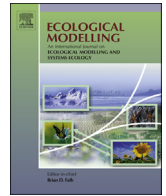




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Non-equilibrium plant metapopulation dynamics challenge the concept of ancient/recent forest species

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ABSTRACT

Previous analyses of the regional distribution of forest plants have revealed that some species have a biased distribution towards either ancient or recent forest patches. It has been therefore proposed to classify forest plant species according to their affinity for ancient or recent patches. In this contribution, we aimed at providing a dynamical perspective on this static concept of ancient/recent forest species. We developed an inference method to estimate the metapopulation dynamics of forest plants based on landscape history and static (and incomplete) biodiversity data accounting for false absence records. We assessed the power of this novel inference method using simulated metapopulation and landscape dynamics. We finally applied this method to occupancy data of 174 and 121 forest species in two networks of 9208 and 9201 forest patches respectively. These patch networks are located in two French regions, with corresponding landscape historical data based on two forest maps conceived in 1840 and 2000. Our analyses revealed that i) the inference method enables to satisfactorily infer three parameters of the metapopulation model: the rates of colonization, extinction and decay of colonization with distance; ii) this three parameter metapopulation model is sufficient to reproduce the occurrence spatial structure of 72% and 61% of the investigated species in the two regions; iii) forest plant species are distributed along a spectrum of turn-over speed, in which small (large) colonization capacity are associated with small (large) propensity to extinction; iv) species position along this spectrum can be partially predicted from plant functional traits; and v) species metapopulation dynamics are driven by the interaction between landscape and species intrinsic properties, suggesting that ancient/recent forest species lists are unlikely to be easily extrapolated to novel landscapes.

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1. Introduction

Since two centuries, reforestation occurs in many ancient agricultural lands in Western Europe (Koerner et al., 2000; Hermý and Verheyen, 2007). Some plant species are better colonizers of these recent forests (hereafter called recent forest species RFS, Hermý et al., 1999), whereas some other species (hereafter called ancient forest species AFS, Hermý et al., 1999) are more confined to ancient forests, i.e. “forests that already existed before a certain threshold date”. Previous studies on ancient/recent forest species have delivered classification of plant species as AFS or RFS according to the age of forests where they are preferentially present (Hermý et al., 1999; Dupouey et al., 2002; Bergès et al., 2015). There is how-

ever no systematic agreement between the different AFS/RFS lists established in different regions (Hermý et al., 1999; Verheyen et al., 2006; Hermý and Verheyen, 2007; Matuszkiewicz et al., 2013). For instance, species classified as AFS may be typical of recent forests in another region (Hermý and Verheyen, 2007). This suggests that the spatial distribution of these plant metapopulations is not solely triggered by species intrinsic properties.

Recruitment of plant individuals is indeed likely to be limited by both dispersal and post-dispersal environmental filters (Wang and Smith, 2002). Biased distributions of plant species towards ancient forests can therefore be due to i) their failure to disperse propagules to newly created forest patches, and ii) the failure of their propagules to pass through local environmental filters encountered in recent forest patches. Biased distributions of plant species towards recent forests can in turn be due to a more efficient dispersal into newly created forest patches than other plants, and ii) a superior ability to pass through local environmental filters in these patches.

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Regarding dispersal processes, several studies were able to detect distinct dispersal syndromes between AFS and RFS. For example, endozoochorous and epizoochorous species, that are good dispersers, are more frequent in recent forests (Brunet et al., 2012; Bergès et al., 2015). In contrast, AFS are more frequently small-size species with a high seed weight and a low seed terminal velocity (Kimberley et al., 2013).

Regarding abiotic filters, AFS tend to be more present in unfertile soils and when soil acidity are intermediate, while RFS tend to be more present when soils are richer in nitrogen and when they are slightly acidic (Brunet et al., 2012; Bergès et al., 2015). Finally, RFS are poorly tolerant to shade and are more able to survive in open woodlands contrary to AFS (Kimberley et al., 2014; Bergès et al., 2015).

To understand how these two components of recruitment limitation, dispersal and environmental filtering, translate into the dynamics of forest plant species, one needs to go beyond static analyses of geographical patterns, and to develop models of plant spatial dynamics (Hanski, 1998; Freckleton and Watkinson, 2002). Models of metacommunity dynamics in which all species are assumed to behave equivalently and to compete for space have been developed and have incorporated either environmental filtering (Jabot et al., 2008) or a spatially-explicit landscape representation (Economio and Keitt, 2008; May et al., 2013). At a finer level of organization, metapopulation models have also been developed and can also integrate environmental filtering and spatially-explicit dispersal processes (Hanski, 1998; Purves et al., 2007). They can be tuned independently for different species but they do not integrate interspecific competition. All these models can be parametrized with snapshot floristic data, under the strong assumption that species spatial dynamics is at equilibrium (Etienne et al., 2004).

However, landscape composition and spatial structure change over time with the creation or destruction of habitats patches (Meeus, 1993; Hermy and Verheyen, 2007) or with gradual changes in patch quality, e.g. following climatic changes (García-Valdés et al., 2015). If the timescale of landscape dynamics is comparable to or shorter than the timescale of a species metapopulation dynamics, this species dynamics cannot be assumed to be at equilibrium anymore (Verheyen et al., 2004; Vellend et al., 2006). Such species may be strongly affected by the turn-over rate of patches over time and current occupancy may be better explained by past landscape structure rather than current landscape structure (Kuussaari et al., 2009; Jackson and Sax, 2010; Hylander and Ehrlén, 2013; Essl et al., 2015).

A first attempt to integrate landscape dynamics into a forest plant metapopulation model was proposed by Verheyen et al. (2004) by adding patch age in Hanski's incidence function model (Hanski, 1994). They also integrated post-dispersal environmental filtering in their framework, through an ad hoc index of patch quality based on Ellenberg indices (Ellenberg et al., 1992). The main limitation of this approach is that it requires an exhaustive sampling of all the landscape patches, so that it is hardly applicable to large scale studies. More recently, Ruete et al. (2014) resolved this limitation by using a Bayesian approach that authorizes non-exhaustive sampling. They applied their methodology to nine lichen metapopulations spanning roughly one hundred patches. This Bayesian approach is however computationally intensive and is therefore difficult to apply to a large number of species in larger landscapes as those we are studying in this contribution.

We therefore developed an innovative inference method, based on an approximate likelihood computation that is faster and scalable to larger landscapes encompassing several thousands of patches. We first tested this novel method with simulated data to assess its reliability and precision. We then applied it to two large forest plant inventory datasets located in two French regions to answer to the following five main questions: (1) how many and

which metapopulation parameters can be reliably inferred from this type of data? (2) Is the resulting metapopulation model studied sufficient to reproduce observed plant metapopulation patterns? (3) Are forest plant metapopulation parameters linked with the observed difference of plant occurrence towards recent or ancient forest patches? (4) Are these colonization-extinction parameters consistent between the two regions studied? And (5) can they be predicted from plant functional traits and environmental characteristics?

2. Materials and methods

We below describe in turn the metapopulation model (section 2.1), the inference method (section 2.2), the power analyses (section 2.3) and the application to forest plant inventory datasets (section 2.4). Analyses are summarized in Fig. 1.

2.1. The metapopulation model

We consider a patch occupancy model that is close to the one proposed by Verheyen et al. (2004). The occupancy dynamics of the network of patches is modelled as a discrete time process, with events of local extinction t , each patch i is either occupied by the focal species ($OCC_i(t) = 1$) or not ($OCC_i(t) = 0$). If a patch is unoccupied, it is colonized between step t and step $t + 1$ by the focal species with probability $C_i(t)$. The time step was fixed to ten years. If it is occupied, the local population of the focal species can go extinct between step t and $t + 1$ with probability $E_i(t)$.

The extinction probability $E_i(t)$ is assumed to be constant through time and given by the following formula:

$$E_i(t) = \min \left(\frac{\sigma}{A_i^\theta}, 1 \right) \quad (1)$$

where σ is the extinction rate parameter and θ regulates the decay of this rate with the area A_i of patch i .

The colonization probability $C_i(t)$ is given by:

$$C_i(t) = \frac{CON_i(t)^2}{CON_i(t)^2 + 1} \quad (2)$$

where $CON_i(t)$ measures the level of connectivity between patch i and the other patches that are occupied at time t . Following Verheyen et al. (2004), it is given by:

$$CON_i(t) = \alpha \cdot \sum_{j \neq i} (A_j \times OCC_j(t) \times \exp^{-\beta d_{ij}}) \quad (3)$$

where d_{ij} is the geographical distance between patches i and j , α is a colonization parameter and β is a parameter assuming a decay of colonization with distance. Note that we did not introduce habitat suitability in this framework (although technically straightforward), contrary to what Verheyen et al. (2004) did. This choice was made to keep the model simple. We will see below that this parsimony is critical to get reasonably accurate inferences. Geographical distances between patches were Euclidian distances computed from patch edge-to-edge.

Finally the modelled landscape is dynamical itself, with events of patch destruction and creation. When a patch i is newly created at time step t , it is considered to be unoccupied ($OCC_i(t) = 0$), until a first colonization event takes place.

2.2. Inference of model parameters

Our aim was to infer the parameters of the metapopulation model described above based on the combined use of two types of data: i) present occupancy data collected in a subset of the landscape patches, and ii) historical maps of landscape patches

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