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Site productivity overrides competition in explaining the disturbance–diversity relationship in riparian forests

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ABSTRACT

The intermediate-disturbance hypothesis (IDH) is frequently invoked to explain the high biodiversity of certain ecosystems and largely permeates forest management guidelines. Although this hypothesis assumes a trade-off between competitive ability and colonization capacities, the key role of competition is still controversial. Here we evaluate the contribution of competition in explaining species richness along a flooding-disturbance gradient in a riparian forest ecosystem, relative to other potential factors acting in combination with flooding disturbance, namely site productivity and water-mediated seed arrival.

Along a flooding-disturbance gradient across three riparian forests of north France, we assessed: (1) the disturbance–diversity relationship for forest herbs, (2) the intensity of competition using a phytometer transplant experiment, (3) the above-ground plant biomass in the herb layer, phytometer performances, and light intensity at the herb layer level, and (4) the contribution of the hydrochorous seed rain using mat traps and the emergence method. We built several candidate models to compare the relative importance of competition, site productivity, and water seed deposit on forest herb species richness.

We found a typical hump-backed relationship between flooding disturbance intensity/frequency and forest herb species richness. Competition intensity did not vary along this gradient and did not contribute to this relationship. Increasing site productivity (via soil resources and light availability) was associated with increasing forest herb species richness, irrespective of disturbance intensity/frequency. Species supply via the hydrochorous seed rain did not significantly contribute to the herb species richness despite a similar hump-backed pattern along the flooding gradient.

The hump-backed relationship between species richness and disturbance intensity/frequency observed in riparian forests can be explained without referring to competition. Instead, site productivity appears a more important factor, which acts in combination with physical disturbance and the likely resulting environment heterogeneity.

1. Introduction

The effects of disturbance on species diversity have been studied by ecologists for decades and disturbance is widely accepted as one of the main factors shaping ecological communities (Sousa, 1984; Hughes et al., 2007). Disturbance removes biomass, freeing up space and resources for other individuals to use, hence reducing establishment limitation (Grime et al., 1987). The influential intermediate-disturbance hypothesis (IDH; Connell, 1978) is frequently invoked to explain patterns of diversity along disturbance gradients (Shea et al., 2004 and references therein), including riparian zones (e.g., Salo et al., 1986; Biswas and Mallik, 2010). The IDH postulates a trade-off between competitive ability and colonization capacities: under high-intensity/frequency disturbances the better competitors and poorer colonizers cannot persist, whilst under low-intensity/frequency disturbances, the better competitors exclude the good colonizers; only at intermediate intensities/frequencies of disturbance can both types co-exist. Though the IDH largely permeates forest management guidelines (e.g. Hartshorn, 1995; Nebel et al., 2001), it remains highly controversial. The IDH is not one mechanism of coexistence, but rather a set of different mechanisms acting at various scales that share

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the same outcome: coexistence under intermediate disturbance (Roxburgh et al., 2004; Shea et al., 2004).

The disturbance–diversity relationship is closely related to the productivity–diversity relationship, productivity and disturbance producing opposite effects on the competitive outcome: higher site productivity favours superior competitors whilst higher disturbance levels favour inferior competitors (Grime, 1973; Kondoh, 2001). In temperate ecosystems, the productivity–diversity relationship is typically unimodal at a fine-grained scale (Grime, 1973; Waide et al., 1999; Fridley et al., 2012). The original explanation presumes a preponderant role for local environmental conditions and competition. Very few species can survive at very low site productivity levels, whilst competitive exclusion is thought to decrease species richness in very productive environments; therefore, diversity peaks at intermediate productivity, at which competition and environmental harshness are not too strong. Kondoh (2001) showed that the productivity level that maximizes species richness increases with increasing disturbance, and similarly the IDH-predicted peak of species richness moves to higher disturbance levels with increasing productivity. Although the relationship between disturbance, productivity and competition has been empirically explored (Campbell and Grime, 1992; Violle et al., 2010), the central role of competition is still controversial. It has been suggested, for example, stronger, rather than weaker competition may follow prolonged disturbance (Lenssen et al., 2004) and facilitation may promote coexistence at low and intermediate levels of disturbance (Michalet et al., 2006). The resource-ratio theory of plant competition predicts that competition intensity is constant along productivity gradients, but shifts from belowground competition for water and nutrients in unproductive habitats to aboveground competition for light in productive habitats (Tilman, 1988). More insight is thus needed about the actual importance of competition compared to productivity in structuring communities along disturbance gradients.

All these niche-based explanations have been recently challenged by dispersal-based assembly mechanisms. It has been argued that dispersal limitation may be more important than competition in shaping the unimodal productivity–diversity relationship (Myers and Harms, 2009; Xiao et al., 2010), due to the lack of dispersal syndromes in harsh conditions and small number of diaspores in productive conditions. Local species richness has indeed been shown to be generally limited by seed arrival across a wide range of plant communities in a recent meta-analysis (Myers and Harms, 2009). This study also revealed that the strength of the positive relationship between seed arrival and species richness is enhanced by disturbance. However, a seed addition experiment revealed that this positive relationship decreased as productivity increased in undisturbed plots, whilst in the presence of disturbance, seed addition led to a relatively constant increase in species richness independently from productivity (Foster, 2001).

In this study, we aim to assess the contribution of competition in shaping the disturbance–diversity relationship within herb communities of a riparian forest, relative to other confounding factors, namely site productivity and seed arrival.

Riparian ecosystems are particularly well suited for this purpose as they provide strong environmental gradients associated with topographic position (incl. lateral distance away from the riverbank and elevation above the lowest water level; Franz and Bazzaz, 1977; van Coller et al., 2000). These gradients represent changes in various environmental factors such as flooding intensity, frequency and duration, water availability, nutrient deposition, substrate, soil texture and depth (Franz and Bazzaz, 1977; Menges and Waller, 1983; Austin and Smith, 1989; van Coller et al., 2000). Close to the riverbank flood-induced recurrent disturbance is thought to limit diversity by preventing poor colonizers (i.e. recruitment-limited species) from establishing whilst towards the uplands the lack of flooding is believed to limit diversity by promoting competitive exclusion (Fig. 1); species richness peaks at intermediate levels of disturbance, hence at intermediate topographic levels within the floodplain (Naiman and Décamps, 1997; Budelsky and Galatowitsch, 2000; Decocq, 2002; Van Looy et al., 2003). The lateral gradient away from the riverbank also represents a gradient of hydrochorous seed rain intensity (e.g. Moggridge et al., 2009). Hydrochory, or dispersal of diaspores by water, acts as a secondary, facultative vector for many species, including incidental hydrochores *sensu* Merritt and Wohl (2006), and is an important factor structuring riparian plant communities (e.g. Schneider and Sharitz, 1986; Nilsson et al., 1991; Moggridge et al., 2009; Merritt et al., 2010).

We chose study sites where floods are periodic and of short duration and where the lateral position to the riverbank is a good surrogate of flooding intensity, frequency and duration (Menges and Waller, 1983) to test the following research hypotheses:

- H1: species richness of the herb layer follows the prediction of the IDH. If this is true, then species richness is the lowest on the frequently flooded riverbanks, peaks at intermediate elevation levels (upper terraces within the floodplain), and decreases above the riparian zone.
- H2: competition intensity is limited by disturbance severity close to the riverbank, increases with relative elevation being the strongest at upper topographic levels, and significantly explains species richness.
- H3: aboveground plant biomass is limited by site productivity which is low close to the riverbank (intense runoff of nutrients) and above the floodplain (no flood-mediated nutrient deposit, low light availability) but high at intermediate topographic levels and significantly explains species richness.
- H4: water-mediated seed deposition is low close to the riverbank (intense runoff) and above the floodplain (no flood-mediated seed deposit) but high at intermediate topographic levels and significantly explains species richness.

2. Methods

2.1. Study sites

The study was conducted in the forest of Hirson–Saint-Michel, located at the border between north France and Belgium (Fig. 2). This mostly deciduous forest covers approximately 6500 ha and is managed as a high forest. The climate is sub-oceanic with submountain influences. The substrate consists of primary schists and sandstones of the Gedinnian and Revinian periods, largely covered by loess on the plateaux. This forest includes several floodplains of the upper Oise watershed. Three of them were used in this study: those formed by the rivers Artoise, Gland and Oise. They consist of an alluvial channel, with bank material composed of sediments transported by the river. The three rivers are spring-fed permanent streams and exhibit a torrential regime with large floods after each episode of abundant precipitation, due to both the impermeable substrate and the difference in altitude between origin and confluence (ca. 80, 130, and 80 m for the Oise, the Gland, and the Artoise, respectively). For example, yearly flows of the Oise range typically from 1.6 to 10.5 $m^3 s^{-1}$ (see Electronic Appendix A for more details on the hydraulic features). Floods are periodic and of short duration: while the areas nearest to the river channel are typically flooded after each substantial rainfall episode, the upper part of the floodplain is flooded at least once a year during winter (December–February), less frequently in spring (March–May). The overall geomorphic pattern is of braided-anastomosed type (Gordon et al., 2004) but not active geomorphologically, hence with