  
22 359 significant in agricultural habitats. In forests, only Ctot, C:N (0.4 and 0.44, respectively) and pH (-  
23  
24 360 0.39) were significantly correlated to species density and only C:N was significantly correlated to  
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26  
27 361 species richness (0.40), but none were correlated to the Shannon index (Fig. 5).

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29 362 As C:N was highly correlated with both Ctot and pH (0.61,  $p < 0.0001$  and -0.69,  $p < 0.0001$   
30  
31 363 respectively), while Ctot and pH were also correlated (0.43,  $p < 0.001$ ) but to a lesser extent than to  
32  
33 364 C:N, we decided to include only Ctot and pH as covariates in two distinct global linear models testing  
34  
35 365 their effect and that of habitat descriptors on species density, species richness and Shannon index and  
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37  
38 366 we implemented a procedure of automatic selection based on AIC. Both models (Ctot and pH) did not  
39  
40 367 detect any significant effect of any variable on the Shannon index. Table 4 displays the results of  
41  
42 368 models analyzing the effects of habitat descriptors and either Ctot or pH on species density and species  
43  
44  
45 369 richness. The Ctot models showed that there was no simple effect of habitat descriptors either on  
46  
47 370 species density or on species richness, whereas pH models showed significant effects of HT and TC  
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49 371 on species density and of TC on species richness. Additionally, pH and Ctot models revealed the effect  
50  
51 372 of several significant interactions. The pH model showed significant effects of the interactions  
52  
53 373 between HT and TC, between HT and SI and between TC and SI on species density. The Ctot models  
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56 374 showed the effect of interactions between HT and SI on species density, and between TC and SI on  
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58 375 both species density and species richness. Indeed, least square means for species density comparison  
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60 376 (Fig. 6a) obtained with the Ctot model showed no difference between both HTs in non-isolated  
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377 habitats (isolated class 0) whereas it showed significantly higher values in forest than in agriculture in  
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 2 378 isolation classes 1 and 2. Moreover, comparisons of least square means for species density showed  
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 4 379 significantly higher values in old than in recent patches for the isolation classes 1 and 2, while it  
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 6 380 showed no difference between age classes for the continuous habitats (Fig. 6b). Similarly, least square  
 7  
 8 381 means for species richness comparison showed significantly higher values in old than in recent patches  
 9  
 10 382 for the isolation class 2, while it showed no difference between age classes for habitats of isolation  
 11  
 12 383 class 0 and 1 (Fig. 6c). Soil pH and Ctot did not have a significant effect on their own, neither on  
 13  
 14 384 species density nor on species richness. The Ctot had significant effects in interaction with HT, and  
 15  
 16 385 TC on species density. According to estimated model parameters, species density increased more with  
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 18 386 Ctot in old than in recent habitats. It also increased more with Ctot in forest than in agricultural land.  
 19  
 20 387 The soil pH had significant effects in interaction with HT, TC and SI on species density and in  
 21  
 22 388 interaction with TC on species richness. Species density decreased with the pH in forests whereas it  
 23  
 24 389 increased with the pH in agricultural habitats. Species density and species richness also decreased with  
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 26 390 the pH in old habitats whereas it did not change according to pH in recent habitats.  
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#### 391 4. Discussion

##### 392 4.1. Effects of habitat temporal continuity on collembolan diversity

393 The total number of species (gamma diversity) was higher in old than in recent forests.  
 394 Species present in recent forests and not in old ones were all rare species (i.e. found in less than 10%  
 395 of the records), except for 3 species (*Isotoma viridis*, *Lepidocyrtus cyaneus* and *Lepidocyrtus*  
 396 *lignorum*). These species are known as agricultural-preferring species in the studied region (Ponge et  
 397 al., 2003, 2006). Furthermore, they were found exclusively in isolation classes 1 and 2. Thus it is  
 398 difficult to know whether they were present as relics of the past HT (i.e. agricultural land) or if they  
 399 colonized forest patches from the neighboring agricultural matrix. However, the fact they were not  
 400 present in the equivalent isolation class of old forests suggests that they benefited from the presence  
 401 of a non-saturated community in recent forests. Indeed, the fact that all niches were not necessarily  
 402 occupied in recent forests was certainly in favor of the persistence of agricultural-preferring species:  
 403 these species might colonize spatially isolated patches but would not be able to persist in the more  
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404 diverse communities present in old forests of comparable spatial isolation. In agricultural land, the  
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2 405 total number of species was also higher in old than in recent sites. Only three species present in recent  
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4 406 sites were absent in old ones. Among the 15 species that were present in old but not in recent sites,  
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6 407 only three were common species (i.e. present in more than 10% of the records) and no common  
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8 408 species were found in recent but not in old agricultural sites. This shows that even in open habitats  
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10 409 such as agricultural land, the total number of species was reduced in recently created habitats. It is still  
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12 410 difficult to draw any conclusion on differences in the number of rare species, but the fact that some  
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14 411 common species were lacking in recent sites only, allows us to conclude that this absence is due to the  
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16 412 temporal continuity of the habitat and not to some random mechanism.  
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20 413 Our results show that habitat temporal discontinuity impacts negatively species density,  
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22 414 species richness and Shannon index but not the total abundance of Collembola. For a similar number  
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24 415 of individuals, recent habitats showed fewer species than old habitats whatever the habitat type or the  
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26 416 spatial continuity. This suggests that resources not taken by species still lacking in recent habitats are  
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28 417 used by larger populations of existing species. Among the variables under study, only the carbon to  
29  
30 418 nitrogen ratio reacted to temporal continuity, but this was due to the particular situation of spatially  
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32 419 continuous (non-isolated) old forests that displayed higher values than every other forest patches  
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34 420 whatever their spatiotemporal structure. All other soil properties (humus type, a proxy of litter amount  
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36 421 and quality, pH, C, N contents and P availability) were similar in old and recent habitats of the same  
37  
38 422 type, suggesting that habitat temporal continuity has a direct effect on collembolan diversity that does  
39  
40 423 not depend on soil properties. Within the limits of our analytical protocol (we did not study all  
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42 424 parameters known to influence Collembola, such as for instance the composition of litter and that of  
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44 425 soil microbial communities, nor did we study interactions between Collembola and higher trophic  
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46 426 levels) this confirms our first hypothesis (H1) predicting a lower collembolan diversity in recently  
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48 427 created habitats.  
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53 428 The direct effect of habitat temporal continuity on collembolan diversity is also supported by  
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55 429 the fact that both species density and species richness were impacted by temporal continuity in the pH  
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57 430 model. This means that habitat temporal discontinuity impacts diversity not only by decreasing the  
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59 431 size of the local pool of species (species density) but also by decreasing the number of species that  
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432 would be present if local soil conditions were strictly similar among all spatiotemporal situations  
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2 433 (species richness). This is supported by the fact that the impact of temporal continuity on Shannon  
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4 434 index must be considered as a direct effect because this index did not show any significant correlation  
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6 435 with soil physicochemical properties.  
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9 436         However, the temporal discontinuity of habitat could also be viewed as an index of  
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11 437 disturbance. According to the intermediate disturbance hypothesis we could expect recent habitats to  
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13 438 host low collembolan diversity, habitats of intermediate age to host a higher biodiversity, and  
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15 439 biodiversity to decrease in older habitats because of exclusive competition (Connell, 1978; Molino and  
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17 440 Sabatier, 2001; but see Fox, 2013). Our results did not support this general scheme. This might be due  
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19 441 to the fact that our study focuses on the landscape scale, so that studied habitat were not homogeneous  
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21 442 and host a high diversity of local niches at scales ranging from units to tens square meters (Ponge and  
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23 443 Salmon, 2013). Nevertheless, we cannot exclude that habitats older than the ones we studied, might  
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25 444 display a decrease in collembolan biodiversity, thus supporting the intermediate disturbance  
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27 445 hypothesis. We did not expect old most isolated habitats to display the lowest alpha diversity predicted  
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29 446 by metacommunity theories (Tilman, 1982; Hubbell, 2001) because the oldest habitats we studied  
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31 447 were certainly not old enough to support such patterns. Additionally, within-patch heterogeneity is  
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33 448 most likely to prevent collembolan alpha diversity from decreasing to such low levels.  
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38 449         Most empirical studies testing the effect of landscape structure on diversity patterns do not  
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40 450 take habitat temporal structure into account (Mouquet et al., 2003). We do not have knowledge of any  
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42 451 other study on Collembola that is strictly comparable to ours although collembolan species have been  
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44 452 shown to be affected by habitat successional stage (Setälä et al., 1995; Loranger et al., 2001; Scheu et  
45  
46 453 al., 2003; Chauvat et al., 2007; Salamon et al., 2008; Chauvat et al., 2011). While in these studies the  
47  
48 454 observed effects were due both to change in habitat type (succession) and to habitat age (time since the  
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50 455 habitat is in place) our results allow us to focus on the effect of habitat age within the same habitat  
51  
52 456 type. Temporally discontinuous (recent) habitats displayed lower diversities due to the poor  
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54 457 colonization/dispersal abilities of Collembola: some species were absent from recent habitats not  
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56 458 because the habitat was not suitable for them but because they did not have enough time to colonize it.  
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58 459 Higher values of the Shannon index in old than in recent habitats support this hypothesis: communities  
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2 461 in recent habitats are dominated by fewer species. Coined as colonization credit, this process has been  
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4 462 suggested to occur in plant communities (Cristofoli et al., 2010), but has so far been documented by  
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6 463 only a few empirical studies on plants (Gijbels et al., 2012) and butterflies (Cristofoli and Mahy,  
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#### 10 464 *4.2. Effect of habitat spatial isolation on collembolan diversity*

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12 465 In this study, we tested two main possible effects of spatial isolation on diversity: the indirect  
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14 466 effect of isolation through its effect on environmental conditions and its direct effect through its  
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16 467 influence on species likelihood to colonize and persist in a patch. We detected no consistent effect,  
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19 468 either direct or indirect, of habitat spatial structure on collembolan diversity, among the two habitat  
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21 469 types and the two age classes here compared.

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23 470 Habitat fragmentation is thought to decrease the local diversity of macroorganisms because  
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25 471 isolated patches (i) are too small to fulfill ecological and demographic requirements of populations  
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27 472 (Allouche et al., 2012), and (ii) are more difficult to colonize (Wamser et al., 2012). We did not find  
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29 473 such effect in Collembola. This is probably because our habitat patches were always large enough to  
30  
31 474 fulfill ecological and demographic requirements of all potentially present collembolan species due to  
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33 475 the small size of these organisms. Schneider et al. (2007) showed indeed that collembolan populations  
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35 476 in patches as small as 50 cm<sup>2</sup> did not change both in diversity and density within 16 months of  
36  
37 477 isolation. Given that our smallest patch was much larger than this restricted surface, this may explain  
38  
39 478 why spatial discontinuity did not affect collembolan populations in our study. Thus, even if the  
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41 479 colonization of isolated patches might be a problem for them (see section 4.3), fragmentation has  
42  
43 480 probably not led to local extinctions, so that colonization is not necessary to maintain diversity. Of  
44  
45 481 course, the connectivity and the size of micro-habitats inside the patches may influence collembolan  
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47 482 diversity at micro-site scale (Hertzberg, 1997; Åstrom and Bengtsson, 2011) but our sampling design  
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49 483 does not allow testing this hypothesis.  
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#### 484 4.3. *Interacting effects of habitat temporal and spatial structure on diversity*

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2 485 Our results showed that spatial and temporal structures of habitats had an interactive effect on  
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4 486 local diversity patterns. In the studied region, we showed that species diversity increased with spatial  
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6 487 isolation in old habitats whereas it decreased with spatial isolation in recent habitats. This resulted in  
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9 488 differences of diversity in isolated habitats while recent and old continuous habitats showed similar  
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11 489 values. This suggests that when in place for a long time, isolated habitats supported more colonization  
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13 490 events than spatially continuous (i.e. non-isolated) habitats, without concomitant extinction events.  
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15 491 This can be due to species from the opposite habitat type being present locally, if they do not have  
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18 492 strict habitat preferences, because of increased edge effects in isolated patches (Slawski and Slawska,  
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20 493 2000; Östman et al., 2009). This also means that the negative effect of spatial isolation on collembolan  
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22 494 diversity can only be unravelled if we take the habitat temporal structure into account. Our results  
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24 495 suggests that Collembola species need time to colonize recently created habitat that are isolated from  
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26 496 other habitats of the same type. This effect should be especially strong for specialist species that do not  
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29 497 survive in a matrix of the opposite habitat type. To our knowledge, it is the first time that such  
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31 498 interacting effects are empirically unravelled.

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33 499 The interaction between habitat spatial and temporal continuity was not strictly similar for  
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35 500 species density and species richness. Indeed, species density was lower in recent than in old habitat of  
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38 501 isolation classes 1 and 2, whereas species richness was lower in recent than in old habitat of isolation 2  
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40 502 only. By definition, species density is affected by the number of individuals present in a sample, while  
41  
42 503 species richness is not. Species density should thus be sensitive to both local factors and landscape  
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44 504 characteristics (regional factors). Local factors determine locally the carrying capacity of the  
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46 505 environment while the number of species that can reach a local patch should be mostly determined by  
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49 506 landscape characteristics. This difference in sensitivity between both diversity indicators reveals that  
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51 507 old habitat of isolation class 1 should benefit from the contribution of many poorly abundant species  
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53 508 (not taken into account in the calculation of species richness) in addition to a few abundant species.  
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55 509 This results in similar values of species richness in old and recent habitats of isolation class 1, but still  
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58 510 different values for species density. In the other hand, old habitats of isolation class 2 benefit from an  
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511 increase in the number of species that are also more evenly distributed, which results in an increase in  
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2 512 both species richness and species density compared to recent habitat of the same isolation class.  
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4 513         These results support the novel idea that habitat fragmentation constrains diversity not only  
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6 514 through spatial but also through temporal continuity: there is a strong positive impact of temporal  
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8 515 continuity on the total number of species, in addition to the distribution of individual numbers within  
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10 516 each species. Thus, in the case of soil organisms, which probably disperse slowly at landscape scale,  
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12 517 regional processes shaping communities must be slow. That is why habitat age has to be taken into  
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14 518 account to better predict soil biodiversity in the context of habitat fragmentation.  
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#### 18 519 *4.4. Effect of soil properties in interaction with habitat spatiotemporal structure on diversity*

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21 520         Few soil characteristics responded to the spatial and /or temporal structure of habitats,  
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23 521 suggesting that indirect effect on diversity should be weak. Additionally, our results showed that both  
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25 522 species density and species richness were submitted to direct effects of habitat descriptors and their  
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27 523 interactions, whereas no indirect effects were detected since neither the Ctot nor the soil pH had  
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29 524 simple effect on diversity. However, the two parameters that were most correlated with species density  
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31 525 (soil pH and total carbon Ctot) interacted with habitat descriptors to affect diversity. Collembolan  
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33 526 diversity was more influenced by Ctot and soil pH in old than in recent patches. This result  
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35 527 corroborates the study of Dzwonko (2001), who showed that plant species indicator values for several  
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37 528 environmental factors (Ellenberg indicators) were more reliable in old than in recent forests. Species  
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39 529 can be good indicators of environmental conditions only if communities have had enough time to  
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41 530 reach equilibrium. Before equilibrium, a bias can occur because some indicator species are lacking due  
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43 531 to dispersal limitation (Seabloom and van der Valk, 2003) or because some species reflecting previous  
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45 532 habitat type still persist (French et al., 2008).  
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48  
49 533         The introduction of Ctot in the model suppressed the significant effect of temporal continuity  
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51 534 on species density. Likewise, the introduction of the pH in the model suppressed the significant effect  
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53 535 of habitat type on species richness. This means that a part of the variability explained by habitat  
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55 536 descriptors is in fact due to a difference in soil properties. Ctot was lower (although not significantly)  
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57 537 in recent than in old habitats, especially in forest and soil pH was significantly lower in forest than in  
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538 agricultural land. Since the carbon content and the soil pH may influence collembolan diversity  
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 2 539 (Chagnon et al., 2000), we cannot totally reject that a part of the observed difference in diversity  
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 4 540 according to habitat descriptors is due to slightly different environmental conditions. This shows that  
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 6 541 discriminating between direct and indirect effects is not straightforward, confirming that when  
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 8 542 studying the impact of landscape structure on soil animals, soil properties should be taken into  
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 10 543 account.

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 13 544 We also showed that effects of habitat descriptors on species density and species richness were  
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 15 545 not strictly similar when taking into account soil properties. Fewer effects were detected on species  
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 17 546 richness than on species density, but all factors impacting species richness also impacted species  
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 19 547 density. This suggests that some factors impacting species density also impact species relative  
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 21 548 abundances in a subtle way and that removing this effect on abundances through the use of species  
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 23 549 richness suppresses the effects detected on diversity. This confirms that using an abundance-free index  
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 25 550 of biodiversity using rarefaction curves allows a better analysis of the impact of local and regional  
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 27 551 factors on local pools of species (Gotelli and Colwell, 2001).

#### 31 32 552 *4.5. Differences in diversity patterns between habitat types*

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 34 553 We defined habitat types as two very broad categories: agriculture or forest without taking the  
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 36 554 precise habitat type (e.g. coniferous and deciduous forests) into account. Nevertheless, we were able to  
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 38 555 reveal some significant effects of landscape characteristics on diversity and differences in patterns  
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 40 556 between the two habitat types. This confirms that for Collembola, the land use is a fundamental factor  
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 42 557 that determines which species can persist locally (Ponge, 1993; Hopkin, 1997; Birkhofer et al., 2012).  
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 44 558 As hypothesized (H2), local diversity in terms of species density and species richness were higher in  
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 46 559 forest than in agricultural habitats. This is likely to be due to differences in soil properties between  
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 48 560 these two contrasted habitat types. (1) Forests display well developed humus profiles and a higher soil  
 49  
 50 561 carbon content, which provide resources for many collembolan species (Chagnon et al., 2000). The  
 51  
 52 562 absence of tree cover and the exportation of organic matter and associated nutrients in agricultural  
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 54 563 land result in a reduced soil organic layer and soil moisture (Batlle-Aguilar et al., 2011) which will  
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 56 564 consequently negatively affect diversity and abundance of soil biota. Additionally, higher soil density  
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565 in agricultural habitats may also reduce collembolan abundance because it provides little pore space  
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2 566 for soil-dwelling populations (Vreeken-Buijs et al., 1998). It is not excluded that other biotic factors  
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4 567 such as predation contributed to drive observed diversity patterns. However, our field study did not  
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6 568 allow assessing the impact of such factor. Surprisingly, in our study, habitat type had no effect on the  
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9 569 Shannon index. Based on the mathematical expression of Shannon's diversity, which associates a  
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11 570 probability of occurrence to each species, this discrepancy suggests that even though the number of  
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13 571 species differed, less frequent species were most affected by change in habitat type (Gorelick, 2006).  
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15 572         The effect of temporal discontinuity was stronger in forest than in agricultural land. This  
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17 573 finding supports our third hypothesis (H3) that predicted a stronger effect of habitat spatiotemporal  
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19 574 structure on collembolan diversity in forest than in agricultural habitats. This could arise because open  
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21 575 habitats lead to more efficient dispersal either through passive or active mechanisms. First, if  
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23 576 Collembola have a preponderant passive dispersal and are directly or indirectly transported by wind,  
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25 577 as suggested for some species by Dunger et al. (2002) and Coulson and Midgley (2012), their  
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27 578 colonization rate might be higher in agricultural habitats since air flow is stronger in the absence of  
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29 579 tree cover (Wright et al., 2010). This result is in accordance with other findings on Collembola in  
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31 580 deglaciaded land (Ingimarsdottir et al., 2012). Indeed these authors showed that in such extremely open  
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33 581 habitat (i.e. with reduced to nil vegetation cover) collembolan dispersal rate was potentially high.  
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35 582 Another explanation could be that collembolan communities in agricultural land are comprised of  
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37 583 more epigeic species than in forests (Sousa et al., 2004), with morphological traits (e.g. long legs, long  
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39 584 furcula) supposed to allow higher mobility in open habitats (Salmon and Ponge, 2012). This result  
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41 585 suggests that dispersal rates and modes are habitat-dependent as shown in other microarthropod  
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43 586 groups (Lindo and Winchester, 2009).  
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49 587         Our results also showed a significant interaction between spatial isolation and habitat type.  
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51 588 With spatial isolation, species density increased in forest but decreased in agricultural habitats. This  
52  
53 589 could be due to better mobility and less strict habitat preferences of species found in agricultural  
54  
55 590 communities (Lauga-Reyrel and Deconchat, 1999; Ponge et al., 2006), likely to be present in remnant  
56  
57 591 forest patches. In contrast, many species from the forest communities show strict habitat preferences  
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59 592 and a reduced mobility (Auclerc et al., 2009) and are thus less prone to colonize remnant agricultural  
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593 patches. Our results also suggest that the forest matrix surrounding agricultural patches is more  
 1  
 2 594 difficult to cross for species than the agricultural matrix surrounding forests. Since passive dispersal  
 3  
 4 595 by wind is likely to be more efficient in agricultural lands than in forests, this suggests that largely  
 5  
 6 596 overlooked passive dispersal mechanisms might be influential for collembolan communities and meta-  
 7  
 8 597 community dynamics.

## 12 598 **5. Conclusion**

14 599 Our study contributes to some extent to disentangle complex effects of habitat characteristics  
 15  
 16 600 (i.e. spatiotemporal structure and local physicochemical conditions) on collembolan diversity. Most  
 17  
 18 601 importantly, we showed that habitat temporal continuity is a key factor shaping collembolan diversity  
 19  
 20 602 and that we must take it into account if we want to understand the effects of habitat spatial structure.  
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 22 603 We also showed that using both species richness and species density as indicators of biodiversity  
 23  
 24 604 allows refining the analysis of the factors influencing collembolan diversity at different scales.  
 25  
 26 605 Unfortunately, it is rather impossible to experiment at landscape scale, and the limits of our study must  
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 28 606 be clearly defined. We controlled only partly the factors thought to influence collembolan diversity:  
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 30 607 climate and litter quality could not be controlled, as they can be in experimental conditions (Åström  
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 32 608 and Bengtsson, 2011; Bokhorst et al., 2012). Similarly, the different levels of isolation and age were  
 33  
 34 609 broadly defined and not totally equivalent in forest and agricultural habitats. However, we were able to  
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 36 610 detect several effects of our treatments (habitat type, isolation and patch age), using landscape past  
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 38 611 dynamics as a surrogate for a strict experimental approach. Some theoretical models predicted such  
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 40 612 patterns (Green and Sadedin, 2005; Gardner and Engelhardt, 2008), but empirical corroborating  
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 42 613 studies are still scarce (Lemaître et al., 2012). Nevertheless, we showed that habitat fragmentation  
 43  
 44 614 constrains diversity not only in space but also in time. The temporal continuity of habitats is one of the  
 45  
 46 615 factors that have a positive effect on diversity. Soil organisms disperse slowly compared to above-  
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 48 616 ground biota and it hence takes longer for a recent habitat to build up soil diversity especially if the  
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 50 617 patch is very isolated.

57 618 Assembly theory is now well recognized in community ecology but still little applied in soil  
 58  
 59 619 ecology. This metacommunity framework predicts four models that could explain species distribution



620 at local scale (Leibold et al, 2004). These models essentially differ in the importance given to dispersal  
1  
2 621 process in explaining metacommunity dynamics. Two of them, ‘species sorting’ (environmental  
3  
4 622 constraints control species distribution) and ‘mass effect’ (dispersal redistributes species among  
5  
6 623 habitats independently of environmental constraints) were found relevant to collembolan communities  
7  
8 624 by da Silva et al. (2012) and Ingimarsdottir et al. (2012). This study also supports the idea that  
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10  
11 625 dispersal plays an important role in structuring collembolan metacommunities and that the magnitude  
12  
13 626 and direction of its effect depend on the type of habitat considered.  
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34 635 the quality of the manuscript.  
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## 1 FIGURE CAPTIONS

2 **Figure 1:** Statistical diagram picturing steps of data analyses. Arrows represent effects of factors on  
3 variables (collembolan diversity and soil properties). Direct effects are represented by continuous  
4 arrows and indirect effects by dotted arrows. Model type 1 (arrow 1) stands for the linear models  
5 testing the effect of the three habitat descriptors on collembolan diversity. Model type 2 (arrow 2)  
6 stands for linear and generalized linear models testing the effect of the habitat descriptors on soil  
7 physicochemical properties. Model type 3 (arrows 1 and 3) stands for linear models testing the effects  
8 of the three habitat descriptors and a soil property on diversity indicators.

9 **Figure 2:** Individual based rarefaction curves old forests (F\_old), recent forests (F\_rec), old  
10 agricultural land (A\_old) and recent agricultural land (A\_rec).

11 **Figure 3:** Mean species density (3a), Shannon index (3b) and species richness (3c) of old (grey) and  
12 recent (white) agricultural and forest habitats. Letters indicate significant differences among means.  
13 “A” and “B” labels represent significant differences between agricultural and forest habitats. Stars  
14 show simple effect of age ( $p < 0.05^*$ ;  $p < 0.01^{**}$ ;  $p < 0.001^{***}$ ). Error bars represent standard errors.

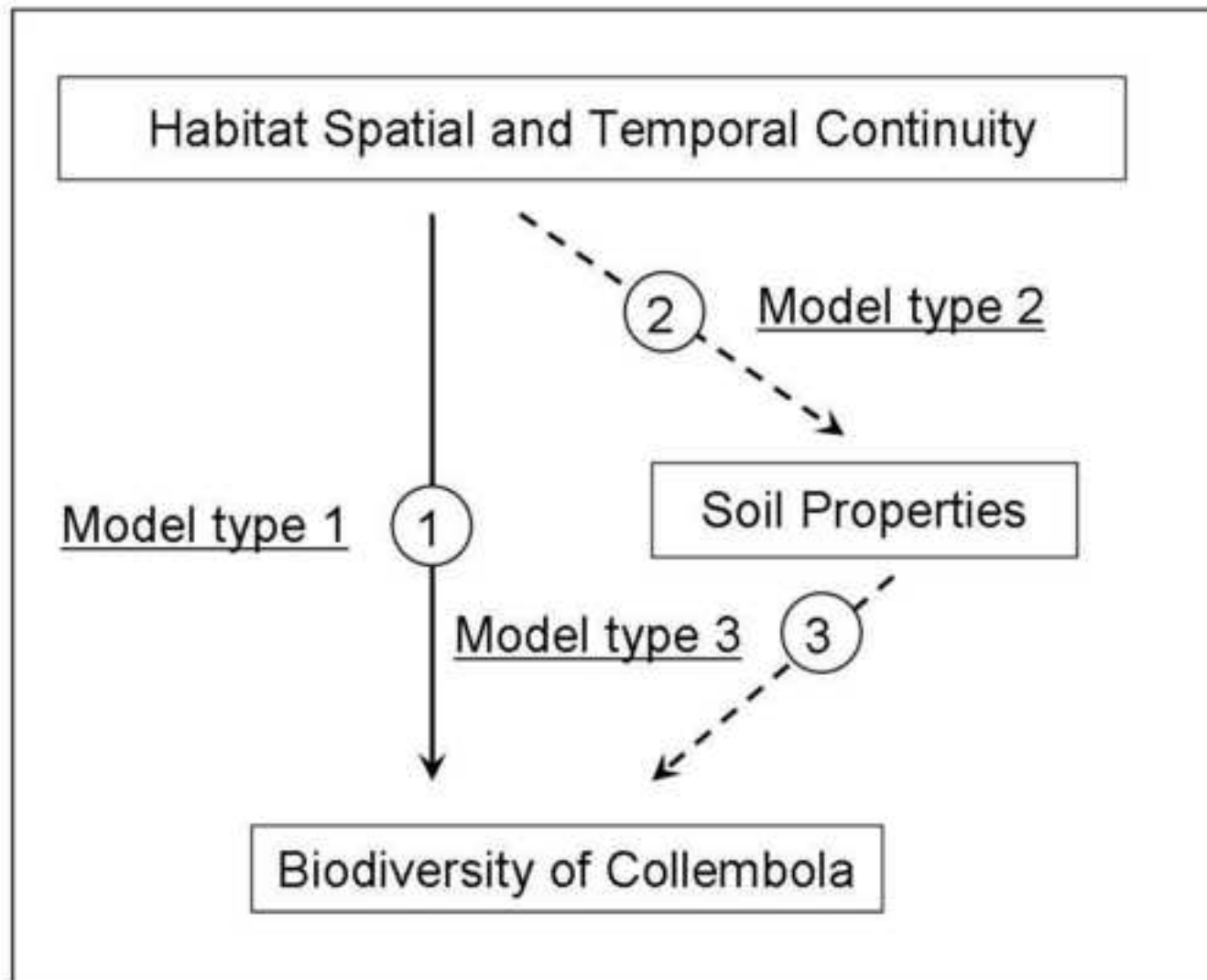
15 **Figure 4:** Mean species density (4a) and species richness (4b) according to Habitat Type, Temporal  
16 Continuity (two age classes: old and recent) and Spatial Isolation (three classes: 0 black bars, 1 white  
17 bars and 2 grey bars). Error bars represent standard errors.

18 **Figure 5:** Correlation coefficients (Pearson) between species density (grey bars), species richness  
19 (dashed bars) or Shannon index (white bars) and soil properties for the complete data set (agricultural  
20 land and forest) (5a) and for forest only (5b). Soil pH: pH, total nitrogen content: Ntot, total carbon  
21 content: Ctot, carbon to nitrogen ration: CN, bioavailable phosphorus: Ph, cation exchange capacity:  
22 CEC, soil moisture: moist, soil density: dens and Humus Index: Humus. Stars show significant  
23 correlation ( $p < 0.05^*$ ;  $p < 0.01^{**}$ ;  $p < 0.001^{***}$ ) between species density, species richness or Shannon  
24 index and each soil parameters listed above.

25 **Figure 6:** Least square means for species density and species richness obtained using the model  
26 testing for the effect of the three habitat descriptors as well as total carbon on species density and  
27 species richness. Least square means for species density are represented according to Habitat Type  
28 (agricultural, grey bars and forested, white bars) and Spatial Isolation (three isolation classes 0, 1 and

29 2) (6a), and least square means for species density and species richness are represented according to  
30 Temporal Continuity (two age classes: old, dashed bars and recent, white bars) and Spatial Isolation  
31 (three isolation classes 0, 1 and 2) (respectively 6b and 6c). Error bars represent standard errors. Stars  
32 show significant differences between habitat types (6a) or ages (6b and 6c) within each isolation class.

Figure1  
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**Direct effects**



**Indirect effects**





Figure2

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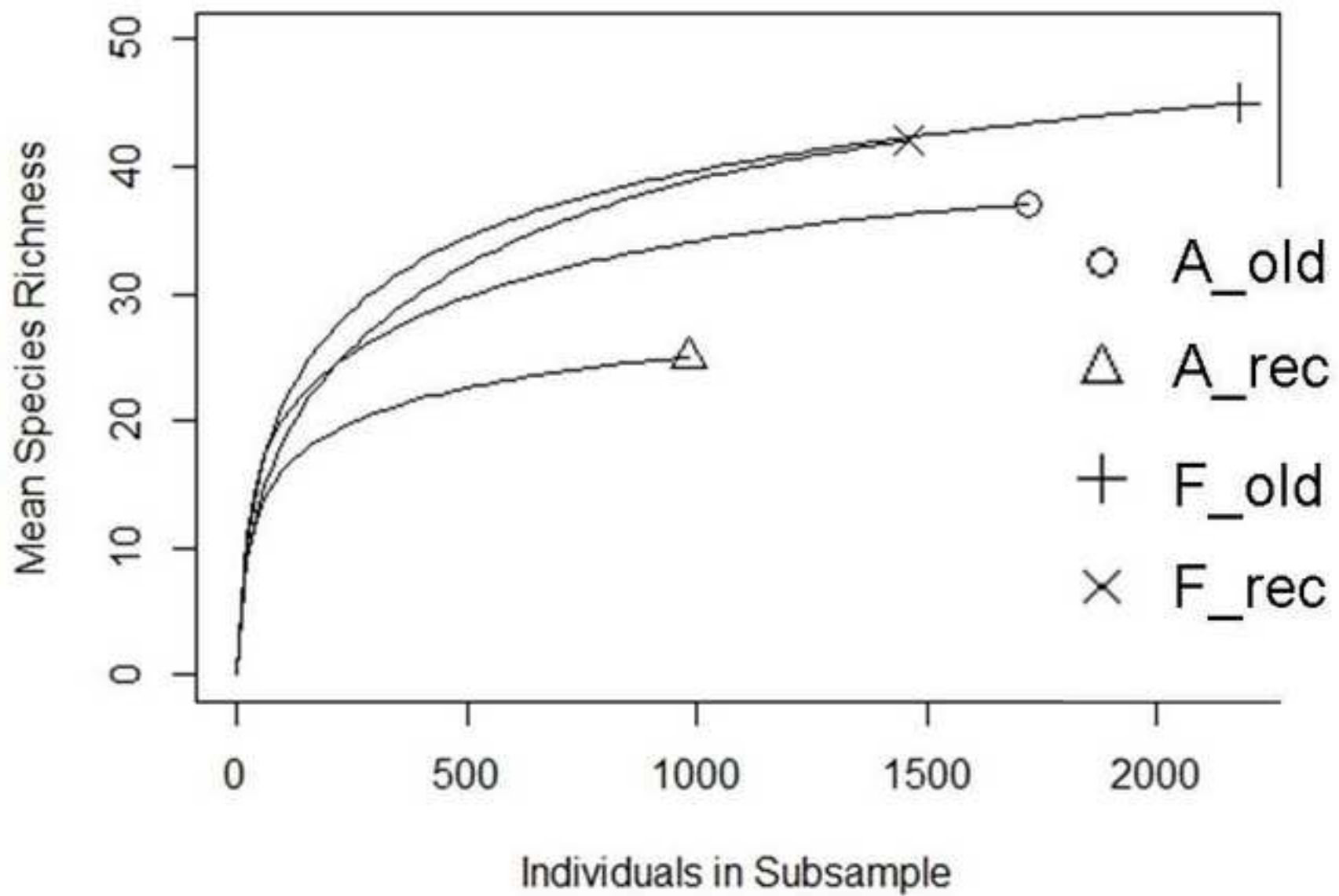
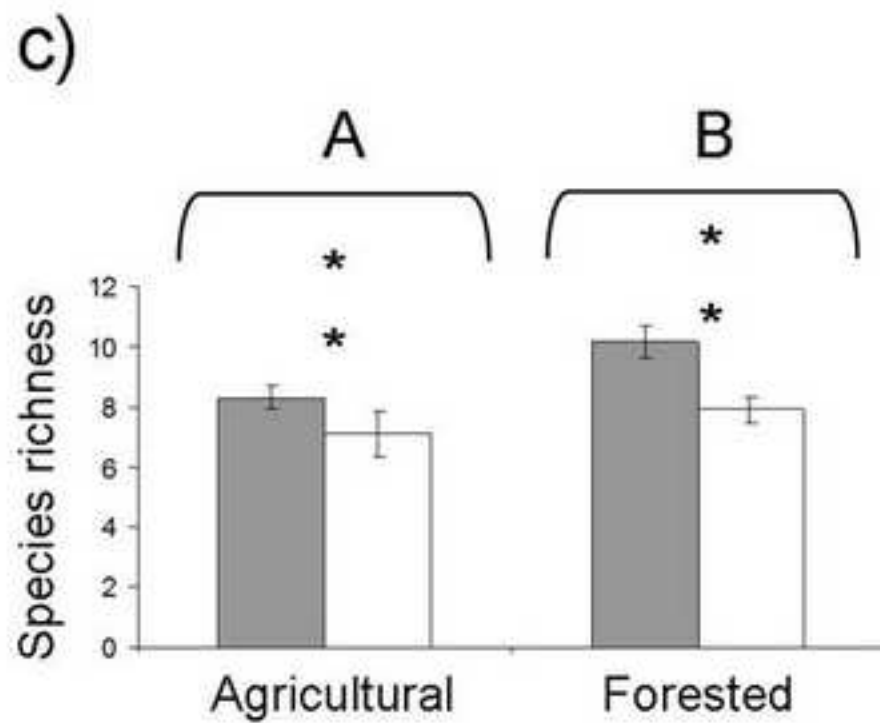
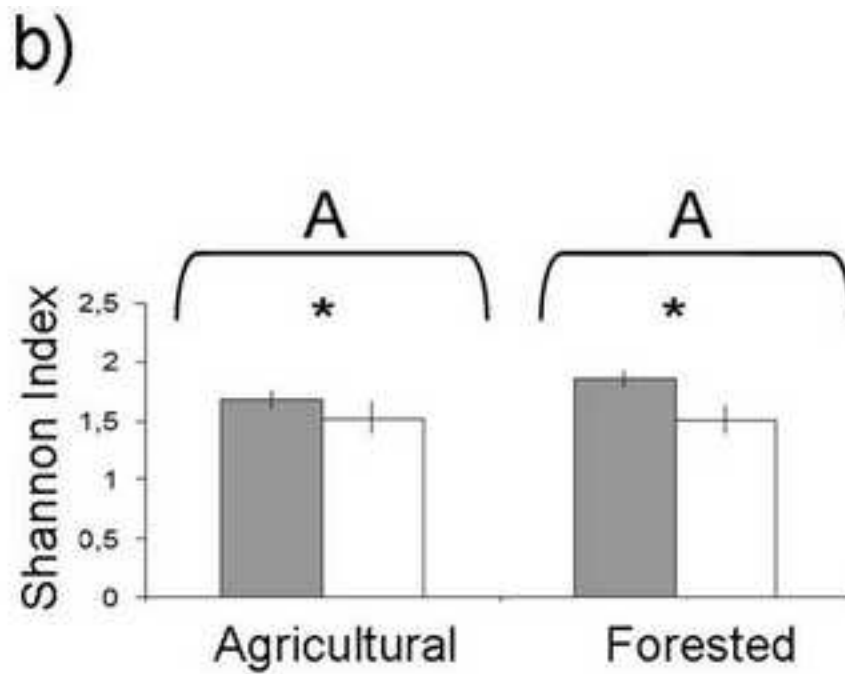
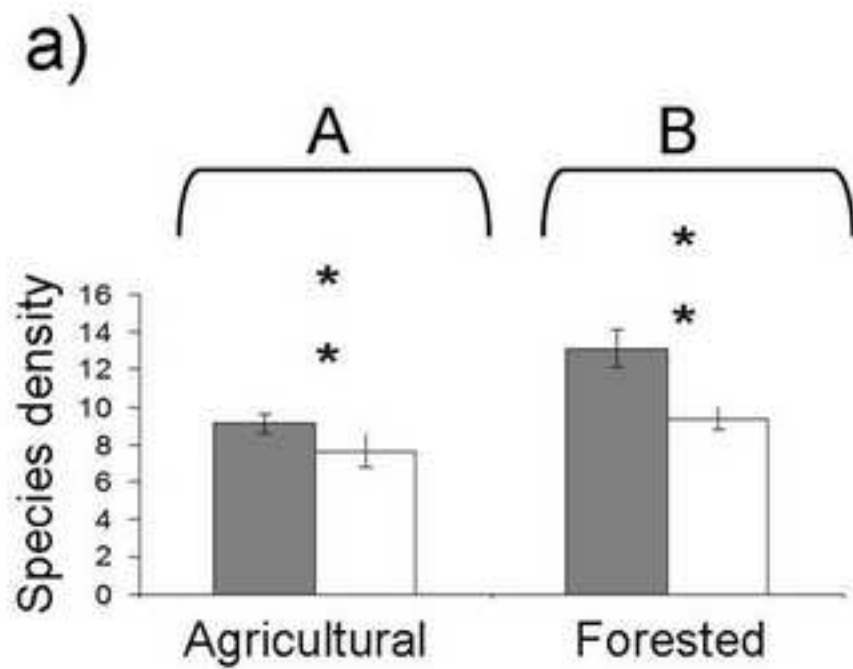


Figure3  
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■ Old  
□ Recent

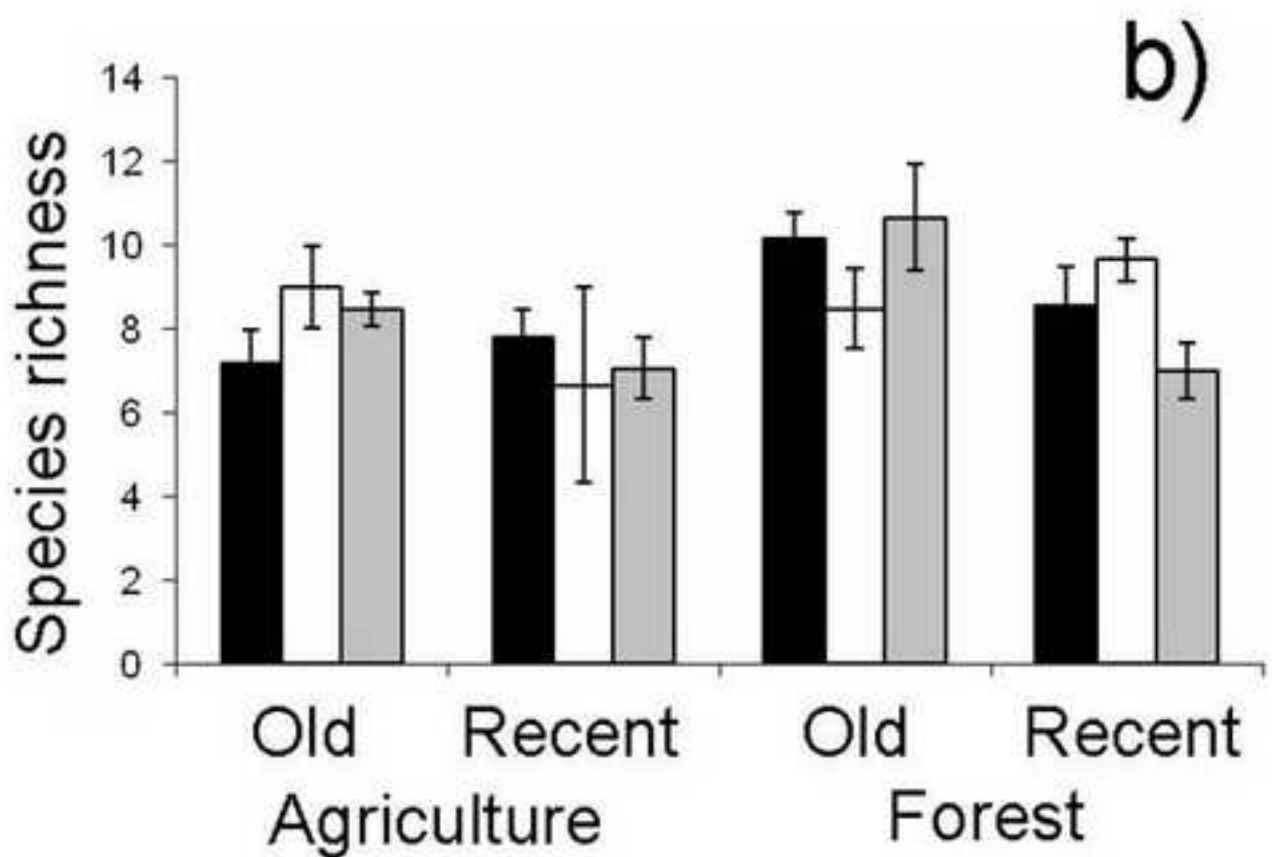
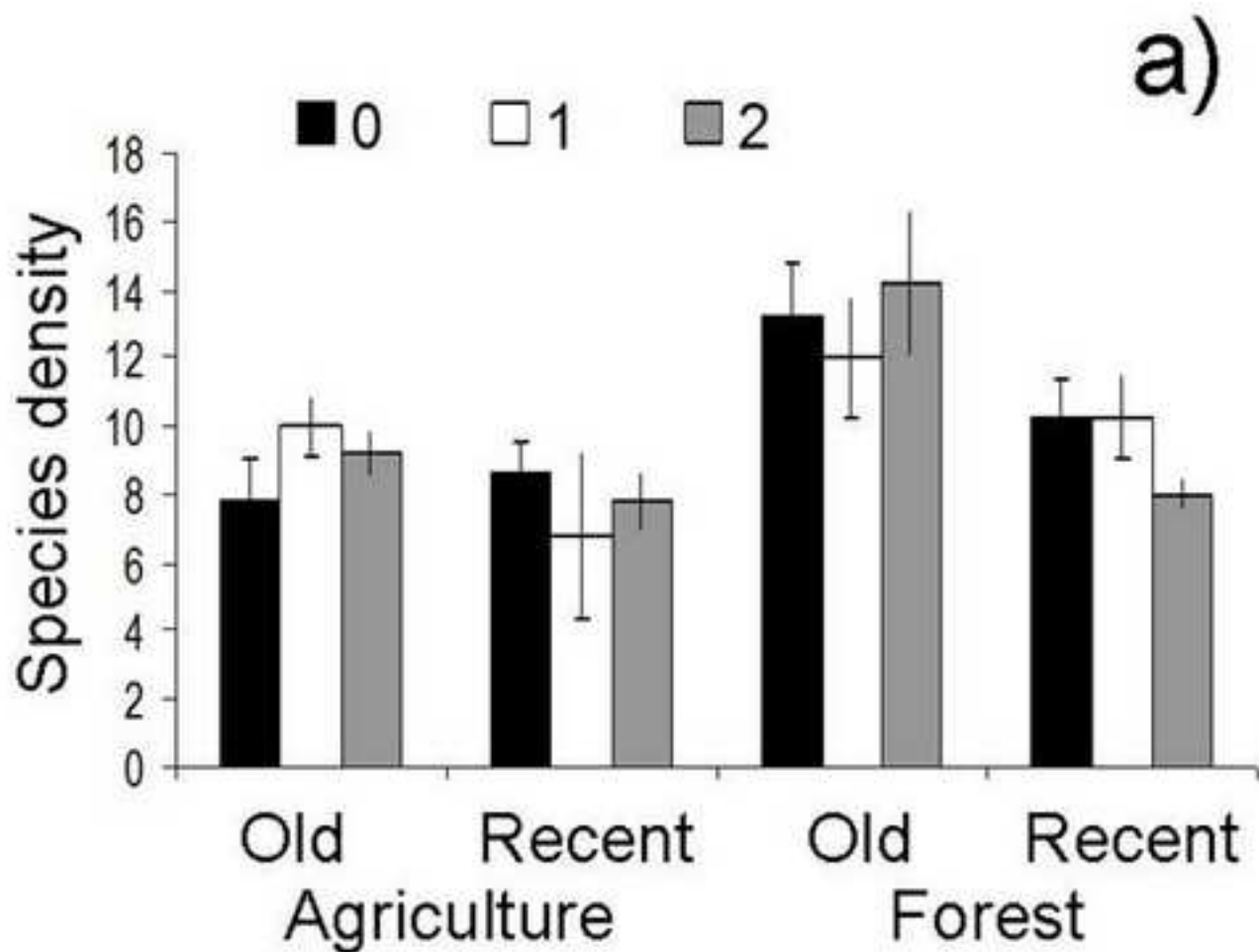


Figure5

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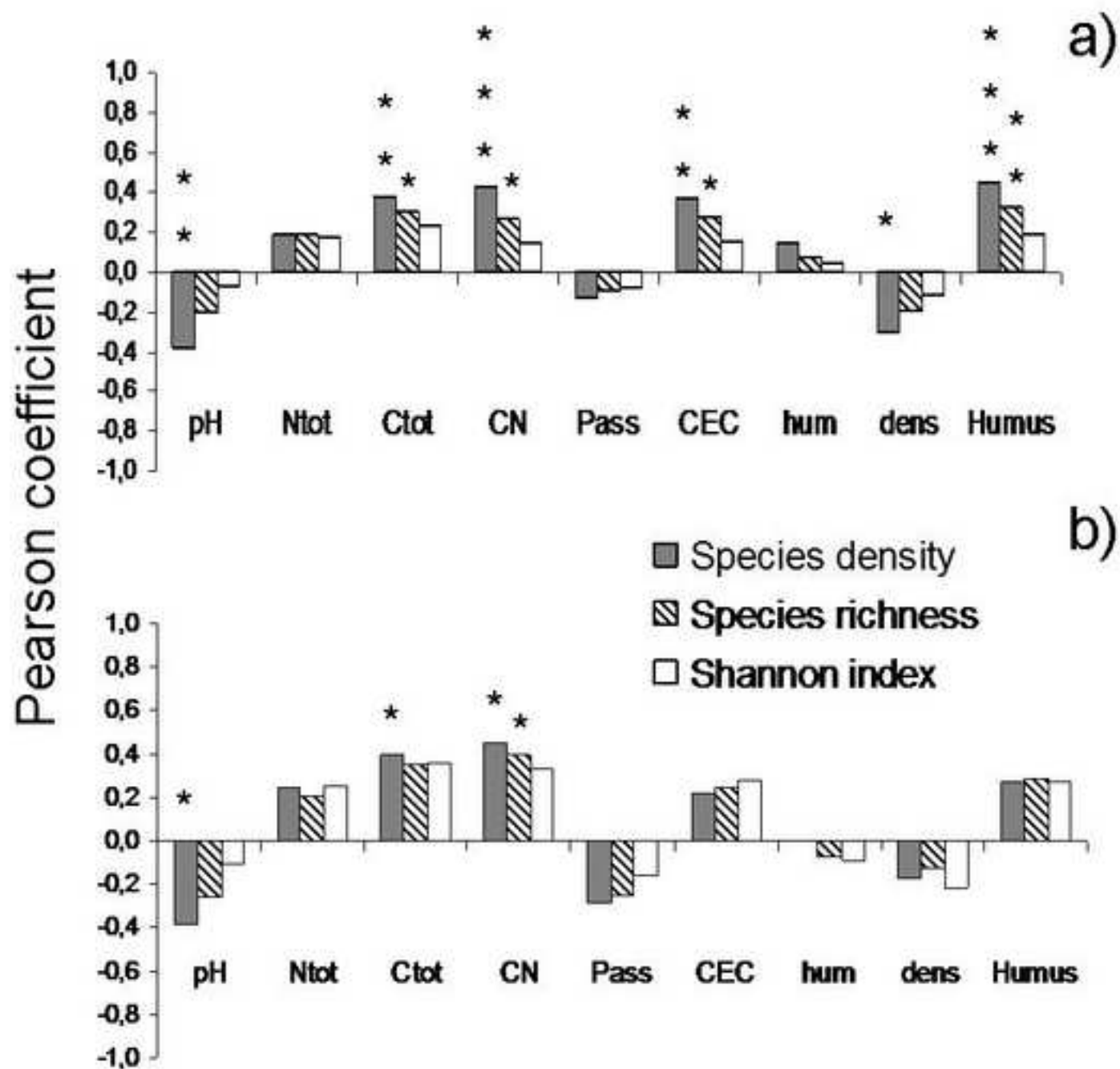
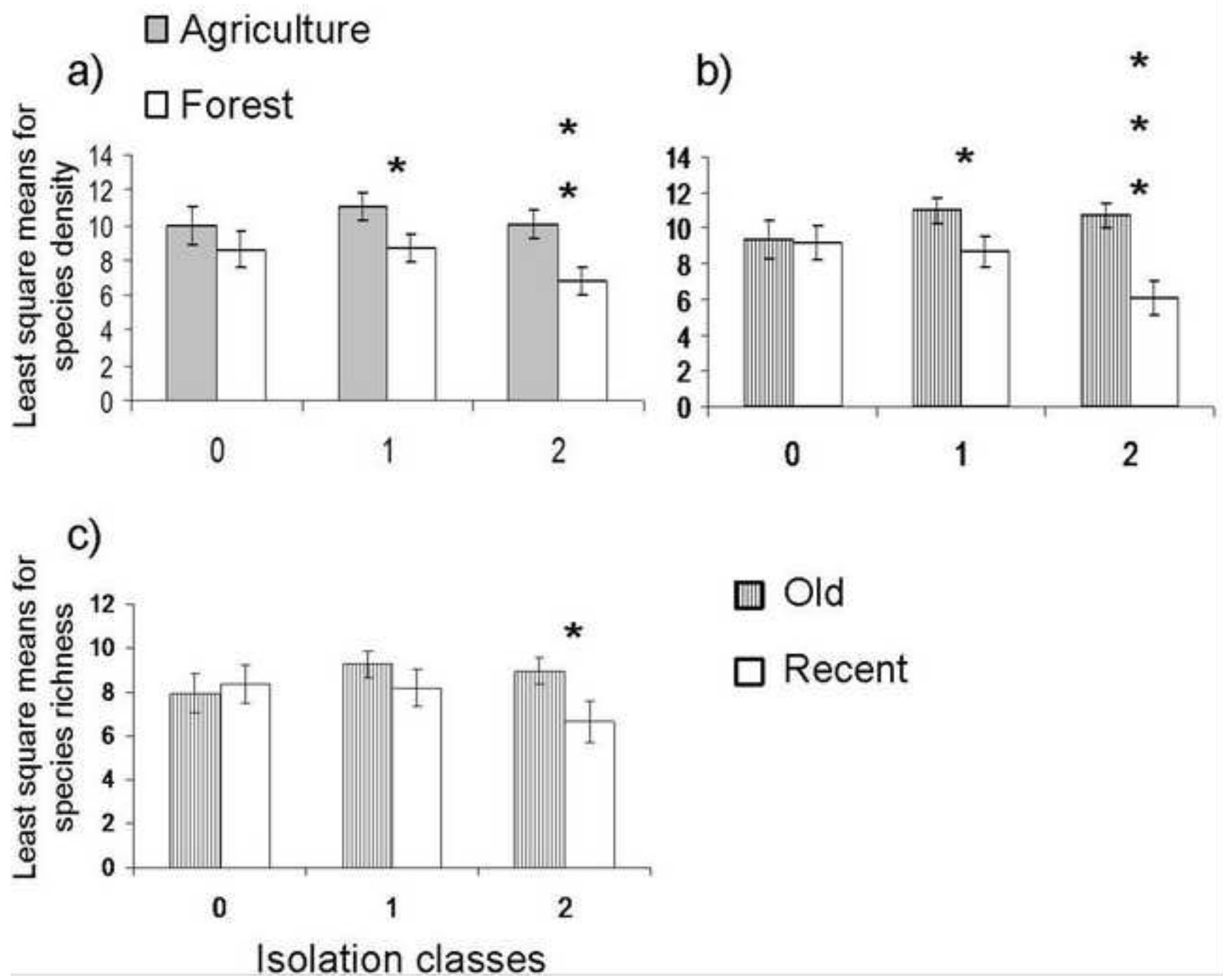


Figure 6

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1 **Table 1.** Effect of habitat descriptors (Habitat Type HT, Temporal Continuity TC and Spatial Isolation  
 2 SI) and all their interactions on Collembola diversity indicators (Species density = total number of  
 3 species collected in a sample of 0.2 dm<sup>2</sup>, Rarefied species richness = number of species estimated for  
 4 57 individuals, Shannon index, Dominance = relative frequency of most abundant species, Abundance  
 5 = total number of individuals per sample). Transformation used on and results of linear models (F  
 6 value and degrees of freedom df). Significance levels: p<0.05\*; p<0.01\*\*; p<0.001\*\*\*.

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		F value				
	df	Species density	Species richness	Shannon Index	Dominance	Abundance
Habitat type (HT)	1	14.2***	0.01*	0.54	0.83	7.09*
Temporal Continuity (TC)	1	9.84**	0.006**	5.23*	0.36	0.99
Spatial Isolation (SI)	2	0.03	0.97	0.23	0.17	0.15
HT : TC	1	2.29	0.33	0.97	0.17	0.71
HT : SI	2	0.12	0.84	0.22	0.17	0.55
TC : SI	2	1.06	0.34	0.44	0.14	0.25
HT : TC : SI	2	1.60	0.36	1.20	0.52	1.75
R <sup>2</sup>		0.40	0.30	0.18	0.06	0.23
Transformation		none	none	none	log <sub>10</sub>	none

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9 **Table 2.** Soil characteristics (mean values and standard deviations) showing differences between  
 10 agricultural and forest habitats. Total carbon content (C<sub>tot</sub>), soil pH (pH), carbon to nitrogen ratio  
 11 (C/N), cation exchange capacity (CEC), soil moisture (Moisture), bulk density (Density) and Humus  
 12 index (Humus). Significance levels: p-values correspond to results of linear and generalized linear  
 13 models presented in Table 3 (p<0.05\*; p<0.01\*\*; p<0.001\*\*\*).

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	Agriculture	Forest	p-value
C <sub>tot</sub> (%)	6.9 ± 2.41	8.74 ± 3.87	*
pH	5.14 ± 0.4	3.95 ± 0.39	***
C/N	12.55 ± 1.46	15.88 ± 2.88	***
CEC (meq%)	24.96 ± 3.82	36.57 ± 8.91	***
Moisture (%)	21.66 ± 14.37	28.78 ± 14.98	*
Density (g/cm <sup>3</sup> )	0.9 ± 0.22	0.68 ± 0.22	***
Humus Index	1 ± 0	3.54 ± 1.55	***

23 **Table 3.** Effect of habitat descriptors (Habitat Type HT, Temporal Continuity TC and Spatial Isolation  
 24 SI) and all their interactions on soil properties. Soil pH (pH), total carbon content (Ctot), total nitrogen  
 25 content (Ntot), carbon to nitrogen ratio (C/N), bioavailable phosphorus (Phosphorus), cation exchange  
 26 capacity (CEC), soil moisture (Moisture), bulk density (Density) and Humus index (Humus).  
 27 Transformation, model type (distribution) and results of linear or generalized linear models (F  
 28 value/Chi square and degrees of freedom df). Significance levels: p<0.05\*; p<0.01\*\*; p<0.001\*\*\*.

		F / Chi square								
	df	pH	Ctot	Ntot	C/N	Phosphorus	CEC	Moisture	Density	Humus
Habitat type	1	185.77***	4.85*	0.12	68.45***	2.74	47.42***	4.13*	13.66***	39.56***
Temporal Continuity	1	2.34	2.16	1.05	9.43**	0.32	0.19	0.08	0.04	0.37
Spatial Isolation	2	6.28**	0.10	0.42	6.07**	3.74*	0.11	0.08	0.54	0.51
HT : TC	1	2.53	0.07	0.86	27.86***	2.69	0.72	2.69	1.14	0.36
HT : SI	2	5.60**	1.47	1.62	5.27**	2.94	1.68	0.66	1.27	0.51
TC : SI	2	1.34	1.12	1.51	1.27	2.92	0.63	0.25	0.21	0.21
HT : TC : SI	2	2.74	1.99	0.70	5.69**	0.85	0.90	0.27	0.78	0.21
R <sup>2</sup>		0.82	0.26	0.12	0.77	0.35	0.55	0.12	0.28	0.63
Model type (distribution)		Normal	Gamma	Gamma	Normal	Normal	Normal	Gamma	Gamma	Poisson
Transformation		none	none	none	none	log <sub>10</sub>	log <sub>10</sub>	none	none	none

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31 **Table 4.** Effect of habitat descriptors (Habitat Type HT, Temporal Continuity TC and Spatial Isolation  
 32 SI), total soil carbon content (Ctot) (left hand side), soil pH (right hand side) and all their interactions  
 33 on species density and species richness. Transformation and results of linear models (F values and  
 34 degrees of freedom df), tested after variable selection based on AIC criterion). Significance levels:  
 35  $p < 0.05^*$ ;  $p < 0.01^{**}$ ;  $p < 0.001^{***}$ .

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Ctot model				Soil pH model			
		Species density	Species richness			Species density	Species richness
	df	F value	F value		df		
Habitat type (HT)	1	0.79	0.15	Habitat type (HT)	1	5.98*	1.38
Temporal Continuity (TC)	1	1.9	0.05	Temporal Continuity (TC)	1	6.00*	6.56*
Spatial Isolation (SI)	2	0.2	0.02	Spatial Isolation (SI)	2	0.33	3.07
Total Carbon (Ctot)	1	0.00	0.66	pH H <sub>2</sub> O (pH)	1	0.02	0.64
HT : TC	1	/	2.36	HT : TC	1	4.4*	2.34
HT : SI	2	4.14*	2.14	HT : SI	2	4.56*	1.80
TC : SI	2	10.13***	5.28**	TC : SI	2	4.04*	1.73
HT : Ctot	1	4.62*	0.02	HT : pH	1	5.23*	0.92
TC : Ctot	1	6.00*	0.03	TC : pH	1	9.84**	5.65*
SI : Ctot	2	0.07	0.07	SI : pH	2	4.89*	2.69
HT : TC : Ctot	1	/	2.07	HT : TC : pH	2	3.2	/
HT : SI : Ctot	2	5.04*	2.31	HT : SI : pH	1	2.56	1.59
TC : SI : Ctot	2	11.34***	5.74**				
R <sup>2</sup>		0.67	0.49	R <sup>2</sup>		0.62	0.49
Transformation		none	none	Transformation		none	none

**Appendix A.** List of study sites with their classification according to habitat type (agriculture vs forest), temporal continuity (old vs recent) and spatial isolation (three isolation classes), followed by % edge contrast with opposite habitat type, matrix type (old or recent or mixed), station code, land use, humus form according to Brêthes et al. (1995) and main community indices of Collembola (total abundance per sample, species density, species richness, Shannon index and dominance). The edge contrast is the % borderline which the patch with the sampling point shares with the opposite habitat in the circle of 300 m around the sampling point. The matrix type is the dominant age of the habitat surrounding the patch with the sampling point. The combination of both defines the level of isolation.

Habitat type	Temporal Continuity	Spatial Isolation	Edge contrast (%)	Matrix type	Station code	Land use	Humus form	Abundance	Species density	Species richness	Shannon index	Dominance	
Agriculture	Ancient	0	0	mostly old	A-old0 N=5	Hay meadow	EUMULL	47	9	9	1.93	0.32	
			0			Christmas tree	EUMULL	50	6	6	1.34	0.48	
			0			Crop	EUMULL	9	5	5	1.58	0.22	
			0			Pasture	EUMULL	41	7	7	1.47	0.51	
		1	both old and recent	0	A-old1 N=6	Hay meadow	EUMULL	212	12	8.89	1.83	0.33	
				25		Pasture	EUMULL	99	7	5.53	0.69	0.84	
				25		Hay meadow	EUMULL	56	8	8	1.82	0.23	
				25		Hay meadow	EUMULL	56	12	11.97	2.21	0.26	
				25		Pasture	EUMULL	75	12	10.94	2.09	0.3	
				25		Crop	EUMULL	128	11	9.75	2.05	0.23	
			2	mostly old	25	A-old2 N=9	Hay meadow	EUMULL	147	10	7.72	1.57	0.39
					61		Hay meadow	EUMULL	101	11	9	1.32	0.66
					74		Hay meadow	EUMULL	90	8	7.63	1.59	0.45
					78		Hay meadow	EUMULL	112	9	7.66	1.69	0.37
	Recent	0	mostly old	A-rec0 N=3	Hay meadow	EUMULL	244	10	7.6	1.78	0.32		
					Hay meadow	EUMULL	63	7	6.8	1.54	0.33		
					Pasture	EUMULL	25	9	9	2	0.27		
			1	both old and recent	A-rec1 N=4	23	Pasture	EUMULL	8	4	4	1.32	0.38
						25	Christmas tree	EUMULL	16	2	2	0.23	0.94
						32	Hay meadow	EUMULL	57	8	8	1.84	0.26
		37				Pasture	EUMULL	60	13	12.6	1.88	0.36	
		2	mostly old	A-rec2 N=5	46	Hay meadow	EUMULL	80	8	7.59	1.59	0.3	
					46	Christmas tree	EUMULL	122	7	6.27	1.41	0.44	
					63	Hay meadow	EUMULL	11	5	5	1.55	0.27	
					80	Christmas tree	EUMULL	104	10	9.38	1.94	0.28	
		83	Hay meadow	EUMULL	191	9	6.97	1.21	0.65				
		Forest	Ancient	0	mostly old	F-old0 N=5	Deciduous	DYSMULL	65	10	9.49	1.64	0.51
							Coniferous	DYSMODER	142	11	8.87	1.63	0.48
Deciduous	DYMULL						227	19	12.4	2.21	0.27		
Deciduous	DYSMULL						247	14	9.44	1.79	0.43		
Deciduous	DYMODER						76	12	10.57	2.09	0.25		
1	both old and recent			F-old1 N=5	25	Deciduous	EUMODER	76	9	8.37	1.67	0.41	
					37	Coniferous	OLIGOMULL	118	13	10.31	1.87	0.41	
					51	Deciduous	DYSMULL	170	16	12.58	2.09	0.34	
					67	Deciduous	MESOMULL	78	7	6.85	1.26	0.63	
					83	Deciduous	DYSMULL	224	15	10.07	2.03	0.22	
					100	Deciduous	OLIGOMULL	115	19	14.74	2.36	0.32	
					100	Deciduous	OLIGOMULL	61	13	11.05	1.8	0.51	
					100	Deciduous	DYSMULL	231	18	9.58	1.7	0.44	
					100	Deciduous	DYSMULL	151	14	10.88	2.07	0.28	
100	Deciduous		EUMULL	26	7	7	1.7	0.37					
Recent	0		mostly old	F-rec0 N=4	Coniferous	OLIGOMULL	86	8	7.07	1.38	0.41		
					Deciduous	OLIGOMULL	101	13	10.67	2.25	0.18		
					Coniferous	OLIGOMULL	180	9	6.78	0.99	0.75		
					Deciduous	OLIGOMULL	120	11	9.59	1.51	0.58		
	1		both old and recent	F-rec1 N=4	11	Deciduous	MESOMULL	82	10	8.52	1.72	0.32	
					19	Deciduous	OLIGOMULL	46	7	7	1.35	0.52	
					23	Deciduous	MESOMULL	165	12	8.94	1.58	0.39	
					24	Deciduous	DYSMODER	222	12	9.45	1.82	0.35	
					69	Deciduous	MESOMULL	18	9	9	2.08	0.17	
					100	Coniferous	MESOMULL	132	8	5.32	0.78	0.79	
	2		mostly old	F-rec2 N=5	100	Deciduous	OLIGOMULL	145	7	6.04	1.4	0.46	
					100	Coniferous	OLIGOMULL	92	9	8.04	1.6	0.48	
					100	Coniferous	OLIGOMULL	64	7	6.51	1.15	0.63	
		100			Coniferous	OLIGOMULL	64	7	6.51	1.15	0.63		

**Appendix B.** List of collembolan species in the 60 studied samples, together with total abundance and frequency (number of samples where the species was present)

Species names	Abundance	Frequency
<i>Arropalithes pygmaeus</i>	1	1
<i>Brachystomella parvula</i>	29	11
<i>Ceratophysella armata</i>	3	2
<i>Ceratophysella denticulata</i>	49	8
<i>Cryptopygus scapelliferus</i>	1	1
<i>Desoria violacea</i>	108	1
<i>Detriturus jubilaris</i>	42	6
<i>Deuteraphorura inermis</i>	53	7
<i>Deuterosminthurus pallipes</i>	11	4
<i>Entomobrya nivalis</i>	4	1
<i>Folsomia candida</i>	8	5
<i>Folsomia fimetaria</i>	4	3
<i>Folsomia listeri</i>	8	1
<i>Folsomia manolachei</i>	1	1
<i>Folsomia quadrioculata</i>	535	20
<i>Folsomia spinosa</i>	694	31
<i>Friesea claviseta</i>	3	1
<i>Friesea mirabilis</i>	6	1
<i>Friesea truncata</i>	8	1
<i>Heteromurus nitidus</i>	351	32
<i>Hypogastrura assimilis</i>	6	4
<i>Isotoma antennalis</i>	83	1
<i>Isotomurus fuscus</i>	37	7
<i>Isotomiella minor</i>	583	37
<i>Isotomurus palustris</i>	39	5
<i>Isotomiella paraminor</i>	75	6
<i>Isotomodes productus</i>	6	1
<i>Isotomodes trisetosus</i>	1	1
<i>Isotoma viridis</i>	161	23
<i>Lepidocyrtus cyaneus</i>	125	22
<i>Lepidocyrtus lanuginosus</i>	687	48
<i>Lepidocyrtus lignorum</i>	195	17
<i>Lipothrix lubbocki</i>	9	5
<i>Megalothorax minimus</i>	48	16
<i>Mesaphorura critica</i>	5	2
<i>Mesaphorura krausbaueri</i>	19	5
<i>Mesaphorura macrochaeta</i>	828	43
<i>Mesaphorura sp.</i>	14	3
<i>Mesaphorura sylvatica</i>	1	1
<i>Mesaphorura yosii</i>	76	7
<i>Micraphorura absoloni</i>	48	6
<i>Micranurida pygmaea</i>	22	8
<i>Micranurida sensillata</i>	2	1
<i>Neanura muscorum</i>	11	1
<i>Neotullbergia ramiscuspis</i>	20	3
<i>Odontella lamellifera</i>	5	1
<i>Orchesella cincta</i>	2	2
<i>Orchesella sp.</i>	12	4
<i>Paratullbergia callipygos</i>	73	15
<i>Parisotoma notabilis</i>	650	42
<i>Protaphorura armata</i>	281	24
<i>Pseudosinella alba</i>	27	8
<i>Pseudanophorus binoculatus</i>	3	1
<i>Pseudosinella decipens</i>	2	1
<i>Pseudosinella maui</i>	53	15
<i>Pseudachorutes parvulus</i>	10	3
<i>Sminthurinus aureus</i>	31	12
<i>Sminthurides schoetti</i>	10	3
<i>Sminthurinus signatus</i>	20	10
<i>Sphaeridia pumilis</i>	72	19
<i>Stenaphorura lubbocki</i>	2	1
<i>Subisotoma pusilla</i>	1	1
<i>Tomocerus minutus</i>	2	1
<i>Willemia anophthalma</i>	3	2
<i>Willemia intermedia</i>	4	3
<i>Xenyllodes armatus</i>	3	2
<i>Xenylla corticalis</i>	1	1
<i>Xenylla grisea</i>	7	3
<i>Xenylla tullbergi</i>	42	6
<i>Xenylla xavieri</i>	3	2