

Emergent properties arising from spatial heterogeneity influence fungal community dynamics

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ABSTRACT

Community dynamics are mediated by species interactions, and within communities spatial heterogeneity and intransitive relationships promote coexistence. However, few experimental studies have assessed effects of heterogeneity on the interactions of competing individuals. Wood decay basidiomycete fungi are ideal for studying community structure and dynamics because they are easy to manipulate in laboratory microcosms, and communities resolve themselves rapidly. Most studies have only used simplistic pair-wise interactions in a 2-D plane, but here we investigate a three-species community in an environmentally realistic novel 3-dimensional system. We show how spatial heterogeneity and patch size dynamics are important for coexistence, and how competitive interactions change over different spatial dimensions. Emergent properties arose with increased spatial heterogeneity: the weakest competitor co-occurred with the community when its territory was less fragmented, and interactions became intransitive.

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1. Introduction

Spatial variation in natural ecosystems affects all aspects of ecology from the level of individual behaviour, to whole population and community dynamics (Holmes et al., 1994). Since interactions between individuals of a community play a pivotal role in shaping the structure of the community, understanding interactions in the context of spatial variation is critical to explaining community development and its contribution to the functioning of the wider ecosystem.

Spatial heterogeneity promotes coexistence by providing spatial refuges and reducing the encounter rate of individuals, hence reducing the risk of attack (Huffaker, 1958; Brockhurst et al., 2005). The classical study by Luckinbill (1973) demonstrated that the

unstable interaction between *Didinium nasutum* and *Paramecium aurelia* (where *P. aurelia* is driven to extinction by *D. nasutum*) was stabilised and coexistence occurred following an increase in viscosity of culture medium. More recently, theoretical models have predicted that the spatial distribution of individuals affects community stability such that greater dispersion of species will result in greater niche partitioning, which promotes coexistence over evolutionary time (Wang et al., 2015). Additionally, long-term investigations of habitat fragmentation show that patchiness has drastic negative effects on biodiversity (Lovejoy et al., 1986; Laurance et al., 2011). Little experimental work, however, has been conducted on the combined effects of spatial variability and patch size or quality on species interaction stabilisation (Daugherty, 2011).

Antagonism (interference competition; often called combat with fungi) between coexisting saprotrophic fungi causes spatial patterning of communities during decomposition (Hiscox et al., 2016b). During this process, wood decay fungi compete with one another in 3-dimensional space for resources whilst maintaining distinct individual territories (even different individuals of the

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same species do not merge). This system is ideal for studying community dynamics as the location of the decay fungi can be determined simply by culturing (Hiscox et al., 2017), and different spatial arrangements can be easily prepared and communities become resolved after a few months. Interference competition (combat) may result in deadlock (neither fungus gains territory held by another fungus), replacement (one fungus gains the territory held by another), partial replacement (one fungus partially gains territory of another) or even mutual replacement (both fungi partially gain territory held by the other) (Boddy, 2000). A hierarchy of combative ability is usually exhibited between specific species combinations where the K-selected characteristics of later stage resource colonisers frequently lend them greater competitive fitness than the earlier resource colonisers (Boddy, 2000), but interactions are sometimes intransitive and can alter depending on different environmental conditions (Woodward and Boddy, 2008).

Intransitivity is a key mechanism in maintaining species coexistence and biodiversity by satisfying an interaction relationship similar to that in a game of 'rock-paper-scissors' (Kerr et al., 2002; Reichenbach et al., 2007). Intransitive interactions often occur in species-rich communities and result in the survival of combatively weaker individuals (Gallien et al., 2017; Maynard et al., 2017a). A study which paired 18 basidiomycetes against each other to investigate the structure of their competitive network, found that diverse communities with high intransitivity showed a positive diversity-function relationship (Maynard et al., 2017b), which in the real world would translate to decomposition processes and carbon cycling.

Fungal community dynamics have been well studied in the past (Caruso et al., 2012; Hannula et al., 2013; Hiscox et al., 2015a; Persoh, 2015; Arnstadt et al., 2016; Van Der Wal et al., 2016), with some attention given to the effects of spatial patterns and individual patch size on interaction outcomes (White et al., 1998; Sturrock et al., 2002; Hiscox et al., 2017). All of these studies, however, have been conducted across essentially a 2-dimensional plane, yet in the real world decomposer communities operate in heterogeneous, 3-dimensional space, and at larger scales emergent properties may arise (Halley et al., 1996). The aim of the present study was to test the effect of spatial heterogeneity and patch size on community interactions in 3-dimensional space, and to determine the effect of such spatial variability on the ecosystem service provided by the community, namely resource decay rate. The decay of dead wood by fungi is crucial to forest ecosystem function and is pivotal to soil biogeochemical processes such as carbon cycling and nutrient release (Eriksson et al., 1990). The rate of decomposition, therefore, has been used as an indicator of fungal productivity and ecosystem service (Hiscox et al., 2015b, 2016a). Individuals compete for territory changing the structure of the community, different species cause different rates of decay and the interaction process itself can alter decay rate (Hiscox et al., 2016a), thus competition causes changes to the rate of wood decay and carbon and nutrient release in forest ecosystems.

Using wood-decay basidiomycetes as experimental organisms, the outcomes of multiple species competitive interactions were tested in both 2- and 3-dimensional systems. The effect of (1) the orientation of woody vessels (an aspect of resource structural complexity), (2) patch size and (3) spatial patterns on species interactions and decay rate were investigated, and the following hypotheses tested: (1) substratum orientation causes combative strength to change; (2) patch fragmentation negatively affects an individual's competitive success; and (3) spatial heterogeneity in a three-species community causes changes to the ecosystem function, in this case wood decay, provided by the community compared to dual-species competitive systems.

2. Methods

2.1. Fungal strains

Three fungal species were selected based on their ecological roles and successional order in the natural environment: a primary resource coloniser (*Stereum gausapatum*), and two early secondary colonisers (*Stereum hirsutum* and *Trametes versicolor*) (Supplementary Table 1). Specific strains were chosen based on their expected combative hierarchy: *T. versicolor* > *S. hirsutum* > *S. gausapatum* (Hiscox et al., 2015a, 2015b, 2016b).

2.2. Experimental design

Interactions were performed by combining precolonised wood blocks (three species, one per block) with different levels of complexity (Fig. 1): (1) 2 wood blocks; (2) 3 wood blocks; (3) a 3×3 (i.e. 9) matrix of blocks; (4) a $3 \times 3 \times 3$ (i.e. 27) matrix of blocks. (1) With pairs of blocks, all combinations of the three species were made, i.e. 3 combinations. (2) With triplicates, all three combinations of three species were made, each with a different species in the middle. (3) In the nine block matrix arrangement, 3 blocks precolonised with each species were arranged with the constraint

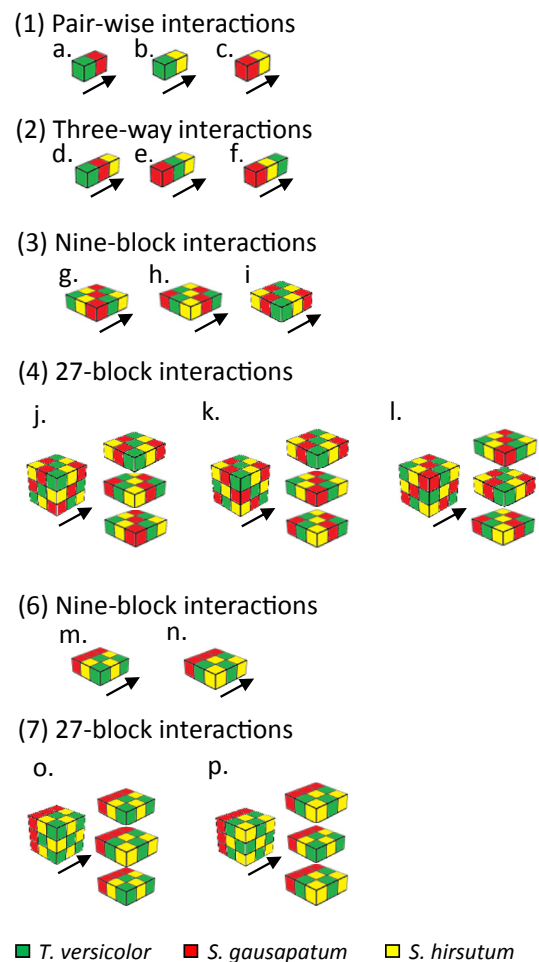


Fig. 1. Spatial distribution of species within the experimental design. Blocks coloured red indicate *S. gausapatum*, green indicates *T. versicolor* and yellow blocks are indicative of *S. hirsutum*. Dispersal patterns of nine-way and 27-block interactions were arranged such that blocks containing the same species do not have adjacent faces. Arrows indicate xylem directional flow.

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