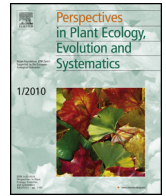




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Research article

Janzen–Connell patterns are not the result of Janzen–Connell process: Oak recruitment in temperate forests



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ABSTRACT

According to the Janzen–Connell hypothesis, seedling mortality is greater close to conspecific (or closely related) adult trees because of higher enemy pressure, ultimately increasing local tree-species diversity. However, this pattern (*i.e.* a decline of seedling performance close to conspecific or closely related adults) could also result from other processes: (1) heterospecific adults might positively affect seedlings; (2) conspecific (or closely related) adults might negatively affect seedlings by causing a deterioration of the microenvironment. We tested these hypotheses, accounting also for sizes of adults. We planted oak-seedlings in a temperate forest, characterized their adult neighbourhoods, measured 26 microenvironmental conditions, seedling mortality during one year, budburst and leaf herbivory. We detected Janzen–Connell-like patterns (frequent lack of budburst close to conspecific adults; high seedling mortality close to closely related adults) that were consistent with the Janzen–Connell process. However, these patterns were either counteracted by non-Janzen–Connell processes such as a favourable microenvironment or were weak with little explained variance. We detected Janzen–Connell-like patterns that were not consistent with the Janzen–Connell process: proximity to heterospecific adults *per se* decreased leaf herbivory partly due to microenvironmental effects, such that a lower leaf herbivory decreased seedling mortality. Overall, the spatial pattern of tree recruitment may resemble that predicted by Janzen–Connell but result from different processes: notably heterospecific adults creating refuges from enemies, facilitating the establishment of oaks below non-oaks without hindering their establishment below oaks.

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1. Introduction

A major challenge in community ecology is to understand mechanisms promoting species diversity in forests. Many mechanisms have been suggested (Wright, 2002), but the Janzen–Connell (JC) hypothesis (Connell, 1971; Janzen, 1970) remains widely used. According to the JC hypothesis, seedlings will suffer from proximity to conspecific adult trees (or closely related adults, see Liu et al., 2012) because of high pressure from specialized natural enemies. Seedlings of other species will thus be able to establish under the adult tree, thereby increasing species diversity of communities. The JC hypothesis has been confirmed multiple times in both trop-

ical (*e.g.* Bagchi et al., 2014; Clark and Clark, 1984; Comita et al., 2014) and temperate forests (*e.g.* Comita et al., 2014; Masaki and Nakashizuka, 2002; Packer and Clay, 2000; Seiwa et al., 2008) but does not always hold true and is still debated (Hyatt et al., 2003). One aspect that has been largely overlooked is that a JC pattern (*i.e.* a decline of seedlings close to conspecific or closely related adults) might also result from other processes: (1) heterospecific adults might positively affect seedlings (rather than negative effect of conspecific or closely related adults), and (2) conspecific (or closely related) adults might negatively affect seedlings by causing a deterioration of the microenvironment (rather than by increasing enemy pressure).

A JC pattern may result from a reduced enemy pressure close to heterospecific adults, rather than from an increased enemy pressure close to conspecific adults. An adult tree is a reservoir of specialized enemies, aggregating nearby the adult tree (Connell,

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1971; Janzen, 1970). Hence, a heterospecific adult attracts its own specialized enemies, which are not able to attack proximate focal seedlings due to a conservatism of biotic interactions (see Winkler and Mitter, 2008). Heterospecifics might even hinder the detection of focal seedlings by their enemies (Jactel et al., 2001). Heterospecific adults may thus represent a refuge for focal seedlings by decreasing enemy pressure, thereby improving seedling survival. Overall, a reduction of the enemy pressure close to heterospecific adults could be a non-JC process inducing a JC-like pattern, but with very different consequences: seedlings of focal species would establish below heterospecifics instead of heterospecifics below focal species (see also Rutten et al., 2016).

A JC pattern may also result from a deterioration of the microenvironment of seedlings by conspecific adults, or from an improvement of the microenvironment of seedlings by heterospecific adults. Adult trees might affect some or all of the following aspects of the microenvironment all influencing seedling survival: litter decomposition and chemistry, the physical structure of the microenvironment, and the microclimate and composition of the herbaceous layer. Moreover, the effect of adult trees on the microenvironment may be species-specific, resulting in a detrimental microenvironment under conspecific adult trees and in a beneficial microenvironment under heterospecific adult trees. This is often the case during ecological succession when a plant species improves the microenvironment for heterospecific seedlings and late-successional species profit from the microenvironments produced by early-successional species depending on repetitive disturbances. For instance, soil characteristics might differ between tree species due to the physical and chemical properties of their litter (Binkley, 1995). Different tree species might also differ in soil moisture because rain interception depends on species-specific tree characteristics (e.g. branch angle, bark type; Crockford and Richardson, 2000). Finally, evolutionarily distant adult trees might have a very different impact on their microenvironment compared to the focal species. For example, Gymnosperms produce less litterfall than Angiosperms, and also a more acidic litter hence resulting in a lower soil pH (Sariyildiz et al., 2005). The stemflow is also very low for Gymnosperms (Crockford and Richardson, 2000). If the impact of adult trees on their proximate microenvironment changed gradually with evolutionary position, the resulting effect on seedling survival may be more similar between a conspecific adult and a closely related than a distantly related adult. Overall, a deterioration of the microenvironment by conspecific (or closely related) adults, and an improvement of the microenvironment by heterospecific (or distantly related) adults could both be non-JC processes inducing a JC pattern.

The impact of a tree on proximate seedlings might be reinforced with the size of that tree. Larger adult trees have a larger crown and a larger root system, so they could accumulate more specialized enemies than smaller adults (see Packer and Clay, 2000; referring to Janzen, 1970). Moreover, larger adult trees are mostly older and have affected their microenvironment for a longer period, intensifying their specific microenvironmental conditions. Also, the impact of a large adult tree on proximate seedlings potentially extends over a greater spatial distance. Size may even impact seedlings more strongly than distance does. Overall, the visibility of a JC pattern might be reinforced with the size of the tree (see Packer and Clay, 2000; referring to Janzen, 1970), regardless of the process involved: the negative effect of a large conspecific adult may increase with the size of that tree, just as the positive effect of a heterospecific adult.

We tested the above hypotheses on alternative processes inducing a JC pattern, using oaks (*Quercus*) as study model, in a temperate forest. Natural regeneration of temperate forests is usually described as depending on light and thus on the creation of canopy gaps (about gap theory, see Yamamoto, 1992). Creation of canopy

gaps induces a gradient of light quality and hence of regeneration niches. Some of those niches will correspond to the high-light requirement of temperate oak trees, known to be relatively shade-intolerant (Ellenberg et al., 1992). We studied seedlings because it is at this stage that the JC signal has been described to be the strongest (Comita et al., 2014; Connell, 1971; Hyatt et al., 2003). We planted oak seedlings as phytometers in order to avoid bias due to local acclimatization or selection. We measured seedling mortality and processes controlling seedling mortality (budburst and leaf herbivory). Mortality decreases with physiological performance, and a core characteristic of performance in seedlings is budburst and particularly an early budburst (Augspurger, 2008; Besford et al., 1996; Seiwa, 1998), allowing photosynthesis and nutrient acquirement during the best light conditions, before the closure of the canopy. Mortality of seedlings also increases with leaf herbivory (Moles and Westoby, 2004; Wada et al., 2000) by removing photosynthetic tissues. Even low levels of herbivory may strongly increase seedling mortality given their small overall leaf area. Firstly, we tested the classical prediction of JC hypothesis, i.e. that proximity to conspecific adult tree increases seedling mortality, lack and delay of budburst and leaf herbivory. Secondly, we expanded the classical JC hypothesis to other aspects of adult neighbourhood by testing whether heterospecifics or distant relatives decrease seedling mortality, lack and delay of budburst and leaf herbivory, and whether size of trees reinforces the effect of distance or exerts an independent effect. Thirdly, we opened JC hypothesis to the microenvironment. We tested if adults affect litter decomposition and chemistry, physical structure of microenvironment, microclimate and composition of herbaceous layer, in order to estimate if previously identified effects of neighbourhood on seedlings are directly determined by the neighbourhood (potentially due to enemy pressure) or mediated by the microenvironment.

2. Material and methods

2.1. Site description

The study was conducted between 2013 and 2015 in the Forest of Rennes, Brittany, France (48°12' N, 1°33' W, ca. 90 m altitude), a semi-natural managed forest with oceanic climate, mean annual temperature of 11.3 °C and average annual rainfall of 836 mm. The soil is a brown-leached soil. This forest is composed of two parcel types dominated by either oak (*Quercus petraea* hybridizing with *Quercus robur*) and beech (*Fagus sylvatica*) or Scots pine (*Pinus sylvestris*) interspersed with other Angiosperms. The other main tree species in the overstorey are typical from European temperate oceanic lowland forests: *Ilex aquifolium*, *Castanea sativa*, *Sorbus torminalis*, *Abies alba* and *Carpinus betulus* (see Yguel et al., 2011 for further details). The herbaceous layer contained seedlings of different tree species: *Quercus* spp., *F. sylvatica*, *C. sativa*, *I. aquifolium*, *A. alba*, *P. sylvestris*; ferns predominantly *Pteridium aquilinum*; grasses mainly *Linum caeruleum*; other Angiosperms such as *Rubus* spp., *Hedera helix*, *Lonicera periclymenum*, and bryophytes.

Ten pairs of two adult oak-trees (ca. 60 years old) were selected within the forest (used by Yguel et al., 2011). Each pair had one tree in the more oak-dominated parcel and one in the more pine-dominated parcel, separated by distances of less than 150 m. Selecting adult oak-trees in both types of parcels ensured a large range of evolutionary distance between seedlings and their adult neighbours. Trees of the same pair were of the same oak species (*Q. petraea* or *Q. robur*, not strictly speaking distinct species are always partly hybridized; Yguel personal communication). This blocked design was essential to control for variation among pairs due to different macroenvironments or different sources of seedlings

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