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Effect of habitat spatiotemporal structure on collembolan diversity

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ABSTRACT

Landscape fragmentation is a major threat to biodiversity. It results in the transformation of continuous (hence large) habitat patches into isolated (hence smaller) patches, embedded in a matrix of another habitat type. Many populations are harmed by fragmentation because remnant patches do not fulfil their ecological and demographic requirements. In turn, this leads to a loss of biodiversity, especially if species have poor dispersal abilities. Moreover, landscape fragmentation is a dynamic process in which patches can be converted from one type of habitat to another. A recently created habitat might suffer from a reduced biodiversity because of the absence of adapted species that need a certain amount of time to colonize the new patch (e.g. direct 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;

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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.