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Pest damage in mixed forests: Disentangling the effects of neighbor identity, host density and host apparency at different spatial scales

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ABSTRACT

Mixed forests are thought to be less prone to pest insect damage than monocultures. This may result from reduced host availability (*i.e.*, density effect) or from non-host trees reducing the physical or chemical apparency of host trees (*i.e.*, associational resistance, AR). However, associational and density effects are often confounded in mixed forests. We aimed to disentangle their relative contribution to attacks of pine trees by a specialist pest, the pine processionary moth (PPM, Thaumetopoea pityocampa). We assessed pine infestation by PPM by counting the number of winter nests during three consecutive years along an experimental gradient of pine density in presence or absence of a fast growing species, namely birch. The total number of PPM nests per plot increased with pine density (maximum in high density monocultures), while the proportion of attacked pine trees decreased along the same gradient. Birch provided associational resistance via reduced pine apparency due to their greatest higher. This mechanism occurred at two spatial scales, whenever birch was planted within pine plots or in adjacent plots. Associational resistance was stronger in dense stands, probably due to reduced distance between pines and neighboring birches. But AR faded with time, pines becoming taller than birches, making density effects preeminent over apparency effects. Our findings suggest that mixing tree species to trigger resistance to pest insects requires taking into account the relative growth rate of associated species together with the relative proportion of associated species, both within and between stands.

1. Introduction

Pest insects and pathogens can compromise tree growth or survival, thus reducing the provisioning of associated ecosystem services (Boyd et al., 2013). In addition to higher productivity found in tree species-rich forests (Gamfeldt et al., 2013; Vilà et al., 2013), tree diversity has been shown to reduce pest damage (Jactel and Brockerhoff, 2007), suggesting associational resistance (AR) in mixed forests. AR occurs when a given plant suffers less damage from herbivores when growing with heterospecific neighbors than amongst conspecific plants (Tahvanainen and Root, 1972). In mixed forests, AR seems the most frequent tree diversity effect, as confirmed by meta-analyses (Castagneyrol et al., 2014a). However, this is still debated and recent studies found neutral effects of tree diversity (Plath et al., 2012) or even associational susceptibility (AS, Brown and Ewel, 1987; White and Whitham, 2000), *i.e.*, increased damage in tree mixtures as compared to monocultures (Haase et al., 2015; Schuldt et al., 2010).

For a given total tree density, mixing non-host trees with host trees leads to a reduction of the density of the latter. Pure associational effects are thus often confounded with host density effects in experiments manipulating tree diversity (Castagneyrol et al., 2013; Muiruri et al., 2015; Schuldt et al., 2012; but see Kim and Underwood, 2015; Underwood et al., 2014). A sound understanding of herbivory in mixed forests requires teasing these two mechanisms apart.

The host density effects involved in AR can operate through a reduction of herbivore density in mixed forests. The "resource concentration hypothesis" (Root, 1973) and its further developments (Hambäck and Englund, 2005) predict that the density of

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specialized herbivores should increase with host plant density (*i.e.*, absolute abundance) and frequency (*i.e.*, relative abundance) in a given vegetation patch, because specialists are more likely to immigrate to and less likely to emigrate from patches where host plants are more abundant (Hambäck et al., 2000; Underwood et al., 2014), which is the case in pure stands. However, within stands, pest abundance on individual trees may depend on absolute host density (Andersson et al., 2013; Hambäck and Englund, 2005), with more abundant hosts resulting in lower likelihood of individual trees being attacked (*i.e.*, dilution of attacks). Resource dilution may then have contrasting effects on the proportion of attacked trees *vs*. on the load of herbivores on each individual attacked tree.

For a given host density, the direction and intensity of pure associational effects depend on the specific composition of mixed stands (Castagneyrol et al., 2014a, 2014b). For instance, AR may be driven by the presence of non-host plants reducing host plant apparency (*i.e.*, affecting the probability of being found by herbivores (Feeny, 1976)). Association between host and non-host trees may disrupt or dilute the visual (Dulaurent et al., 2012; Finch et al., 2003; Finch and Collier, 2000) and chemical cues (Bruce and Pickett, 2011; Hambäck et al., 2000; Jactel et al., 2011) that herbivores use to locate and select their host trees. In addition, natural enemies (predators or parasitoids) are assumed to be more diverse and more abundant in mixed stands due to a greater diversity of alternative feeding resources, thus providing a better top-down regulation of herbivores in mixtures than in monocultures (Quayle et al., 2003; Riihimäki et al., 2005).

Density and pure associational effects are likely to be scale dependent. For instance, AR was shown more likely to occur in small patches of plant mixtures (Bommarco and Banks, 2003). This spatial effect could be due to the distance at which herbivores perceive their environment (Stutz et al., 2015; Vehviläinen and Koricheva, 2006). At long distance, resource density may be more important for herbivores relying on chemical cues to locate their host, while herbivores using visual or contact cues may be more sensitive to patch size. At short distance however, all cues might be used and herbivores should respond to diversity irrespective of host patch size (Andersson et al., 2013). However these spatial changes have been rarely studied in forests, due to the lack of proper herbivory surveys in spatially explicit experiments.

The pine processionary moth (PPM, *Thaumetopoea pityocampa*, Denis and Schiff.) is the main pine defoliator in southern Europe and northern Africa (Battisti et al., 2005). It is an oligophagous insect, feeding mainly on pine species (*Pinus*). According to the AR hypothesis, monocultures of pines are expected to be more vulnerable to PPM than mixed stands of pines and deciduous trees (Jactel et al., 2015). More specifically, Castagneyrol et al. (2014b) showed that although tree species richness *per se* had no effect on PPM infestation, the composition of mixed pine plots was a key driver of resistance to PPM, AR being significant only in pine - birch mixtures. A likely mechanism was the reduction of pine apparency by this fast growing broadleaved species. Yet, the study did not disentangle the relative effects of pine density and composition of mixed stands.

The objective of the present study was to address this issue and investigate the effects of pine apparency at two spatial scales. We specifically tested the following hypotheses: (**1**) Pure associational resistance to PPM in mixed pine stands is mainly driven by reduced pine apparency; (**2**) Pine apparency toward PPM is reduced by the presence of taller neighboring trees but also by taller neighboring stands; (**3**) Pure associational resistance effects are counterbalanced by effects of pine density, with PPM attacks affecting a larger proportion of pines in mixed stands where pines are less abundant.

2. Materials and methods

2.1. The ORPHEE experiment

The ORPHEE experiment belongs to the worldwide Tree Diversity Network (TreeDivNet). It is located 40 km south of Bordeaux (France) and was established in 2008 on a 12 ha clear cut of maritime pine stands. In total, 25,600 trees belonging to five species were planted (European birch: *Betula pendula*, Roth; Pedunculate oak: *Quercus robur*, Linne; Pyrenean oak: *Q. pyrenaica*, Willdenow; Holm oak: *Q. ilex*, Linne; and Maritime pine: *Pinus pinaster*, Aiton). These common five species are native and can naturally co-occur in forests in southwestern France.

Eight blocks were established with 32 plots in every block corresponding to the 31 possible combinations of 1–5 species, with an additional replicate of the combination of the five species. In particular 17 species combinations contain pines, either alone, or in

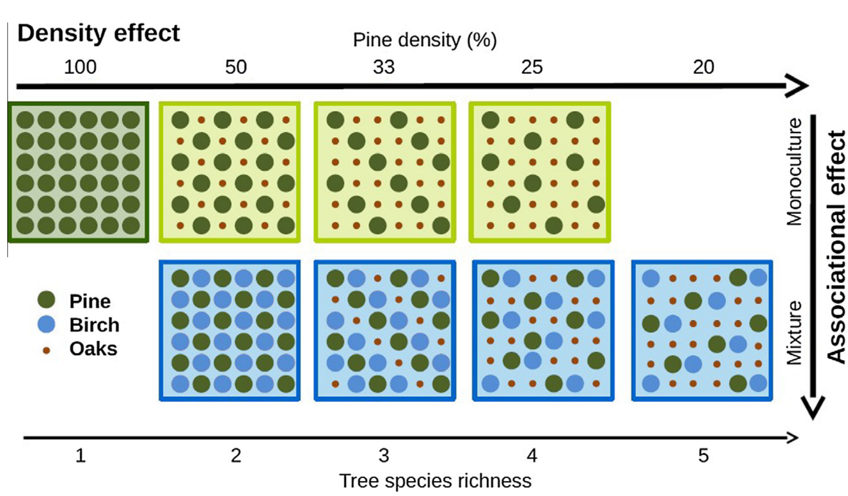

Fig. 1. Conceptual diagram representing how tree diversity can be decomposed into density and associational effects in the ORPHEE experiment. The diameter of dots reflects mean tree species height. The *pure associational* effect was tested comparing monocultures and pine-birch mixtures (blue squares) while controlling pine density The effect of *pine density* was tested for pine-birch mixtures and for monocultures, using high-density pine monoculture (dark green square) and different low density monocultures corresponding to mixtures of pine with increasing number of oak species (light green squares). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)