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Aligning spatial ecological theory with the study of clonal organisms: the case of fungal coexistence

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ABSTRACT

Established ecological theory has focused on unitary organisms, and thus its concepts have matured into a form that often hinders rather than facilitates the ecological study of modular organisms. Here, we use the example of filamentous fungi to develop concepts that enable integration of non-unitary (modular) organisms into the established community ecology theory, with particular focus on its spatial aspects. In doing so, we provide a link between fungal community ecology and modern coexistence theory (MCT). We first show how community processes and predictions made by MCT can be used to define meaningful scales in fungal ecology. This leads to the novel concept of the unit of community interactions (UCI), a promising conceptual tool for applying MCT to communities of modular organisms with indeterminate clonal growth and hierarchical individuality. We outline plausible coexistence mechanisms structuring fungal communities, and show at what spatial scales and in what habitats they are most likely to act. We end by describing challenges and opportunities for empirical and theoretical research in fungal competitive coexistence.

Key words: modular organisms, clonal growth, fungal competition, fungal community ecology, modern coexistence theory, metacommunity, intransitive coexistence, competition–colonisation trade-off, growth–density covariance, spatial storage effect.

CONTENTS

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I. INTRODUCTION

From the perspective of ecological dynamics in space, it is useful to divide organisms into two groups: unitary and modular. The former is represented by motile animals, single-celled microbes, and non-clonal plants. Although all plants are modular from a morphological standpoint, we focus here on ecological interactions in space. Thus, the *ecologically modular* organisms include a range of life forms such as coral polyps, colonial bryozoans, slime molds, clonal plants, colonial Prokaryota (e.g. Actinobacteria; Wink, Mohmmadipanah & Hamedi, 2017) and most notably, filamentous fungi (Booth, 2014; Pringle & Taylor, 2002). We argue that mainstream ecological theory has focused on unitary organisms and that its concepts often hinder the inclusion of ecologically modular life forms. The most obvious example is the clear dichotomy between individual and population, which is central to population and community ecology and yet difficult to apply to ecologically modular organisms. However, there are further, less-obvious examples of conceptual obstacles, including the common understanding of reproduction or the definition of growth, movement and dispersal (Bielčik *et al.*, 2019; Chaudhary *et al.*, 2022; Pringle & Taylor, 2002). Here, we develop a conceptual framework which allows translation of features of modular biology and ecology into existing ecological theory. The central theoretical topic is spatial competitive coexistence (Amarasekare, 2003; Chesson, 2000*a*), but the concept is applicable to other areas of spatial ecology. As a model life form, we chose to focus on one of the most abundant and intensively studied forms of ecologically modular organisms: filamentous fungi.

Due to their roles in organic matter decomposition, soil carbon storage and plant symbiosis, filamentous fungi are of great importance in all terrestrial ecosystems. The question of fungal coexistence is thus not only interesting in itself, as a precursor to our understanding of community dynamics in ecologically modular organisms but is also relevant to challenges of the Anthropocene. Understanding the mechanisms that maintain fungal biodiversity is essential to make predictions about the impacts of global change factors acting at different spatial and temporal scales, and to improve our mitigation and conservation capabilities (Catford, Bode & Tilman, 2018; Godoy, 2019; Valladares *et al.*, 2015).

The importance of spatial properties of the environment has been documented in fungi for diverse scales (Boddy, 1999; Held *et al.*, 2009; O'Leary *et al.*, 2020). Yet it remains unknown exactly which spatial processes drive persistence or decline of fungal biodiversity. As a way forward, in line with Peay (2014), we argue for theory-driven, mechanism-focused research on fungal communities, which we believe has potential to bridge the gap between reductionist and holistic approaches in microbial ecology (as described in Tecon *et al.*, 2019). Our focus on spatial aspects of modern coexistence theory (MCT) enables us to tackle two interrelated problems of fungal ecology. First, it enables us to delineate the meaningful spatial scales on which research should focus (Dini-Andreote *et al.*, 2021; Nemergut *et al.*, 2013). Second, it enables us to address the challenges posed by implementing theory developed largely for unitary

organisms into the realm of modular organisms (Booth, 2014; Ma *et al.*, 2016; Pringle & Taylor, 2002).

The network-like bodies of filamentous fungi and spatial complexities of their habitats cause each mycelium to interact with others on multiple spatial scales simultaneously, from microscopic hyphal tips to macroscopic mycelia (see Table 1 for glossary) (Bielčik *et al.*, 2019; Boddy, 2000; Hanson *et al.*, 2006). Moreover, many empirical approaches in MCT require measurements of population dynamics over multiple generations (Godwin, Chang & Cardinale, 2020; Siepielski & McPeek, 2010). In filamentous fungi, the distinction between an individual and its population is not clear, nor is the definition of the temporal scale of a generation (Booth, 2014). Therefore, we begin by showing how MCT can be employed in identifying the relevant spatial scale and the level of biological organisation practical for a given study (Pringle & Taylor, 2002). In doing so, we introduce the concept of unit of community interaction (UCI) as a practical surrogate for the concept of individuality.

Following this, we introduce pertinent spatial coexistence mechanisms, show under what circumstances they can drive fungal coexistence, and what spatial scales and UCIs are practical to follow for each mechanism. In accordance with established theory, we organise spatial coexistence

Table 1. Glossary.

Clonal subsidizing	Ability of a physiologically integrated genet to support ramets that grow under less-favourable conditions (e.g. lower nutrient availability, higher competitive pressure).
Competitive coexistence	In the context of modern coexistence theory, the term 'coexistence' has a narrower meaning than in the current ecological literature. In the broader ecological literature, the term can be used to describe the coexistence of, for example, prey and predators, hosts and parasites, or humans and wildlife. In modern coexistence theory, the term refers to competitive coexistence: the coexistence of ecologically similar species that compete for resources without competitively displacing each other.
Competitive rankings and intransitive competition	This refers to competitive hierarchies between ecologically similar species. Competitive ranking is often expressed by arrows, e.g., pointing from species A that outcompetes species B (A → B). It is important to note that competitive rankings are context dependent. They can be reversed if, for example, the environment changes (from A → B, to A ← B). In communities with three or more species, competitive rankings can be transitive (i.e. hierarchical), where species A is competitively dominant over both B and C (A → B → C ← A), or intransitive (non-hierarchical), where species A outcompetes species B but is outcompeted by species C (A → B → C → A).
Competitively homogeneous and competitively heterogeneous environment	This describes the relationship between competitive rankings of species and space. The environment is competitively homogeneous if competitive rankings remain the same throughout the area. That is, species 1 is a superior competitor of species 2 throughout the area, even if abiotic and biotic heterogeneities are present (but not in a quality or quantity that alters the competitive ranking). If environmental heterogeneities change the competitive ranking within the area, the area is competitively heterogeneous.
Hierarchical individuality	This describes life forms where the distinction between individual and population is not clear. Instead, multiple levels of organisation of the organism can be described as an individual (e.g. ramets and genets).
Hypha, hyphal tip	The hypha is the basic cellular unit of the morphology of filamentous fungi. It grows (elongates) at its end, called the hyphal tip. It has the shape of a long, branched thread.
Indeterminate clonal growth	A property of ecologically modular organisms, this refers to the ability to spread into adjacent favourable habitat in the form of a physiologically integrated genet, spatially constrained only by habitat availability.
Mutual invasibility	In the context of modern coexistence theory, the term (mutual) invasibility has a different meaning than in invasion biology. It refers to the key condition of species coexistence: as the population size of a species decreases, that species will experience reduced competition from conspecifics. If competition from heterospecifics is lower due to lower niche overlap, overall competition decreases and the species experiences population growth. Thus, when a small number of individuals are added to the equilibrium state of a population or community of competing species, the new species can invade it, i.e. reproduce and coexist. This scenario must apply in a mutual manner to all species in the community if they are to coexist.
Mycelial cord, mycelium	A mycelium is the collection of interconnected hyphae that form a single organism, i.e. a body of a filamentous fungus. Mycelia may have the character of a simple network of microscopic hyphae. In some species, intertwined aggregations of hyphae may form pseudo-organs. An example of this is mycelial cords, which are elongated, often macroscopic structures formed by a parallel alignment of multiple hyphae. Through their growth, mycelial cords can seek out and colonize new resource units.
Mycelial interference	Interference competition is manifested as a direct, aggressive behaviour between competing individuals. In fungi, it occurs at the level of entire mycelia. Mycelia can interfere with each other by producing chemical agents or morphological structures designed to harm or protect against the competitor.
Mycophagous bacteria	Species of bacteria able to feed on living fungal mycelia.
Propagule	A life stage dedicated to dispersal to new habitats. A typical example is a plant seed or hyphal spore. In organisms with clonal growth, elongated growing structures (e.g. mycelial cords) can also play the role of a propagule.
Source-sink dispersal	In competitively heterogeneous habitats, species can maintain continuous dispersal from a favourable area (i.e. the source population) to an unfavourable area. Without this continuous dispersal from the source, the local population in the unfavourable area (i.e. the sink population) would go extinct.

mechanisms into two major blocks (Amarasekare, 2003): those which can function in a competitively homogeneous environment, and those which require environmental heterogeneity. The former are colonisation-related trade-offs and intransitive coexistence (Amarasekare, 2003; Barabás, D'Andrea & Stump, 2018; Kerr *et al.*, 2002). The latter are spatial storage effect and growth–density covariance (Barabás *et al.*, 2018; Chesson, 2000*a*). Even though intransitive coexistence currently stands outside the MCT framework, we argue that no account on fungal coexistence can be complete without it. Each section on a particular coexistence mechanism ends with a subsection on where to look for it. This contains the likely spatial scales at which a given mechanism operates and the UCIs involved. We consider our selection of coexistence mechanisms sufficient to demonstrate conceptual principles, and to serve as a bridge between MCT and fungal community ecology. We do not discuss the coexistence mechanisms of heteromyopia and spatial relative non-linearity in order to prevent overly speculative discussion, given the insufficient state of knowledge relating to these mechanisms in fungi (Amarasekare, 2003; Chesson, 2000*a*; Murrell & Law, 2002). In the last section, we outline knowledge gaps and perspectives for both empirical and theoretical research, focusing on natural history and experimental approaches in fungal competition and coexistence (Peay, 2014).

We hope to achieve two interrelated goals in our review. In addition to conceptual developments around the UCI concept, we also hope to provide fungal ecologists with an accessible bridge to the MCT framework. In explaining modern coexistence theory, there is a trade-off between intuitive language and language that is faithful to the mathematical foundations of MCT. Given our second goal to introduce coexistence theory to (fungal) ecologists and to motivate cross-talk between MCT and the ecology of modular organisms, we tend to use intuitive language. For explanations of coexistence mechanisms more directly linked to the mathematical models of coexistence, we recommend Amarasekare (2003) and Barabás *et al.* (2018). For application of MCT in empirical studies, we recommend Ellner *et al.* (2019), Grainger, Levine & Gilbert (2019*b*), and Godwin *et al.* (2020). Finally, Grainger *et al.* (2021) provide help navigating the theory for empirical ecologists.

Unlike previous work that concentrated on fungal symbionts of plants (Kennedy, 2010), we focus on the saprobic guild of filamentous fungi since more is known about the nature of their competition, growth, dispersal, and interactions with environmental heterogeneities (Peay, Kennedy & Bruns, 2008). In addition, the problem of coexistence in symbionts is likely more complex due to sophisticated interactions with the host, and different community interactions within and outside of the host (Bogar *et al.*, 2019; Kummel & Salant, 2006; Valyi *et al.*, 2016). Yet, some aspects of our review are relevant to symbiotic species, and we use empirical knowledge on these whenever relevant.

Finally, it is important to note that the list of potential coexistence mechanisms in filamentous fungi and other ecologically modular organisms presented here is not exhaustive. For example, we have not considered mechanisms related to resource partitioning or temporal niche partitioning (e.g. the temporal storage effect) (Chesson, 2000*b*). While these mechanisms likely play an important role in the coexistence of ecological communities, we focus on the spatial aspects of coexistence. It is alongside the spatial niche dimension where the modular organisation and multi-scale interactions of fungi pose the most challenges (Chaudhary *et al.*, 2022; Valyi *et al.*, 2016). And it is in the spatial niche dimension where we see the most potential to advance the discussion of fungal fitness and individuality, and to align this discussion with the requirements of community ecology research (Booth, 2014; Lakovic & Rillig, 2022; Pringle & Taylor, 2002).

II. SPATIAL AND BIOLOGICAL SCALES

(1) General overview

A frequent problem of microbial ecology is a tendency for arbitrary approaches to space and spatial scales (Dini-Andreote *et al.*, 2021). There is a growing recognition of the need for, and the difficulty of defining a meaningful spatial scale (Dini-Andreote *et al.*, 2021; Ladau & Eloe-Fadrosh, 2019; Mony *et al.*, 2020). Specifically for fungi, complex life histories, network-like bodies and hierarchical individuality can make application of even elementary spatial concepts difficult (Booth, 2014; Pringle & Taylor, 2002; Valyi *et al.*, 2016). Thus, the possibility of using MCT to delineate the relevant spatial scale and level of biological organisation in fungal mycelium (hereafter biological scale) is of great interest. For dispersal, we always use its broad definition, as movement that drives spatial population dynamics within the current or into new habitat patches (Schlägel *et al.*, 2020). In fungi, dispersal can include mycelial outgrowth (Bielčik *et al.*, 2019; Boddy *et al.*, 2009; Chaudhary *et al.*, 2022).

(2) Meaningful spatial scale

Here, we show that meaningful spatial scale can be the one at which a given community process is expected to take place. For instance, for intransitive coexistence (see Section III.3) driven by mycelial interference (see Table 1) (Hiscox *et al.*, 2017; Maynard *et al.*, 2017), the focal spatial scale covers local neighbourhoods of interfering mycelia. In Euclidian space, the extent of this scale will differ based on the size of mycelia and range of interactions (which may differ from the mycelium size if the competition is at a distance) (Evans *et al.*, 2008).

Similarly, for coexistence mechanisms in metacommunities, the meaningful scales will be local and regional (Amarasekare, 2003; Shoemaker & Melbourne, 2016). Here, not only the Euclidian extent of scales varies, but also the definition of local and regional will depend on a particular coexistence mechanism (or metacommunity model to which the

mechanism refers). In coexistence mechanisms related to the metacommunity model of patch dynamics (e.g. competition–colonisation trade-off), a particular habitat patch equals locality, and the assemblage of separated patches represents the region (see Section III).

For coexistence mechanisms related to the metacommunity model of species sorting (e.g. spatial storage effect), locality can be either an isolated patch, or not isolated area (see Section IV) (Fournier *et al.*, 2017; Melbourne *et al.*, 2007; Shoemaker & Melbourne, 2016). Whether the locality is isolated or not, it must extend over the space in which the environmental conditions remain favourable for the focal species i.e. competitive rankings are unchanged (Amarasekare, 2003; see Table 1), and that is large enough for the dispersal not to prevent aggregation of individuals in their favoured locality (Amarasekare, 2003; Chesson, 2000*a*; Snyder, 2008). Hence, local and regional are defined by the processes of interest and species traits (e.g. size, dispersal range) (see Section IV).

Based on this, we briefly outline for soil habitats (see also Ritz & Young, 2004) the role of spatial coexistence processes on the Euclidian microscale, a topic gaining considerable attention in fungal ecology. First, microstructure properties can contribute to habitat connectivity (see Section III) influencing dispersal between two patches (Falconer *et al.*, 2012; Kravchenko *et al.*, 2011). Second, we speculate that they can act as environmental variables in heterogeneous environments: if species are adapted to different microstructures and the belowground areas differ in microstructural properties, each species can have a competitive advantage in a different locality. Our speculation is based on current research on micro-environments (Aleklett *et al.*, 2021; Fukuda *et al.*, 2021; Hanson *et al.*, 2006; Held, Edwards & Nicolau, 2008; Held *et al.*, 2009; Hopke *et al.*, 2021), which additionally identified species-specific responses (traits) in navigating microstructures (Aleklett *et al.*, 2021; Fukuda *et al.*, 2021; Held *et al.*, 2009; Hopke *et al.*, 2021).

(3) Meaningful biological scale: concept of unit of community interactions

The concepts used by MCT (e.g. individual, propagule, population growth) fit better to unitary organisms than to networked mycelia with hierarchical individuality, indeterminate growth and convoluted life histories (Booth, 2014; Pringle & Taylor, 2002). For instance, operational definitions of fitness and population growth in MCT are often based on quantifying the number of discrete propagules produced per individual and established new individuals that share common anatomical and physiological characteristics (e.g. seeds, established seedlings) (Adler, Ellner & Levine, 2010; Angert *et al.*, 2009; Godoy, Kraft & Levine, 2014). However, this definition of fitness is problematic in fungi, as they can reproduce and disperse *via* anatomically and physiologically diverse structures such as spores, mycelial fragments, growing mycelium or even as symbiotic life stages (e.g. pre-colonised wood) (Bielčik *et al.*, 2019; Chaudhary *et al.*, 2022; Ortiz-Urquiza, 2021; Pringle & Taylor, 2002; Song *et al.*, 2017). Thus, even though the MCT has potential to increase mechanistic understanding of community assembly and biodiversity persistence, the task of applying MCT to fungi can become troublesome to unfeasible because it is being framed using definitions restrictive to unitary organisms. In order to simplify this task, we propose a broader and universally applicable concept termed 'unit of community interactions' (UCI), analogous to Booth's unit of selection (Booth, 2014), or to unit of reproduction (Ma *et al.*, 2016). This concept allows for the operational definition of community assembly agents (units). UCIs are defined based primarily on their role in community processes, rather than on physiological, structural, or developmental details of an ecologically modular organism and its segments, (pseudo)organs and tissues. That is, rather than focusing on how the fungus is organised biologically (e.g. hyphal segment *versus* spore, symbiotic phase *versus* free-living), the UCI concept highlights what role particular segments or biological scales play in a particular community process or coexistence mechanism, and thus enables a comparison of fitness between fungal competitors with different life-history strategies. For instance, in defining UCIs it is of primary interest whether the dispersal is local or regional. It is secondary or irrelevant if the dispersal is by spore, mycelial outgrowth, or another life-history stage (Boddy *et al.*, 2009; Chaudhary *et al.*, 2022). Similarly, a mycelium can be defined as a single UCI, or as a population of lower-level UCIs. Crucially, the choice depends less on the degree of physiological integration within the mycelium than on the coexistence mechanism on which the researcher aims to focus (but see the example below). In a research design, UCIs are meant to serve as a tractable, simplifying substitute for the individuals and propagules of MCT. We first provide a glimpse of the concept's usefulness by using an example, then provide the definition, followed by our reasoning behind the definition.

Let us say a researcher aims to model the coexistence of wood-decomposing species, driven by a competition–colonisation trade-off among wood logs across a given area (i.e. among patches) (Amarasekare, 2003; Boddy *et al.*, 2009; Levins & Culver, 1971). Some mycelia may extend between multiple wood blocks (Bebber *et al.*, 2007; Boddy *et al.*, 2009; Boddy, 1999). Using the concept of the individual and quantifying its fitness is challenging as mycelia can remain physiologically integrated (i.e. contiguous mycelia) across all wood blocks (Booth, 2014; Simonin *et al.*, 2012) (Fig. 1A). In other words, an 'individual' can be present in two different patches (and local communities) at the same time, a situation that hinders the applicability of MCT, as there is no concept or framework within MCT that could accommodate this situation. The problem can be easily solved if we shift the focus from biological individuals to UCIs. Applying the concept of UCI in the context of a competition–colonisation trade-off, the mycelium in each patch is perceived as a separate UCI regardless of the physiological integration (Fig. 1B,D), and mycelial cords (see Table 1) spreading from a parental patch are regarded as a form of highly competitive propagule-type UCI (Kennedy *et al.*, 2011) (Fig. 1C). Thus, the degree of

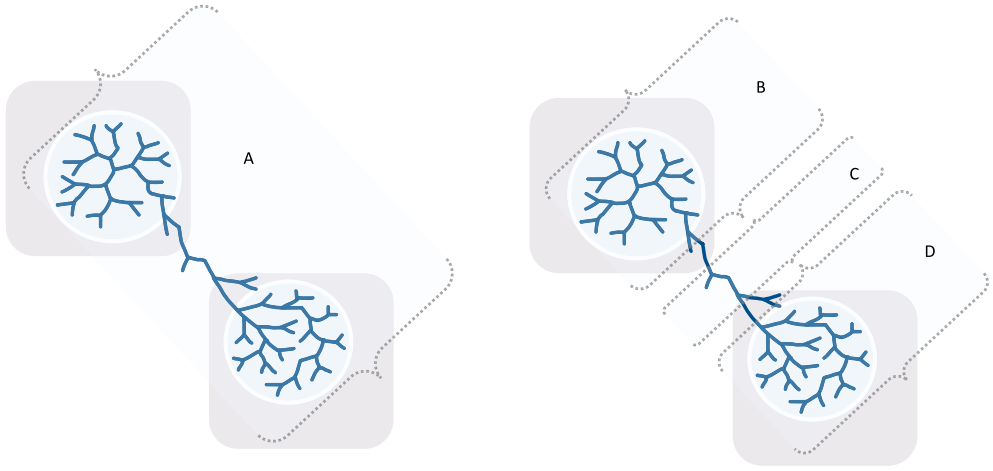

Fig. 1. Concept of unit of community interaction (UCI) in modular organisms, illustrated for the example of a patch dynamics model in fungi. Patches are depicted as rectangles, mycelia and mycelial cords as pale blue circles and blue lines, respectively. From a biological perspective (A), the entire physiologically integrated modular organism is a single unit (an individual). This remains the case also if it spreads between multiple resource patches. Within the framework of coexistence in competitive metacommunities, it is useful to distinguish (regardless of the physiological integration) between adult-like UCIs (B and D) and propagule-like UCIs (C), i.e. mycelia in local patches and mycelial cords dispersing between patches, respectively.

physiological integration matters in a manner analogous to the degree of investment by a parental plant into a single seed (Levine & Rees, 2002).

By introducing the UCI concept, instead of attempting to fit the complexities of fungal organisation into the concepts and mechanisms developed largely by studying unitary organisms, we show that the mechanisms of coexistence can be utilised to define operationally the organisational units of interest. In other words, the meaningful biological scale becomes the one at which important community processes or coexistence mechanisms are hypothesised to act.

We define UCI as: (*i*) a physiologically integrated entity (propagule, segment or a whole organism), (*ii*) whose growth influences (and can be influenced by) its external competitive environment, and (*iii*) and has the capacity to either produce, or to act as agent(s) of dispersal. This capacity is defined as having both the pluripotency, and available biomass/resources. Necessary biomass (energy) can be either contained within the structure of dispersal (e.g. spore, sclerotium), or provided by the hyphal network (e.g. mycelial cords subsidised by parental mycelium). Dispersal is defined as any movement, by a spore or mycelial outgrowth, capable of reaching new habitat both in the immediate vicinity or at a larger spatial scale, and thus contributing to (meta)population dynamics (Chaudhary *et al.*, 2022; Schlägel *et al.*, 2020).

Our definition of UCI covers all biological and spatial scales at which fungi interact in a fashion predicted by MCT, i.e. engage in (meta)community competitive dynamics driven by an interplay between niche differences, competitive differences, habitat variability and dispersal (Barabás *et al.*, 2018; Chesson, 2000*a*; Shoemaker & Melbourne, 2016). Following this definition, individual contiguous mycelia, their local segments (i.e. ramets), and specialised propagules can act as UCIs.

The first condition (*i*) of physiological integration prevents two or more disconnected mycelia from being considered as a single UCI, even if they have the same genetic identity (i.e. single genet). If they re-establish connection through hyphal fusion (i.e. anastomosis), they once again meet the condition of physiological integration (Wu *et al.*, 2012).

The condition of physiological integration must be fulfilled to ensure that UCIs can be perceived as individual-surrogates that are internally organised and potentially compete with each other (within a population of multiple UCIs). Thus, while each UCI must be physiologically integrated, the converse is not true. Each physiologically integrated mycelium does not need to be a single UCI, but instead can be regarded as a population of lower-level UCIs (e.g. see the above example of UCIs in competition–colonisation trade-off). The operational choice depends, again, on the community process of interest (Fig. 2). For instance, if the aim is to study interference competition, the contiguous mycelia are the best candidate for the UCI. During interference, the response can be organised at the level of entire mycelium (Boddy, 2000; Kolesidis *et al.*, 2019). Partitioning it into lower-level UCIs would likely obscure, rather than elucidate important processes. By contrast, in coexistence *via* growth–density covariance (see below), of primary importance is the ability to concentrate (population) growth in a favourable area (Barabás *et al.*, 2018; Chesson, 2000*a*; Melbourne *et al.*, 2007; Shoemaker & Melbourne, 2016). It is of secondary importance whether this growth remains physiologically integrated or not. What is crucial is that the MCT can justify simplification and address all growth at the population level. The UCI concept offers the flexibility to meet theoretical expectations, and thus all spores or mycelial segments are assorted regardless of their biological character into populations of locally dispersing UCIs, or

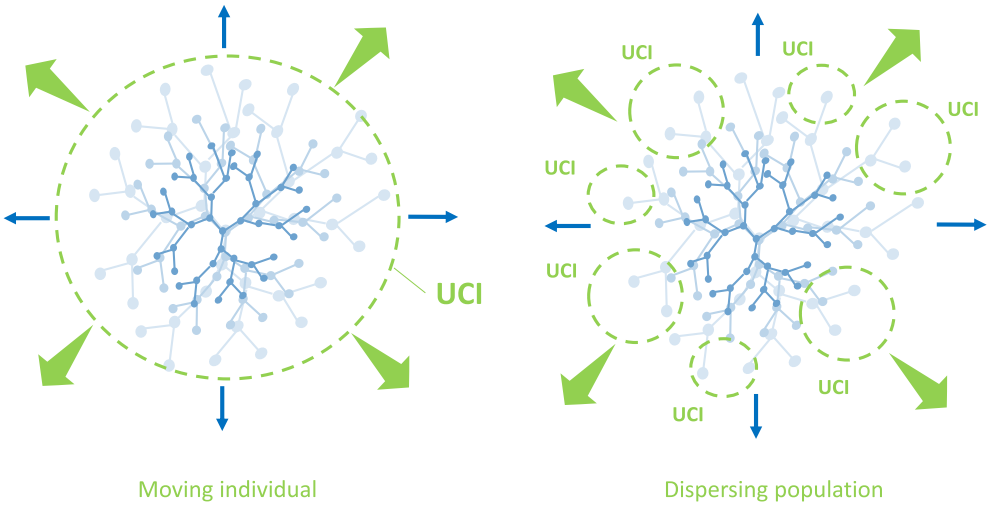

Fig. 2. Flexibility in defining units of community interaction (UCIs; green dashed circles) in ecologically modular organisms. The figure shows growth of the same mycelium (blue dots and lines and blue arrows), which can be viewed as the movement (green arrows) of a single individual (left) or the dispersal of a population (right). The choice is operational, and it depends on the ecological context and the research question.

regionally dispersing UCIs. To summarise, a physiologically integrated mycelium can be treated as a single UCI or as a population of lower-level UCIs, depending on the nature of the respective coexistence mechanisms.

The second condition (*ii*) of growth influencing (and can be influenced by) the external competitive environment excludes (for instance) individual nuclei (the units of selection of Booth, 2014) from having the status of a UCI. In accordance with MCT, the growth of any UCI is affected by and affects the competitive environment (e.g. resources, predators, competitors) (Chesson, 2000*a*,*b*). From the perspective of a nucleus, the environment is the cytoplasm, and does not directly influence the competitors or external resources (Lakovic & Rillig, 2022).

The last condition (*iii*) of the UCI (i.e. the capacity to either produce or to act as agent(s) of dispersal) points to the ability of UCIs to contribute to the (meta)population dynamics described by MCT (e.g. patch colonisation, source–sink dispersal; see Table 1) (Amarasekare *et al.*, 2004; Shoemaker & Melbourne, 2016), and simultaneously sets the lower limit for a mycelial segment (or fragment) that can still have the status of a UCI. In theory, any segment/fragment can start a new mycelium following an outgrowth into a new resource patch, or fragmentation by external forces (Boddy *et al.*, 2009; Pringle & Taylor, 2002; Rayner, 1991). While in laboratory conditions, a mycelium can re-establish from a single hyphal tip, in natural communities the threshold for available biomass/resources to act as a unit of dispersal might be higher (Nix-Stohr, Moshe & Dighton, 2008; Qandah & Del Rio Mendoza, 2012). Similarly, mycelia of wood decomposers can persist in wood patches after depletion of the resource base necessary to build a fruiting body (i.e. available biomass/resources to produce unit(s) of dispersal) (Kubartová *et al.*, 2012). From the perspective of population dynamics, unless the species routinely disperses vegetatively, these mycelia are destined for local extinction, unable to contribute to population dynamics as described by MCT (Kubartová *et al.*, 2012).

Note that the definition of UCI is intentionally ambiguous to account for the hierarchical individuality and indeterminate growth of filamentous fungi. Thus, for proper use of the concept, it is critical to explain clearly what is defined as the UCI in a given study and why, i.e. based on what mechanism and context.

Finally, we illustrate how the concept of UCI and the resulting rigorous approach to biological and spatial scales can benefit study of the fungal coexistence program, with examples from previous studies. Pringle & Bever (2002) proposed that temporal niche partitioning supports coexistence in mycorrhizal fungi. They quantified fungal activity using spore production as a proxy, based on the assumption that an increase in spore counts is driven by an increase in physiological activity in the recent past. While this assumption is reasonable for certain species, the ability to disperse both by spore and mycelial growth prevents a similar approach to defining fitness for a wider range of competitors (Valyi *et al.*, 2016). To conduct similar studies on a wider range of species, propagule-like UCIs can be used as a surrogate for spores in fitness definitions (Chaudhary *et al.*, 2022; Valyi *et al.*, 2016).

Besides the definition of fitness (Pringle & Taylor, 2002), fungal ecology also faces the challenge of establishing robust links between patterns of co-occurrence and putative mechanisms of coexistence. There is a tendency to oversimplify the task of coexistence testing by focusing only on one potentially relevant UCI, namely the fully grown mycelia in the resource patch. The observation of a pattern of mycelia unable to displace each other within the local neighbourhood (i.e. interference deadlock) can be interpreted as coexistence driven by the directly observed UCIs (Cui, Yue & Cao, 2023; Fukasawa & Matsukura, 2021). The absence of competitive differences at the mycelial level can actually lead

to competitive exclusion when all relevant UCIs of the life cycle and their corresponding scales are considered. For instance, if two species are competitively similar at the level of mycelia (local UCIs), but one of the two species is superior in dispersal through any form of propagule-like UCIs, competitive exclusion may eventually take place because the conditions for a trade-off between competition and colonisation are not met (Amarasekare, 2003; Levins & Culver, 1971; Tilman, 1994). These topics are discussed in more detail in the following sections.

III. COEXISTENCE IN SPATIALLY HOMOGENEOUS ENVIRONMENTS

(1) General overview

To begin, we clarify the relevant terminology of spatial ecology. MCT makes a clear distinction between habitat heterogeneity (i.e. qualitative differences between patches) and habitat structure where all patches can have the same properties [also referred to as patchiness or physiognomy (Amarasekare *et al.*, 2004; Dunning, Danielson & Pulliam, 1992)]. If competitive rankings among species remain the same in all patches, the environment is structured, but competitively homogeneous (Amarasekare, 2003) (Fig. 3A, Table 1). Whenever we discuss heterogeneity or homogeneity, we mean (unless specified otherwise) the spatial, rather than temporal properties of habitat (Chesson, 2000*a*).

Habitat connectivity refers to the interplay between movement capacity of the organism (in fungi both by spores and/or mycelial outgrowth; Bielčik *et al.*, 2019), and habitat features that influence the movement and survival rates between patches (Henein & Merriam, 1990; Taylor *et al.*, 1993). In fungi, these can include diverse environmental variables such as soil porosity and micro-geometry (Aleklett *et al.*, 2021; Arellano-Caicedo *et al.*, 2021; Falconer *et al.*, 2012; Kravchenko *et al.*, 2011), distances between patches, wind characteristics (Norros *et al.*, 2012), presence of animal mobile linkers (da Silva *et al.*, 2016; Danks *et al.*, 2020),

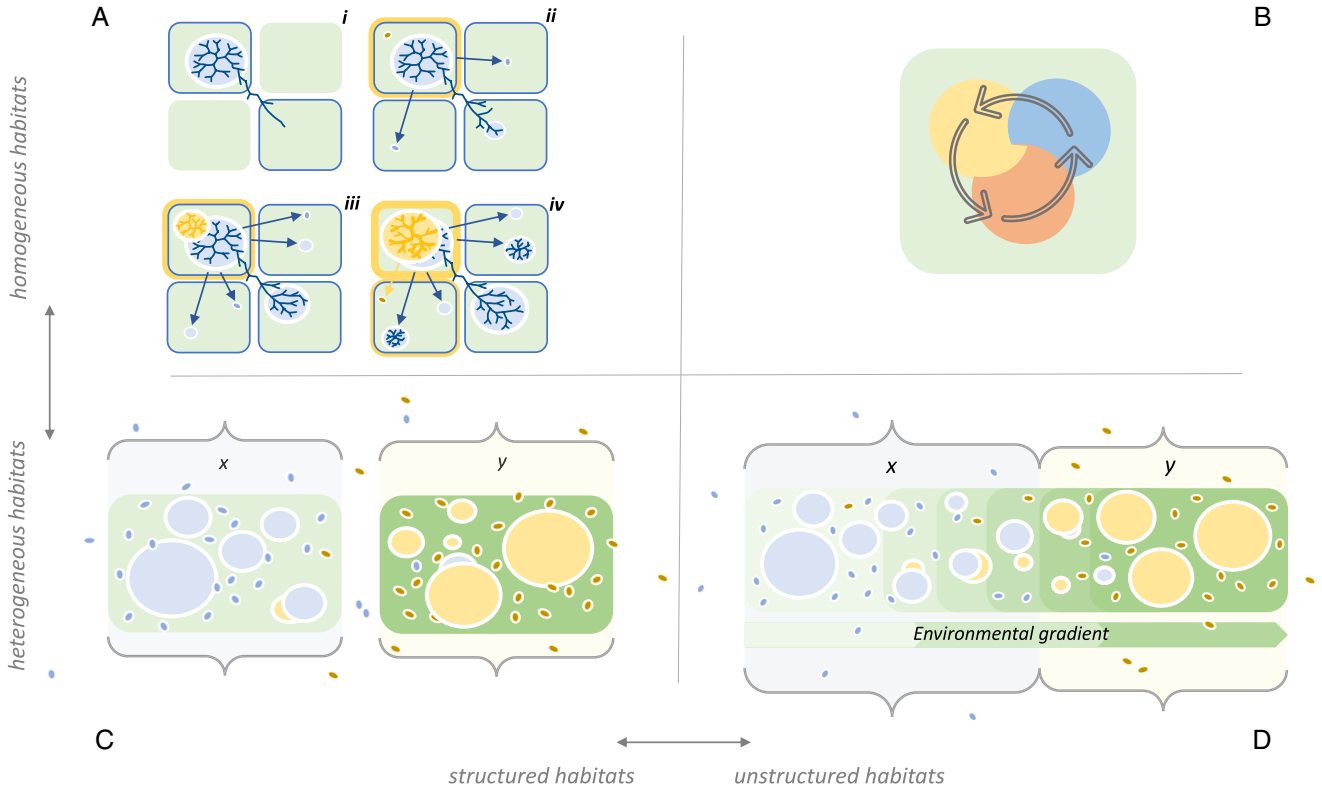

Fig. 3. Coexistence in homogeneous and heterogeneous habitats. Habitat patch(es) are depicted as rectangles. Green shading represents habitat heterogeneity. Coexistence to which spatial processes are relevant can take place in habitats which are homogeneous-structured (A), homogeneous-unstructured (B), heterogeneous-structured (C), and heterogeneous-unstructured (D). (A) Coexistence *via* colonisation–competition trade-off is depicted as successive events (*i–iv*) within the same array of four habitat patches. A superior coloniser arrives first (*i*) and its mycelial structures and spores are depicted in blue. A superior competitor is depicted in orange. (B) Intransitive coexistence is possible in homogeneous and unstructured habitats, provided the competition maintains a certain spatial property, i.e. is limited to local neighbourhoods. Intransitive competitive dominance is depicted as the circle of arrows. (C, D) Coexistence in heterogeneous habitats is possible regardless of the habitat structure, provided dispersal towards the unfavourable patches is limited. The competitive rankings must shift with environmental gradient, so the blue species is competitively dominant in one area (*x*), while the yellow species is dominant in another (*y*).

or microclimate enabling the growth of mycelial cords between habitat patches (Dowson, Rayner & Boddy *et al.*, 1988*a*). In modular organisms, each life stage and morphological type involved in connecting patches can be treated as a propagule-like UCI, bearing in mind that different types of propagule-like UCIs may have different interactions with connectivity-influencing environmental variables.

Note that the categorisation of spatial coexistence mechanisms (along the axis of homogeneous or heterogeneous environment) does not mean that different coexistence mechanisms cannot act simultaneously and combine in nature (Gómez-Llano *et al.*, 2023; Kennedy, 2010). Also, the fact that some coexistence mechanisms can operate in homogeneous environments does not mean that they necessarily require homogeneous environments.

(2) Life-history trade-offs in systems with patch dynamics

Previous studies have reported various physiological and morphological trade-offs in fungi that may contribute to the trade-off between colonisation and competition. For instance, mutations that reduced colonisation ability increased local competitiveness in *Penicillium expansum* (Luciano-Rosario *et al.*, 2022). Among fungal species, there is a trade-off between spore number and spore size, with spore number possibly related to a colonisation capacity and spore size to competitive capacity (Aguilar-Trigueros *et al.*, 2019; Löbel & Rydin, 2010; Norros *et al.*, 2023). In saprobic fungi, there is another relevant trade-off between enzymatic capacity (associated with local competitiveness) and growth rate (associated with colonisation capacity) (Zheng *et al.*, 2020). The conditions under which these biological trade-offs can lead to coexistence are outlined below.

(*a*) *Competition–colonisation trade-off*

In fungal habitats, substrates often occur as patches with continual turnover, possibly enabling coexistence of multiple species *via* a competition–colonisation trade-off (CC trade-off) (Amarasekare, 2003; Kneitel & Chase, 2004; Levins & Culver, 1971; Tilman, 1994). New patches appear on a smaller scale due to the addition of new resource units (e.g. fallen trees) (Boddy, 2000; Krah *et al.*, 2018), or on a larger scale through disturbances like forest fire (Junninen, Kouki & Renvall, 2008). The coexistence mechanism is based on species being either superior at local competition, or superior at regional colonisation. Thus, inferior competitors can maintain their populations through a fugitive strategy at the regional scale, arriving first at a new patch (Fig. 3A).

Conversely, coexistence *via* CC trade-off will be prevented if a species evolves to be superior both in competition and colonisation (Kneitel & Chase, 2004; Levine & Rees, 2002), or if the inferior competitor cannot benefit sufficiently from its advantage of superior colonisation ability (Amarasekare, 2003). This can happen if propagules of the superior competitor are *a priori* present (waiting) in the environment, or if the connectivity between patches is too high (Amarasekare, 2003; Shoemaker & Melbourne, 2016). In fungi, superior competitors can arrive first as a mycelium spreading through and/or waiting in leaf litter (note that in this case the entire mycelium will play the role of a propagule-like UCI) (Allmér, Stenlid & Dahlberg, 2009; Boddy & Jones, 2007; Boddy, 1999; Dowson *et al.*, 1988*a*). Hence, it might be no coincidence that the best evidence for CC trade-off structuring fungal communities comes from symbiotic species in a habitat where patches of host trees are isolated by grassland not supporting the symbiont (Smith *et al.*, 2018). In this case, habitat connectivity between patches is low and does not support *a priori* propagule presence in form of mycelial outgrowth (Smith *et al.*, 2018).

In wood-decomposing fungi, species typical of later successional stages tend to be competitively superior (Boddy, 2000; Chapela, Boddy & Rayner, 1988), a pattern that is, in principle, in line with a CC trade-off. However, we suggest that in many habitats this pattern is driven not by the CC trade-off, but rather by a similar, yet distinguishable trade-off between competition and growth rate.

(*b*) *Competition–growth rate trade-off*

If superior competitors are not dispersal limited, inferior competitors can still coexist, provided they maintain a fugitive strategy based on fast growth at the early habitat stage, instead of superior colonisation ability (Amarasekare, 2003). The trade-off is then not between competition and colonisation, but rather between competition and fast growth (CFG trade-off), which has also been referred to as coexistence in successional niche (Amarasekare, 2003; Pacala & Rees, 1998). In fungi, fast growth can be enabled by specialising on substrates that do not require high enzymatic investments (e.g. simple sugars, amino acids), and investing less into structures and metabolites needed for stress resistance and/or interference ability (Boddy, 2000; Zheng *et al.*, 2020). Eventually, fast-growers will be locally replaced by species that specialise on recalcitrant substrates, tolerate stress and invest in interference abilities (Boddy, 2000). Thus, the CFG trade-off in fungi could be also called a persistence–growth rate trade-off, with superior competitors increasing their persistence by both stress tolerance and interference ability (Boddy, 2000; Jonsson, Edman & Jonsson, 2008; Maynard *et al.*, 2019*a*).

(*c*) *Where to look for it: UCIs and spatial scales*

Compared to the CC trade-off, conditions for coexistence under CFG trade-off differ (Amarasekare, 2003), and are likely more permissive for a wider range of fungal systems. As coexistence mechanisms, both trade-offs depend on patch dynamics and do not require environmental heterogeneity. Crucially, in the CFG trade-off, the degree of isolation between patches can be lower (i.e. the expected spatial scales smaller) (Amarasekare, 2003). The CC trade-off is likely to drive fungal coexistence only at larger spatial scales (e.g. landscape level), where the dispersal of superior competitors is sufficiently limited. As mentioned above, for symbiotic

species this can be patches of host plants isolated by areas that do not support the symbiont. For saprobic species, ecosystems that undergo periodic large-scale disturbances (e.g. fire, logging), could be a candidate for coexistence *via* CC trade-off (Junninen *et al.*, 2008). The involved UCIs are likely to be restricted to contiguous mycelia engaging in mycelial interference at the local scale. For inferior competitors, spores (possibly succeeded by a pre-colonising endosymbiotic stadium) will act as propagule-like UCIs, enabling dispersal across larger distances (Boddy, Gibbon & Grundy, 1985; Parfitt *et al.*, 2010).

For the CFG trade-off, coexistence of saprobes is more likely, and could be possible also at smaller scales and in less spatially structured environments (e.g. single forest floor), as long as there is a possibility for continuous turnover of patches, so that patches in various successional stages of decomposition are always available (Amarasekare, 2003).

The UCIs involved can be more variable. While at the local patch scale, these will be still contiguous mycelia, colonisation of new patches (e.g. wood blocks) can be driven either by spores, or by mycelial cords and mycelial networks waiting in the forest floor (Allmér *et al.*, 2009; Boddy & Jones, 2007; Boddy, 1999), or by pre-colonisation by an endosymbiotic stadium (Boddy *et al.*, 1985; Parfitt *et al.*, 2010).

(3) Intransitive coexistence in local neighbourhoods

(*a*) *Intransitive coexistence and fungal biology*

To our knowledge, intransitive coexistence has not been integrated into the MCT framework (Levine *et al.*, 2017), and its development was largely parallel to the development of MCT (Gallien *et al.*, 2017). One reason for this is that multi-species interactions are more difficult to tackle analytically than interactions between two species (Spaak & Schreiber, 2023; Ulrich *et al.*, 2014). Other reasons might be biological. Significant MCT developments are linked to research in plant communities (Siepielski & McPeek, 2010) and it has been suggested that plants compete in ways that do not support emergence of intransitive networks (Wilson, 2011; but see Soliveres *et al.*, 2015). While in principle any kind of competition can be intransitive (Allesina & Levine, 2011), interference [ubiquitous in fungi (Boddy, 2000; Hiscox, O'Leary & Boddy, 2018; Soliveres *et al.*, 2018)] results in numerous possibilities for species-pair-specific competitive responses and outcomes (Evans *et al.*, 2008; Hiscox *et al.*, 2010; Stahl & Christensen, 1992), which in turn increases the likelihood of competitive hierarchies to become intransitive (Boddy, 2000; Boswell, 2012).

Analogous to a rock–paper–scissors game, intransitive competition emerges in multi-species (i.e. a minimum of three) interactions where no species is dominant over all others (Fig. 3B). Intransitive competition is well documented in fungi (Boddy, 2000; Hiscox *et al.*, 2015; Maynard *et al.*, 2017; Soliveres *et al.*, 2018), and competition shifts towards less-hierarchical interactions were shown to decrease/delay competitive exclusion (Maynard *et al.*, 2017; O'Leary *et al.*, 2018).

In addition to competition rankings being intransitive, the requirement for lower competitive differences (Soliveres *et al.*, 2018), and competitive reversals match fungal biology well (Soliveres & Allan, 2018). In wood-decomposing saprobes, each successional stage is often occupied by many species (Hiscox *et al.*, 2018). The competitive differences among species of the same successional stadium are expected to be less pronounced than between species from different successional stages (Hiscox *et al.*, 2018). Competitive rankings and competition outcomes can be reversed by environmental variability (Chapela *et al.*, 1988; Sturrock *et al.*, 2002), by changing spatial relationships between competing mycelia (Hiscox *et al.*, 2017; O'Leary *et al.*, 2018; Sturrock *et al.*, 2002), by size differences (Connolly & Muko, 2003; Kolesidis *et al.*, 2019), or by the presence of the third species (Hiscox *et al.*, 2017), with higher-order interactions other than intransitive ones (Barabás, 2021; Levine *et al.*, 2017).

(*b*) *Where to look for it: UCIs and spatial scales*

Intransitive coexistence is predicted to be tied to local UCIs, with a limited role of propagule-like UCIs, and to be more frequent in organisms with limited dispersal competing in local neighbourhoods (Kerr *et al.*, 2002; Reichenbach, Mobilia & Frey, 2007; Soliveres & Allan, 2018) (Fig. 3B). In communities of interfering bacteria, intransitive coexistence was possible when interactions happened in local neighbourhoods, and mixing prevented intransitive coexistence (Kerr *et al.*, 2002). This is reminiscent of the spatial scale of mycelial local neighbourhoods, where fungal intransitive coexistence has been documented or suggested (Hiscox *et al.*, 2017; Maynard *et al.*, 2017; O'Leary *et al.*, 2018). Given the importance of mycelium-level organisation in interference competition, the entire physiologically integrated mycelium should be considered as the UCI (Kolesidis *et al.*, 2019), with emphasised importance of interference-relevant morphological and physiological characteristics of these UCIs [e.g. transport efficiency, mycelial barrages, or interference at distance (Bebber *et al.*, 2007; Boddy, 2000; Hiscox *et al.*, 2010)].

While intransitivity promoting species persistence has been well documented in fungi, future research will need to reconcile the MCT requirement of growth when rare (i.e. mutual invasibility, see Table 1) (Grainger *et al.*, 2019*b*; Siepielski & McPeek, 2010). In fact, most of the empirical evidence in fungi comes from interacting mycelia of similar size. This is problematic from the MCT perspective. For species coexistence to be stabilised, each species should be able to rebound from rarity (see Section V.7).

IV. COEXISTENCE IN SPATIALLY HETEROGENEOUS ENVIRONMENTS

(1) General overview

There are three coexistence mechanisms dependent on environmental heterogeneity: spatial storage effect,

growth–density covariance, and spatial relative non-linearity (Amarasekare, 2003; Barabás *et al.*, 2018; Chesson, 2000*a*). Alone or in combination, each can generate a pattern of correlation between environmental heterogeneity and community composition: populations of competitors are concentrated each in its preferred locality (Fournier *et al.*, 2017), and coexistence is stabilised at the regional level (see Section II.2) (Fig. 3C,D). We demonstrate herein fungal coexistence in heterogeneous habitats for spatial storage effect and growth–density covariance. Both mechanisms concentrate species in their respective favourable areas. However, the processes by which this is achieved are different (Barabás *et al.*, 2018; Chesson, 2000*a*).

The spatial storage effect is driven by an interaction between the direct effect of the environment on population growth of a focal species, and the competition that the focal species experiences in this given environment (Snyder, Borer & Chesson, 2005). When the high-quality habitat of a focal species is at the same time a low-quality habitat for a competitor, then competition is low where growth conditions are good (Amarasekare, 2003; Barabás *et al.*, 2018; Shoemaker & Melbourne, 2016). This enables the focal species to grow when rare and build up its population in a favourable area.

Thus, the spatial storage effect can be seen as a bottom-up mechanism, where local responses to the environment are the primary driver. By contrast, growth–density covariance relies on the existence of a physical spatial process that drives individuals (or more broadly UCIs) of rare species into their favourable areas (patches) (Shoemaker & Melbourne, 2016; Snyder *et al.*, 2005). Along these lines, Shoemaker & Melbourne (2016), rather intuitively, called it a concentration mechanism. In motile organisms, this can be achieved by directed movement towards favourable localities (Zhang *et al.*, 2021), a process analogous to mycelial growth directed into favourable areas (Boddy & Abdalla, 1998; Thompson & Rayner, 1983).

(2) Conditions for heterogeneity-dependent coexistence and evidence in fungi

The general conditions for coexistence in heterogeneous habitats can be summed up as follows:

There must be a species-specific response to the environmental conditions. These environmental conditions must vary in space, so the competitive rankings between competitors can vary across the region (Amarasekare, 2003; Amarasekare *et al.*, 2004) (Fig. 3C,D; Table 1). Next, species must be able to concentrate their population growth in their preferred localities (Snyder, 2008). While the local areas can be adjacent, dispersal between areas must be maintained under a critical threshold (Fig. 3C,D). What follows is that the spatial scale of the local area must be sufficiently large relative to the scale of dispersal (Snyder, 2008), regardless of the type (spores or mycelial segments) of propagule-like UCIs. Among small-scale heterogeneities, intensive dispersal would lead to mixing of species, preventing spatial niche segregation and coexistence. In the spatial storage effect, intermediate levels of dispersal can maintain unprotected coexistence also at a local spatial scale (Amarasekare, 2003). Unprotected coexistence is a situation in which a species is maintained in its unfavourable locality by a buffering effect of source–sink dispersal from its favourable locality (Amarasekare, 2003; Amarasekare *et al.*, 2004).

The last condition relates to the temporal dimension: to build up populations in favourable areas, species need sufficient time for population growth to take place. Hence, the spatial heterogeneity must be sufficiently long-lasting (Chesson, 2000*b*; Snyder, 2008). In the following, we examine how these coexistence conditions relate to fungal biology and ecology.

We expect that coexistence based on spatial heterogeneity plays a significant role in community assembly of filamentous fungi. This type of coexistence is generally predicted to be common in diverse systems (Kneitel & Chase, 2004; Levine & Rees, 2002), and several aspects of fungal ecology make it likely: (*i*) the observed correlation between environmental parameters and community structure (Baldrian *et al.*, 2012; Gehring *et al.*, 1998; Krah *et al.*, 2018; Kubartová *et al.*, 2012; Odriozola *et al.*, 2023); (*ii*) the influence of environment on competitive rankings (Hiscox *et al.*, 2016; Kennedy, 2010); (*iii*) the presence of directed and indeterminate clonal growth (Boddy & Abdalla, 1998; Dowson *et al.*, 1988*b*; Thompson & Rayner, 1983); (*iv*) indications of spore dispersal being, at least in some species, concentrated at close range (Abrego *et al.*, 2020; Galante, Horton & Swaney, 2011; Norros *et al.*, 2012; Peay & Bruns, 2014; Smith *et al.*, 2018; but see also Chaudhary *et al.*, 2022); and (*v*) the existence of life-history trade-offs in response to environmental parameters (Maynard *et al.*, 2019*a*). According to Kneitel & Chase (2004), species differential responses to the environment always imply that habitat utilisation has evolved alongside a trade-off, so in a heterogeneous region no species becomes a perfect utiliser of all local conditions. One class of trade-offs that can enable coexistence is between (broadly defined) competitive dominance and a density-independent trait, such as mortality (Adler & Mosquera, 2020), stress tolerance (Haegeman, Sari & Etienne, 2014), or susceptibility to predation (Holt, Grover & Tilman, 1994). Thus, it is of interest that a trade-off between competitive ability and abiotic stress tolerance has been shown to structure fungal communities (Maynard *et al.*, 2019*a*).

The empirical evidence reviewed above makes heterogeneity-driven coexistence a promising area for research. Yet, caution is needed as none of these findings directly demonstrate coexistence and it is important not to confuse patterns with processes/mechanisms. For instance, spatial heterogeneities at smaller scale (e.g. within a fallen tree trunk; Krah *et al.*, 2018) can be correlated with community composition, but the coexistence can be driven by heterogeneities at larger spatial scale (e.g. among tree trunks), or even by non-spatial mechanisms.

(3) Where to look for it: coexistence in heterogeneous habitats

For heterogeneous habitats, we discuss the likely conditions and scales of coexistence detection in two separate sections. In the first, we describe the likely habitat characteristics. In the second, we describe the importance of biological details and scales, i.e. the UCIs.

(a) *Where to look for it: habitat properties*

The best candidates for heterogeneity-driven coexistence are habitats where (*i*) the environment is heterogeneous in parameters known to alter competitive rankings (Amarasekare, 2003; Amarasekare *et al.*, 2004); (*ii*) the local areas (patches) are sufficiently large that most of the dispersing UCIs stay within them (Snyder, 2008); and (*iii*) they are sufficiently durable in time, so the species' populations have time to build up (Chesson, 2000*b*; Snyder, 2008).

Several environmental variables have been shown to alter competitive rankings in fungi, including temperature, pH, nitrogen levels, concentrations of gases, or water potential (Hiscox *et al.*, 2016, 2018; Kennedy, 2010). Unlike competitive rankings, the spatio-temporal aspects of points *ii* and *iii* are relative to characteristics of fungal species and the spatial scales of the chosen UCIs. Fungal species are likely highly diverse in terms of dispersal ranges, growth rate and generation time (Abrego, Norberg & Ovaskainen, 2017; Bässler *et al.*, 2014; Halbwachs, Simmel & Bässler, 2016; Norros *et al.*, 2014; Zheng *et al.*, 2020). Spatial characteristics of the UCIs, such as dispersal ranges, will affect what area (patch) is sufficiently large. Growth rate and generation times will affect what area (patch) is sufficiently durable in time. Therefore, it is impossible to make universally valid predictions about the scale of coexistence. Yet, it is possible to outline some preliminary expectations. When environmental heterogeneities exist at a small scale (i.e. they have high granularity), they are less likely to maintain coexistence. For instance, small saprobic habitats (e.g. a single pine needle, herbivore dung; Bruns, 2019), are ephemeral and the majority of propagules land outside of favourable habitat (unless dispersal is primarily by propagule-like mycelial UCIs that are capable of actively seeking favourable conditions). At least for species dispersed mainly by spores, coexistence is more likely at a larger scale, for instance if single ephemeral habitats (and heterogeneity among them) aggregate both in space and time. Thus, rather than being driven by heterogeneities among single pine needles, coexistence may be driven by heterogeneities of pine litter aggregated under the canopy of different tree species, or at the spatial scale of microclimatic differences between forest edges and forest interiors (Brabcová *et al.*, 2022). At this scale, habitats are more durable and dispersing UCIs are more likely to remain within the species' favourable area (Nordén & Larsson, 2000).

The above is intended only as preliminary guidance. While it is true that larger spatial heterogeneities are more likely to promote coexistence, if the spatial scales of UCIs and their dispersal are microscopic, it is possible that even a single log or root is sufficiently large for the spatial coexistence of saprobic or symbiotic species.

(b) *Where to look for it: UCIs*

For heterogeneity-dependent coexistence, the ability to concentrate population growth within a preferred area is a key spatial process (Amarasekare *et al.*, 2004; Shoemaker & Melbourne, 2016; Snyder, 2008). We argue that for fungi, it is of secondary importance whether this population growth is physiologically integrated (but see below), and even whether it takes the form of mycelial outgrowth or short-range spore dispersal (Abrego *et al.*, 2020; Boddy *et al.*, 2009; Junninen & Komonen, 2011). Therefore, as a starting point, the total biomass and its ability to concentrate growth in favourable areas should be considered as the population of local UCIs (including mycelial segments and spores). More important than distinction between spores and mycelial segments is the distinction between the fraction of UCIs that stays within a favourable habitat and the fraction that leaves it (Amarasekare, 2003; Shoemaker & Melbourne, 2016).

Let us recall that the definition of a particular UCI type is always based on the characteristics of a particular spatial coexistence mechanism to which it is to be applied. Since the canonical definitions of the spatial storage effect and growth–density covariance are rather abstract and general, it follows that the definition of a UCI based on these mechanisms is of a rather low resolution (locally growing UCIs *versus* regionally dispersing UCIs). However, the situation changes when these coexistence mechanisms are applied in more detailed models (see Section V.6).

To conclude, we provide two relevant points. First, the fraction of regionally dispersing UCIs also includes biomass of fruiting bodies (e.g. mushrooms) and other structures dedicated to spore dispersal. Even though fruiting bodies physically do not leave the original location, they do 'leave it' in terms of no longer contributing to local community interactions. The biomass and energy used for their growth no longer can be used for local mycelial outgrowth or competition, thus it is better considered as a regionally dispersing, not locally competing UCI (Chan *et al.*, 2019). From the perspective of competitive metacommunity, this biomass is analogous to unitary individuals leaving the original locality without ever reaching a new one (i.e. dispersal mortality; Ruxton, Gonzalez-Andujar & Perry, 1997).

Secondly, while the degree of mycelial physiological integration does not affect the choice of meaningful UCIs in heterogeneous habitats, it can affect the spatial scale and character of the favourable habitat patch. Growth of species with a lower degree of physiological integration is more likely to follow the boundaries of their favourable patches/areas (Olsson, 1995) (Fig. 4A). Conversely, species with a higher degree of physiological integration may employ the process of clonal subsidising in order to expand their area further (Fig. 4B, Table 1). We may call the former selective species,

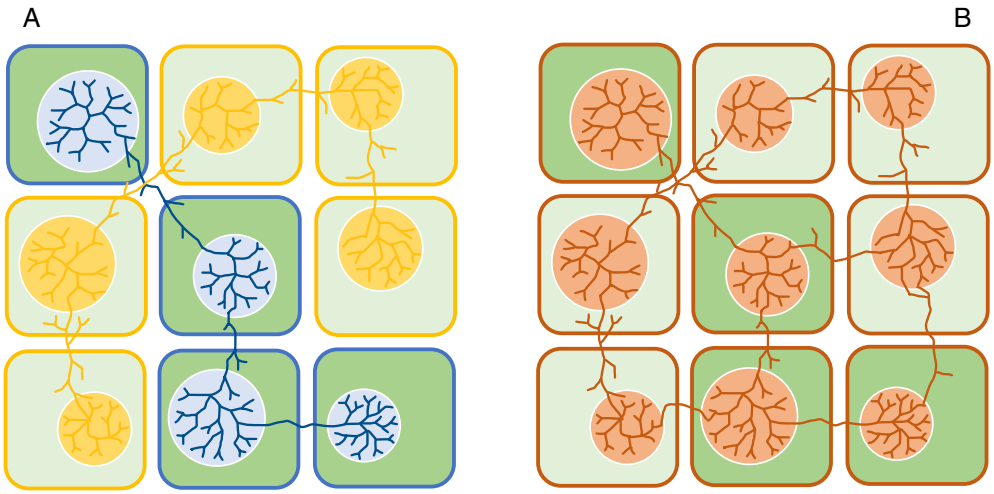

Fig. 4. Spatial niche partitioning in heterogeneous habitats and clonal subsidising. A and B both depict the same structured and heterogeneous habitat. Two modular species, both with a lower degree of physiological integration (selective/specialist species) are depicted in A as blue and yellow, respectively. They are expected to have greater options for coexistence in heterogeneous habitats, as compared to the averaging-generalist species (B) with higher physiological integration. Thus, a higher degree of network transport and clonal subsidising can lead to lower biodiversity (B).

and the latter averaging species. For selective species, environmental heterogeneities are likely to provide more coexistence options, since clonal averaging may diminish spatial niche segregation (Bielčik *et al.*, 2019; Eilts *et al.*, 2011) (Fig. 4B).

Thus, the degree of clonality is one trait with direct relevance to spatial coexistence. In the next section, we introduce other relevant traits as part of perspectives for future research.

V. FUTURE PERSPECTIVES

(1) General overview

A comprehensive discussion of MCT-inspired future research in fungi would exceed the scope of this review. Instead, we focus on topics that we believe are most urgent, and provide examples for the further development and application of the UCI concept in future studies.

We begin by outlining how MCT can inspire and provide directions for empirical research on fungal natural history (Peay, 2014), with special attention to the spatial properties of mycelia. This is followed by a discussion of a broader approach towards fungal competition, one that would be more compatible with coexistence tests (Boddy, 2000; Hiscox *et al.*, 2018). Then we apply insights from these two sections into how a fungal coexistence experiment may be set up. Following this, we provide examples of the use of the UCI concept for the correct selection and parameterisation of coexistence models. Finally, we introduce ongoing theoretical discussions with special relevance to fungi.

(2) Importance of basic knowledge on natural history

To design a coexistence experiment, and to make decisions about UCIs and their properties of interest, sufficient knowledge about the life history of competing species is needed. When animal ecologists decide on the design of a coexistence study, they already know that studying competition between two predators as different as mantises and lions is unreasonable, and can readily hypothesise that a single lion may act as a local habitat for various flea species. They also do not need to define UCIs of interest, as these are usually synonymous with unitary individuals. Analogous knowledge about trophic dependencies and sizes of fungi in natural habitats is mostly lacking (Peay, 2014). Similarly, plant ecologists can select an appropriate place in the landscape for coexistence experiments with perennial herbs: beneath the tree canopy for understory species, or away from it for open grassland species. These crucial choices are based on space-related life-history knowledge, which appears trivial until one wishes to study microbes (Dini-Andreote *et al.*, 2021; Mony *et al.*, 2020).

For most fungal species and communities, we do not have an estimate of the temporal and spatial scales, trophic interactions, and life-history traits that coexistence experiments should encompass to mimic and capture the community dynamics realistically. For example, are co-occurring species differentially competitive in the same layer of soil (Mujic *et al.*, 2016)? Are both species affected by micro- and meso-fauna of the soil (Visser, Parkinson & Hassall, 1987)? What is the viability of their persistent UCIs in time? How do they reproduce and propagate: *via* spores, or as propagule-like mycelial UCIs (Boddy *et al.*, 2009; Kennedy *et al.*, 2011)? Is spore production a suitable ecological fitness estimate for both species,

analogous to seed counting in plants (Godwin *et al.*, 2020; Pringle &Taylor, 2002)?

We argue that one of the first tasks in empirical research on fungal coexistence is to broaden knowledge on basic natural history (Peay, 2014). Below we develop two aspects: size differences, and trophic interactions of co-occurring species. The former is directly relevant to spatial coexistence mechanisms and thus to the definition and choice of the relevant UCIs. The latter is chosen since fungal competition is mostly studied as mycelial interference. Relevant knowledge on all forms of competition is crucial for a comprehensive understanding, but also for the design of microcosms for coexistence experiments.

(3) Size of the saprobic fungus

Visual observations of wood decomposers indicate that an entire tree branch can be shared by only a few large territorial mycelia (Boddy *et al.*, 1985; Rayner & Todd, 1980, 1977). Yet, studies based on environmental sequencing or collection of fruiting bodies show dozens to hundreds of taxa in a single log (Baldrian *et al.*, 2012; Dickie, Wakelin & Richardson, 2020; Krah *et al.*, 2018; Kubartová *et al.*, 2012). RNA-based studies showed that this large biodiversity at small scale cannot be all explained by non-active DNA from dead fungi (Baldrian *et al.*, 2012). It is therefore likely that while some of the numerous mycelia do not extend beyond the sample volume (e.g. freshly germinated spores, or species with small mycelia), others can extend across much larger scales, and sample volumes represent only a fragment of their mycelia. Without knowledge of spatial scales of competition among species, it will be harder to define the relevant UCIs and we risk conducting coexistence studies at inappropriate scales – 'between lions and fleas'. Under laboratory conditions, without consumers and with abundant nutrients, most cultivatable fungi grow as a thick, disc-shaped mycelium that can be intuitively defined as a single UCI (Camenzind *et al.*, 2020; Zheng *et al.*, 2020). As resource supplies decrease, intra-specific variability relevant to the spatial characteristics of the mycelium (and thus to the definition and extent of UCIs) occurs, with some species remaining rather compact (i.e. a single UCI), while others begin to spread as relatively isolated ramets (increasing the possibility of treating them as multiple UCIs) (Camenzind *et al.*, 2020; Veresoglou *et al.*, 2018). The established practice of growing fungi on sterile, resource-rich media distorts not only our perception of their morphology and relevant UCIs, but also of competitive interactions, a topic we address below.

(4) Competition other than interference

Fungal competition is routinely studied in sterile conditions, and mostly from the perspective of mycelial interference and space pre-emption, treating each mycelium implicitly as a single UCI. We argue for a greater focus on other forms of competition, including competition driven by trophic interactions [e.g. apparent competition (Bonsall & Hassell, 1997; Holt & Bonsall, 2017)]. In nature, trophic interactions can interfere with fungal competition in several ways, all potentially important for coexistence (Chesson, 2000*b*; Crowther, Boddy & Jones, 2012). For instance, they can (*i*) drive apparent competition (Grover & Holt, 1998), (*ii*) enable trade-offs between grazing resistance and other traits (Kneitel & Chase, 2004), or (*iii*) alter the outcomes of interference competition (A'Bear *et al.*, 2013; Crowther *et al.*, 2012). As grazing can act as a biotic disturbance to established mycelia, we argue that experiments without grazing may overestimate the role of pre-emptive priority effects (i.e. underestimate coexistence; Grainger *et al.*, 2019*a*) in fungal communities. It is easy to imagine that in enclosed microcosms, the fast-growing species will quickly pre-empt the available space and resources as a single UCI, driving their system into stasis and other species to local extinction.

The importance of grazing is indicated by multiple empirical studies. Top-down control can be driven by invertebrates regulating fungal population growth (Crowther *et al.*, 2015), or influencing interference outcomes [acting as an equalising mechanism (Crowther *et al.*, 2013; Crowther, Boddy & Jones, 2011)]. It has been hypothesised that top-down control is predominant in nutrient-rich environments, where bottom-up control becomes less significant (Crowther *et al.*, 2015). Yet studies on mycophagous bacteria show the potential for apparent competition to be important in a wider range of nutrient conditions (see Table 1). In oligotrophic soils (e.g. mineral layers, dune soils), mycophagous bacteria can feed on fungi and potentially affect community composition (de Boer *et al.*, 1998; Höppener-Ogawa *et al.*, 2007; Leveau, Uroz & de Boer, 2010). Interestingly, mycophagous bacteria can feed on fungi in a species-preferential manner (Ballhausen *et al.*, 2015; De Boer *et al.*, 1998), can reduce the growth of fungi *in vitro* (De Boer *et al.*, 1998), and have been shown to alter community composition in field experiments (Höppener-Ogawa *et al.*, 2009).

In addition to excluding trophic interactions (compare with field plot experiments on plants), Petri plate competition experiments may overestimate the role of space pre-emption and interference if rich media are used, while also biasing our perception of mycelia towards always treating them as individual UCIs. When fungal mycelia grow with limited resources, they tend to be less territorial. Mycelia spread in space, and they can create an intermingled mesh of multiple species (Stahl & Christensen, 1992), growing in the form of populations composed of multiple local, lower-level UCIs.

Intermingling has been documented for saprobes on agar media (Stahl & Christensen, 1992), and for symbiotic fungi in soil (Koide *et al.*, 2004). It is therefore likely that just as for plant roots, interference prevails in resource-rich conditions and exploitative competition in resource-restricted environments (McNickle & Brown, 2012). Different UCIs and coexistence models will be appropriate for each scenario.

Another good reason for fungal competition studies to go beyond the realm of equal-sized mycelia on an agar plate comes from theoretical research on intra-specific variability and interference coexistence (Maynard *et al.*, 2019*b*).

Phenotypic plasticity has been shown to promote coexistence in intransitive communities, with the underlying mechanism analogous to bet-hedging: the more phenotypes a species has, the more likely it is to persist (Maynard *et al.*, 2019*b*; Milles *et al.*, 2023). It would be intriguing to explore how coexistence can be affected in fungi, where phenotypic plasticity can be accompanied by dramatic changes in competing UCIs. For example, a mycelium can be outcompeted as a single, large UCI under laboratory conditions in homogeneous environments, but in more natural and structured environments it can be split into a population of small UCIs with each of these smaller UCIs consequently adopting a different phenotype in response to its local competitive environment (Evans *et al.*, 2008; Hiscox *et al.*, 2010).

(5) Microcosms to study species coexistence

Once relevant life-history traits are identified, it is possible to design coexistence experiments and define the UCIs in a way that is relevant to the dynamics of biodiversity in real environments (Gómez-Llano *et al.*, 2023; Siepielski & McPeek, 2010). Here we outline what features the microcosms should have. Ideally, microcosms should enable establishment of community equilibria and measurement of population-level competition (Barabás *et al.*, 2018; Siepielski & McPeek, 2010). For this, microcosms should contain model species with smaller UCIs (either as multiple small mycelia, or as loosely spread mycelia with defined ramet-level UCIs). To mimic long-lived natural systems (e.g. soil), microcosms should have an option for resupplying the system with nutrients, and include representatives of other trophic levels that are likely to modulate population-level competitive interactions between fungi and enable the establishment of realistic equilibrium states (e.g. bacterial communities, selected protists and invertebrate species) (Crowther *et al.*, 2013; Hart, Freckleton & Levine, 2018).

While time series data are ideal to measure population dynamics (as a response to competition and signal of coexistence) (Hart *et al.*, 2018; Siepielski & McPeek, 2010), acquiring time series in systems that can not be visually accessed (e.g. soil communities) is a troublesome task. Fortunately, not all coexistence studies require time series (Grainger *et al.*, 2019*b*). Notably in annual plant systems, seed production is a fitness measure obtained from a single destructive harvest. Similar approaches could be applied in fungal species with analogous life histories. For fungi with a semelparous life history, i.e. sporulating once in the life cycle, destructive-harvest experiments analogous to seed counting in annual plants can be a feasible option (Pringle & Taylor, 2002). In addition, an argument can be made that in these species, allocation of resources between mycelial growth and sporulation is of lesser concern (Damialis *et al.*, 2015; Pringle & Taylor, 2002).

The requirement for ecological relevance, continuous supply of resources and the presence of consumers for the establishment of an equilibrium state make soil microcosms particularly attractive candidates for experiments on fungal coexistence. Yet, their construction and maintenance will require significant effort. They also have the disadvantage that processes in soil microcosms cannot be observed non-destructively. Alternative experimental systems with properties essential for coexistence experiments (e.g. establishment of community equilibrium, natural context of interactions) include 'cheesy and shitty' systems, i.e. microcosms of cheese rind and dung communities, respectively (Bruns, 2019). Ultimately, the development of easily observable laboratory systems (e.g. agar plate or microfluid-based systems) that meet the above requirements would be a great contribution to the study of fungal communities (Aleklett *et al.*, 2021; Mafla-Endara *et al.*, 2021). Such systems, which allow direct, continuous observation of competing UCIs, would expand the scope of available coexistence models and empirical approaches. We introduce these topics in the following section.

(6) The role of the UCI concept in model parameterisation and tests of coexistence

Empirical tests of species coexistence often struggle to account correctly for the necessary scale, life stages, and system complexity that must be incorporated into experimental design (Gómez-Llano *et al.*, 2023; Hawlena *et al.*, 2022). This can be challenging even for unitary organisms where there is no difficulty in defining the individual. In the case of fungi, the challenge is exacerbated by their indeterminate individuality and complex life history. The concept of UCI can help address the challenges of empirical studies in at least four ways.

First, the UCI concept can bring clarity to thinking about which levels of biological organisation are important for which coexistence mechanisms. As exemplified above, some mechanisms focus on physiologically integrated mycelia in local neighbourhoods, while others focus on lower-level UCIs and their role within and between environmental patches.

Second, the UCI concept helps to design studies in which the relevant spatial scales for specific coexistence mechanisms and fungal species are correctly identified. For ecologically modular organisms, there is no reason to assume that physiologically integrated individuals are always local (Smith, Bruhn & Anderson, 1992). That is, a physiologically integrated mycelium may extend over a heterogeneous region. In this case, lower-level UCIs are needed to design the study properly.

Third, there is no reason to believe that the above works the same way for all competing species. Different competitors may use different morphological structures as UCIs with the same competitive function. For instance, different competitors may use different morphological types for dispersal within a region, and competitors may span different spatial scales, with some mycelia acting as local UCIs while in other species mycelia are better represented as populations of UCIs (Boddy, 1999; Hiscox *et al.*, 2018). Thus, the UCI concept provides a robust, theory-based comparison between

competing species with different life histories, helping to avoid pitfalls of inappropriate comparisons.

Finally, the UCI concept facilitates the definition of relevant vital rates and variables used for quantitative tests of species coexistence (Barabás *et al.*, 2018). So far, we have explained the utility of the UCI concept to define clearly the competing entities in organisms with indeterminate individuality. This is important to provide clarity in defining research questions, scales, selecting models, and designing experiments.

Once the competing units are delineated, the next step in empirical coexistence studies is to determine which UCIs (and aspects thereof) should be used as a fitness proxy to measure the effects of environment and competition (Barabás *et al.*, 2018; Chesson, 2000*b*; Pringle & Taylor, 2002). That is, we need to define which UCIs and their characteristics are appropriate to quantify the key parameter of growth rate for residents and invaders (Barabás *et al.*, 2018; Grainger *et al.*, 2019*b*).

For organisms such as unitary microbes, this is straightforward, and the same unit, the single cell, which is expected to interact in the community, is used to quantify the competitive and environmental responses of the population (Narwani *et al.*, 2013).

Once the organism has a modular morphology and/or multiple life stages, the competing and quantified UCIs may differ, and in general, the quantified UCIs may be more variable. To illustrate, in plants, researchers quantified the number of seeds per individual (Angert *et al.*, 2009; Godoy *et al.*, 2014), the number of newly established seedlings (Adler *et al.*, 2010; Angert *et al.*, 2009; Chu & Adler, 2015), the proportion of surviving seeds (Godoy *et al.*, 2014), the number of inflorescences in annual plants (Sears & Chesson, 2007), or the area covered by an adult plant (Adler *et al.*, 2010; Chu & Adler, 2015). In these plant studies, the decision about quantified UCIs was made based on species life history, and the particular coexistence model applied to this life history.

Similarly, fungal ecologists must consider the variability of life histories and the characteristics of coexistence mechanisms to quantify coexistence. For example, if the environment can be idealised as two-dimensional and the coexistence mechanism does not involve regional dispersal, then the change in area covered by mycelia over the period of competition may be a useful vital rate to measure, similar to some plant studies (Adler *et al.*, 2010; Chu & Adler, 2015). If the coexistence mechanism involves persistent stages, the survival rate of persistent UCI (which can have many morphological forms, such as spores or mycelial structures) can be quantified (Hopkins & Bennett, 2023; Willetts & Bullock, 1992). If the coexistence mechanism is based on patch dynamics and involves both local competition and dispersal between patches, then depending on the model, researchers can quantify the results of local competition, dispersal kernels or the number of newly colonised patches (Shoemaker & Melbourne, 2016; Tilman, 1994).

Before providing examples, it is useful to clarify the relationship between two levels of abstraction in MCT: canonical coexistence mechanisms and coexistence models adapted for specific systems. Coexistence research operates at several levels of abstraction. At the core are the most general concepts of MCT, i.e. the mechanisms of species coexistence (Amarasekare, 2003; Barabás *et al.*, 2018; Chesson, 2000*b*). They can be viewed as ecological principles that provide insight into the general conditions under which species can or cannot coexist. As such, their parameters are general and broadly defined.

To adapt them to a specific system, it is often necessary to introduce more detailed parameters and relationships (Fig. 5; Adler *et al.*, 2010; Warner & Chesson, 1985). These more detailed models should inform in a straightforward manner what UCIs we quantify and what aspects should be measured. In Fig. 5 and in the text below, we present two simple example models and show how the choice of a particular model affects the definition of a UCI and its properties that need to be quantified.

Warner & Chesson (1985) developed a model of coexistence based on the storage effect and recruitment fluctuations in species with overlapping generations. Similar models could be adapted to iteroparous fungi. The key step in this adaptation is to use the UCI concept to distinguish between generations (i.e. parent mycelia and new recruits) (Fig. 5). Adler *et al.* (2010) developed an agent-based model for perennial plants that captures multiple stabilising mechanisms arising from both competitive interactions in local neighbourhoods and temporal environmental fluctuations. The structure of the model takes into account competition for space and competition at a distance, processes that are important in fungal communities (Adler *et al.*, 2010; Kolesidis *et al.*, 2019). In fungi, competing agents in similar agent-based models could be defined as UCIs at different levels of organisation (Fig. 5).

To conclude, testing species coexistence through model parameterisation offers several advantages. This approach can provide insights into which coexistence mechanism, vital rates (e.g. recruitment, growth, mortality), or which UCI (submycelial regions, entire mycelia, propagule-like UCIs) contribute to coexistence and to what extent (Adler *et al.*, 2010; Chu & Adler, 2015; Hawlena *et al.*, 2022). The use of models provides a mechanistic, quantifiable insight into species coexistence. However, if this approach is not feasible, ecologists can still test coexistence at a more phenomenological level by applying the mutual invasibility test (Adler *et al.*, 2010; Narwani *et al.*, 2013; Siepielski & McPeek, 2010).

(7) Future theoretical perspectives

In order to introduce fungi into MCT, we offered the theory mostly in its established form (Amarasekare *et al.*, 2004; Chesson, 2000*a*,*b*), and contributed the novel concept of the UCI. However, we do not want to give the impression that the final, conclusive state of theory has been reached. The field is undergoing theoretical developments, and we highlight those that are most relevant to fungi and ecologically modular organisms, together with our further suggestions for theoretical developments beyond the UCI concept

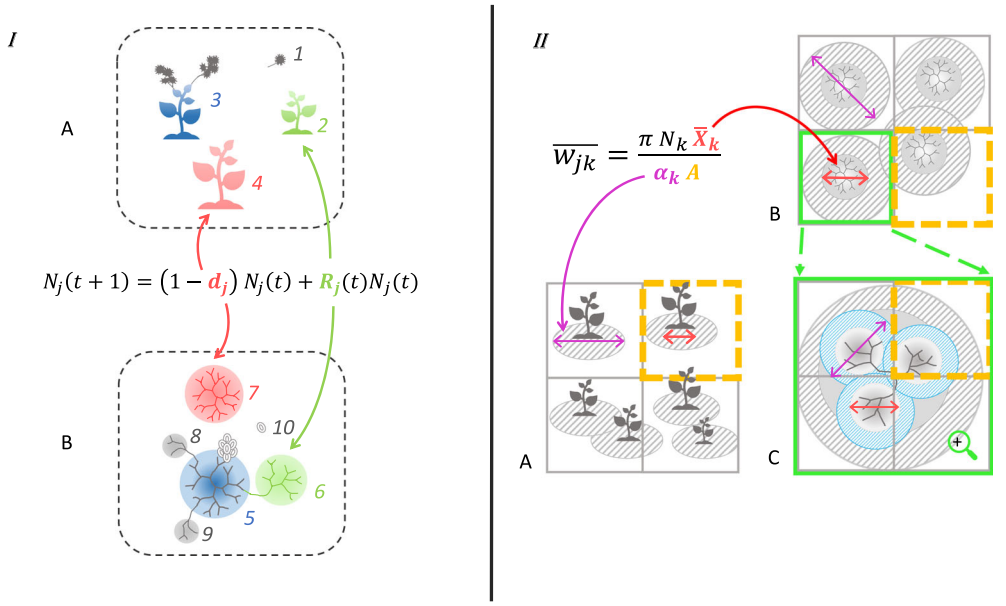

Fig. 5. (I) The equation $N_j(t+1) = (1-d_j)N_j(t) + R_j(t)N_j(t)$, adapted from Warner & Chesson (1985), represents a simple model for the population dynamics of a species j over time. In this equation, the population size at time $t+1$, $N_j(t+1)$, is influenced by the population size N_j at the previous time step, the fluctuating recruitment rate R_j (green), and the constant mortality rate d_j (red). This model is applicable in situations where the environmental and competitive factors affect new recruits and older individuals (units of community interaction, UCIs) differently. Originally developed for plants (I.A), the model does not explicitly consider seeds, i.e. pre-recruitment UCIs, in its basic form (grey, 1). The model does consider and distinguishes between three types of UCIs: UCIs newly recruited in the current time step (green, 2), the sum of living older UCIs and new recruits (blue, 3 and green, 2), and UCIs that perished in the current time step (red, 4). I.B illustrates the flexibility of the UCI concept in modifying the plant model for modular organisms. A specific property of UCIs (e.g. threshold size, degree of physiological autonomy, or variations in environmental responses) is predetermined to categorise some UCIs as individual-surrogates (5, 6 and 7), while the remaining ramets and spores, i.e. pre-recruitment UCIs, are not quantified (8, 9 and 10). (II) Adapted from Appendix S1 in Adler *et al.* (2010), the equation $\overline{w_{jk}} = \frac{\pi N_k \overline{X}_k}{\alpha_k A}$ provides another example from a plant model with potential applications in fungi. This equation is employed in the model to define the crowding effect in local plant neighbourhoods (II.A). $\overline{w}_{jk}$ can be interpreted as the impact of neighbourhood competition imposed by species k on species j in sessile systems where spatial competition can be coupled with other forms of more distant interactions, such as chemically driven interference competition. These effects are accounted for by the terms $\overline{X}_k$ (red arrows), representing the average size of an individual of species k, and α_k (pink arrows and dashed areas), denoting the spatial scale of the effect of species k on all other species in its vicinity. N_k represents the number of individuals (UCIs), and A signifies the unit of modelled area (orange). We use this equation to demonstrate the utility of UCIs in the rigorous definition of processes and variables in local neighbourhoods of modular organisms at different spatial and biological scales (II.B, C). The model can be applied to fungi at different levels of organisation: either mycelia (II.B), or ramets within the mycelium (II.C). While doing so, the UCI concept helps maintain conceptual clarity and aids in answering questions about the characteristics of UCIs that are essential for correct application of the model. For instance, it helps in assigning the average size of the ramet or genet, the unit of area (A), or it helps in navigating the model's assumptions. For example, the assumption of randomness in UCI distribution is acceptable in (II.B), but not in (II.C): here, we should expect the mycelium to tend to space lower-level UCIs in an orderly fashion.

that are desirable specifically for ecologically modular organisms. We also provide examples of how the UCI concept can be used in the design and communication of fungal studies related to priority effects, agent-based modelling or neutral coexistence.

First, original work by Chesson (2000*a*,*b*) assumes a fully deterministic mutual invasibility, i.e. there is no lower bound for the invader's population size. In fact, theory suggests that the lower the invader's initial density, the faster will be its initial growth. However, species with positive within-species interactions (e.g. Allee effect) may only invade from a certain initial threshold density (Grainger *et al.*, 2019*b*; Schreiber, Yamamichi & Strauss, 2019). When interference is a substantial component of competition, and interference ability is positively dependent on density (UCI size, or UCI counts) (Kolesidis *et al.*, 2019), even potentially coexisting species may be incapable of mutual invasion from low numbers (or spore count, or mycelium size) (Nix-Stohr *et al.*, 2008). Hence, fungal ecologists should observe and contribute to the ongoing theoretical debate on the mutual invasibility criterion (Ellner *et al.*, 2022).

Second, further theoretical research is needed to clarify the role of priority effects in fungal coexistence. Priority effects in the narrow sense of the term (i.e. as niche

pre-emption; Fukami, 2015) have been proposed as one of the drivers of coexistence in symbiotic fungi (Kennedy, 2010). However, in the coexistence literature, priority effects are now perceived as preventing rather than driving the coexistence (Fukami, Mordecai & Ostling, 2016; Grainger *et al.*, 2019*a*). Still, priority effects are characterised by small fitness differences between species. Small fitness differences could potentially promote coexistence, if coupled with niche differentiation that occurs at a different scale from that at which pre-emption is observed (Kennedy, 2010). Since the priority effects of modular organisms depend on scale and UCI type, it should always be made clear which UCIs prevent invasion (e.g. compact or loosely grown mycelia) and in what form of propagule-like UCIs the competitor arrives. For example, if we show that colonisation by spores results in priority effects, this may not be true if dispersal is by propagule-like UCIs in the form of mycelial outgrowth. We suggest the results should be communicated with similar resolution.

Another theoretical challenge is the role of within-species variability in coexistence (Hart, Schreiber & Levine, 2016). Mathematical models of MCT imply no within-species variability. Yet in fungi, competitive ability depends not only on species identity but also on an individual's mycelium size (Kolesidis *et al.*, 2019). Therefore, it is likely that approaches such as individual-based modelling will become a valuable tool in fungal coexistence research, as they can readily address the influence of within-species variability (Grimm, Aylión & Railsback, 2017; Jeltsch *et al.*, 2019; Milles, Dammhahn & Grimm, 2020). For agent-based models, the use of UCI concepts is straightforward, as agent and UCI can often be treated as synonyms. UCI can then help to define and communicate the state variables, properties of agents and their interactions (Grimm *et al.*, 2020).

An important conceptual feature of MCT is the dualism between within-species (i.e. intra-specific) and among-species (i.e. interspecific) competition. Yet in fungi and some other groups of ecologically modular organisms, this dualism may be imprecise, since within-species interactions differ dramatically based on the ability of interacting mycelia to fuse (Paoletti, 2016; Shahi *et al.*, 2016; Stahl & Christensen, 1992). Mycelia of a single species that do not fuse (i.e. anastomose) will compete for space and resources without establishing any degree of cooperation (Stahl & Christensen, 1992). By contrast, if mycelia fuse, their constituent, lower-level UCIs can interact in both a competitive and cooperative manner (Richard, Glass & Pringle, 2012). Therefore, for fungi and similar organisms capable of somatic fusion, we propose adaptation of MCT terminology to distinguish between three types of competitive interactions: intra-clonal, intra-specific and inter-specific.

Furthermore, it is important to note that the theoretical assumptions on which MCT is based have not been fully resolved. For example, debate continues about the importance of higher order interactions, coexistence in communities of multiple species or in systems with alternative stable states (Barabás *et al.*, 2018; Singh & Baruah, 2021; Spaak & Schreiber, 2023). Similarly, discussion is ongoing on the importance of equilibria and fully deterministic, stable coexistence (Revilla & Weissing, 2008). It is debated to what degree biodiversity can be maintained by unstable coexistence, with overlapping concepts of effective coexistence, unprotected coexistence, and coviability (Amarasekare, 2003; Jeltsch *et al.*, 2019). The latter framework highlighted the importance of stochastic processes within local neighbourhoods, which could be of great significance for fungal coexistence (Jeltsch *et al.*, 2019). Fungal ecologists can contribute to this debate by using UCIs to define the scales at which local neighbourhoods drive important processes, and by using UCIs to define agents in agent-based models of species co-viability (Jeltsch *et al.*, 2019).

Finally, in addition to deterministic biodiversity concepts based on niche theory, such as MCT, a neutral theory of species coexistence has been proposed (Hubbell, 2005). Recent developments in MCT state that neutral coexistence is a rather special, unlikely case that is only possible when both niche and fitness differences between competitors are zero (Grainger *et al.*, 2019*a*). While this scenario seems unlikely, the really interesting scientific question might not be whether coexistence is neutral or not, but to what extent it is neutral (Adler, HilleRisLambers & Levine, 2007; Grainger *et al.*, 2019*a*). And while the scenario of perfect neutrality seems unlikely indeed, the abundance of interactions in species-rich communities can act as an equalising factor. This has been hypothesised for intransitive networks: while competitive difference between two species may be high, a third species can lower this by giving an advantage to the weaker competitor (Allesina & Levine, 2011; Levine *et al.*, 2017). Thus, neutral processes of emigration, immigration, and drift have received attention in explaining biodiversity persistence in species-rich systems such as tropical rainforests (Bongalov *et al.*, 2019; Vandermeer, 1996). Fungal communities exhibit similarly high species richness, and although studies have shown a relationship between fungal community composition and environmental gradients (as would be expected from the determinism of niche theory; Brown *et al.*, 2013), it is also important to note that each locality (defined here as an area where environmental variables are homogeneous) can host multiple species simultaneously (Baldrian *et al.*, 2012; Krah *et al.*, 2018; Kubartová *et al.*, 2012). Fungal ecology is just beginning to explain the processes that produce these patterns, but neutral processes may also play a role. Research on symbiotic fungi suggests that both niche-based and neutral processes structure fungal communities in space (Caruso *et al.*, 2012; Dumbrell *et al.*, 2010). Unravelling the contribution of possible niche-based and neutral processes will require mechanistic insights based on a clear definition of spatial scales, local and propagule-like UCIs, and their role in the respective processes (Brown *et al.*, 2013).

VI. CONCLUSIONS

(1) Existing theory in spatial ecology has been developed focusing on unitary organisms. In effect, the concepts and

frameworks of spatial ecology, represented here by modern coexistence theory, do not facilitate research on modular life forms. We argue that conceptual development is an essential step in designing feasible coexistence research for complex modular life forms, as represented here by filamentous fungi.
(2) In addition, a closer integration of fungal community ecology and modern coexistence theory is missing. This integration could facilitate both fundamental and applied research on mechanisms that govern fungal biodiversity, and could benefit both disciplines.
(3) Answering these requirements for theoretical development, we used modern coexistence theory to define a practical concept of unit of community interaction. This is a conceptual development that facilitates feasible coexistence research for complex clonal life forms. This concept enables a focus on biological features that are primarily relevant to the process a researcher intends to study, and distinguishes them from complexities of clonal life forms that are of secondary interest.
(4) We showed that modern coexistence theory can be a very practical framework for navigating empirical research in the community ecology of fungi and other clonal organisms. It provides insight into which spatial scales and levels of biological organisation are meaningful to study. It places competitive interactions into a wider, holistic framework and elucidates natural history gaps.
(5) Our novel concept of UCI is defined as process-centric, always based on how the coexistence mechanism/model is defined. In this way, the concept is a simplifying one, meant to improve the tractability of the morphological and physiological complexity of modular organisms, enabling a focus only on those aspects of modular biology that are likely to be important to the ecological mechanism under study.

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