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Spatial patterns of seedling-adult associations in a temperate forest community

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ABSTRACT

The spatial patterns of seedling recruitment were examined in a temperate deciduous forest stand of NW Spain. The emergence and survival of individual seedlings were sampled during two recruitment seasons for the five dominant tree species (*Corylus avellana*, *Crataegus monogyna*, *Fagus sylvatica*, *Ilex aquifolium* and *Taxus baccata*). Point pattern analyses based on the mark correlation functions and the independent marking null model were used to explore the relationship between seedling density and the location of individual adults of the same and of different species. Overall, we found that negative or null patterns of association dominated at intermediate to large scales in our study site. Surprisingly, there were almost no positive associations at small scales, except for some pairs of fleshy-fruited species. At the same time, the massive recruitment of *F. sylvatica* following a mast event was accompanied by positive associations at larger scales. Spatial changes in seedling abundance were demonstrated to depend not only on the distribution of conspecific adult trees, but to lay a spatial signature of the location of adults from other species. The temporal persistence of some of these patterns and changes associated to varying production highlight the need for a community approach to study tree recruitment.

1. Introduction

The spatial arrangement of recruits relative to their parent trees is a challenging question in plant ecology, with important consequences for both population and community dynamics (Crawley, 1997; Murrell et al., 2001). The main framework for this is provided by the so called Janzen–Connell hypothesis (Janzen, 1970; Connell, 1971), which predicts that specialized predators, including pathogens, will reduce seedling density beneath parent trees, thereby enhancing the recruitment of other species. This hypothesis has been criticized both in empirical and theoretical grounds (Hubbell, 1980; Clark and Clark, 1984; Condit et al., 1992; Barot et al., 1999; Hyatt et al., 2003; Freckleton and Lewis, 2006). However, the Janzen–Connell hypothesis has also received broad support, which could explain contrary results by chance events linked to predator saturation (Schupp, 1992; Burkey, 1994; Hulme and Benkman, 2002) or plant–soil feedbacks (Bever, 1994; Packer and Clay, 2000, 2003).

Most of the studies focusing on the Janzen–Connell hypothesis have ignored spatiotemporal effects on plant recruitment dynamics. Indeed, only a few studies have examined these effects and, in most cases, they have studied only one species or they have been conducted under laboratory conditions (but see Augspurger, 1983; Cintra, 1997; Peters, 2003; Miriti, 2007; Queenborough et al., 2007). Here, we examined in a temperate forest not only the spatial relationship between adults and seedlings within species, but also the relationships with heterospecifics (i.e., community level patterns of association). The adoption of this framework is needed because of the variable importance of different factors during the recruitment season (e.g., different climatic conditions favoring seedling emergence and survival in a species specific manner), and because of different patterns of temporal overlap among species (e.g., intra- and inter-specific competition and facilitation, storage effects, preemption of space, etc. Chesson, 2000). Also, a community approach is important because of the potential interaction among different tree species in terms of the temporal variability in seed production (e.g., masting years and other cycles of less amplitude), and the changing response of both dispersers and predators driven by selection of resources with varying availabilities (Martínez and González Taboada, 2009).

Different ecological processes may leave a particular signature on the spatial arrangement of individuals and therefore, studying spatial associations may help to reveal the importance of underlying mechanisms (McIntire and Fajardo, 2009). A powerful tool to characterize the spatial structure of plant communities is point pattern analysis, which studies the spatial distribution of the mapped position of individuals within a given study region

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(Wiegand and Moloney, 2004; Perry et al., 2006; Illian et al., 2008; Law et al., 2009). Although mainly used to study static patterns in detail, point pattern analysis can be also applied to study their temporal variation (Zang and Skarpe, 1995; Wiegand et al., 1998; Riginos et al., 2005; Felinks and Wiegand, 2009). Contrasting the observed patterns to null models derived from specific hypotheses can help to identify the relative importance of different mechanisms (Wiegand and Moloney, 2004). However, causal relationships need to be carefully stated because different processes may result in the same spatial pattern (Levin, 1992; Moloney, 1993; Jeltsch et al., 1999; Wiegand and Moloney, 2004). Finally, results of spatial point pattern analysis can suggest hypotheses about the underlying processes which can then be proven experimentally (Levin, 1992; Silvertown and Wilson, 1994; Crawley, 1997).

In this study, we take advantage of a detailed sampling of spatial changes in seedling density during two consecutive recruitment seasons to gain understanding about the recruitment process in a temperate forest of the Cantabrian range (NW Spain). Previous work demonstrated a predominance of small scale positive associations between adult individuals of different species in this study site (Martínez et al., 2010). Here, we used point-pattern analysis to describe the spatial association of seedlings and adults at the community level. This allowed us to find out if similar positive associations occurred also between adults and seedlings, and to derive hypotheses on the underlying mechanisms and their relative importance. We further examined potential changes in patterns of association with time, which are expected due to the presence of a mast event of the main canopy species *Fagus sylvatica* L. In particular, we were interested in answering the following questions: (1) Is there any spatial relationship between seedlings and either conspecific or heterospecific adults? (2) Do these relationships remain constant within and between seasons? (3) Is seedling recruitment enhanced or inhibited under the canopy of heterospecific trees? (4) Are spatial patterns of recruitment enough to explain the relationship between adults?

2. Materials and methods

2.1. Study area

The study was conducted during two consecutive recruitment seasons (May–September in 2004 and 2005) at the Teixeu site (43°17′49″N, 5°30′25″W, 1000 m a.s.l., Asturias province, NW Spain). The Teixeu site is located at the Northern edge of a temperate deciduous beech forest (*F. sylvatica*), and its name refers to the presence of yew *Taxus baccata* L., which is the other main canopy species. The forest understory is composed of fleshy-fruited species (hawthorn *Crataegus monogyna* Jacq., holly *Ilex aquifolium* L. and rowans *Sorbus* sp.), and hazel *Corylus avellana* L. The study area is located on a steep North-east facing slope (average incline is 25.6°) which is bounded in the west by the mountain ridge, in the east by flatter pasture areas, and in the North by a rocky area where no trees grow. Soil conditions are nearly homogeneous in the plot, with a poor development caused mainly by the steep slopes and limestone outcrops. The climate of the region is Atlantic, with annual temperature of 9.4 °C (mean, 1970–2009) and rainfall distributed throughout the year (1609 mm per year, mean 1970–2009). Snow is abundant from December up to early April.

From the early twenty century until now, the site has been used for extensive farming with seasonal occurrence of cattle *Box taurus* and goats *Capra hicus*. Additionally, red deer *Cervus elaphus* and wild boar *Sus scrofa* are abundant. Consumption and trampling of seedlings and saplings by these species have been detected at the study site, and all but *S. scrofa* browse also on leaves and buds from lower branches of adult and juvenile trees. No major logging event or fire has occurred in the study region, although some firewood collection has occurred sporadically. Other perturbations like slope effects or strong storms are less frequent at the site, although they are important in forest renewal because of the creation of gaps.

2.2. Plant species

We focused on the five most abundant tree species at the study site (Martínez et al., 2010); *I. aquifolium* (Aquifoliaceae, 73.1 stems/ha); *C. avellana* (Corylaceae, 66.2); *F. sylvatica* (Fagaceae, 28.4); *C. monogyna* (Rosaceae, 24.4); and *T. baccata* (Taxaceae, 20.9). Hereafter we will refer to these species by their genus name.

Crataegus, *Ilex* and *Corylus* are understory species, while *Fagus* and *Taxus* are late-successional, shade-tolerant species. *Crataegus*, *Ilex* and *Taxus* are fleshy-fruited trees (arils, not true fruits in the case of *Taxus*) whose seeds are dispersed during the autumn by migrant bird frugivores, almost exclusively thrushes (*Turdus* spp., Turdidae), (Snow and Snow, 1988; Martínez et al., 2008). In contrast, *Fagus* and *Corylus* produce large dry-fruits dispersed at first by barochory (i.e., by gravity), and after by dyszoochory as a result of caching rodents (mainly the wood mouse *Apodemus sylvaticus*, yellow-necked mouse *A. flavicollis*; both mouse species also prey upon dispersed seeds of the fleshy-fruited species). A comparative study on predators' preferences of seeds of fleshy-fruited trees in the field showed a selection order *Taxus* > *Ilex* > *Crataegus* (García et al., 2005). Nevertheless, seed predation on dry-fruited species is more intense (Martínez and González Taboada, 2009).

Almost all seeds of *Fagus* and *Corylus* germinate the same year they are dispersed, but seeds of *Ilex*, *Crataegus* and *Taxus* need up to 4 years of dormancy to complete embryo development (Hu, 1975; Beckett and Beckett, 1979; Thomas and Polwart, 2003). In addition, as mentioned above, herbivores could exert strong pressures on the following plant stages. Previous work demonstrated a predominance of small scale positive associations between adult individuals of different species in our study site (Martínez et al., 2010). Indeed, multi-species clumps up to 2.5 m in diameter and comprising a few individuals, frequently from *Ilex* and *Corylus*, were common in the study plot. See Martínez et al. (2010) for further details of the study plot, as well as for a detailed account of adult intra- and inter-specific spatial patterns of association between tree species. Finally, it is also interesting to note that these forests currently have a relict character in the Cantabrian range, and that some of the species are locally endangered (*Taxus* and *Ilex*) or declining (*Fagus*, Jump et al., 2006; Peñuelas et al., 2007).

2.3. Data collection

In May 2004, we established 105 fixed 0.5×0.5 m quadrats within the ~3 ha study stand (180 m × 170 m, Fig. 1) to evaluate seedling emergence and survival. Quadrats were located in all of the microhabitats present to include the different types of vegetation cover. This distribution ensured at the same time a good representation of different distance intervals among sampling quadrats and adult trees of each species. We distinguished among tree species and between female and male individuals in dioecious ones. Open gaps within the forest covered by herbaceous vegetation were also included. In the microhabitats corresponding to forest areas (i.e., different canopies), quadrats were located randomly near trees with $\geqslant$10 cm dbh, and spaced $\geqslant$5 m apart to reduce or eliminate canopy overlap among conspecific trees. For open microhabitats, quadrats were randomly selected but spaced >2 m apart to maximize spatial variation.

Quadrats were visited three times per season, and the presence of each emerged seedling was recorded and mapped to the nearest 1 cm. For each seedling, we recorded its survival in each successive survey during the sampling season. Seedling age was distinguished