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Contrasting processes drive alpha and beta taxonomic, functional and phylogenetic diversity of orthopteran communities in grasslands

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A B S T R A C T

Taxonomic, functional and phylogenetic diversities can respond differently to biotic and abiotic filters. However, biodiversity management tends to focus on a single index, generally taxonomic diversity, assuming a strong positive correlation among biodiversity components across scales. This can result in a mismanagement of functional and phylogenetic diversities with negative consequences for ecosystem functioning and long-term maintenance of services. Understanding the relationships among biodiversity components, how they change across scales and which their main drivers are can lead to more sustainable management of biodiversity and its associated ecosystem services and functions.

We used an integrative approach of biodiversity where we investigated alpha and beta taxonomic (TD), functional (FD) and phylogenetic (PD) diversity of orthopteran communities as well as species and functional traits composition and their associated drivers at the local and landscape scales in permanent mesic grasslands of the French Jura Mountains. We assessed whether orthopteran TD, FD and PD were positively correlated. We also determined the drivers of TD, FD and PD and their changes across scales and among indices using data related to soil, agricultural practices, elevation, and biotic interactions with plants.

Our results showed that (i) elevation was a strong driver of orthopteran community trait composition, (ii) orthopteran alpha TD, FD and PD were correlated among themselves and increased with plant species richness, and (iii) local beta diversity was not correlated with alpha diversity. Beta diversity had different drivers at local and landscape scale: it was influenced by soil chemistry and texture at the local scale and increased with the difference in elevation among plots at the landscape scale.

This study evidences distinct processes driving alpha and beta diversity of orthopteran communities at both the local and landscape scales. It supports the hypothesis that less intensive agricultural practices enhance orthopteran diversity and highlights the importance to consider beta diversity at both local and landscape scale when designing and assessing the management regimes of grassland ecosystems. Prioritizing the importance of the different biodiversity components and spatial scales constitutes an important challenge for sustainable grassland management.

1. Introduction

The biodiversity of ecological communities is a multi-faceted concept that includes not only the diversity of species (taxonomic diversity, TD) but also functional trait differences among species (functional diversity, FD) and the phylogenetic dissimilarity among species (phylogenetic diversity, PD). Functional traits and their associated diversity inform about biotic interactions, niche complementarity, and environmental filtering, which in turn allows discriminating between neutral and niche assembly processes (McGill et al., 2006). Phylogenetic diversity informs about the evolutionary relationships among species and can link community structure to ecosystem functions and stability (Cadotte et al., 2012). Evidences reveal various degrees of divergence among biodiversity components (Devictor et al., 2010; Pavoine and Bonsall, 2011). For instance, two communities with equal TD can have different FD and PD as a result of their evolutionary and ecological histories (Webb et al., 2002). True species turnover following disturbance or land use change can lead to higher TD but

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lower FD and PD (Concepción et al., 2015; Knapp et al., 2012). Theories describing changes in biodiversity along environmental dimensions such as the ecological gradient theory (Scheiner and Willig, 2005) tend to focus on species richness. An integrative theory that encompasses the changes of the various biodiversity facets over environmental dimensions and over scales is still lacking. Such a theoretical framework would increase our capacity to understand and predict the changes of the different components of biodiversity and their consequences for ecosystem functioning.

1.1. Drivers of biodiversity

Soberón (2007) proposed that dispersal limitations, abiotic constraints and biotic interactions are the main factors determining the composition of local communities from the global pool. These drivers of biodiversity are likely to vary in importance with the spatial scale considered and/or along environmental gradients (Boulangeat et al., 2012; Kneitel and Chase, 2004; Lortie et al., 2004). Dispersal limitations are more likely to occur at broader spatial scales (beyond species dispersal capacity), abiotic constraints are well documented at the regional to landscape scale (Thuiller et al., 2004), and biotic interactions occur locally (Soberón, 2007). Similarly, assembly mechanisms are likely to change along environmental gradients where, for example, the cold and short growing season of high elevation sites imposes stronger filters on plant growth and reproduction than in lower elevation sites (Pellissier et al., 2010). A detailed study of the drivers of functional and phylogenetic components of orthopteran communities in grasslands can lead to a more integrative and multi-scale perspective of species assembly that can provide key information to help improve grassland management.

1.2. Biodiversity and ecosystem management

Preserving diversity was shown to be essential to maintain stable ecosystem services such as productivity (Tilman et al., 1996). For instance, decrease in species richness can lead to overall decreased levels of ecosystem functioning (Hooper et al., 2005) and stability (Tilman et al., 2006). However, this effect depends on the types of species that are lost (community composition, functional groups). The spatio-temporal divergences of TD, FD and PD may inform about possible consequences of community change on ecosystem functioning and underlying services (e.g., Díaz et al., 2007; Hooper et al., 2005). The additional information provided by phylogenetic and functional diversity is often neglected in ecosystem management, but it is critical to understand, predict and manage future changes of ecosystem properties and functions.

1.3. Orthopteran diversity and its drivers

In the present study, we test the filtering effect of elevation, soils, agricultural practices, dispersal limitation and biotic interactions with plants on the diversity (alpha and beta TD, FD and PD at local and landscape scale) of orthopteran communities in the mesic permanent grasslands of the French Jura Mountains. We focus on orthopterans because they are (*i*) key actors of grassland ecosystems as they are very abundant and diverse, (*ii*) they occupy a central position in the foodweb and can consume up to 30% of the plant biomass in alpine grassland ecosystems (Blumer and Diemer, 1996) and (*iii*) they can mediate the negative impact of grazing by large herbivores on plant diversity (Zhong et al., 2014).

The drivers of orthopteran diversity were shown to vary across spatial scales in grasslands (Sutcliffe et al., 2015). At the local scale, studies demonstrated the importance of environmental conditions, habitat complexity, soils (Janssens et al., 1998), management practices (Fonderflick et al., 2014; Humbert et al., 2012), eutrophication and acidification (Stevens et al., 2010) and biotic interactions (Bakker et al., 2006; Borer et al., 2014; Deraison et al., 2015). For example, Marini et al. (2008) showed that intensive management (frequent cuttings and application of high amounts of nitrogen fertilizer) lead to impoverished communities dominated by few Caelifera species such as *Chorthippus parallelus* in the European Alps. At the landscape scale, studies demonstrated the impact of habitat loss and fragmentation (Helm et al., 2006), climate change (Harrison et al., 2015), land use change (Weiner et al., 2011) and landscape heterogeneity (Ovalle et al., 2006) on orthopteran diversity. Several studies demonstrated the trait-mediated relations between plant and orthopteran communities (Deraison et al., 2015; Ibanez et al., 2013; Moretti et al., 2013) and the effects of orthopterans on ecosystem functioning (Deraison et al., 2015; Ibanez et al., 2013). The beta TD of orthopteran communities was shown to decrease in the presence of highly mobile species as well as from the landscape to the local scale (Marini et al., 2012). Nevertheless, integrative approaches comparing taxonomic, functional and phylogenetic components of orthopteran communities over various spatial scales are still lacking, yet they are critical for optimizing grassland management efforts.

1.4. Aims and hypotheses

Our study acknowledges the complexity and multiple causality of ecological patterns and aims at generating integrative knowledge regarding biodiversity changes across scales, following an approach based on empirical constructivism and scientific realism (Pickett et al., 2007). More specifically, we challenge the dominant paradigm in conservation management that states that changes in species richness parallel those in TD, FD and PD, which was observed for plants in the same grasslands (Mauchamp et al., 2014). To do so, we investigate the drivers of orthopteran alpha and beta TD, FD and PD as well as of their species and trait composition at both the local and landscape scales. We expect beta diversity to be higher at the landscape scale than at the local scale because of the more pronounced spatially heterogeneous filtering effect of environmental conditions (difference in elevation, climate, soil and agricultural practices) and the stronger dispersal contingencies at landscape scale. We also expect high stocking rates and frequent cuttings to decrease TD, FD and PD of orthopteran communities as a result of the filtering of poorly adapted species and functional groups, and their replacement by few species better adapted to the more intensive agricultural practices.

2. Materials and methods

2.1. Study site

We studied semi-natural permanent grasslands mainly used for dairy farming and Protected Designation of Origin cheese production (mainly Comté cheese, a major economic sector, with constraining specifications for agricultural practices) located in the NW part of the French Jura Mountains (Fig. 1). The area is located between 391 and 1195 m a.s.l. and is characterized by a nemoral climate with a strong suboceanic influence. Permanent grasslands growing on cambisols developed on limestone and loess cover about 22% of the total surface of the study area. We selected 46 mesic grasslands encompassing a gradient in mowing and grazing practices (from strictly grazed to frequently mown) as well as in fertilization regime (Mauchamp et al., 2014). We excluded grasslands that have been ploughed or sown within the ten past years or that are located on steep slopes to avoid potential confounding effects.

2.2. Agricultural practices and soil surveys

Interviews with the 23 farmers who manage the selected grasslands were organized to quantify (1) the mean number of cuts per year (*cutting*; 0 in strictly grazed parcels); (2) the stocking rate (*grazing*) expressed in livestock units day per hectare and per year (available for