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Research paper

Landscape effects on plants in forests: Large-scale context determines local plant response

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HIGHLIGHTS

- In forests, local plant response to landscape features changed with landscape extent.
- Landscape features at large scale (>500 m) better predicted local plant response.
- A better consideration of the large-scale effects of landscape on plants is needed.
- This may imply to take better account of time-lag effects of landscape.

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ABSTRACT

Most studies of landscape effects on plants in forests have explored only relatively small landscape scales (size of spatial extent) considering the poor-dispersal ability generally reported for forest plants, or failed to verify confidently that the scales at which landscape is considered best predicts plant patterns. We investigated the effect of landscape composition on response of plant communities according to three scales - 400 ha, 100 ha and 25 ha - in 263 forests in the northern half of France. We hypothesized that landscape composition at the 400-ha scale better predicted plant responses than smaller scales. We built models to compare the effects of each scale on individual species response and plant composition of 1902 700-m^2 vegetation plots, considering the shared and pure effects of scales. Only landscape composition at the 400-ha scale showed a critical pure effect on plant composition. Similarly, the 400-ha scale better predicted individual species response. Using a large dataset, we brought evidence that landscape composition further than 100 ha and at least up to 400 ha had more effects on local plant diversity in forests, which means that smaller-scale investigations may miss the influence of landscape on plant patterns. The effects of large spatial scale may reflect the legacies of past landscape or the long-distance dispersal capacity of plants. Our findings call for better consideration of the large-scale effects of landscape on plants both in scientific studies and management plans.

1. Introduction

Landscape effects on biodiversity have received increasingly greater attention and several syntheses have shown that landscape context has an important effect on organisms in interaction with other processes occurring at patch scale (Bender & Fahrig, 2005; Ewers & Didham, 2006; Jules & Shahani, 2003; Kupfer, Malanson, & Franklin, 2006; Murphy & Lovett-Doust, 2004; Vandermeer & Lin, 2008; Wiser & Buxton, 2008). It may be more difficult to identify relations between landscape context and plant response than animal response, as plants are generally dependent on other agents for dispersal and pollination, and many have a long life-span (or long-lived seed bank) or use vegetative propagation (Jules & Shahani, 2003; Krauss et al., 2010). Landscape context can exert its influence at various scales depending not only on species attributes but also on the landscape features under consideration (Dungan et al., 2002; Graf, Bollmann, Suter, & Bugmann, 2005; Holland, Bert, & Fahrig, 2004; Vos, Verboom, Opdam, & Ter Braak, 2001). In this paper, landscape scale refers to the size of area – centered on the focal vegetation plot – within which habitat predictor variables are measured, and therefore the extent (and not the grain) of the predictor variable (see Holland et al., 2004). Studies designed

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to capture landscape effects on plants rarely compare the effect of several landscape scales, which means they fail to verify that the scale used better or best explains the plant response patterns observed. In forests, investigations into landscape effects on plants are very often restricted to a small radius, i.e. less than 500 m (De Sanctis, Alfo, Attorre, Francesconi, & Bruno, 2010; Guirado, Pino, & Roda, 2006; Marini, Scotton, Klimek, & Pecile, 2008), which is a methodological choice justified by the limited dispersal distance conventionally reported (Dzwonko, 1993; Dzwonko & Loster, 1992; Matlack, 1994; Vanruremonde & Kalkhoven, 1991). Moreover, landscape studies on plants are generally based on very small datasets (e.g. Schindler, von Wehrden, Poirazidis, Wrbka, & Kati, 2013; but see Martin-Queller, Diez, Ibanez, & Saura, 2013), which reduces the general validity of the results and may even lead to misspecification of the scale at which landscape influences plant diversity. Consequently, there is still a dearth of understanding of how well the scale at which landscape predictors are measured predicts plant patterns, whereas this scale strongly affects both the efficiency of study designs to identify landscape effects on species (Holland et al., 2004; Jackson & Fahrig, 2012, 2015) and the knowledge on the spatial extent of the effects of management practices. Determining appropriate spatial scales is crucial for biodiversity conservation, as it necessarily dictates the scales at which conservation actions and sustainable management schemes need to be established (Aviron, Burel, Baudry, & Schermann, 2005; Forman, 1995; Jackson & Fahrig, 2012; Martin-Queller et al., 2013).

A common method for estimating appropriate scale is to measure landscape features at several nested spatial scales and determine which scale fits the best model of species response to landscape context (Fahrig, 2003; Grashof-Bokdam, 1997; Lindborg & Eriksson, 2004). The scale at which landscape features such as habitat amount best predict local species or community responses is qualified as "characteristic scale" (Holland et al., 2004) or "scale of effect" (Jackson & Fahrig, 2012); it would be also qualified as "functional spatial scale" when related to species traits like dispersal distance or home-range size that are thought to be important elements of species response (Jackson & Fahrig, 2012). In particular, it is reasonable to assume that plant species with long-distance dispersal are influenced by landscape composition at a larger scale than plant species with short-distance dispersal, as demonstrated for animal species (Jackson & Fahrig, 2012). In plants, long-distance dispersal can explain the presence of certain species when neighbouring sources are absent (Cain, Milligan, & Strand, 2000; Pearson & Dawson, 2005), but it can also be argued that landscape effects on plants are time-delayed (Krauss et al., 2010). This temporal effect of landscape can be seen in large-scale landscape effects on plants, as shown in grasslands (Lindborg & Eriksson, 2004). Hence, it is essential to explore landscape effects at large scale, and to assess whether plants in forests could also be impacted by relatively distant landscape habitats, and not just by well-known local factors like light conditions, soil constraints and forest stand characteristics.

Our hypothesis was that plants are affected by the effect of landscape composition (habitat amount) at a larger scale than generally thought, i.e. that the characteristic scale is larger than the typical 500-m radius that corresponds to a 100-ha squared buffer. We also hypothesized that a common landscape scale can be identified among plant species responses i.e. there is a scale at which landscape composition best predicts the response of most species. We used a comprehensive approach to investigate how the relationship between forest plant species occurrence and landscape composition changes with scale using a national countryside survey. The large study area (about 56,000 km^2) and large sample size (1902 plots) allowed us to sample a broad range of landscape types and work with many replicates in each category of landscape, thus avoiding the pseudo-replication problem in landscape-scale studies (Fahrig, 2003). Indeed, landscape studies tend to sample a handful of landscape situations and then go on to infer landscape effects from them, which can yield biased results since other environmental factors can be spuriously correlated with landscape variables (Fahrig, 2003). Moreover, we considered effects exclusively attributable to landscape features and eliminated effects that can be explained by site factors. Indeed, site factors count among the drivers of local forest plant presence and a large part of plant community variation is jointly explained by landscape and site effects (e.g. Kolb & Diekmann, 2004; Marini et al., 2008). The ability to consider "pure effects" of landscape is therefore a key issue for landscape studies.

Here we investigated how well landscape composition at several landscape scales predicts forest plant community composition and presence of individual species. Using three nested spatial scales, i.e. 25 ha, 100 ha and 400 ha, we specifically addressed the following questions:

- What is the landscape effect at each landscape scale, and is there an advantage to enlarging the landscape scale in order to study forest plant responses?
- Is there a common landscape scale that better predicts both community and individual species responses?
- Can plant response to landscape scale be explained by ecological traits of species?

2. Materials and methods

2.1. Study area and data

Data were provided by the Inventaire Forestier National (IFN), a national organization entrusted with inventorying and monitoring forest resources throughout France (http://inventaire-forestier.ign.fr/spip/). Here, IFN plots were selected in the northern half of France to cover a homogenous temperate climate zone, and to reduce the time-lag between field surveys and aerial photographs, that ultimately varied between 0 to 4 years. This allowed us to define a study area that covered 56,208 km^2 across 15 French administrative départements (Fig. 1). The dataset comprised a total of 1902 plots distributed in 263 forest patches ranging from 77 to 230,939 ha. The study area belongs to the geological structure of the Paris Basin (centre and close periphery), and altitude was low (under 400 m a.s.l.). The climate is essentially oceanic with a gradual continental influence depending on proximity of the sea. Geological substrates vary and give very acidic to alkaline soils and dry to wet soil conditions (Appendix A). We selected only plots located at least at 300 m from the external forest edge in order to have a landscape composed mainly of forest habitat, as our analysis was focused on forest communities. All plots were located in forest stands composed mainly of *Quercus petraea* Liebl. and *Quercus robur* L., and managed as even-aged high forest systems (issued from natural regeneration or plantation), coppices with standards and coppices (Appendix A). The plant database was composed of 700-m^2 circular plots surveyed for plant presence during the growing season between 2001 and 2005. A total of 428 species was identified. Species traits were compiled from Julve (2011) and Biolflor (Kuhn, Durka, & Klotz, 2004): Raunkiaer's life form and bryophyte type, dispersal vector of vascular plants, a combination of weight and length of seeds, and habitat preference (preference for forest, forest edge or non-forest habitats).

2.1.1. Landscape data

Landscape habitats were mapped in 2009 by photo-interpretation using aerial orthophotos (BD ORTHO®) with a spatial resolution of 0.5 × 0.5 m and GIS in 400-ha (2000 × 2000 m)