Pedobiologia 57 (2014) 103–117

Contents lists available at ScienceDirect

Pedobiologia - Journal of Soil Ecology

journal homepage: www.elsevier.de/pedobi

Effect of habitat spatiotemporal structure on collembolan diversity

Charlène Heiniger[a,*], Sébastien Barot[b], Jean-François Ponge[c], Sandrine Salmon[c], Léo Botton-Divet[a], David Carmignac[d], Florence Dubs[a]

[a] IRD, UMR BIOEMCO, Centre France Nord, 93143 Bondy, France
[b] IRD, UMR BIOEMCO, ENS, 75006 Paris, France
[c] MNHN, UMR 7179, 91800 Brunoy, France
[d] ENS, UMR BIOEMCO, ENS, 75006 Paris, France

ARTICLE INFO

Article history:
Received 25 April 2013
Received in revised form
25 December 2013
Accepted 17 January 2014

Keywords:
Landscape structure and dynamics
Collembolan diversity
Colonization credit
Patch age
Patch isolation
Forest versus agriculture

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 meta-population effect). Thus landscape dynamics lead to complex habitat spatiotemporal structured, 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 structure of habitats for collembolan diversity, taking soil properties into account. In an agroforested landscape, we set up a sampling design comprised of two types of habitats (agriculture versus forest), a gradient of habitat isolation (three isolation classes) and two contrasting ages of habitats. Our results showed that habitat temporal structure is a key factor shaping collembolan diversity. A reduced diversity was detected in recent habitats, especially in forests. Interactions between temporal continuity and habitat quality were also detected by taking into account soil properties: diversity increased with soil carbon content, especially in old forests. Negative effects of habitat age on diversity were stronger in isolated patches. We conclude that habitat temporal structure is a key factor shaping collembolan diversity, while direction and amplitude of its effect depend on land use type and spatial isolation.

Introduction

Habitat fragmentation is well known to be a major threat to biodiversity in many macroorganisms (Saunders et al., 1991; Tilman, 1994; Tilman et al., 1994; Finlay et al., 1996; Stratford and Stouffer, 1999; Cushman, 2006; Mapelli and Kittlein, 2009; Krauss et al., 2010). Biodiversity is not only driven by local environmental conditions, but also by spatial processes (Hanski, 1994; Ettema and Wardle, 2002; Holyoak et al., 2005). It is now largely recognized that ecological processes shaping communities occur at least at two distinct organization levels (Shmida and Wilson, 1985; Ricklefs, 1987; Wardle, 2006). (1) Regional processes occur since habitats within a landscape are interconnected by dispersal, which gives birth to meta-community dynamics (Gilpin and Hanski, 1991; Hubbell, 2001; Leibold et al., 2004). At the regional scale, an increase in habitat spatial connectivity increases the probability of a species to reach an unoccupied habitat and thus may enhance local diversity (Bailey, 2007; Brückmann et al., 2010). (2) Local factors such as environmental conditions and competition between organisms act as filters enabling species to maintain a viable population in a patch of habitat (Decaëns et al., 2011;

---

* Corresponding author. Tel.: +33 0642135945; fax: +33 0148025970.
E-mail addresses: charlene.heiniger@ird.fr, charlene.heiniger@gmail.com (C. Heiniger).

http://dx.doi.org/10.1016/j.pedobi.2014.01.006
0031-4056/

Petit and Fried, 2012) and thus reduce local diversity. Within this framework, patches are defined as spatial units of habitat differing from the surrounding area (Forman and Godron, 1986). Even though patches may display an internal heterogeneity at a finer scale, e.g. microhabitat (Leibold et al., 2004), they contain a single type of habitat defined by relatively homogeneous biotic and abiotic factors such as temperature, humidity or vegetation cover.

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

Recent insights into the influence of landscape structure on collembolan diversity showed that at the patch scale, collembolan (alpha) diversity in forests may respond negatively to habitat diversity at the landscape scale (Ponge et al., 2003; Sousa et al., 2006). In these cases, the decrease in local or alpha diversity was attributed to habitat fragmentation occurring in diverse landscapes. Indeed, patch isolation, which increases most of the time in fragmented habitats, may reduce the chances of colonization by species, especially if these have poor dispersal ability (Hewitt and Kellman, 2002). In contrast, Querner et al. (2013) showed that landscape heterogeneity may increase local (alpha) collembolan diversity in oilseed rape fields (i.e. in agricultural habitats). In this case, species are thought to express preferences for different habitat types so that regional (gamma) diversity increases with habitat heterogeneity (Vanbergen et al., 2007). Since these preferences are not strict, and species move between patches, habitat heterogeneity in the neighbouring landscape would also increase diversity at the patch scale (alpha diversity). These results suggest that it is difficult to predict a priori the impact of habitat isolation on local (alpha) species diversity and that this impact depends on the ecosystem under investigation. Here, we compare the effect of patch isolation in two broad habitat types, open versus closed vegetation, within the same landscape.

Most empirical studies on meta-community dynamics assume that local communities have reached equilibrium at sampling time. However, some authors have suggested that the time elapsed, since the first species successfully colonized a patch of habitat, is essential for the understanding of observed diversity patterns (Mouquet et al., 2003). These authors assume that communities at the first stages of the assembly process are unsaturated because only a subset of the regional species pool has yet been able to colonize the patch. Besides spatial structure, patch temporal structure may thus also influence collembolan alpha diversity. Ponge et al. (2006) showed that landscape heterogeneity might come with a more dynamic patch temporal structure. They suggest that regions comprising more diverse habitat types may also include more patches of habitat that have experienced a recent change in land use (e.g. patches that switched from forest to agriculture or the reverse, and thus are not continuous through time). This may have subsequently reduced collembolan diversity at the patch scale (alpha diversity). In this sense, the lack of diversity observed in most heterogeneous landscape might be due to patch history (i.e. to temporal discontinuity) rather than to patch spatial structure (i.e. fragmentation).

Another source of complexity for understanding the influence of habitat structure on diversity patterns is that patch characteristics (age, spatial isolation, land use type) may influence local communities either directly or indirectly. They directly impact local communities through their effect on meta-community dynamics (Driscoll et al., 2012). Patch characteristics may also impact communities through complex links between landscape dynamics and local environmental properties (Wu and Loucks, 1995). For example, isolation and age of a patch can impact local microclimatic conditions (Saunders et al., 1991; Magura et al., 2003), and increased edge effects in isolated patches can be responsible for changes in soil properties. In this case, patch spatial structure would be responsible for changes in local conditions, which would consequently affect local (alpha) diversity (e.g. indirect effect). Conversely, pre-existing local conditions may impact land use changes (e.g. if the forest soil is fertile, the forest is more likely to be turned into a field). Such direct and indirect effects must be disentangled to determine the effects of landscape structure on local communities.

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

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

Materials and methods

Study site

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

Sampling design

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

Habitat type

Collembolan communities are likely to depend on the dichotomy between open and closed vegetation (Ponge et al., 2003; Vanbergen et al., 2007). Hence we decided to split the landscape into two major habitat types: forest and agricultural land. Thus, sampled sites were either meadows, pastures, crops, or Christmas tree plantations for agricultural habitats and coniferous or deciduous stands for forest habitats (Appendix A). Christmas tree plantations might at first be thought of as forest habitats. However, they display many characteristics of agricultural habitats: the absence of litter and developed humus profiles (due to low stature and density of Christmas trees), use of ploughing and pesticides, i.e. same characteristics as agricultural land. They are generally constituted by no more than five-year-old trees and have been shown to support collembolan communities typical of agricultural habitats (Ponge et al., 2003). It is well known that the transition from deciduous to coniferous stands implies an abrupt change in soil physicochemical properties (pH, humus form, etc.) (Gauquelin et al., 1996; Augusto et al., 2003). However, Ponge et al. (2003) showed that in the Morvan region, collembolan communities do not differ between coniferous and deciduous stands, contrary to often-reported detrimental effects of coniferous plantations, mostly ascribed to changes in humus form and soil acidity (Cassagne et al., 2004; Hasegawa et al., 2009). In any case, collembolan communities of both forest types differ less from each other than they differ from agricultural communities. The absence of pronounced reaction of collembolan communities to tree species composition was also observed in similar acidic soil conditions in Germany (Salamon and Alphei, 2009). This is explained by the fact that on acidic bedrocks of the studied region, similar humus forms with thick litter layers and strong soil acidity (moder) develop under both stand types (Ponge, 1993). It has been shown that Collembola mostly feed on microorganisms and animal faeces, and rarely directly consume leaves or needles (Ponge, 1991; Caner et al., 2004). As such, they are most of all influenced by humus forms regardless of the forest canopy composition (Ponge, 1993). Additionally, coniferous tree species planted in the Morvan region (Douglas fir, silver fir and more rarely Norway spruce) have a more nutrient rich litter and do not acidify the soil to the same extent as pines (Augusto et al., 2003). This allowed us to group both forest types into a single broader category. We avoided sampling in special habitats such as humid areas or clear-cuts so as to minimize the influence of particular environmental conditions within forests and agricultural land.

Habitat temporal continuity

In order to assess the temporal continuity of each habitat within the focus area, we implemented a dynamic cartography (i.e. picturing both spatial and temporal continuity) approach using aerial photographs. In total, about two hundred aerial photographs (IGN, France) were required from 1948 to 2008 with a photograph taken approximately every five years. We categorized each habitat into two age classes (Appendix A). Those in place at least since 1948 were classified as old. Recent forests were agricultural habitats until conversion to forest 30–40 years ago (in our classification, a change from deciduous to coniferous stand is not a temporal discontinuity). Recent agricultural habitats were forests until conversion to agricultural land 20–30 years ago. Studied local collembolan communities were thus included in habitats that were homogeneous in type and age. In the context of this study, we considered that a patch is not only a continuous block of the same habitat type but also a continuous part of the same habitat type over time, meaning that we mapped four types of patch: old forest, recent forest, old agricultural and recent agricultural.

Habitat spatial isolation

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

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

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

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

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

Collection of fauna and soil data

Sampling took place from June 27 to July 9, 2010. Each site was sampled for litter/soil mesofauna using a cylindrical soil corer (5 cm diameter × 7 cm depth, one sample at each sampling site). We thus sampled exactly the same volume of soil at each site, meaning that values of species density (i.e. the number of species per unit area sensu according to Gotelli and Colwell, 2001) presented here correspond to the number of species found over 0.2 dm^2. Litter/soil were brought back to the laboratory within a week and placed in a Berlese dry-funnel extractor for 10 days. Animals were collected and stored in 70% ethyl alcohol until identification. Collembola were mounted, cleared in chloral-lactophenol and identified to species level under a light microscope (400× magnification), according to Hopkin (2007), Potapov (2001), Thibauld et al. (2004) and Bretfeld (1999). A list of species is given in Appendix B.

We also sampled soils (organo mineral horizon, between 0 and 10 cm) in each site in order to characterize soil physicochemical properties at each sampling site. Three samples were taken around soil fauna samples and were pooled together. Soils were air-dried and sieved to 2 mm before measuring total carbon (C_{tot}) and total nitrogen (N_{tot}) contents (gas chromatography), pH (H_2O), bioavailable phosphorus (Olsen method) and cation exchange capacity (CEC). Additionally, the top five soil centimetres were sampled using a Burger cylinder (0.1 L volume) and immediately packed in waterproof bags in order to determine soil moisture and bulk density. The humus form was characterized according to Brêthes et al. (1995) and the Humus index was calculated according to Ponge et al. (2002), and was used as a proxy for litter amount and recalcitrance to decay (Ponge et al., 1997; Ponge and Chevalier, 2006).

Statistical analyses

The following diversity indicators were calculated for each site: species density (sensu Gotelli and Colwell, 2001), i.e. the actual number of species found in each sample, species richness (sensu Gotelli and Colwell, 2001), i.e. the local number of species estimated to be found in a smaller sample containing 25% of the mean individual density (i.e. 57 individuals), Shannon index, dominance (relative frequency of the most abundant species), and abundance (total number of individuals).

These diversity indicators were analysed using linear models (type III sums of squares used for unbalanced design and because significant interactions were expected, see Appendix B), testing for habitat type (HT), spatial isolation (SI), and temporal continuity (TC) effects as well as effects of all interactions between these factors. To fulfil linear model assumptions, dominance had to be log-transformed. In order to detect possible effects of habitat spatiotemporal structure (regional factors) on soil quality that could influence diversity indicators, we tested the effect of habitat descriptors on soil physicochemical properties. Most of natural or log-transformed data fulfilled the assumptions of linear models. When this was not the case, we used generalized linear models with a Gamma link function or a Poisson link function. All possible correlations (Pearson) between diversity indicators and soil properties were calculated and tested. We also calculated and tested these correlations in both habitat types separately.

Finally, we constructed complete linear models, testing the effects of the three habitat descriptors on diversity indicators and including most important soil parameters as covariates, together with all their interactions. Since there were many combinations of habitat descriptors and many soil parameters, it was not possible to include all of them and their interactions in a single model. Therefore, we focussed our analysis on the two soil parameters that were the most correlated with diversity and/or that were significantly affected by habitat descriptors, i.e. C_{tot} and pH. These two variables can be considered as proxies for two main physico-chemical factors which impact collembolan communities at two different scales (species or community): C_{tot} is a proxy for general habitat and resource availability and thus determines the total abundance; and pH is a proxy for local environmental filter which selects species within communities, since several collembolan species are only adapted to low or high soil acidity (Ponge, 1993; Salmon, 2004). We analysed two models testing separately for the effect of these two variables, the three habitat descriptors and all their interactions (two-, three- and four-way interactions). Simple effects of variables and interactions that were kept in each final model were selected using an automatic selection procedure based on AIC (procedure step, with backward direction, Bodzogan, 1987; Posada and Buckley, 2004). Combinations of habitat descriptors were compared using least square means and associated multiple comparisons of means (Tukey). All statistical analyses were performed using Mass, car, vegan and Lsmeans packages of R software (R Development Core Team, 2010).

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

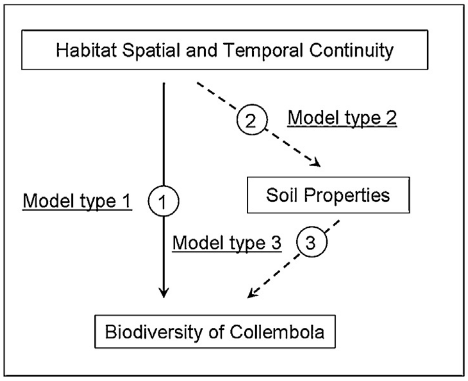

Fig. 1. Statistical diagram picturing steps of data analyses. Arrows represent effects of factors on variables (collembolan diversity and soil properties). Direct effects are represented by continuous arrows and indirect effects by dotted arrows. Model type 1 (arrow 1) stands for the linear models testing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

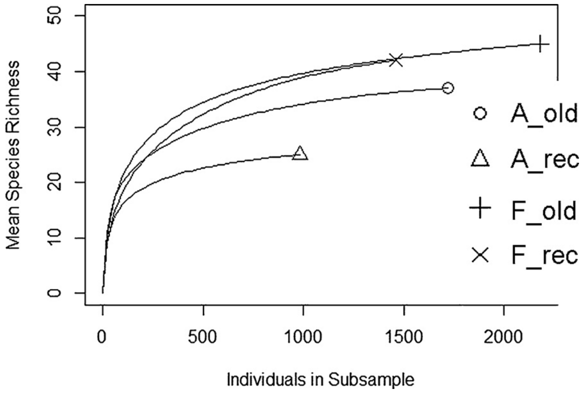

Fig. 2. Individual based rarefaction curves old forests (F_old), recent forests (F_rec), old agricultural land (A_old) and recent agricultural land (A_rec).

Results

Effects of the three habitat descriptors on collembolan diversity

In total, 6339 individuals were identified to 70 species. We found 3639 from 57 species in forest and 2700 individuals from 39 species in agricultural habitats. In forests, 44 species were found in old sites and 42 in recent sites. In agricultural land, 36 species were found in old sites and 24 species in recent sites. Thirteen species were present in recent forests but not in old forests and 15 species were present in old forests and not in recent forest. In agricultural sites, 15 species were present in old but not in recent sites and only 3 species not present in old sites were found in recent sites. Rarefaction curves (Fig. 2) showed that our sampling was nearly exhaustive for both habitat types whatever old or recent, and that forests (both recent and old) harboured more species in total (gamma diversity) than agricultural land (old > recent). Statistical models implemented on diversity indicators (Model type 1 in Fig. 1, Table 1) showed that habitat type (HT) exerted an effect on species density, species richness and total abundance. Species density, species richness as well as abundance of Collembola were higher in forest compared to agricultural habitats (on average, respectively, 11.4 versus 8.6 for species density and 9.1 versus 7.9 for species richness). However, no effect of HT was detected either on Shannon index or on dominance. Furthermore, only Shannon index, species richness and species density responded to habitat temporal continuity (TC), old habitats showing higher values than recent habitats (on average 10.8 versus 9.3 for species density, 1.8 versus 1.6 for Shannon index, and 9.1 versus 7.5 for species richness). Multiple comparisons among means (Tukey) showed that this effect was mainly due to differences between old and recent forests (on average, respectively, 13.1 and 9.4 for species density, 1.9 and 1.5 for Shannon index, and 10.2 versus 7.9 for species richness), whereas old and recent agricultural lands showed closer values (on average, respectively, 9.1 versus 7.7 for species density, 1.7 versus 1.5 for Shannon index, and 8.3 versus 7.1 for species richness) (Fig. 3). Both coniferous and deciduous forests displayed significantly lower values for species density, species richness and Shannon index in the recent age class compared to the old one (data not shown). We did not detect any effects of spatial isolation (SI) on diversity indicators, either in forest or in agricultural habitats, and no interaction between habitat descriptors (Fig. 4).

Effects of the three habitat descriptors on soil characteristics

Most soil properties were significantly different according to HT. Models testing the effect of HT on soil properties showed that CEC, C_{tot}, C:N and humus index had significantly higher values in forest than in agricultural habitats, whereas soil density, soil moisture and pH showed opposite trends (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, responded to the two other habitat descriptors (SI and TC). Soil pH, bioavailable phosphorus, and carbon to nitrogen ratio (C:N) showed differences

Table 1
Effect of habitat descriptors (habitat type HT, temporal continuity TC and spatial isolation SI) and all their interactions on Collembola diversity indicators (species density = total number of species collected in a sample of 0.2 dm^2, rarefied species richness = number of species estimated for 57 individuals, Shannon index, dominance = relative frequency of most abundant species, abundance = total number of individuals per sample). Transformation used on and results of linear models (*F* value and degrees of freedom df).

	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^2		0.40	0.30	0.18	0.06	0.23
Transformation		None	None	None	$\log_{10}$	None

* $p < 0.05$ (significant level).
** $p < 0.01$ (significant level).
*** $p < 0.001$ (significant level).

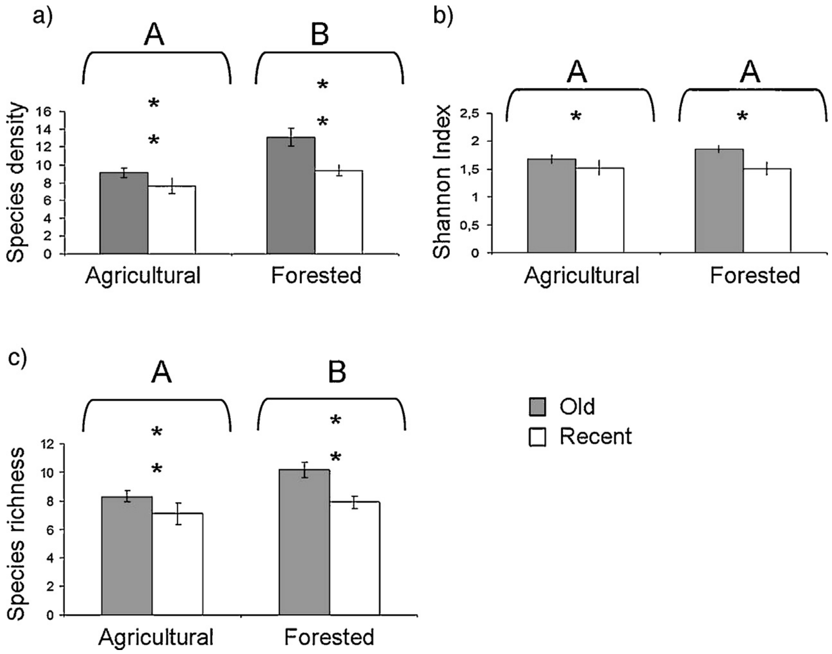

Fig. 3. Mean species density (3a), Shannon index (3b) and species richness (3c) of old (grey) and recent (white) agricultural and forest habitats. Letters indicate significant differences among means. "A" and "B" labels represent significant differences between agricultural and forest habitats. Stars show simple effect of age (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$). Error bars represent standard errors.

between isolation classes. Soil pH was higher in isolation class 1 (on average 4.3) than in isolation classes 0 and 2 (on average, respectively, 3.7 and 3.8), but only in forest patches, resulting in a significant interaction between HT and SI. Bioavailable phosphorus content was higher in isolation class 2 than in isolation classes 0 and 1 (on average, respectively, 74, 55 and 44 mg/kg). Only C:N was significantly impacted by TC and was higher in old habitats than in recent ones. Moreover, for C:N, many interactions between habitat descriptors were significant (Table 3). Multiple mean comparisons showed that these effects were mostly due to non-isolated old forest habitats (isolation class 0) that showed significantly higher values (on average 20.6) than every other forest habitats whatever their SI or TC (in old habitats: isolation 1, 15.8; isolation 2, 16; in recent habitats: isolation 0, 14.5; isolation 1, 14.3; isolation 2, 13.8). In agricultural land, no effect of the spatiotemporal descriptors on C:N was detected.

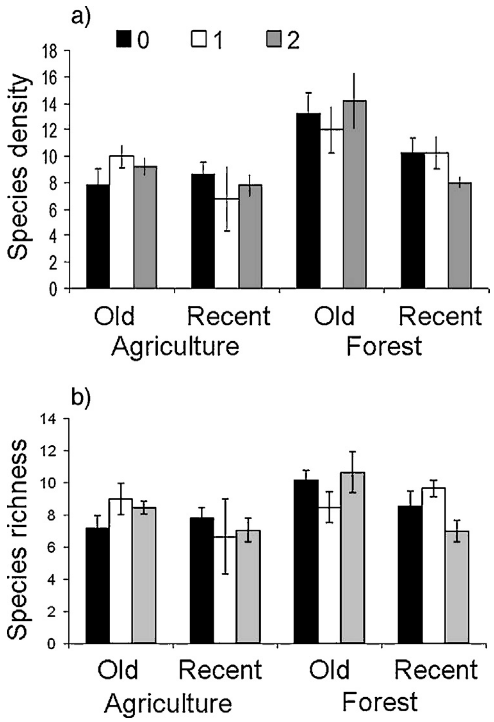

Fig. 4. Mean species density (4a) and species richness (4b) according to habitat type, temporal continuity (two age classes: old and recent) and spatial isolation (three classes: 0 black bars. 1 white bars and 2 grey bars). Error bars represent standard errors.

Effects of the three habitat descriptors and soil characteristics on collembolan diversity

When data from both forest and agricultural habitats was tested, no correlations between Shannon index and soil properties were significant (Fig. 5). On the other hand, many correlations between species density and soil properties were significant at the 5% level. Species density was positively correlated with CEC, C_{tot}, C:N and humus index (0.37, 0.38, 0.43 and 0.44, respectively) and negatively correlated with bulk density and pH (−0.3 and −0.38, respectively) (Fig. 5). Only positive correlations between species richness and C_{tot}, C:N, CEC and humus index (respectively, 0.30, 0.27, 0.28 and

Table 2
Soil characteristics (mean values and standard deviations) showing differences between agricultural and forest habitats. Total carbon content (C_{tot}), soil pH (pH), carbon to nitrogen ratio (C/N), cation exchange capacity (CEC), soil moisture (moisture), bulk density (density) and humus index (humus).

	Agriculture	Forest	*p*-Value
C_{tot} (%)	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^3)	0.9 ± 0.22	0.68 ± 0.22	***
Humus index	1 ± 0	3.54 ± 1.55	***

Significance levels: *p*-values correspond to results of linear and generalized linear models presented in Table 3.

[*] $p < 0.05$ (significant level).

[**] $p < 0.01$ (significant level).

[***] $p < 0.001$ (significant level).

Table 3

Effect of habitat descriptors (habitat type HT, temporal continuity TC and spatial isolation SI) and all their interactions on soil properties. Soil pH (pH), total carbon content (C_{tot}), total nitrogen content (N_{tot}), carbon to nitrogen ratio (C/N), bioavailable phosphorus (phosphorus), cation exchange capacity (CEC), soil moisture (Moisture), bulk density (density) and humus index (humus). Transformation, model type (distribution) and results of linear or generalized linear models (*F* value/Chi square and degrees of freedom df).

	F/Chi square									
	df	pH	C_{tot}	N_{tot}	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^2		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	$\log_{10}$	$\log_{10}$	None	None	None

[*] $p < 0.05$ (significant level).
[**] $p < 0.01$ (significant level).
[***] $p < 0.001$ (significant level).

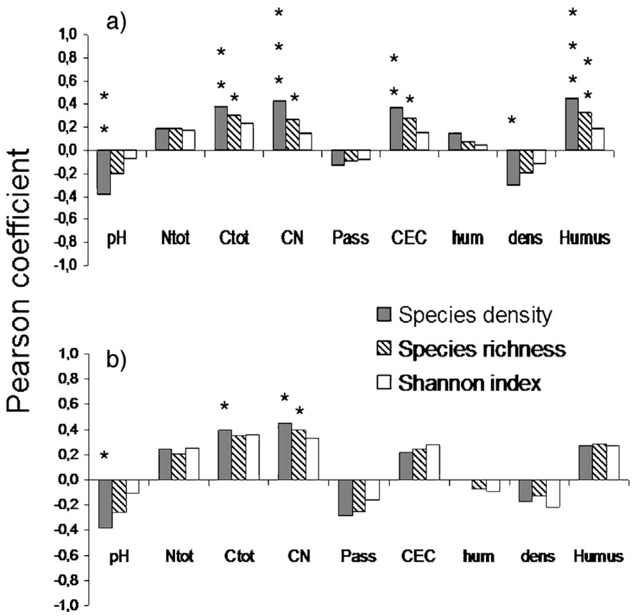

Fig. 5. Correlation coefficients (Pearson) between species density (grey bars), species richness (dashed bars) or Shannon index (white bars) and soil properties for the complete data set (agricultural land and forest) (5a) and for forest only (5b). Soil pH: pH, total nitrogen content: N_{tot}, total carbon content: C_{tot}, carbon to nitrogen ratio: C:N, bioavailable phosphorus: Ph, cation exchange capacity: CEC, soil moisture: moist, soil density: dens and humus index: humus. Stars show significant correlation ($^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$) between species density, species richness or Shannon index and each soil parameters listed above.

0.33) were observed. However, most of these correlations reflected the above-mentioned differences in soil properties between forest and agricultural habitats. When implemented separately in the two HTs no correlations with species density, species richness or Shannon index were significant in agricultural habitats. In forests, only C_{tot}, C:N (0.4 and 0.44, respectively) and pH (−0.39) were significantly correlated to species density and only C:N was significantly correlated to species richness (0.40), but none were correlated to the Shannon index (Fig. 5).

As C:N was highly correlated with both C_{tot} and pH (0.61, $p < 0.0001$ and −0.69, $p < 0.0001$ respectively), while C_{tot} and pH were also correlated (0.43, $p < 0.001$) but to a lesser extent than to C:N, we decided to include only C_{tot} and pH as covariates in two distinct global linear models testing their effect and that of habitat descriptors on species density, species richness and Shannon index. To facilitate this, we implemented a procedure of automatic selection based on AIC. Both models (C_{tot} and pH) did not detect any significant effect of any variable on the Shannon index. Table 4 displays the results of models analysing the effects of habitat descriptors and either C_{tot} or pH on species density and species richness. The C_{tot} models showed that there was no simple effect of habitat descriptors either on species density or on species richness, whereas pH models showed significant effects of HT and TC on species density and of TC on species richness. Additionally, pH and C_{tot} models revealed the effect of several significant interactions. The pH model showed significant effects of the interactions between HT and TC, between HT and SI, and between TC and SI on species density. The C_{tot} models showed the effect of interactions between HT and SI on species density, and between TC and SI on both species density and species richness. Indeed, least square means for species density comparison (Fig. 6a) obtained with the C_{tot} model showed no difference between both HTs in non-isolated habitats (isolated class 0), whereas it indicated significantly higher values in forest than in agriculture in isolation classes 1 and 2. Moreover, comparisons of least square means for species density showed significantly higher values in old than in recent patches

Table 4
Effect of habitat descriptors (habitat type HT, temporal continuity TC and spatial isolation SI), total soil carbon content (Ctot) (left hand side), soil pH (right hand side) and all their interactions on species density and species richness. Transformation and results of linear models (*F* values and degrees of freedom df), tested after variable selection based on AIC criterion).

C_{tot} model				Soil pH model			
	df	Species density *F* value	Species richness *F* value		df	Species density	Species richness
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_2O (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^2		0.67	0.49	R^2		0.62	0.49
Transformation		None	None	Transformation		None	None

* $p < 0.05$ (significant level).
** $p < 0.01$ (significant level).
*** $p < 0.001$ (significant level).

for the isolation classes 1 and 2, while it indicated no difference between age classes for the continuous habitats (Fig. 6b). Similarly, least square means for species richness comparison showed significantly higher values in old than in recent patches for the isolation class 2, while there were no differences between age classes for habitats of isolation class 0 and 1 (Fig. 6c). Soil pH and C_{tot} did not have a significant effect on their own, neither on species density nor on species richness. C_{tot} had significant effects on the interaction with HT, and TC on species density. According to estimated model parameters, species density increased more with C_{tot} in old than in recent habitats. It also increased more with C_{tot} in forest than in agricultural land. The soil pH had significant effects in interaction with HT, TC and SI on species density and in interaction with TC on species richness. Species density decreased with the pH in forests whereas it increased with the pH in agricultural habitats. Species density and species richness also decreased with the pH in old habitats whereas these parameters did not change with pH in recent habitats.

Discussion

Effects of habitat temporal continuity on collembolan diversity

The total number of species (gamma diversity) was higher in old than in recent forests. Species present in recent forests and not in old ones were all rare species (i.e. found in less than 10%

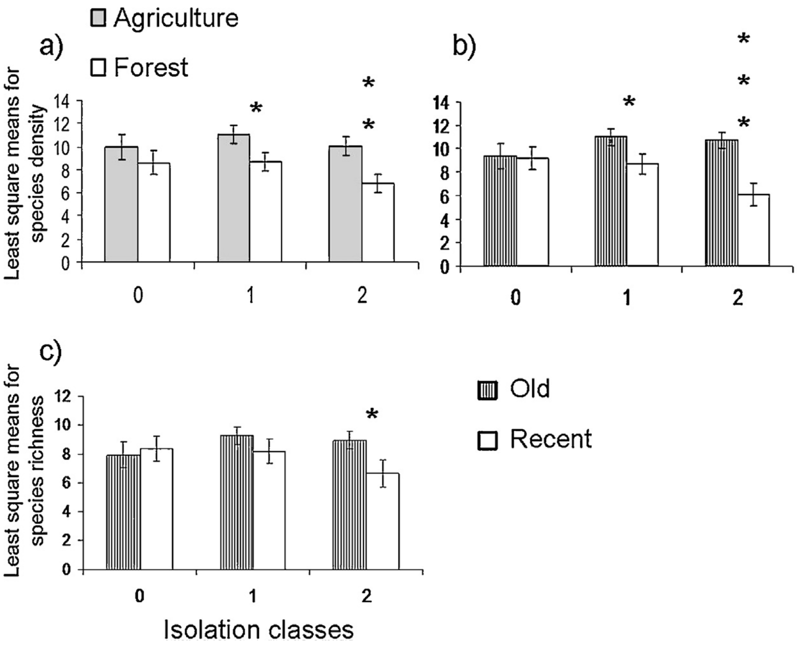

Fig. 6. Least square means for species density and species richness obtained using the model testing for the effect of the three habitat descriptors as well as total carbon on species density and species richness. Least square means for species density are represented according to habitat type (agricultural, grey bars and forested, white bars) and spatial isolation (three isolation classes 0, 1 and 2) (6a), and least square means for species density and species richness are represented according to temporal continuity (two age classes: old, dashed bars and recent, white bars) and spatial isolation (three isolation classes 0, 1 and 2) (respectively, 6b and 6c). Error bars represent standard errors. Stars show significant differences between habitat types (6a) or ages (6b and 6c) within each isolation class.

of the records), except for 3 species (*Isotoma viridis*, *Lepidocyrtus cyaneus* and *Lepidocyrtus lignorum*). These species are known as agricultural-preferring species in the studied region (Ponge et al., 2003, 2006). Furthermore, they were found exclusively in isolation classes 1 and 2. Thus it is difficult to know whether they were present as relics of the past HT (i.e. agricultural land) or if they colonized forest patches from the neighbouring agricultural matrix. However, the fact they were not present in the equivalent isolation class of old forests suggests that they benefitted from the presence of a non-saturated community in recent forests. Indeed, the fact that all niches were not necessarily occupied in recent forests certainly favoured the persistence of agricultural-preferring species: these species might colonize spatially isolated patches but would not be able to persist in the more diverse communities present in old forests of comparable spatial isolation. In agricultural land, the total number of species was also higher in old than in recent sites. Only three species present in recent sites were absent in old ones. Among the 15 species that were present in old but not in recent sites, only three were common species (i.e. present in more than 10% of the records) and no common species were found exclusively in recentagricultural sites. This shows that even in open habitats such as agricultural land, the total number of species was reduced in recently created habitats. It is still difficult to draw any conclusion on differences in the number of rare species, but the fact that some common species were lacking in recent sites only, allows us to conclude that this absence is due to the temporal continuity of the habitat and not to some random mechanism.

Our results show that habitat temporal discontinuity impacts negatively species density, species richness and Shannon index but not the total abundance of Collembola. For a similar number of individuals, recent habitats had fewer species than old habitats whatever the habitat type or the spatial continuity. This suggests that resources, not appropriated by species not yet colonizing recent habitats, are used by larger populations of existing species. Among the variables under study, only the carbon to nitrogen ratio reacted to temporal continuity, but this was due to the particular situation of spatially continuous (non-isolated) old forests that displayed higher values than every other forest patches regardless of their spatiotemporal structure. All other soil properties (humus type, a proxy of litter amount and quality, pH, C, N contents and P availability) were similar in old and recent habitats of the same type, suggesting that habitat temporal continuity has a direct effect on collembolan diversity that does not depend on soil properties. Within the limits of our analytical protocol (we did not study all parameters known to influence Collembola, such as the composition of litter and of soil microbial communities, nor did we study interactions between Collembola and higher trophic levels) this observation confirms our first hypothesis (H1) predicting a lower collembolan diversity in recently created habitats.

The direct effect of habitat temporal continuity on collembolan diversity is also supported by the fact that both species density and richness were impacted by temporal continuity in the pH model. This means that habitat temporal discontinuity impacts diversity not only by decreasing the size of the local pool of species (species density) but also by decreasing the number of species that would be present if local soil conditions were strictly similar among all spatiotemporal situations (species richness). This is supported by the fact that the impact of temporal continuity on the Shannon index must be considered as a direct effect because this index did not show any significant correlation with soil physicochemical properties.

However, the temporal discontinuity of habitat could also be viewed as an index of disturbance. According to the intermediate disturbance hypothesis we could expect recent habitats to host low collembolan diversity, habitats of intermediate age to host a higher biodiversity, and biodiversity to decrease in older habitats because of exclusive competition (Connell, 1978; Molino and Sabatier, 2001; but see Fox, 2013). Our results, however, did not support this general scheme. This might be due to the fact that our study focuses on the landscape scale, where studied habitats were not homogeneous and where they host a high diversity of local niches at scales ranging from units to tens of square metres (Ponge and Salmon, 2013). Nevertheless, we cannot exclude that habitats older than the ones we studied, might display a decrease in collembolan biodiversity, thus supporting the intermediate disturbance hypothesis. We did not expect old and mostly isolated habitats to display the lowest alpha diversity predicted by meta-community theories (Tilman, 1982; Hubbell, 2001) because the oldest habitats we studied were certainly not old enough to support such patterns. Additionally, within-patch heterogeneity is most likely to prevent collembolan alpha diversity from decreasing to such low levels.

Most empirical studies testing the effect of landscape structure on diversity patterns do not take habitat temporal structure into account (Mouquet et al., 2003). We do not have knowledge of any other study on Collembola that is strictly comparable to ours although collembolan species have been shown to be affected by habitat successional stage (Setälä et al., 1995; Loranger et al., 2001; Scheu et al., 2003; Chauvat et al., 2007; Salamon et al., 2008; Chauvat et al., 2011). While in these latter studies the observed effects were due both to change in habitat type (succession) and to habitat age (time since the habitat is in place), our results allow us to focus on the effect of habitat age within the same habitat type. Temporally discontinuous (recent) habitats displayed lower diversities due to the poor colonization/dispersal abilities of Collembola: some species were absent from recent habitats not because the habitat was not suitable for them but because they did not have enough time to colonize it. The higher values of the Shannon index observed in old compared to recent habitats support this hypothesis: communities in recent habitats are dominated by fewer species. Coined as colonization credit, this process has been suggested to occur in plant communities (Cristofoli et al., 2010), but has so far been documented by only a few empirical studies on plants (Gijbels et al., 2012) and butterflies (Cristofoli and Mahy, 2010). All these studies showed that specialist species are more affected than generalist species.

Effect of habitat spatial isolation on collembolan diversity

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

Habitat fragmentation is thought to decrease the local diversity of macro-organisms because isolated patches (i) are too small to fulfil ecological and demographic requirements of populations (Allouche et al., 2012), and (ii) are more difficult to colonize (Wamser et al., 2012). We did not find such an effect in Collembola. This is probably because our habitat patches were always large enough to fulfil ecological and demographic requirements of all potentially present collembolan species due to the small size of these organisms. Indeed, Schneider et al. (2007) showed that collembolan populations in patches as small as 50 cm^2 did not change both in diversity or in density within 16 months of isolation. Given that our smallest patch was much larger than this restricted surface, this may explain why spatial discontinuity did not affect collembolan populations in our study. Thus, even if the colonization of isolated patches might be a problem for them (see Interacting effects of habitat temporal and spatial structure on diversity section), fragmentation has probably not led to local extinctions, so that colonization is not necessary to maintain diversity. Of course, the connectivity and the size of micro-habitats inside the patches may influence collembolan diversity at micro-site scale (Hertzberg, 1997; Åström and Bengtsson, 2011) but our sampling design does not allow us to test this hypothesis.

Interacting effects of habitat temporal and spatial structure on diversity

Our results showed that spatial and temporal structures of habitats had an interactive effect on local diversity patterns. In the studied region, we showed that species diversity increased with spatial isolation in old habitats whereas it decreased with spatial isolation in recent habitats. This resulted in differences of diversity in isolated habitats while recent and old continuous habitats showed similar values. This suggests that when in place for a long time, isolated habitats supported more colonization events than spatially continuous (i.e. non-isolated) habitats, without concomitant extinction events. This can be due to species from the opposite habitat type being present locally, if they do not have strict habitat preferences, because of increased edge effects in isolated patches (Sławski and Sławska, 2000; Östman et al., 2009). This also means that the negative effect of spatial isolation on collembolan diversity can only be unravelled if we take the habitat temporal structure into account. Our results suggest that Collembola species need time to colonize recently created habitat that are isolated from other habitats of the same type. This effect should be especially strong for specialist species that do not survive in a matrix of the opposite habitat type. To the best of our knowledge, it is the first time that such interacting effects are empirically unravelled.

The interaction between habitat spatial and temporal continuity was not strictly similar for species density and species richness. Indeed, species density was lower in recent than in old habitat of isolation classes 1 and 2, whereas species richness was lower in recent than in old habitat of isolation 2 only. By definition, species density is affected by the number of individuals present in a sample, while species richness is not. Species density should, thus, be sensitive to both local factors and landscape characteristics (regional factors). Local factors determine the carrying capacity of the local environment while the number of species that can reach a local patch should be mostly determined by landscape characteristics. This difference in sensitivity between both diversity indicators reveals that old habitat of isolation class 1 should benefit from the contribution of many poorly abundant species (not taken into account in the calculation of species richness) in addition to a few abundant species. This results in similar values of species richness in old and recent habitats of isolation class 1, but still different values for species density. In the other hand, old habitats of isolation class 2 benefit from an increase in the number of species that are also more evenly distributed, which results in an increase in both species richness and species density compared to recent habitat of the same isolation class.

These results support the novel idea that habitat fragmentation constrains diversity not only through spatial but also through temporal continuity: there is a strong positive impact of temporal continuity on the total number of species, in addition to the distribution of individual numbers within each species. Thus, in the case of soil organisms, which probably disperse slowly at the landscape scale, regional processes shaping communities must be slow. That is why habitat age has to be taken into account to better predict soil biodiversity in the context of habitat fragmentation.

Effect of soil properties in interaction with habitat spatiotemporal structure on diversity

Few soil characteristics responded to the spatial and/or temporal structure of habitats, suggesting that the indirect effect on diversity is likely to be weak. Additionally, our results showed that both species density and species richness were submitted to direct effects of habitat descriptors and their interactions, whereas no indirect effects were detected since neither the C_{tot} nor the soil pH had simple effects on diversity. However, the two parameters that were most correlated with species density (soil pH and total carbon C_{tot}) interacted with habitat descriptors to affect diversity. Collembolan diversity was more influenced by C_{tot} and soil pH in old compared to recent patches. This result corroborates the study of Dzwonko (2001), who showed that plant species indicator values for several environmental factors (Ellenberg indicators) were more reliable in older forests. Species can be good indicators of environmental conditions only if communities have had enough time to reach equilibrium. Before equilibrium, a bias can occur because some indicator species are absent due to dispersal limitation (Seabloom and van der Valk, 2003) or because some species reflecting previous habitat type still persist (French et al., 2008).

The introduction of C_{tot} in the model suppressed the significant effect of temporal continuity on species density. Likewise, the introduction of the pH in the model suppressed the significant effect of habitat type on species richness. This means that a part of the variability explained by habitat descriptors is in fact due to a difference in soil properties. C_{tot} was lower (although not significantly) in recent compared to old habitats, especially in forest and soil pH was significantly lower in forest than in agricultural land. Since the carbon content and the soil pH may influence collembolan diversity (Chagnon et al., 2000), we cannot totally reject that a part of the observed difference in diversity according to habitat descriptors is due to slightly different environmental conditions. This shows that discriminating between direct and indirect effects is not straightforward, confirming that when studying the impact of landscape structure on soil animals, soil properties should be taken into account.

We also showed that the effects of habitat descriptors on species density and species richness were not strictly similar when considering soil properties. Fewer effects were detected on species richness than on species density, but all factors impacting species richness also impacted species density. This suggests that some factors affecting species density also impact the relative abundance of species in a subtle way and that removing this effect on abundances through the use of species richness suppresses the effects detected on diversity. This confirms that an abundance-free index of biodiversity using rarefaction curves allows a better analysis of the impact of local and regional factors on local pools of species (Gotelli and Colwell, 2001).

Differences in diversity patterns between habitat types

We defined habitat types as two very broad categories: agriculture or forest without taking the precise habitat type (e.g. coniferous and deciduous forests) into account. Nevertheless, we were able to reveal some significant effects of landscape characteristics on diversity and differences in patterns between the two habitat types. This confirms that for Collembola, land use is a fundamental factor that determines which species can persist locally (Ponge, 1993; Hopkin, 1997; Birkhofer et al., 2012). As hypothesized (H2), local diversity in terms of species density and species richness were higher in forest than in agricultural habitats. This is likely due to differences in soil properties between these two contrasted habitat types. (1) Forests display well developed humus profiles and a higher soil carbon content, which provide resources for many collembolan species (Chagnon et al., 2000). The absence of tree cover and the exportation of organic matter and associated nutrients in agricultural land result in a reduced soil organic layer and decreased soil moisture (Batlle-Aguilar et al., 2011), which will consequently negatively affect diversity and abundance of soil biota. Additionally, higher soil density in agricultural habitats may also reduce collembolan abundance because it provides little pore space for soil-dwelling populations (Vreeken-Buijs et al., 1998). We cannot exclude, however, that other biotic factors such as predation contributed to drive observed diversity patterns, yet our field study did not allow assessing the impact of such other factors. Surprisingly, in our study, habitat type had no effect on the Shannon index. Based on the mathematical expression of Shannon's diversity, which associates a probability of occurrence to each species, this discrepancy suggests that even though the number of species differed, less frequent species were most affected by change in habitat type (Gorelick, 2006).

The effect of temporal discontinuity was stronger in forest than in agricultural land. This finding supports our third hypothesis (H3) that predicted a stronger effect of habitat spatiotemporal structure on collembolan diversity in forest than in agricultural habitats. This could arise because open habitats lead to more efficient dispersal either through passive or active mechanisms. First, if Collembola have a preponderant passive dispersal and are directly or indirectly transported by wind, as suggested for some species by Dunger et al. (2002) and Coulson and Midgley (2012), their colonization rate might be higher in agricultural habitats since air flow is stronger in the absence of tree cover (Wright et al., 2010). This result is in accordance with other findings on Collembola in deglaciated land (Ingimarsdottir et al., 2012). Indeed these authors showed that in such extremely open habitat (i.e. with reduced to nil vegetation cover) collembolan dispersal rate was potentially high. Another explanation could be that collembolan communities in agricultural land are composed of more epigeic species than in forests (Sousa et al., 2004), with morphological traits (e.g. long legs, long furcula) that allow higher mobility in open habitats (Salmon and Ponge, 2012). This result suggests that dispersal rates and modes are habitat-dependent as shown in other microarthropod groups (Lindo and Winchester, 2009).

Our results also showed a significant interaction between spatial isolation and habitat type. With spatial isolation, species density increased in forest but decreased in agricultural habitats. This could be due to better mobility and less strict habitat preferences of species found in agricultural communities (Lauga-Reyrel and Deconchat, 1999; Ponge et al., 2006), likely to be present in remnant forest patches. In contrast, many species from forest communities show strict habitat preferences and reduced mobility (Auclerc et al., 2009) and are thus, less prone to colonize remnant agricultural patches. Our results also suggest that the forest matrix surrounding agricultural patches is more difficult to cross for species than the agricultural matrix surrounding forests. Since passive dispersal by wind is likely to be more efficient in agricultural lands than in forests, this suggests that largely overlooked passive dispersal mechanisms might be influential for collembolan communities and meta-community dynamics.

Conclusion

Our study, to some extent, disentangles the complex effects of habitat characteristics (i.e. spatiotemporal structure and local physicochemical conditions) on collembolan diversity. Most importantly, we showed that habitat temporal continuity is a key factor shaping collembolan diversity and that we must take it into account if we want to understand the effects of habitat spatial structure. We also showed that using both species richness and species density as indicators of biodiversity allows us to refine the analysis of the factors influencing collembolan diversity at different scales. Unfortunately, it is not realistic to experiment at the landscape scale, and the limits of our study must be clearly defined. We only partly controlled the factors thought to influence collembolan diversity: climate and litter quality could not be controlled, as they can be in experimental conditions (Åström and Bengtsson, 2011; Bokhorst et al., 2012). Similarly, the different levels of isolation and age were broadly defined and not totally equivalent in forest and agricultural habitats. However, we were able to detect several effects of our treatments (habitat type, isolation and patch age), using landscape past dynamics as a surrogate for a strict experimental approach. Some theoretical models predicted such patterns (Green and Sadedin, 2005; Gardner and Engelhardt, 2008), but empirical corroborating studies are still scarce (Lemaître et al., 2012). Nevertheless, we showed that habitat fragmentation constrains diversity not only in space but also in time. The temporal continuity of habitats is one of the factors that have a positive effect on diversity. Soil organisms disperse slowly compared to aboveground biota and it hence takes longer for a recent habitat to build up soil diversity especially if the patch is very isolated.

Assembly theory is now well recognized in community ecology but still little applied in soil ecology. This meta-community framework predicts four models that could explain species distribution at local scale (Leibold et al., 2004). These models essentially differ in the importance given to dispersal process in explaining meta-community dynamics. Two of them, 'species sorting' (environmental constraints control species distribution) and 'mass effect' (dispersal redistributes species among habitats independently of environmental constraints) were found relevant to collembolan communities by da Silva et al. (2012) and Ingimarsdottir et al. (2012). This study also supports the idea that dispersal plays an important role in structuring collembolan meta-communities and that the magnitude and direction of its effect depend on the type of habitat considered.

Acknowledgements

This study was sponsored by the R2DS program of the Conseil Régional d'Ile-de-France. We would like to thank the public and private owners of the sampling sites for allowing the study to be carried out on their land. We would also like to thank the IRD (Centre France Nord) and the MNHN (Brunoy) for the access to their facilities and material; the Laboratoire des Moyens Analytiques (IRD, Dakar) for performing the soil analysis; the IGN (France) for providing aerial photographs; Joshua Lobe for correction of the English language; Thibaud Decaëns for helpful advice about the use of species rarefaction curves; anonymous reviewers for their useful comments, which improved the manuscript considerably.

Appendix A.

List of study sites with their classification according to habitat type (agriculture versus forest), temporal continuity (old versus recent) and spatial isolation (three isolation classes), followed by % edge contrast with opposite habitat type, matrice 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
			0			Hay meadow	EUMULL	212	12	8.89	1.83	0.33
		1	25	Both old and recent	A-old1 $N = 6$	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
			25			Hay meadow	EUMULL	147	10	7.72	1.57	0.39
		2	61	Mostly old	A-old2 $N = 9$	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
			81			Hay meadow	EUMULL	50	8	8	1.4	0.48
			100			Hay meadow	EUMULL	32	7	7	1.68	0.34
			100			Pasture	EUMULL	59	8	7.9	1.7	0.31
			100			Hay meadow	EUMULL	86	8	7.99	1.99	0.21
			100			Christmas tree	EUMULL	156	13	10.33	2.08	0.25
			100			Pasture	EUMULL	63	11	10.6	1.6	0.56
	Recent	0	0	Mostly old	A-rec0 $N = 3$	Hay meadow	EUMULL	244	10	7.6	1.78	0.32
			0			Hay meadow	EUMULL	63	7	6.8	1.54	0.33
			0			Pasture	EUMULL	25	9	9	2	0.27
		1	23	Both old and recent	A-rec1 $N = 4$	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	46	Mostly old	A-rec2 $N = 5$	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	0	Mostly old	F-old0 $N = 5$	Deciduous	DYSMULL	65	10	9.49	1.64	0.51
			0			Coniferous	DYSMODER	142	11	8.87	1.63	0.48
			0			Deciduous	DYMULL	227	19	12.4	2.21	0.27
			0			Deciduous	DYSMULL	247	14	9.44	1.79	0.43
			0			Deciduous	DYMODER	76	12	10.57	2.09	0.25
		1	25	Both old and recent	F-old1 $N = 5$	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
		2	100	Mostly old	F-old2 $N = 5$	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	0	Mostly old	F-rec0 $N = 4$	Coniferous	OLIGOMULL	86	8	7.07	1.38	0.41
			0			Deciduous	OLIGOMULL	101	13	10.67	2.25	0.18
			0			Coniferous	OLIGOMULL	180	9	6.78	0.99	0.75
			11			Deciduous	OLIGOMULL	120	11	9.59	1.51	0.58
		1	19	Both old and recent	F-rec1 $N = 4$	Deciduous	MESOMULL	82	10	8.52	1.72	0.32
			23			Deciduous	OLIGOMULL	46	7	7	1.35	0.52
			24			Deciduous	MESOMULL	165	12	8.94	1.58	0.39
			69			Deciduous	DYSMODER	222	12	9.45	1.82	0.35
		2	100	Mostly old	F-rec2 $N = 5$	Deciduous	MESOMULL	18	9	9	2.08	0.17
			100			Coniferous	MESOMULL	132	8	5.32	0.78	0.79
			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

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

References

Allouche, O., Kalyuzhny, M., Moreno-Rueda, G., Pizarro, M., Kadmon, R., 2012. Area-heterogeneity tradeoff and the diversity of ecological communities. Proceedings of the National Academy of Sciences of the United States of America 109, 17495–17500.

André, H.M., Noti, M.I., Lebrun, P., 1994. The soil fauna: the other last biotic frontier. Biodiversity and Conservation 3, 45–56.

Åström, J., Bengtsson, J., 2011. Patch size matters more than dispersal distance in a mainland-island metacommunity. Oecologia 167, 747–757.

Auclerc, A., Ponge, J.F., Barot, S., Dubs, F., 2009. Experimental assessment of habitat preference and dispersal ability of soil springtails. Soil Biology and Biochemistry 41, 1596–1604.

Augusto, L., Dupouey, J.L., Ranger, J., 2003. Effects of tree species on understory vegetation and environmental conditions in temperate forests. Annals of Forest Science 60, 823–831.

Bailey, S., 2007. Increasing connectivity in fragmented landscapes: an investigation of evidence for biodiversity gain in woodlands. Forest Ecology and Management 238, 7–23.

Batlle-Aguilar, J., Brovelli, A., Porporato, A., Barry, D.A., 2011. Modelling soil carbon and nitrogen cycles during land use change. A review. Agronomy for Sustainable Development 31, 251–274.

Birkhofer, K., Schöning, I., Alt, F., Herold, N., Klarner, B., Maraun, M., Marhan, S., Oelmann, Y., Wubet, T., Yurkov, A., Begerow, D., Berner, D., Buscot, F., Daniel, R., Diekötter, T., Ehnes, R.B., Erdmann, G., Fischer, C., Foesel, B., Groh, J., Gutknecht, J., Kandeler, E., Lang, C., Lohaus, G., Meyer, A., Nacke, H., Näther, A., Overmann, J., Polle, A., Pollierer, M.M., Scheu, S., Schloter, M., Schulze, E.D., Schulze, W., Weinert, J., Weisser, W.W., Wolters, V., Schrumpf, M., 2012. General relationships between abiotic soil properties and soil biota across spatial scales and different land-use types. PLos ONE 7, e43292.

Bodzogan, H., 1987. Model selection and Akaike's Information Criterion (AIC)! The general theory and its analytical extensions. Psychometrika 52, 345–370.

Bokhorst, S., Phoenix, G.K., Bjerke, J.W., Callaghan, T.V., Huyer-Brugman, F., Berg, M.P., 2012. Extreme winter warming events more negatively impact small rather than large soil fauna: shift in community composition explained by traits not taxa. Global Change Biology 18, 1152–1162.

Bretfeld, G., 1999. Synopses on Palaearctic Collembola, II Symphypleona. Abhandlungen und Berichte des Naturkundemuseums, Görlitz.

Brêthes, A., Brun, J.J., Jabiol, B., Ponge, J.F., Toutain, F., 1995. Classification of forest humus forms: a french proposal. Annales des Sciences Forestières 52, 535–546.

Brückmann, S.V., Krauss, J., Steffan-Dewenter, I., 2010. Butterfly and plant specialists suffer from reduced connectivity in fragmented landscapes. Journal of Applied Ecology 47, 799–809.

Caner, L., Zeller, B., Dambrine, E., Ponge, J.F., Chauvat, M., Llanque, C., 2004. Origin of the nitrogen assimilated by soil fauna living in decomposing beech litter. Soil Biology and Biochemistry 36, 1861–1872.

Cassagne, N., Bal-Serin, M.C., Gers, C., Gauquelin, T., 2004. Changes in humus properties and collembolan communities following the replanting of beech forests with spruce. Pedobiologia 48, 267–276.

Chagnon, M., Paré, D., Hébert, C., 2000. Relationships between soil chemistry, microbial biomass and the collembolan fauna of southern Quebec sugar maple stands. Écoscience 7, 307–316.

Chauvat, M., Titsch, D., Zaytsev, A.S., Wolters, V., 2011. Changes in soil faunal assemblages during conversion from pure to mixed forest stands. Forest Ecology and Management 262, 317–324.

Chauvat, M., Wolters, V., Dauber, J., 2007. Response of collembolan communities to land-use change and grassland succession. Ecography 30, 183–192.

Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science 199, 1302–1310.

Coulson, S.J., Midgley, N.G., 2012. The role of glacier mice in the invertebrate colonisation of glacial surfaces: the moss balls of the Falljokull, Iceland. Polar Biology 35, 1651–1658.

Cristofoli, S., Mahy, G., 2010. Colonisation credit in recent wet heathland butterfly communities. Insect Conservation and Diversity 3, 83–91.

Cristofoli, S., Piqueray, J., Dufrêne, M., Bizoux, J.P., Mahy, G., 2010. Colonization credit in restored wet heathlands. Restoration Ecology 18, 645–655.

Cushman, S.A., 2006. Effects of habitat loss and fragmentation on amphibians: a review and prospectus. Biological Conservation 128, 231–240.

da Silva, P.M., Berg, M.P., Serrano, A.R.M., Dubs, F., Sousa, J.P., 2012. Environmental factors at different spatial scales governing soil fauna community patterns in fragmented forests. Landscape Ecology 27, 1337–1349.

Davies, K.F., Melbourne, B.A., Margules, C.R., Lawrence, J.F., 2005. Metacommunity structure influences the stability of local beetle communities. In: Holyoak, M., Leibold, M.A., Holt, R.D. (Eds.), Metacommunities: Spatial Dynamics and Ecological Communities. University of Chicago Press, Chicago, pp. 170–188.

Decaëns, T., 2010. Macroecological patterns in soil communities. Global Ecology and Biogeography 19, 287–302.

Decaëns, T., Margerie, P., Renault, J., Bureau, F., Aubert, M., Hedde, M., 2011. Niche overlap and species assemblage dynamics in an ageing pasture gradient in north-western France. Acta Oecologica 37, 212–219.

Driscoll, D.A., Whitehead, C.A., Lazzari, J., 2012. Spatial dynamics of the knob-tailed gecko *Nephrurus stellatus* in a fragmented agricultural landscape. Landscape Ecology 27, 829–841.

Dzwonko, Z., 2001. Assessment of light and soil conditions in ancient and recent woodlands by Ellenberg indicator values. Journal of Applied Ecology 38, 942–951.

Dunger, W., Schulz, H.J., Zimdars, B., 2002. Colonization behaviour of Collembola under different conditions of dispersal. Pedobiologia 46, 316–327.

Ettema, C.H., Wardle, D.A., 2002. Spatial soil ecology. Trends in Ecology and Evolution 17, 177–183.

Finlay, B.J., Esteban, G.F., Fenchel, T., 1996. Global diversity and body size. Nature 383, 132–133.

Forman, R., 1995. Land Mosaics: The Ecology of Landscapes and Regions. Cambridge University Press, Cambridge.

Forman, R., Godron, M., 1986. Landscape Ecology. Wiley, New York.

Fox, J.W., 2013. The intermediate disturbance hypothesis should be abandoned. Trends in Ecology and Evolution 28, 86–92.

French, L.J., Smith, G.F., Kelly, D.L., Mitchell, F.J.G., O'Donoghue, S., Iremonger, S.E., McKee, A.-M., 2008. Ground flora communities in temperate oceanic plantation forests and the influence of silvicultural, geographic and edaphic factors. Forest Ecology and Management 255, 476–494.

Gardner, R.H., Engelhardt, K.A.M., 2008. Spatial processes that maintain biodiversity in plant communities. Perspectives in Plant Ecology Evolution and Systematics 9, 211–228.

Gauquelin, T., Gers, C., Deharveng, L., 1996. Physico-chemical heterogeneity of superficial soil layers in conifer plantations versus original broad leaf forests in Ariege (Pyrenees, France). Communications in Soil Science and Plant Analysis 27, 2361–2380.

Gijbels, P., Adriaens, D., Honnay, O., 2012. An orchid colonization credit in restored calcareous grasslands. Écoscience 19, 21–28.

Gilpin, M.E., Hanski, I.A., 1991. Metapopulation Dynamics: Empirical and Theoretical Investigations. Academic Press, London.

Gorelick, R., 2006. Combining richness and abundance into a single diversity index using matrix analogues of Shannon's and Simpson's indices. Ecography 29, 525–530.

Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4, 379–391.

Green, D.G., Sadedin, S., 2005. Interactions matter: complexity in landscapes and ecosystems. Ecological Complexity 2, 117–130.

Hågvar, S., 1983. Collembola in Norwegian coniferous forest soils. II. Vertical distribution. Pedobiologia 25, 383–401.

Hanski, I., 1994. Patch-occupancy dynamics in fragmented landscapes. Trends in Ecology and Evolution 9, 131–135.

Hasegawa, M., Fukuyama, K., Makino, S., Okochi, I., Tanaka, H., Okabe, K., Goto, H., Mizoguchi, T., Sakata, T., 2009. Collembolan community in broad-leaved forests and in conifer stands of *Cryptomeria japonica* in Central Japan. Pesquisa Agropecuária Brasileira 44, 881–890.

Hertzberg, K., 1997. Migration of Collembola in a patchy environment. Pedobiologia 41, 494–505.

Hewitt, N., Kellman, M., 2002. Tree seed dispersal among forest fragments. II. Dispersal abilities and biogeographical controls. Journal of Biogeography 29, 351–363.

Hillebrand, H., Blenckner, T., 2002. Regional and local impact on species diversity - from pattern to processes. Oecologia 132, 479–491.

Holyoak, M., Leibold, M.A., Holt, R.D., 2005. Metacommunities: Spatial Dynamics and Ecological Communities. University of Chicago Press, Chicago.

Hopkin, S.P., 1997. Biology of the Springtails (Insecta: Collembola). Oxford University Press, Oxford.

Hopkin, S.P., 2007. A Key to Collembola (Springtails) of Britain and Ireland. Field Studies Council, Shrewsbury.

Hubbell, S.P., 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton.

Ingimarsdottir, M., Caruso, T., Ripa, J., Magnusdottir, O.B., Migliorini, M., Hedlund, K., 2012. Primary assembly of soil communities: disentangling the effect of dispersal and local environment. Oecologia 170, 745–754.

Kotliar, N.B., Wiens, J.A., 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos 59, 253–260.

Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R.K., Helm, A., Kuussaari, M., Lindborg, R., Öckinger, E., Partel, M., Pino, J., Poyry, J., Raatikainen, K.M., Sang, A., Stefanescu, C., Teder, T., Zobel, M., Steffan-Dewenter, I., 2010. Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. Ecology Letters 13, 597–605.

Lauga-Reyrel, F., Deconchat, M., 1999. Diversity within the Collembola community in fragmented coppice forests in south-western France. European Journal of Soil Biology 35, 177–187.

Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P., Rossi, J.P., 2006. Soil invertebrates and ecosystem services. European Journal of Soil Biology 42, S3–S15.

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., Gonzalez, A., 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7, 601–613.

Lemaître, J., Darveau, M., Zhao, Q., Fortin, D., 2012. Multiscale assessment of the influence of habitat structure and composition on bird assemblages in boreal forest. Biodiversity and Conservation 21, 3355–3368.

Lindo, Z., Winchester, N.N., 2009. Spatial and environmental factors contributing to patterns in arboreal and terrestrial oribatid mite diversity across spatial scales. Oecologia 160, 817–825.

Loranger, G., Bandyopadhyaya, I., Razaka, B., Ponge, J.F., 2001. Does soil acidity explain altitudinal sequences in collembolan communities? Soil Biology and Biochemistry 33, 381–393.

Magura, T., Tothmeresz, B., Elek, Z., 2003. Diversity and composition of carabids during a forestry cycle. Biodiversity and Conservation 12, 73–85.

Mapelli, F.J., Kittlein, M.J., 2009. Influence of patch and landscape characteristics on the distribution of the subterranean rodent *Ctenomys porteousi*. Landscape Ecology 24, 723–733.

Molino, J.F., Sabatier, D., 2001. Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis. Science 294, 1702–1704.

Morecroft, M.D., Taylor, M.E., Oliver, H.R., 1998. Air and soil microclimates of deciduous woodland compared to an open site. Agricultural and Forest Meteorology 90, 141–156.

Mouquet, N., Munguia, P., Kneitel, J.M., Miller, T.E., 2003. Community assembly time and the relationship between local and regional species richness. Oikos 103, 618–626.

Östman, Ö., Mellbrand, K., Hamback, P.A., 2009. Edge or dispersal effects – Their relative importance on arthropod densities on small islands. Basic and Applied Ecology 10, 475–484.

Petit, S., Fried, G., 2012. Patterns of weed co-occurrence at the field and landscape level. Journal of Vegetation Science 23, 1137–1147.

Ponge, J.F., 1991. Food resources and diets of soil animals in a small area of Scots pine litter. Geoderma 49, 33–62.

Ponge, J.F., 1993. Biocenoses of Collembola in Atlantic temperate grass-woodland ecosystems. Pedobiologia 37, 223–244.

Ponge, J.F., 2000. Vertical distribution of Collembola (Hexapoda) and their food resources in organic horizons of beech forests. Biology and Fertility of Soils 32, 508–522.

Ponge, J.F., Arpin, P., Sondag, F., Delecour, F., 1997. Soil fauna and site assessment in beech stands of the Belgian Ardennes. Canadian Journal of Forest Research 27, 2053–2064.

Ponge, J.F., Chevalier, R., 2006. Humus index as an indicator of forest stand and soil properties. Forest Ecology and Management 233, 165–175.

Ponge, J.F., Chevalier, R., Loussot, P., 2002. Humus index: an integrated tool for the assessment of forest floor and topsoil properties. Soil Science Society of America Journal 66, 1996–2001.

Ponge, J.F., Dubs, F., Gillet, S., Sousa, J.P., Lavelle, P., 2006. Decreased biodiversity in soil springtail communities: the importance of dispersal and landuse history in heterogeneous landscapes. Soil Biology and Biochemistry 38, 1158–1161.

Ponge, J.F., Gillet, S., Dubs, F., Fedoroff, E., Haese, L., Sousa, J.P., Lavelle, P., 2003. Collembolan communities as bioindicators of land use intensification. Soil Biology and Biochemistry 35, 813–826.

Ponge, J.F., Salmon, S., 2013. Spatial and taxonomics correlates of species and species trait assemblages in soil invertebrate communities. Pedobiologia 56, 129–136.

Posada, D., Buckley, T.R., 2004. Model selection and model averaging in phylogenetics: advantages of Akaike Information Criterion and Bayesian approaches over likelihood ratio tests. Systematic Biology 53, 793–808.

Potapov, M., 2001. Synopses of Palearctic Collembola. III. Isotomidae. Abhandlungen und Berichte des Naturkundemuseums, Görlitz.

Querner, P., Bruckner, A., Drapela, T., Moser, D., Zaller, J.G., Frank, T., 2013. Landscape and site effects on Collembola diversity and abundance in winter oilseed rape fields in eastern Austria. Agriculture, Ecosystems and Environment 164, 145–154.

R Development Core Team, 2010. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Ricklefs, R.E., 1987. Community diversity: relative roles of local and regional processes. Science 235, 167–171.

Salamon, J.A., Alphei, J., 2009. The Collembola community of a Central European forest: influence of tree species composition. European Journal of Soil Biology 45, 199–206.

Salamon, J.A., Scheu, S., Schaefer, M., 2008. The Collembola community of pure and mixed stands of beech (*Fagus sylvatica*) and spruce (*Picea abies*) of different age. Pedobiologia 51, 385–396.

Salmon, S., 2004. The impact of earthworms on the abundance of Collembola: improvement of food resources or of habitat? Biology and Fertility of Soils 40, 323–333.

Salmon, S., Ponge, J.F., 2012. Species traits and habitats in springtail communities: a regional scale study. Pedobiologia 55, 295–301.

Saunders, D.A., Hobbs, R.J., Margules, C.R., 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5, 18–32.

Scheu, S., Albers, D., Alphei, J., Buryn, R., Klages, U., Migge, S., Platner, C., Salamon, J.A., 2003. The soil fauna community in pure and mixed stands of beech and spruce of different age: trophic structure and structuring forces. Oikos 101, 225–238.

Schneider, K., Scheu, S., Maraun, M., 2007. Microarthropod density and diversity respond little to spatial isolation. Basic and Applied Ecology 8, 26–35.

Seabloom, E.W., van der Valk, A.G., 2003. Plant diversity, composition, and invasion of restored and natural prairie pothole wetlands: implications for restoration. Wetlands 23, 1–12.

Setälä, H., Marshall, V.G., Trofymow, J.A., 1995. Influence of micro-habitat and macro-habitat factors on collembolan communities in Douglas-fir Stumps during forest succession. Applied Soil Ecology 2, 227–242.

Shmida, A., Wilson, M.V., 1985. Biological determinants of species diversity. Journal of Biogeography 12, 1–20.

Sławski, M., Sławska, M., 2000. The forest edge as a border between forest and meadow. Vegetation and Collembola communities. Pedobiologia 44, 442–450.

Sousa, J.P., Bolger, T., da Gama, M.M., Lukkari, T., Ponge, J.F., Simon, C., Traser, G., Vanbergen, A.J., Brennan, A., Dubs, F., Ivitis, E., Keating, A., Stofer, S., Watt, A.D., 2006. Changes in Collembola richness and diversity along a gradient of land-use intensity: a pan European study. Pedobiologia 50, 147–156.

Sousa, J.P., da Gama, M.M., Pinto, P., Keating, A., Calhoa, F., Lemos, M., Castro, C., Luz, T., Leitao, P., Dias, S., 2004. Effects of land-use on Collembola diversity patterns in a Mediterranean landscape. Pedobiologia 48, 609–622.

Stratford, J.A., Stouffer, P.C., 1999. Local extinctions of terrestrial insectivorous birds in a fragmented landscape near Manaus, Brazil. Conservation Biology 13, 1416–1423.

Tanner, J.E., 2003. Patch shape and orientation influences on seagrass epifauna are mediated by dispersal abilities. Oikos 100, 517–524.

Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M.C., Schwager, M., Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography 31, 79–92.

Thibauld, J.M., Schultz, H.J., da Gama, M.M., 2004. Synopses on Palearctic Collembola. IV. Hypogastruridae. Abhandlungen und Berichte des Naturkundemuseums, Görlitz.

Tilman, D., 1982. Resource Competition and Community Structure. Princeton University Press, Princeton.

Tilman, D., 1994. Competition and Biodiversity in spatially structured habitats. Ecology 75, 2–16.

Tilman, D., May, R.M., Lehman, C.L., Nowak, M.A., 1994. Habitat destruction and the extinction debt. Nature 371, 65–66.

Vanbergen, A.J., Watt, A.D., Mitchell, R., Truscott, A.-M., Palmer, S.C.F., Ivits, E., Eggleton, P., Jones, T.H., Sousa, J.P., 2007. Scale-specific correlations between habitat heterogeneity and soil fauna diversity along a landscape structure gradient. Oecologia 153, 713–725.

Vreeken-Buijs, M.J., Hassink, J., Brussaard, L., 1998. Relationships of soil microarthropod biomass with organic matter and pore size distribution in soils under different land use. Soil Biology and Biochemistry 30, 97–106.

Wamser, S., Diekötter, T., Boldt, L., Wolters, V., Dauber, J., 2012. Trait-specific effects of habitat isolation on carabid species richness and community composition in managed grasslands. Insect Conservation and Diversity 5, 9–18.

Wardle, D.A., 2006. The influence of biotic interactions on soil biodiversity. Ecology Letters 9, 870–886.

Wright, T.E., Kasel, S., Tausz, M., Bennett, L.T., 2010. Edge microclimate of temperate woodlands as affected by adjoining land use. Agricultural and Forest Meteorology 150, 1138–1146.

Wu, J.G., Loucks, O.L., 1995. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. Quarterly Review of Biology 70, 439–466.