THE ROLE OF SPACE, DISPERSAL AND ACTIVE MOVEMENT IN FUNGAL COMMUNITY ASSEMBLY

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Herewith I certify that I have prepared and written my thesis independently and that I have not used any sources and aids other than those indicated by me.

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SUMMARY

Most of the theory of community ecology has been developed studying the unitary organisms. Therefore, the applicability of established theory to modular organisms remains unclear. Here we present theoretical developments that allow the community ecology of modular organisms to be firmly embedded within the established community ecology frameworks of modern coexistence theory and movement ecology. Within modular organisms, our primary focus is on filamentous fungi. The interplay of space and movement of organisms is critical for community assembly and species coexistence. Several research areas such as metacommunity theory, modern coexistence theory, and movement ecology aim to describe this interplay for animals and plants. These disciplines have assembled theoretical knowledge about the persistence and dynamics of biological diversity that is intended to be universally applicable to living systems. Applying theoretical concepts largely developed for unitary macro-organisms to filamentous fungi is challenging given their modular, network-like body structure. Here, we reviewed relevant knowledge from modern coexistence theory, movement ecology, and fungal ecology and developed two concepts that enable the application of established community ecology to filamentous fungi. We named these concepts unit of community interactions (UCI) and active movement of fungi. The first concept provides an operational definition of individual and population that is central to modern coexistence theory, but is problematic for clonal/modular life forms. This concept is introduced in the first chapter of this thesis along with modern coexistence theory applied to fungal systems. In the second chapter, we introduce the concept of active movement in fungi, demonstrating how the framework of movement ecology can be applied to filamentous fungi at all relevant spatial scales. We show that in modular organisms, physiological and morphological movements have a coupled ecological function and can thus influence community assembly via processes predicted by movement ecology. We further demonstrate this in the third chapter, where we describe the development of an agent-based model of hyphal dispersal in micro-structured environments and provide an initial evaluation of the model.

ZUSAMMENFASSUNG

Theorien zur Ökologie von Lebensgemeinschaften wurden großteils bei der Untersuchung unitärer Organismen entwickelt. Daher bleibt die Anwendbarkeit der etablierten Theorie auf modulare Organismen unklar. Hier stellen wir theoretische Entwicklungen vor, die es ermöglichen die Gemeinschaftsökologie modularer Organismen fest in die etablierten gemeinschaftsökologischen Rahmenwerke der modernen Koexistenztheorie und der Bewegungsökologie einzubetten. Innerhalb der modularen Organismen liegt unser Hauptaugenmerk auf filamentösen Pilzen. Das Zusammenspiel von Raum und Bewegung von Organismen ist entscheidend für den Aufbau von Lebensgemeinschaften und die Koexistenz von Arten. Verschiedene Forschungsbereiche wie die Metagemeinschaftstheorie, die moderne Koexistenztheorie und die Bewegungsökologie zielen darauf ab, dieses Zusammenspiel für Tiere und Pflanzen zu beschreiben. Diese Disziplinen haben theoretisches Wissen über den Erhalt und die Dynamik der biologischen Vielfalt zusammengetragen, das universell auf lebende Systeme anwendbar sein soll. Die Anwendung theoretischer Konzepte, die weitgehend für unitäre Makroorganismen entwickelt wurden, auf filamentöse Pilze ist angesichts ihres modularen, netzwerkartigen Körperaufbaus eine Herausforderung. Hier haben wir relevante Erkenntnisse aus der modernen Koexistenztheorie, der Bewegungsökologie und der Pilzökologie überprüft und zwei Konzepte entwickelt, die die Anwendung der etablierten Gemeinschaftsökologie auf filamentöse Pilze ermöglichen. Wir haben diese Konzepte Unit of Community Interactions (UCI) und Active Movement of Fungi genannt. Das erste Konzept liefert eine operationelle Definition von Individuum und Population, die für die moderne Koexistenztheorie von zentraler Bedeutung ist, aber für klonale/modulare Lebensformen problematisch ist. Dieses Konzept wird im ersten Kapitel dieser Arbeit zusammen mit der modernen Koexistenztheorie, angewandt auf Pilzsysteme, vorgestellt. Im zweiten Kapitel stellen wir das Konzept der aktiven Bewegung bei Pilzen vor und zeigen, wie der Rahmen der Bewegungsökologie auf filamentöse Pilze auf allen relevanten räumlichen Skalen angewendet werden kann. Wir zeigen, dass bei modularen Organismen physiologische und morphologische Bewegungen eine gekoppelte ökologische Funktion haben und somit den Aufbau von Lebensgemeinschaften durch Prozesse beeinflussen können, die von der Bewegungsökologie vorhergesagt werden. Wir demonstrieren dies im dritten Kapitel, in dem wir die Entwicklung eines *agent-based* Modells der Hyphenausbreitung in mikrostrukturellen Umgebungen beschreiben und eine erste Bewertung des Modells vornehmen.

THESIS OUTLINE

This thesis is a monograph work, consisting of introduction followed by three chapters, out of which one has been published (Chapter 2), and two are ready for submission to a peer-reviewed journal (Chapter 1 and 3). The general concluding remarks summarize all three chapters. All references are provided in a common reference section at the end of the thesis. Co-authors of the three chapters and their contributions are stated below.

Chapter 1:

Bielčik M, Schlägel UE, Schäfer M, Aguilar-Trigueros CA, Lakovic M, Sosa-Hernández MA, Hammer EC, Jeltsch F, Rillig MC. Fungal competitive coexistence and space: Bridging modern coexistence theory and fungal ecology.

Author contributions: All authors contributed to the conceptualization and writing of this review paper.

Chapter 2:

Bielčik M, Aguilar-Trigueros CA, Lakovic M, Jeltsch F, Rillig MC. The role of active movement in fungal ecology and community assembly.

Author contributions: All authors contributed to the conceptualization and writing of this review paper.

Chapter 3:

Bielčik M, Milles A, Aguilar-Trigueros CA, Lakovic M, Jeltsch F, Rillig MC. Model of interaction between hyphal movement and micro-structured environments.

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INTRODUCTION

General introduction to the thesis

With their role in organic matter decomposition and plant symbiosis, filamentous fungi are of tremendous importance in all terrestrial ecosystems. They are important human, plant, and animal pathogens, and they are widely used in the biotechnological and food industry. Despite this importance, research on their community assembly has been lagging behind the relatively more easily assayed communities of plants and animals. Due to methodological developments in microbiology, we have now opportunities to expand our knowledge on fungal community assembly(1).

Our initial attempts to derive hypotheses for fungal systems from established macro-organismal theory encountered a confusing cocktail of conceptual and technical challenges. It became obvious that before anything else, there was a need for conceptual development, a development which resulted in this thesis.

The thesis is divided into three sections, all focused on developing theoretical concepts and a framework that would facilitate research on the space- and movement- dependent community assembly of filamentous fungi.

The first section is focused on spatial aspects of fungal competitive coexistence, and introduces the concept of *unit of community interactions* (UCI) to tackle the problem of hierarchical individuality in filamentous fungi. The second section introduces the concept of *fungal active movement* to facilitate research on fungal community assembly at all relevant spatial scales(2). In the final section, we describe the development and details of an agent-based model (ABM) and provide an initial evaluation that highlights the potential role of fungal active movement in spatial niche partitioning at the microscopic scale.

Introduction to the first section

More in detail, in the first section we outline the meaningful spatial scales that fungal coexistence experiments should cover. In addition, we tackle topics related to context dependency of fungal competition and we argue for expanding our knowledge on basic natural history of fungi(3). Overall, we hope the first section will serve fungal ecologists as an introduction and invitation to the topics of modern coexistence theory (MCT). In explaining modern coexistence theory, there is a trade-off between intuitive language and language that is faithful to the mathematical foundations of MCT. Since one of the aims of this thesis is to *introduce* coexistence theory to fungal ecologists and to *motivate* fungal ecology for more cross-talk with MCT, we incline towards intuitive language. For explanations of coexistence mechanisms which are more directly linked to the mathematical models of coexistence, we recommend Amarasekare(4) and Barabás et al.(5). For application of MCT in empirical studies, we recommend Ellner et al.(6), Grainger et al.(7), and Godwin et al.(8). Finally, Grainger et al.(9) helps empirical ecologist to navigate theory.

The importance of spatial properties of the environment has been documented in fungi for diverse scales (10–12). Yet what are the spatial processes behind persistence or decline of the fungal biodiversity remains unknown. As a way forward, in line with the opinion by Peay, in the first section we argue for a theory driven, mechanism-focused research of fungal communities(3), which we believe has potential to bridge the gap between reductionist and holistic approaches in microbial ecology(13). Our focus on spatial aspects of MCT enables us to tackle two interrelated problems of fungal ecology: First, it enables us to delineate the *meaningful* spatial scales which research should focus on (14,15). Second, it enables us to address the challenge posed by implementing theory (developed largely for unitary organisms) into the realm of modular organism with hierarchical individuality (16–18).

Understanding the mechanisms that maintain fungal biodiversity is essential to make predictions about the impact of global change factors acting at different spatial and temporal scales, and to improve our mitigation and conservation capabilities (19–22).

However, applying the spatial aspects of MCT to filamentous fungi is not a trivial task. The network-like bodies of filamentous fungi and spatial complexities of their habitats cause each fungus to interact with others on multiple spatial scales simultaneously, from single hyphal tips to entire mycelia (2,23,24). Moreover, many empirical approaches in MCT require measurements of population dynamics over multiple generations (8,25). In filamentous fungi, the distinction between an individual and its population is not clear, nor is the definition of a temporal scale of generation (16).

Therefore, in the first section of this thesis, we begin by showing how MCT can be utilized to delineate the meaningful spatial scale and the level of biological organization practical for given study (18). 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 structure fungal communities, what spatial scales and *UCIs* are practical to follow for each mechanism (i.e. where the requirement for individual-hierarchy resolution can be lowered). In accordance with established theory, we organize spatial coexistence mechanisms into two major blocks(4): Those which can function in a spatially homogeneous environment, and those which require environmental heterogeneity. The former are colonization-related trade-offs and intransitive coexistence(4,5,26). The latter are spatial storage effect and growth-density covariance(5,27). Even though the intransitive coexistence stands (so far) outside of the MCT framework, no account of fungal coexistence can be complete without it. Each segment on particular coexistence mechanism ends with a section of *Where to look for it*. This contains the likely spatial scales and *UCIs* involved, in some cases also related additional considerations. On the one hand, we consider our selection of coexistence mechanism sufficient to demonstrate conceptual principles, and to serve as a bridge between MCT and fungal community ecology. On the other hand, the choice of not discussing coexistence mechanisms of *heteromyopia* and *spatial relative nonlinearity* has been made in order to prevent overly speculative discussion, given the insufficient state of knowledge in fungi related to them(4,27,28).

Thus, around the MCT framework, we first organize relevant knowledge in fungal competition, growth, dispersal, succession or interactions with environmental heterogeneity. Later, in the last section, we outline knowledge gaps and perspectives both for empirical and theoretical research, focusing on natural history and experimental approaches in fungal competition and coexistence(3).

Unlike previous similar work(29), we focus on the saprobic guild of filamentous fungi. That said, within the saprobic guild some species may have symbiotic phases (e.g. saprobes pre-colonizing resource as endophytes or parasites of trees(30,31)), and competitive interactions can be modulated by intraguild trophic interactions(32,33). Some aspects of this work are relevant to mycorrhizal species, and we use empirical knowledge on them whenever relevant. Yet, we choose to focus on saprobic fungi since more is known about the nature of their competition(34). In addition, the problem of coexistence in symbionts is likely more complex due to sophisticated trophic interactions with the host, and different community interactions within and outside of the host(35,36).

Introduction to the second section

In the second section of this thesis, we introduce concept of *fungal active movement*, in order to complement the connection of fungal ecology to spatial coexistence theory(2). The movement-related aspects of each organism are essential for studying spatial coexistence, yet in filamentous fungi movement is often reduced to the dispersal by spores. We provide arguments for this being inadequate. In the third section of the thesis, we then support these arguments by simulating the growth of mycelia in soil-like modeled microstructures.

In living organisms, movement occurs in a myriad of ways and on all levels of organization. This has been traditionally reflected in the division of life sciences into disciplines: cellular biology considers cytoplasmic flow or movement of organelles; physiology studies blood flow; while developmental biology describes changes in body part positions during growth. Movement ecology focuses on the movement of entire organisms and their propagules within the environment when searching for food, suitable habitats, reproduction, or avoiding danger.

However, this traditional distinction of biological movement into different domains of life sciences applies only for motile unitary organisms and propagules of sessile organisms. It becomes problematic once we consider modular organisms such as filamentous fungi. Their bodies are composed of filaments (hyphae) interconnected into a mycelial network. In the form of this network, hyphae forage by growing into new areas, and resource patches are integrated through cytoplasmic transport (37). Fungi use these very specific movement means to respond to the universal challenges presented by a heterogeneous environment. In filamentous fungi, the physiological, developmental and ecological functions of movement are not present as distinctive physical phenomena. They are intertwined within the dynamic processes of a filamentous body, and this often leads to the ecological function of movement being rather overlooked by researchers.

We argue that research in fungal community assembly can benefit from the explicit recognition of what we refer to as *active moment* in filamentous fungi: the translocation of biomass within the environment brought about by the organism's own energy resources. Using this term, we proceed to introduce fungi into the movement ecology framework in two steps which correspond to the conceptual developments within the field of movement ecology itself: In the first step, we draw upon the original concept by Nathan et al. (38) to demonstrate the presence of navigation and motion capacity in filamentous fungi. We also propose a definition of *active movement* which is: **i)** inclusive of all groups of organisms, unitary and non-unitary, motile and sessile, **ii)** and thus also extends the concept of the movement path towards a more diverse array of active biomass translocations.

In the second step, we use the extended movement ecology framework by Jeltsch et al. (39) that links movement ecology with biodiversity research to further strengthen our case for the recognition of *active movement* in filamentous fungi by showing that just like in other groups, the movement of a filamentous fungus has an effect on (microbial) community assembly both via mobile linkers (for example, bacteria can use fungi for dispersal), or by acting as a factor of intraspecific and interspecific interactions between fungi(39,40).

With the link between movement and species coexistence at the center of this thesis, the second section has two related aims: One aim is to use the movement ecology framework to define the *active movement* in filamentous fungi and to provide theoretical background to disentangle the ecological function of hyphal and mycelial movements from physiological and developmental functions. In doing so, we provide a concept which enables movement ecologists to tap into the research in filamentous fungi ecology. Second, we argue that the explicit recognition of *active movement* and adoption of movement ecology terminology will provide a more comprehensive treatment of the ecological implications of movement in fungi, and will fuel a new line of research in fungal ecology and community assembly.

As an important remark, we want to prevent our concept of *mycelial active movement* from being (mis)interpreted as an antipode to the seemingly *passive* dispersal by spores. First, spores can be actively moved by forces generated by the parental mycelium (41) (42). Second, we support the broad definition of navigation and motion capacity *sensu* Nathan (38), which accommodates evolved traits such as *when* or *how many* spores are released as a part of mycelial navigation capacity; as well as traits which make spores stick to mobile linkers (i.e. animal dispersal), or survive longer journeys, as a part of movement capacity (43) (44). In the second section, we also demonstrate universal applicability of our concepts to all clonal organisms, on examples of slime molds and clonal plants. While we demonstrate this on the concept of *active movement*, same applies also to the concept of *unit of community interactions.*

Introduction to the third section

The third section of this thesis covers the development and application of an agent-based model (ABM) developed with the aim of studying spatial niche partitioning in microstructures. The first fungal studies in *PDMS landscapes* demonstrated inter-specific variability of movement and navigation at the microscale, and evidence suggests that fungal navigation and movement capacities are tightly controlled and evolved as species-specific traits(12,24,45). Comparative studies of fungal species showed differences in traits such as branching angle, branching distance, or in responses triggered by the collision with obstacle (e.g. directional memory, sliding, collision-induced branching) (12,24,45).

Not only do fungi differ in the way they navigate microstructures, but natural micro-environments are themselves variable. They differ in their *architecture*, defined here as a composite term involving the degree of porosity and geometric properties of soil particles (46,47).

This opens the possibility that particular fungal species express different degrees of adaptation to different architectures, and the spatial features of microstructures alone can modulate fungal community interactions and assembly. One of the important functions of fungal hyphae and mycelium is foraging for new resources (11). Therefore, we chose foraging ability (defined as the maximum distance the mycelium can reach during the simulation) to demonstrate the potential of our ABM to study the spatial ecology of fungi at the microscale. We simulated the growth of fungi with different movement traits in various degrees of environmental porosity, and analyzed the differences in foraging ability between trait-porosity combinations.

The model has been constructed in NetLogo. This provides a user-friendly environment, which we hope will further stimulate the trait-based approach across research groups studying diverse fungal species. In order to increase the accessibility of the model to the broader audience, we provide a short introduction into individual/agent-based models (ABM), and a detailed model description.

1. FUNGAL COMPETITIVE COEXISTENCE AND SPACE: BRIDGING MODERN COEXISTENCE THEORY AND FUNGAL ECOLOGY.

In the first section, we develop the concept of unit of community interaction, and outline the connections and challenges for applying modern coexistence theory in fungal community assembly.

1.1. Spatial and biological scales

One problem of microbial ecology is a tendency for arbitrary approaches to space and spatial scales(14). Specifically for fungi, complex life histories, network-like body and hierarchical individuality can make application of even elementary concepts difficult(16,18,36). Here we show how MCT-related processes can be utilized to delineate the relevant spatial scale and level of biological organization in fungal mycelium (hereafter biological scale). For dispersal, we always refer to its broad definition, as movement that drives spatial population dynamics in the current or into new habitat patches(40). In fungi, active dispersal can include mycelial outgrowth(2,48).

1.1.1. Meaningful spatial scale

In microbial ecology, there is a growing recognition of the need for, and the difficulty of defining a meaningful spatial scale(14,49,50). 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 coexistence via heteromyopia or in intransitive networks (driven by mycelial interference(51,52)), 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.

Similarly, for coexistence mechanisms in metacommunities, the meaningful scales will be *local* and *regional*(4,53). Here, not only the Euclidian extent of scales varies. Also, the definition of *local* and *regional* depends on particular coexistence mechanism (or more broadly, metacommunity model): In the patch dynamics model, a particular habitat patch equals *locality,* and the assemblage of patches sufficiently isolated in space represents the *region*. (see below: *Coexistence in spatially homogeneous environments*).

For coexistence mechanisms related to the metacommunity models of *species sorting* and *mass effect*(53–55), *locality* is either an (isolated) patch, or (not isolated) area. In each case, locality must extend over the space in which the environmental conditions remain favourable for the focal species (i.e. *competitive rankings* are unchanged(4)), and which is large enough so the dispersal does not prevent aggregation of individuals in their favoured locality(4,27,56) (see below: *Coexistence in* *spatially heterogeneous environments*). Hence, *local* and *regional* is defined by the processes of interest and species traits (e.g. size, dispersal range).

Based on this, we briefly outline (exemplified on soil habitats(57)) what role in spatial coexistence we expect for Euclidian microscale, which is gaining considerable attention in fungal ecology. First, microstructure properties can contribute to habitat *connectivity* (see: below), influencing the dispersal between two patches(58,59). Second, we speculate that they can act as environmental variables of 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 in micro-environments (12,24,45,60–62), which also showed species-specific responses (traits) in navigating microstructures (12,60–62). This possibility of spatial niche partitioning is discussed in detail in the third section of this paper.

1.1.2. Meaningful biological scale: concept of unit of community interactions

The concepts utilized by MCT (e.g. *individual*, *propagule*, *population growth*) fit better to unitary organism than to networked mycelia with hierarchical individuality, indeterminate growth and convoluted life history(16,18). For instance, fungi have the ability to disperse as a spore, as a growing mycelium, or even as a symbiotic life stage(2,18,63,64). Thus, the task of applying MCT to fungi can become troublesome to unfeasible.

In order to simplify this task, we propose a novel concept termed *unit of community interactions* (*UCI*), analogical to Booth's *units of selection*(16), or to *unit of reproduction*(17). We argue the *UCI* concept is essential to facilitate the crosstalk between MCT and fungal ecology.

The concept allows for 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 a modular organism and its segments, (pseudo)organs and tissues. That is, rather than focusing on how the fungus is organized biologically (e.g. hyphal segment vs. spore, symbiotic phase vs. free-living), the concept highlights what role particular segments or biological scales play in a particular community process or coexistence mechanism. For instance, in defining *UCIs* it is of primary interest whether the dispersal is *local* or *regional*. It is secondary to irrelevant if the dispersal is by spore, mycelial outgrowth, or another life-history stage(48). Similarly, a mycelium can be defined as a single *UCI*, or as a population of lower-level *UCIs*. Crucially, the choice does not depend so much on the degree of physiological integration within the mycelium, as it depends 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 MCT's *individuals* and *propagules*. We first provide a glimpse of the concept's usefulness using an example, then the definition, followed by reasoning behind the definition.

Let us say a researcher aims to model coexistence of wood decomposing species, driven by competition-colonization trade-off among wood blocks (i.e. patches)(4,48,65). Some mycelia may extend between multiple resource units(11,48,66). As long as they stay physiologically integrated (contiguous), they can function as single networks, biological individual(16,67) (Fig.1,A). However, one individual being located *simultaneously* in two different patches (and local communities) creates a conceptual problem. MCT does not expect this kind of situation, and there is no concept or framework within MCT that could accommodate it. The problem can be easily solved if we refocus from biological individuals (i.e. contiguous mycelia) to *UCIs*. Then, the mycelium in each patch is perceived as a separate *UCI* regardless of the physiological integration, and mycelial cords spreading from parental patch are regarded as a form of highly competitive propagule-type *UCI*(68) (Fig.1,B, C, D). The degree of physiological integration matters in a manner analogous to the degree of parental plant's investment into a single seed(69).

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

The definition of UCI is as follows:

> *Unit of community interaction is* ***i)*** *a physiologically integrated entity (propagule, segment or a whole organism),* ***ii)*** *whose growth influences (and can be influenced) by its external competitive environment,* ***iii)*** *and has the capacity* to either produce, or to act as agent(s) of dispersal**.*

** capacity: 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. growth fronts, or mycelial cords subsidized by parental mycelium).*

*** dispersal is here any movement, by a spore or mycelial outgrowth, capable of reaching new habitat both in immediate vicinity or at larger spatial scale, and thus contribute to (meta)population dynamics*(40).

Our definition of *UCI* covers all biological 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*, *relative competitive differences*, *habitat variability* and *dispersal*(5,27,53). Following this definition, ***i)*** individual contiguous mycelia, ***ii)*** their local segments (ramets), and ***iii)*** specialized propagules can act as *UCIs*.

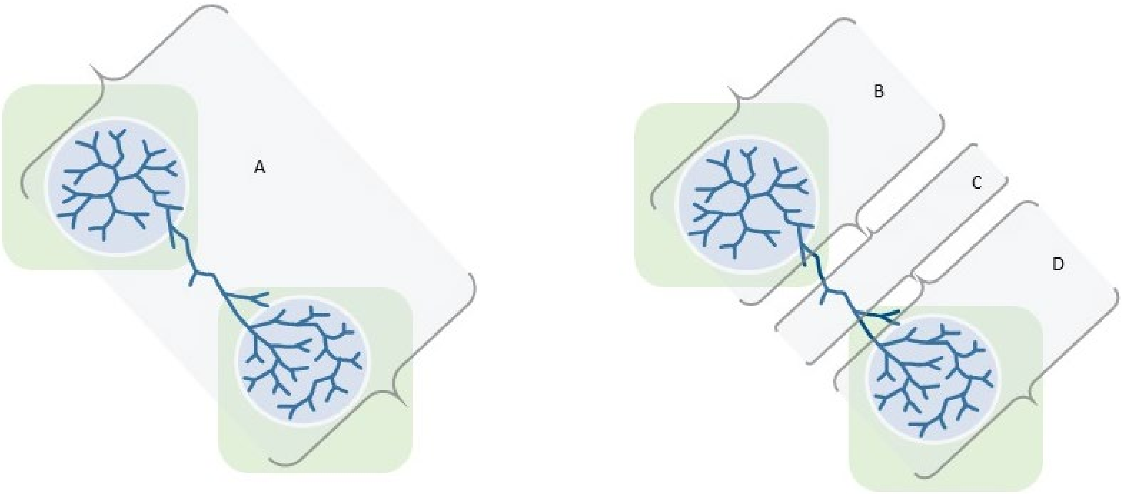

Figure 1. Concept of unit of community interaction (UCI).

*Depicted on the example of patch dynamics model. From biological perspective (**A**), the entire physiologically integrated mycelium is a single unit, an individual. Within the framework of coexistence in metacommunities, it is useful to distinguish (regardless of the physiological integration) between adult-like UCIs (**B, D**) and propagule-like UCIs (**C**), i.e. mycelia in local patches and mycelial cords dispersing between patches, respectively.*

The first condition of *physiological integration* excludes disconnected mycelia on the one hand. On the other hand, it includes physiologically contiguous mycelia created by fusion of genetically different individuals. If the mycelia descend from the same parental mycelium and keep the same genetic identity (i.e. single *genet*), they are likely to re-establish connection through anastomosis, meeting the condition of *physiological integration* again(70). However, we choose to be precautions over whether this is the case for all fully grown mycelia of all species, as it has been shown that also genetically similar conspecifics can engage in interspecific competition for space and resources (i.e. *mycelial deadlock*)(71). On the other hand, genetically different individuals of fungi can fuse into one mycelium, can then act as a single *UCI*(72,73).

To reiterate, while each *UCI* must be physiologically integrated, the converse is not true. Not each physiologically integrated mycelium must be a single *UCI*. It can be regarded as a population of lower-level *UCIs*. The operational choice depends, again, on the community process of interest. For instance, if the aim is to study interference competition, the contiguous mycelia are the best candidate for *UCI*. During interference, the response can be organized at the level of entire mycelium(23,74). Partitioning it into lower-level *UCIs* would likely obscure, rather than elucidate important processes. In contrast, in coexistence via growth-density covariance (see below), of *primary* importance is the ability to concentrate (population) growth in a favorable area(5,27,53,54). It is of *secondary* importance whether this growth remains physiologically integrated, or even whether it has the form of germinating spores or mycelial outgrowth. Thus, the theory justifies for simplification: All *UCIs*; spores or mycelial segments (contiguous or not) are assorted into one of the meta-community types, regardless of their biological character: population of locally dispersing *UCIs*, and regionally dispersing *UCIs*.

The second condition of *growth influencing (and can be influenced) by the external competitive environment* excludes (for instance) individual nuclei (*units of selection* by Booth(16)) from having the status of *UCI*. In accordance with MCT, the growth of any *UCI* must be affected by and affecting competitive environment (e.g. resources, predators, competitors)(27,75). From the perspective of a nucleus, the environment is the cytoplasm, not *directly* influencing the interspecific competitors or external resources.

The last condition of the *UCI* of having *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 colonization, mass effect dispersal)(53,76), and simultaneously sets the lower limit for mycelial segment (or fragment) which can still have the status of UCI. In theory, any segment/fragment can start a new mycelium following an outgrowth into new resource patch, or fragmentation by external forces(18,48,77). While in laboratory conditions, a mycelium can re-establish form a single hyphal tip, this is unlikely in natural communities, where the threshold for available biomass/resources to act as a unit of dispersal are likely higher. Similarly, mycelia of wood decomposers can persist in wood patches after the depletion of the resource base necessary to build a fruiting body (i.e. *available biomass/resources to produce unit(s) of dispersal*). 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 coexistence theory (78)

1.2. Coexistence in spatially homogeneous environments

To begin, we clarify the terminology of spatial ecology. Species coexistence theory makes a clear distinction between habitat *heterogeneity* (i.e. qualitative differences between patches) and habitat *structure* where patches can have the same properties (also referred to as *patchiness* or *physiognomy*(76,79)). If the environment consists of isolated patches, but the competitive rankings between species remain the same in all patches, the environment is structured, but competitively *homogeneous*(4) (Fig.2, A). Habitat *connectivity* refers to the interplay between movement capacity of the organism (in fungi both by spores and/or mycelial outgrowth(2)), and habitat features that influence the movement and survival rates between patches(80,81). In fungi, these can include diverse environmental variables such as soil porosity and microgeometry(58,59,62,82), distances between patches, wind characteristics(83), presence of animal mobile linkers(84,85), or microclimate enabling the growth of mycelial cords between habitat patches(86). Whenever we write about *heterogeneity* or *homogeneity*, we mean (unless specified otherwise) the *spatial*, not *temporal* properties of habitat(27).

1.2.1. Life history trade-offs in systems with patch dynamics

Competition-colonization trade-off

In fungal habitats, substrates often occur as patches with continual turnover, possibly enabling coexistence of multiple species via *competition – colonization trade – off* (later *CC-trade-off*)(4,65,87,88). New patches appear on a smaller scale due to the addition of new resource units (e.g. fallen trees)(89,90), or on larger scale through disturbances like forest fire(91). The coexistence mechanism is based on species being either superior at *local* competition, or superior at *regional* colonization. Thus, inferior competitors can maintain their populations through a fugitive strategy at the regional scale, arriving first at a new patch(Fig.2, A).

Conversely, coexistence via *CC-trade-off* will be prevented, if a species evolves to be superior both in competition and colonization(69,88), or if the inferior competitor can't benefit sufficiently from its advantage of superior colonization ability(4). This can happen if propagules of the superior competitor are a priori present (awaiting) in the environment, or the *connectivity* between patches is too high (4,53). In fungi, superior competitors can arrive first as a mycelium spreading through and/or awaiting in leaf litter(11,92–94). Hence, it might be no coincidence that the best evidence for *CC-trade-off* to structure fungal communities comes from ectomycorrhizal species in a habitat, where patches of trees are isolated by grassland not supporting ectomycorrhiza. That is, the habitat connectivity between patches is low, not supporting a priori propagule presence in form of mycelial outgrowth(95).

Still, in wood decomposing fungi, the species typical of later successional stages actually tend to be competitively superior(90,96). 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.

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 colonization ability(4). The trade-off is then not between *competition* and *colonization*, but rather between *competition* and *fast growth* (later *CFG-trade-off,* also can be referred to as coexistence in *successional niche*(4,97)). In fungi, this can be enabled by specializing 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(90,98). Eventually, fast-growers will be locally replaced by species that specialize on recalcitrant substrates, tolerate stress and invest in interference abilities(90). This means, the *CFG-trade-off* in fungi could be also called *persistence – growth rate* trade-off, depending to a varying degree on a mixture of stress tolerance and interference ability (90,99,100).

Where to look for it

When compared to *CC-trade-off*, conditions for coexistence under *CFG-trade-off* differ (4), 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 *CFG-trade-off*, the degree of isolation between patches can be lower (i.e. the expected spatial scales smaller)(4). *CC-trade-off* is likely to drive fungal coexistence only at larger spatial scales (e.g.

landscape level), so the dispersal of superior competitors can be sufficiently limited (4,95). As mentioned above, for mycorrhizal species this can be patches of mutualist plants isolated by areas which do not support the mycorrhiza. For saprobic species, ecosystems that undergo periodic larger scale disturbances (e.g. fire, logging), could be a candidate for coexistence via *CC-trade-off*(91). The involved *UCIs* are likely to be restricted to contiguous mycelia engaging in mycelial interference at local scale, and spores enabling dispersal across larger distances (plus pre-colonizing endosymbiotic stadium for inferior competitors (30,31)).

For *CFG-trade-off*, coexistence of saprobes is more likely, and could be possible also at smaller scales and less spatially structured environments (e.g. single forest floor), as long as there is a possibility for continuous turnover of patches, so there are always some in each successional stage of decomposition(4).

The *UCIs* involved can be more variable. While at the local patch scale, these will be still contiguous mycelia, colonization of new patches (i.e. wood blocks) can be driven either by spores, or by mycelial cords and mycelial networks awaiting in forest floor (11,92,93), or has a form of pre-colonization by endosymbiotic life stadium (30,31).

1.2.2. Intransitive coexistence in local neighbourhoods

To our knowledge, intransitive coexistence has not been integrated into the MCT framework(101). The reasons for this might be (partially) biological. Significant MCT developments are linked to research in plant communities. It has been suggested that plants compete in ways not supportive for emergence of intransitive networks(102) (but see:(103)). While in principle any kind of competition can be intransitive(104), interference (ubiquitous in fungi (90,105,106)) results in numerous possibilities for species-pair-specific competitive responses and outcomes(71,107), which in turn increases the likelihood of competitive hierarchies to become intransitive(23,108).

Analogous to a rock-paper-scissors game, intransitive (i.e. non-hierarchical) competition emerges in multi-species (i.e. minimum three) interactions, where no species is dominant over all others (Fig.2, B). Intransitive competition is well documented in fungi(52,90,105,109), and competition shifts towards less hierarchical interactions were shown to decrease/delay competitive exclusion(52,110).

In addition to competition rankings being intransitive, the requirement of lower competitive differences(105), and competitive reversals match fungal biology well(111). In wood decomposing saprobes, each successional stage is often occupied by many species(106). The competitive differences among species of the same successional stadium are expected to be less pronounced than between species from different successional stages(106). Competitive rankings and competition outcomes can be reversed by environmental variability(96,112), by changing spatial relationships between competing mycelia (51,110,112), by size differences(74,113), or by presence of a third species(51) (with another than intransitive higher-order interaction(101,114)).

Where to look for it

Intransitive coexistence is predicted to be more frequent in organisms with limited dispersal competing in local neighbourhoods(26,111,115)(Fig.2, B). In communities of interfering bacteria, intransitive coexistence was possible when interactions happened in local neighbourhoods, and mixing prevented coexistence(26). This is reminiscent of spatial scale of mycelial local neighbourhoods, where intransitive coexistence has been documented or suggested for fungi(51,52,110). Given the importance of mycelium-level organization in interference competition, the entire mycelium should be considered as *UCIs*, with emphasis on the degree of physiological integration(74). In fact, models of fungal competition show that intransitivity can be increased by the influence of mycelial resource transport (108).

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)(7,25). 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 stabilized, each species should be able to rebound from rarity.

1.3. Coexistence in spatially heterogeneous environments

There are three coexistence mechanisms dependent on environmental heterogeneity: *spatial storage effect*, *growth-density covariance,* and *spatial relative nonlinearity*(4,5,27). Each of them, or in combination, can generate a *pattern* of correlation between environmental heterogeneity and community composition: populations of competitors are concentrated (*sorted*(55)) each in its preferred *locality*, and coexistence is stabilized at the *regional* level (see above: *Meaningful spatial scale*)(Fig.2, C, D). We demonstrate fungal coexistence in heterogeneous habitats on *spatial storage effect* and *growth-density covariance*.

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(116): When the high quality habitat of a focal species is at the same time a low quality habitat for a competitor, then the high quality habitat is simultaneously the habitat of the low interspecific competition(4,5,53). This enables the focal species to grow when rare and build up population in a favourable area, and concentrates intraspecific over interspecific competition.

Growth-density covariance. We believe this mechanism is a highly intuitive one, with a very counter-intuitive name. In a more intuitive manner, it was called by Shoemaker and Melbourne a *concentration mechanism* (53): a *spatial process* must exist that concentrates species in their respective favourable areas (patches)(116). In sessile organisms, short-scale dispersal is crucial to the functioning of this mechanism (including the local dispersal by clonal outgrowth). In motile organisms, this can be further strengthened by directed movement towards favourable *localities*(117), a process analogical to mycelial growth directed into favourable areas (118,119).

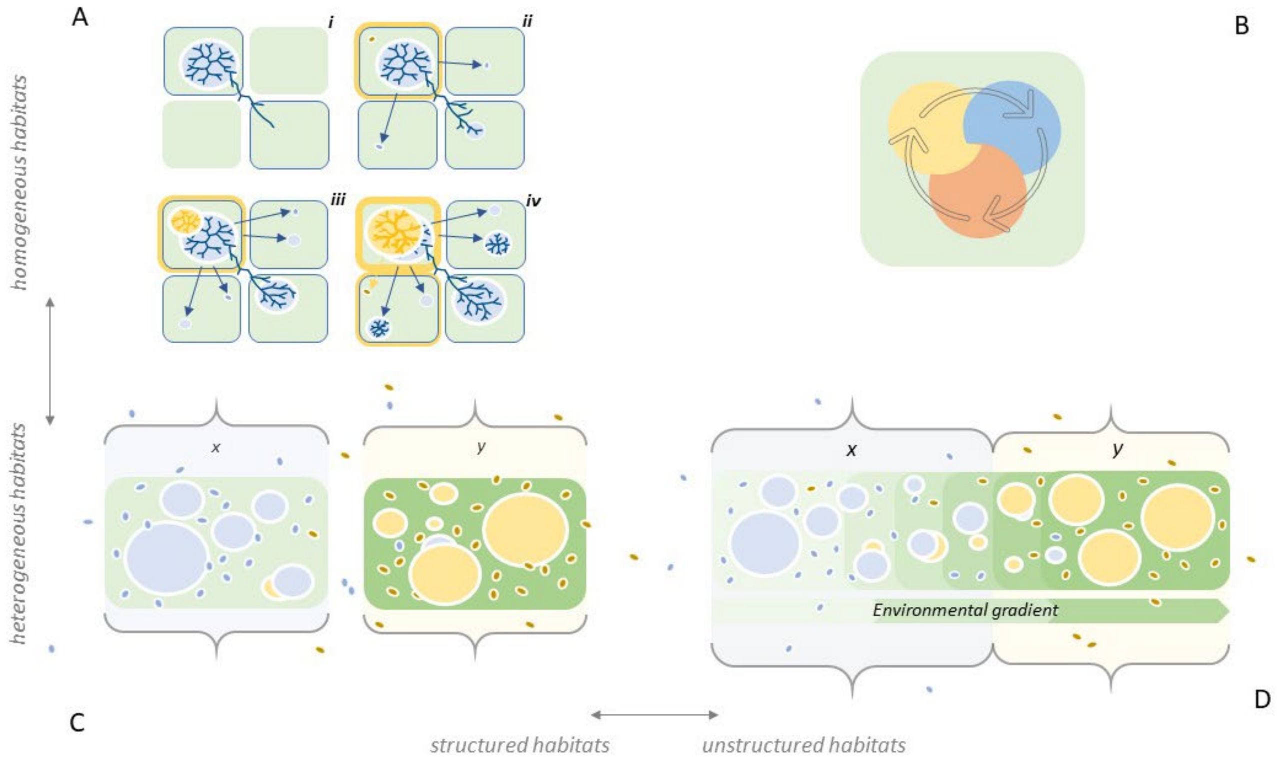

Figure 2. Types of spatial coexistence habitats.

*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**). Coexistence via colonization-competition trade-off (**A**) is depicted as a series of events (**i-iv**). Intransitive coexistence is possible in homogeneous and unstructured habitats, provided the competition maintains a certain spatial property, i.e. is limited to local neighbourhoods (**B**). Coexistence in heterogeneous habitats (**C, D**) is possible regardless of the habitat structure, provided the dispersal towards the unfavourable patches is limited. The competitive rankings must shift with environmental gradient, so blue species is competitively dominant in one area (**x**), yellow species in another (**y**).*

General 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 conditions must vary in space, so the competitive rankings between competitors can vary across the *region*(4,76)(Fig.2, C, D). Next, species must be able to concentrate their population growth in their preferred localities(56). While the *local* areas can be adjacent, dispersal between areas must be maintained under a critical threshold (i.e. concentrated within the favourable area) (Fig.2, C, D). What follows is that the spatial scale of the *local* area must be sufficiently large relative to the scale of dispersal(56). Among small scale heterogeneities, intensive dispersal would lead to mixing of species, preventing spatial niche segregation and coexistence. In *spatial storage effect*, not-too-high, *intermediate* levels of dispersal can maintain *unprotected coexistence* also at *local* spatial scale(4). *Unprotected coexistence* is a situation, in which a species is maintained in its *unfavorable* locality by a buffering effect of *source-sin*k (*mass effect*) dispersal from its favorable locality(4,76).
The last condition relates to the temporal dimension: For building up populations in favorable areas, species need sufficient time for population growth. Hence, the spatial heterogeneity must be sufficiently long-lived (i.e. rather spatial, than spatiotemporal(56,75)). In the following text, we examine how the outlined 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(69,88), and several aspects of fungal ecology make it likely: ***i)*** the observed correlation between environmental parameters and community structure(78,89,120,121), ***ii)*** the influence of environment on competitive rankings(29,122), ***iii)*** the ability of directed and indeterminate clonal growth(2,94,118,119), ***iv)*** spore dispersal being limited (83,95,123–126), and ***v)*** existence of life history trade-offs in response to the environmental parameters(99).

According to Kneitel and Chase, species differential responses to the environment always imply that habitat utilization has evolved alongside a trade-off, so in a heterogeneous region no species becomes a perfect utilizer of all local conditions(88). One class of trade-offs that can enable coexistence is between (broadly defined) competitive dominance and a density independent trait, e.g. mortality (127), stress tolerance(128), susceptibility to predation(129). Thus, it is of interest that a trade-off between competitive ability and abiotic stress tolerance has been shown to structure fungal communities(99).

The empirical evidence reviewed above makes heterogeneity-driven coexistence a promising area of research. Yet, none of these findings provide direct evidence of coexistence, and alternative explanations exist. The correlation between environmental heterogeneity and species distribution can be driven by processes other than the coexistence mechanisms discussed in this section, or by a similar mechanism, but on a spatial scale different that the one which was sampled in a particular study.

Where to look for it: spatial scales and environment types

Best candidates for heterogeneity-driven coexistence are habitats ***i)*** where the environment is heterogeneous in parameters known to alter competitive rankings(4,76)., ***ii)*** the *local* areas (patches) are sufficiently large so most of the dispersing *UCI*s stay within them(56), and ***iii)*** they are sufficiently durable in time, so the species have time to build up populations(56,75).
Regarding the characteristics of environment under ***ii)*** and ***iii)***, fungal species are likely highly diverse in terms of dispersal kernels and growth rate (or generation time). The former trait will affect what area (patch) is *sufficiently large*, the latter 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.

Small heterogeneities are less likely to maintain coexistence. For instance, in saprobic species able to grow and reproduce in small habitats (e.g. single pine needle, herbivore dung(130)), each of these microhabitats is ephemeral. Coexistence is more likely at the scale where these single ephemeral habitats aggregate both in space and time, e.g. a pine needle litter under a specific tree species, or a local population of herbivores.
At a larger spatial scale, coexistence is more likely. For example, microclimatic differences between forest edges and forest interiors may stabilize coexistence alongside the competition-stress tolerance trade-offs(99). At this scale, it is easier to imagine how diverse ecosystem processes (e.g. predation and disturbances) can enable rare species to invade favorable areas. Moreover, dispersal driven either by spores or mycelial outgrowth can easily remain allocated within the species favorable area (which is also likely to be more stable in time)(131).

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(53,56,76). 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 form of mycelial outgrowth or short-range spore dispersal (48,124,132). Therefore, all biomass of a given species (mycelial segments and spores) can be perceived as a sum (population) of lower level *UCI*s. More important than distinction between spores and mycelial fragments is the distinction between the fraction of biomass that stays within a favorable habitat and the fraction that leaves it(4,53). The latter fraction also includes biomass of sporocarps and other structures dedicated to dispersal of spores. Even though sporocarps *physically* do not leave the original location, they do “leave it” in terms of no longer contributing to competition in local community. The biomass and energy used for their growth can be no longer used for local mycelial outgrowth or competition(133). From the perspective of competitive metacommunity, this biomass is analogous to unitary individuals leaving the original locality, without ever making it to the new one (i.e. dispersal mortality).

While physiological integration does not affect the choice of meaningful *UCIs*, it can affect the spatial scale and character of the favorable habitat patch. Growth of species with a lower degree of physiological integration is more likely to follow the boundaries of their favorable patches/areas(134)(Fig.3, A). Conversely, species with higher degree of physiological integration may employ the process of clonal subsidizing in order to expand their area further (Fig.3, B). We may call the former *selective species*, and the latter *averaging species*. For *selective* species, the environmental heterogeneities are likely to provide more coexistence options, since the clonal *averaging* may diminish the spatial niche segregation (2,135)(Fig.3).

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

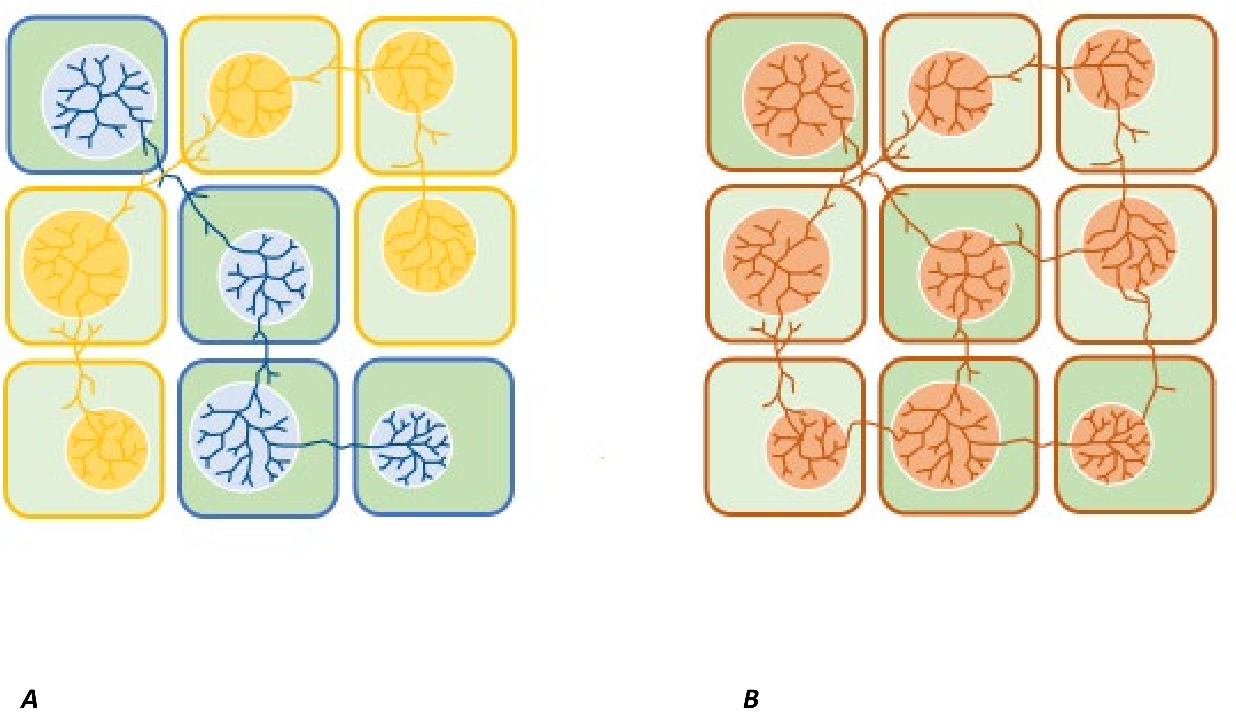

Figure 3. Spatial niche partitioning in heterogeneous habitats and mycelial integration. Fungal species with lower degree of mycelial integration (selective/specialists species, ***A****) have wider options for coexistence in heterogeneous habitats, as compared to the averaging-generalist species (****B****) with more intensive mycelial integration. Higher degree of mycelial transport and clonal subsidizing can lead to decreased biodiversity (****B****)*

1.4. Future perspectives

While a comprehensive discussion of MCT-inspired research in fungi would exceed the scope of this work, we focus on topics that we believe are most urgent. Our focus will be on soil systems, as here knowledge gaps are perhaps most prevalent. Thus, we begin outlining how MCT can inspire and navigate empirical research on fungal natural history(3). This is followed by a discussion of a broader approach towards fungal competition(90,106). Then we apply insights from these two blocks into how a fungal coexistence experiment may be set up. Finally, we introduce ongoing theoretical discussions with special relevance to fungi.

Importance of basic knowledge on natural history

To design a coexistence experiment, sufficient knowledge about the life history of competing species is needed. We demonstrate this with an intuitive example from the aboveground, macroscopic world.

Let us imagine we were to apply methods of environmental sequencing to study competitive interactions between the predators of a savanna. We target a gene of a hypothetical enzyme, dubbed *carnivorase*. It enables digestion of animal biomass (analogous to cellulases of fungal saprobes). Without knowledge of space-related traits usually unavailable in soil fungi (e.g. size, exact location and growth form in 3D space), we may conclude that in addition to hyenas, lions also compete with snakes, spiders, mantises, and even with blood sucking ectoparasites of lions. Needless to say, this would hinder our ability to estimate community interactions (and in effect, design a meaningful coexistence study).

The moment animal ecologists decide on the design of a coexistence study, they already know that studying competition between mantises and lions is unreasonable, and they can readily hypothesize that a single lion may act as a local habitat for various flea species. Similarly, plant ecologists can select an appropriate place in the landscape for coexistence experiment with perennial herbs. Beneath the tree canopy for understory species, away from it for open grassland species. These crucial choices are based on space-related life history knowledge, which appears trivial, as long as one does not study (soil) microbes(14,49).

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 realistically mimic and capture the community dynamics. For example, are co-occurring species differentially competitive in the same layer of soils(136)? Are both species affected by micro- and mesofauna of the soil(137)? How do they reproduce and propagate? Rather via spores, or mycelial outgrowth(48,68)? That is, is spore production a suitable ecological fitness estimate for both species, analogous to seed counting in plants(8,18)? We argue that one of the first tasks in the empirical research on fungal coexistence is to broaden knowledge on size differences, other spatial characteristics and trophic interactions of co-occurring species.

Size of the saprobic fungus

Upon visual observation in wood decomposers, an entire tree branch can be shared by only few large territorial individuals(30,138,139). Yet, sequencing-based and sporocarp-collection studies show dozens to hundreds of species (or operational taxonomic unites, OTUs) in a single log(78,89,121,140). RNA-based studies showed that this large biodiversity at small scale cannot be explained by the non-active DNA alone(121). It is therefore likely, that while some of the numerous mycelia do not expand 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.

Competition different than interference

Fungal competition is routinely studied in sterile conditions. In nature, trophic interactions can interfere with fungal competition in several ways, all of them potentially important for coexistence(75,141). For instance, they can ***i)*** drive apparent competition(142), ***ii)*** enable trade-offs between grazing resistance and other traits(88), ***iii)*** or alter the outcomes of interference competition(141,143). As grazing can act as biotic disturbance to established mycelia, we argue that experiments without grazing may overestimate the role of pre-emptive priority effects (i.e. underestimate coexistence) in fungal communities(144). It is easy to imagine that in enclosed microcosms, the fast-growing species will quickly pre-empt the available space and resources, driving systems into a 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(145), or influencing interference outcomes (acting as an equalizing mechanism(146,147)). Authors working with invertebrates hypothesized that top-down control is predominant in nutrients rich environments, where bottom-up control becomes less significant(145). Yet studies on mycophagous bacteria show potential of apparent competition to be important in a wider range of nutrient conditions. In oligotrophic soils (e.g. mineral layers, dune soils), mycophagous bacteria can feed on fungi and potentially affect community composition(148–150). Interestingly, mycophagous bacteria can feed on fungi in a speciespreferential manner(150,151), can reduce the growth of fungi in vitro(150), and have been shown to alter the community composition in field experiments(152).

In addition to excluding trophic interactions (compare to field plot experiments with plants), Petri plate experiments may overestimate the role of pre-emption and interference if rich media are used. 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 heterospecifics(71). Intermingling has been documented for saprobes on agar media(71), and for EMF in soil(153). It is therefore likely that just as in plant roots, interference prevails in resource rich conditions and exploitative competition in resource restricted environments(154).]

Microcosms to study soil species coexistence

Once species with known relevant traits are identified, we argue for development of soil community microcosms as a fungal analogy of plots used by plant community ecologists. Ideally, microcosms should enable establishment of community equilibria and measurement of population-level competition. For this, microcosms should contain model species of smaller mycelia sizes, should have an option for resupplying the system with nutrients, and include representatives of other trophic levels that are likely to modulate the population-level competitive interactions between fungi (e.g. bacterial communities, selected protists and invertebrate species)(147,155).

Important to note, not all coexistence studies require time series(7). Notably in annual plants systems, seed production is a fitness measure that enables one-time destructive harvest. Similar approaches could be applied in fungal species with analogous life history. Hence, another important trait to focus on is the life cycle. For fungi sporulating once in the life cycle (*semelparous*), destructive harvest experiments analogous to seed counting in annual plants may be feasible(18). In addition, an argument can be made that in these species conditions altering the resource allocation between mycelial growth and sporulation are of lesser concern (18,156).

While the understanding of fungal coexistence in soil is of high importance, we recognize that construction and maintenance of soil microcosms will require a significant effort. In the meantime, there are readily available experimental systems with properties essential for coexistence experiments (e.g. establishment of community equilibrium, natural context of interactions). These are the nectar yeast, and for filamentous fungi the Brun’s *cheesy and shitty* systems, i.e. microcosms of cheese rind and dung communities, respectively (130).

Future theoretical perspectives

In order to introduce fungi into MCT, we offered the theory mostly in its established form(27,75,76). Yet the field is undergoing theoretical developments. We highlight those that are most relevant to fungi. In addition, we outline theoretical developments that should be carried out specifically for the purposes of fungi.

First, original work by Chesson expects a fully deterministic mutual invasibility, i.e. there is no lower bound for invader's population size(27,75). In fact, theory expects that the lower the invader's initial density, the faster its initial growth. Importantly for fungi, species with positive intraspecific interactions (e.g. Allee effect) may only invade from a certain initial threshold density(7,157). When interference is a substantial component of competition, and interference ability is positively dependent on density (or mycelium size)(74), even potentially coexisting species may be unable of mutual invasion from low numbers (or spore count, or mycelium size)(158).

Another theoretical challenge is the role of intraspecific variability in species coexistence(159). Mathematical models on which MCT is based imply no within-species variability. Yet in fungi, the competitive ability depends not only on species identity but also on individual's mycelium size(74). Therefore, it is likely that theoretical approaches that address within species variability (especially for competition in local neighbourhoods) will become a valuable tool in fungal coexistence research(160,161).

Finally, an important conceptual feature of MCT is the dualism between *intraspecific* and *interspecific* competition. Yet in fungi, this dualism may be imprecise, since *intraspecific* interactions differ dramatically based on the ability of interacting mycelia to fuse(71–73). Mycelia of a single species that do not anastomose will compete for space and resources without establishing any degree of cooperation(71). In contrast, if mycelia anastomose, their constituent ramets will interact in both a competitive and cooperative manner(162). Therefore, we propose as future development to adapt MCT so it distinguishes between three types of competitive interactions: *intra-strain* (or *intra-clonal*), *intraspecific* and *interspecific*.

2. THE ROLE OF ACTIVE MOVEMENT IN FUNGAL ECOLOGY AND COMMUNITY ASSEMBLY

To provide comprehensive framework for studying movement- and space- related features of fungal community assembly and coexistence, we argue that the traditional view of fungi as sessile organisms that move only by spore dispersal must be abandoned. In the next section, we provide argument for this and introduce the concept of *fungal active movement.*

2.1. Active movement: definition

Movement is one of the means by which organisms interact with their environment. It enables them to respond to environmental challenges and to access resources. The first step in the process of adding fungal *active movement* to the movement ecology framework requires a revision of the definition of movement itself. We propose definition inclusive for all organisms that interact with their environment in the ways described by the movement ecology framework of Nathan et al. (38) and Jeltsch et al. (39):

The definition of *active movement* is as follows:

> *Active movement is any translocation of biomass sustained by organism's own energy resources, which is steered (navigated) in response to environmental clues and stimuli, or by environmental selection pressures, and can in turn result in a direct effect on the biotic and abiotic environment.*

Based on this definition, we show below how features of fungal morphology and physiology can be described as movement traits, how those traits enable the fungus to respond to its environment, and how these responses affect fungal community assembly. In doing so, we also align the (most important) movement ecology and fungal biology terminology.

2.2. Active movement in filamentous fungi; Nathan's movement ecology framework

Just like in motile organisms, in filamentous fungi the environmental cues and stimuli can influence the *internal state* of the filamentous fungus, and steer (*navigation capacity*) the translocation of the biomass (*motion capacity*) (38). This results in a particular spatial location of the fungal biomass in a particular time (*movement path*) (38).

Motion capacity

Three different kinds of translocation in hyphae and mycelium can enable a direct response to the environment, and can be recognized as forms of active movement: Hyphal (mycelial) growth (163)

(164), transport within the cytoplasm (165) (166), and migration (retraction) of the entire cytoplasm within a hypha (167).

In motile unitary organisms, the following is realized as three distinct, decoupled processes (Fig. 4):

(**A**) translocation of the entire organism (engaging with the heterogeneous environment, resource integration from different locations, escaping or attacking), studied by movement ecology.

(**B**) growth studied by developmental biology, and

(**C**) movement of the physiological fluids, maintaining homeostasis.

In contrast, filamentous fungi must respond to the challenges of their heterogeneous environment, homeostasis maintenance and developmental growth by intertwining all (**A+B+C**): Translocation of the organism is intertwined with growth (**A+B**). Movement of the physiological fluids can have both a homeostatic function, as well as the function of integrating resources from different patches in the environment (**A+C**). Also the entire cytoplasm can be moved from one location to another along hyphae (called the “hyphal channel” in fungal biology), and it is worth mentioning that in fungi several forms of cellular death can be seen as movement traits. If the mycelium at older locations degenerates (possibly recycling some of its own biomass) while outgrowing to new locations, the summary result can be a change in position of the entire organism, which is very similar to situations in typical motile organisms. Therefore, also processes such as autophagy should be recognized as movement related traits (168).

We point out that just like in other actively moving groups, motion capacity in fungi differs radically between species. For example, Olsson (169) let different species grow in Petri dishes with a source of concentrated C on one end, and a source of concentrated N on the opposite end, with the gradient of concentrations in between. While some species were able to actively integrate resources across all space and grow in the entire Petri dish, others were only growing in the central part.

In our concept, it is pivotal to make a clear distinction between the two main forms of ecologically relevant movements (movement capacities) in filamentous fungi, i.e. the translocation by informed growth, and the translocation by cytoplasmic transports (Fig.4). For example, the growth of hyphae is of primary interest in the dispersal of bacteria in soil environment, while the cytoplasmic transport acts in clonal subsidizing. However, it should be noted that in the development of fungal body, cytoplasmic streaming and hyphal growth are closely interrelated. For more details, we refer to the mycofluidics review by Ropert and Seminara (42).

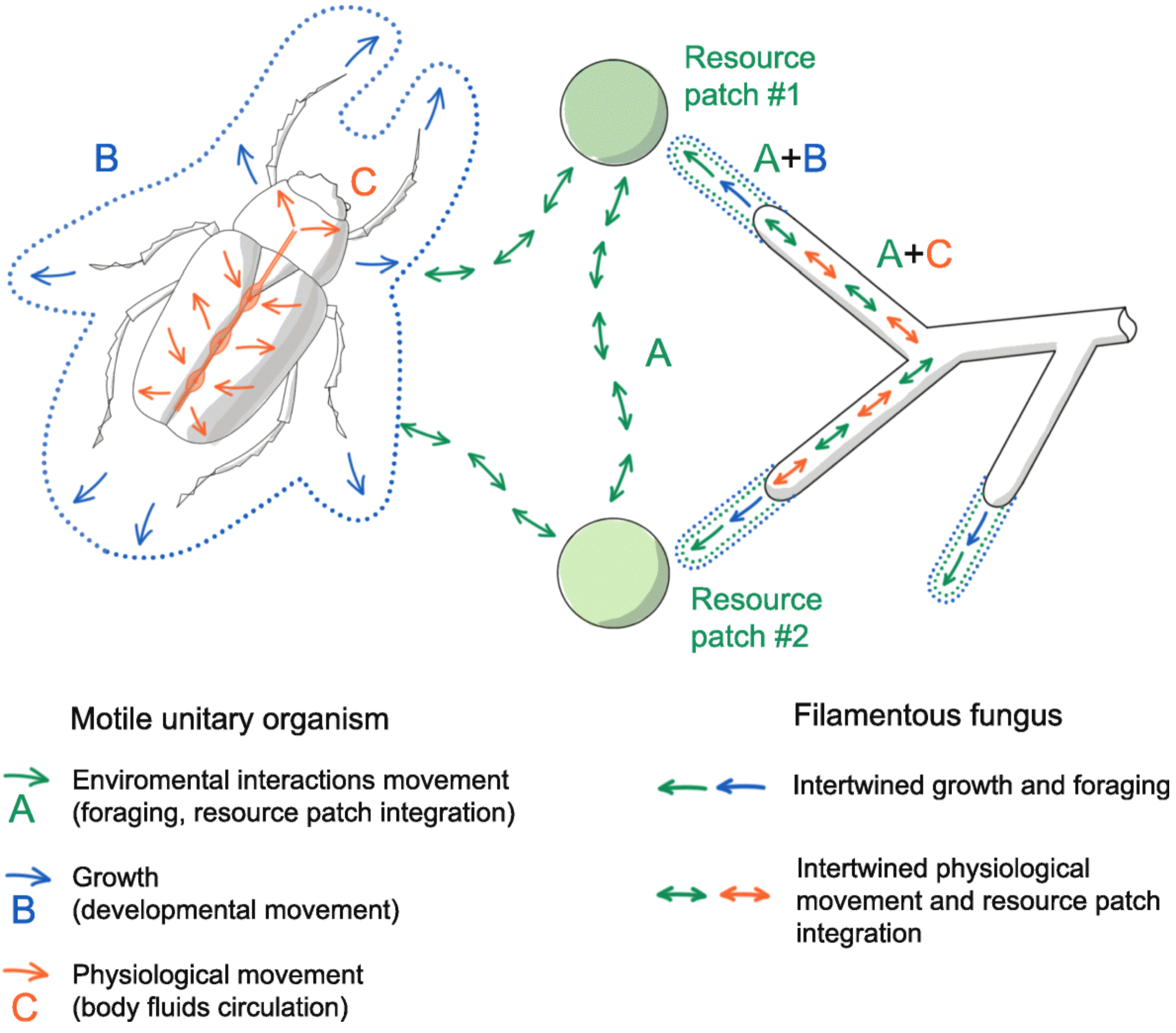

Figure 4. Main movement functions in unitary motile and modular organism (filamentous fungus). In motile unitary organism (left), the individual interacts with the environment by moving its entire body from one point to another (green arrows; ***A****). Physiological movements (orange arrows;* ***C****) and developmental movement (i.e. growth and morphology, blue arrows and dots;* ***B****) are present as distinctive processes. A filamentous fungus (right) has no capacity to move its entire body. Instead it intertwines the foraging with growth and morphology (green + blue arrows and dots;* ***A*** *+* ***B****), and resource patch integration with physiological movements (green arrows + orange arrows;* ***A*** *+* ***C****)*

Navigation capacity, internal state and movement path

Both, the growth of hyphae and transport of biomass within the mycelium can be *informed*, i.e. they react to environmental stimuli in order to facilitate interaction of the organism with the environment (170) (171). In terms of movement ecology, fungi clearly have navigation capacity (Fig. 5). Remarkable navigation capacities are known for example in the grass pathogen *Claviceps purpurea* (the ergot fungus), in which the hypha must pass through several different tissues in order to find its way from the spore germination site to the young floret which it targets (172).

The environmental factors which inform the navigation response (*"Where and when to move?")*, and thus alter the movement of hypha and other active biomass translocations (*movement path*) include:

(i) the availability and distribution of resources (173) (171) (174). The species specific variability in the morphology of the mycelium, for example "phalanx vs. guerilla" foraging strategy is an example of navigation capacity possibly enabled by the genetically coded memory (i.e. potentially selected for on the population level) (173).

(ii) presence of danger in the form of toxic substances or grazers (175) (176). When fungal mycelium is grazed, the interplay between the internal state (motivation to move and the physiological ability to move), and the navigation capacity can be complex: While intense grazing results (unsurprisingly) in decreased growth, moderate grazing can trigger reactions which can be either interpreted as compensatory growth, or escape mechanisms. Hedlund et al. (176) showed how the fungus *Mortierella isabellina* switches from the normal morphology to the faster growth and increased production of aerial hyphae, in response to the grazing by collembola. Authors suggest that aerial hyphae which grow in 3D space have a higher chance to escape the grazer within the pores of a natural substrate. In the Fomina et al. study (175), four different fungal species grew away from the localized sources of Cu and Cd. Interestingly, the response (negative chemotropism) decreased with enhanced availability of sucrose in the medium. Translated to the movement ecology terms, this study investigated navigation capacity also in the context of the internal state (i.e. improved physiological options for growing into areas with toxic metals, if enough energy is available).

(iii) presence of conspecific hyphae and mycelia. Hyphae of filamentous fungi are able to use chemotaxis to navigate growth towards other hyphae of the same species, for example between mating partners (177). Wood decomposing species were also shown to distinguish between different species of competitors, and change their growth between patches accordingly (178).

(iv) the physical structure and other physicochemical characteristics of the environment (179) (180) (181). For instance, in the Hanson et al. study (180), the hyphae were observed within the microstructured environment: Once the fungus grown on an open agar surface enters the microscopic maze, it is able to detect this change, and several growth (movement) parameters are altered. For example, the frequency of branching was increased. This study is also a good example of directional memory in fungi, and its role in navigation. Perera et al. (181) gives an example of how hyphae of dermatophytic fungi use contact-sensing in their navigation through the structures of the host tissues.

(v) the presence of a suitable host (in case of a parasitic or mutualistic fungi). For example, plant roots are known for releasing chemoattractants, which the hyphae use for navigation (174).

2.3. Active movement in filamentous fungi; Jeltsch's movement ecology framework

The extended movement ecology framework predicts that not only does the environment have an effect on the *movement path* (see examples mentioned above), but also the interactions that take place along the *movement path* have an effect on the environment, influencing community assembly (39) (Fig. 5). Just like in other groups, in filamentous fungi the focal individual (with its particular movement path) can act as a mobile link (see below) for populations of other guilds. At the same time and within the same guild, movement of this individual is an important factor of the fungal community assembly affecting intraspecific and interspecific interactions. Below we expand on these two effects of *active fungal movement*.

2.3.1. Hyphae as mobile linkers

The effect of nutrients transport by fungi (i.e. resource mobile links) has been intensively studied in the context of fungus – plant mutualism (182), but the fungi also act as resource mobile linkers for the members of microbial ecosystem. In analogy to the migration of salmon and feeding habits of bears, which results in creation of nutrient mobile link (183), also the nutrients transported by hyphae can be accessed and released by mycophagous bacteria (184). However, the nutrient links can have a less dramatic form, where the fungus is not destroyed: In nutrient poor and dry microhabitats, populations of bacteria can be maintained by hyphal transport and excretion of nutrients and water (185). Mycelia are also able to transport organic contaminants, making them available for biodegradation by soil bacteria (186).

Hyphae of filamentous fungi also act as genetic mobile linkers for populations of soil bacteria (187) (188) (189), by providing a network of pathways, which bacterial species can use for their dispersal.

In soil, bacteria can typically only move in the water phase. In dry conditions, this can decrease the habitat connectivity. However, connectivity can be improved again by the presence of hyphae surrounded by a water film (188). The dispersal ability of bacteria on fungal hyphae appears to be a result of a complicated interplay between the traits of both partners. Different fungus - bacteria species combinations show different dispersal potential (190) (191), and the effect has been already shown to influence bacterial community composition (191). Hydrophobicity decreases the dispersal potential of the fungus (190) (192). On the bacterial side, the ability to actively move within the water film is important (188), although evidence for passive dispersal also exists (190). The example of *fungal highways* and *fungal pipelines* (the terms often used in fungal biology for genetic and resource mobile linkers, respectively) also demonstrates how the adoption of general movement ecology concepts in fungal ecology needs to take into account the specifics of microbial communities. For example, since in bacteria the dispersal propagules are usually metabolically active cells, often the function of genetic and resource mobile linker is closely related. As shown above, the fungus not only serves as a passive scaffold, but the dispersal can be further facilitated by provision of nutrients. Dispersal can be also accompanied by the function of *process linkers*. These can be localized pH alterations (193), or *antibiosis*: By creating microenvironments with antibacterial properties, fungi can preferentially spread antibiotic resistant strains (194). An interesting example is the movement based mutualism between the filamentous fungus *Aspergillus fumigatus* and the swarming bacterium *Paenibacillus vortex* in soil. The conidia of the fungus, unable to actively move, can be transported by bacterial populations for distances of at least 30 cm, including from places which do not support fungal growth, into the niches of *A. fumigatus*. In return, the hyphae of the fungal partner serve as bridges for *P. vortex* across soil pore air gaps, which *P. vortex* would be not able to cross on its own (195).

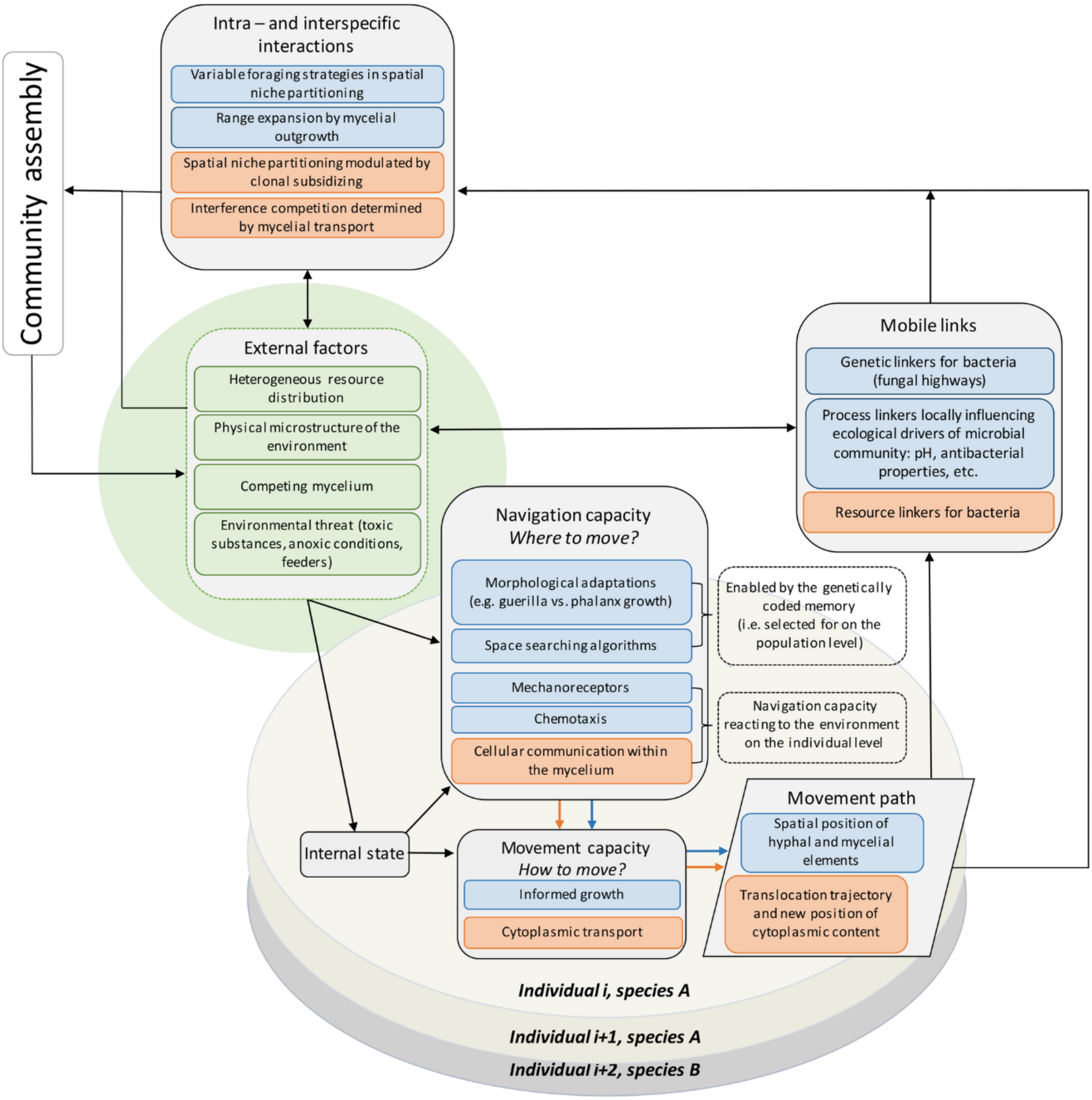

Figure 5. Movement ecology framework adapted for the biology and ecology of filamentous fungi. Original graphical representation of the framework by Jeltsch et al. [4] is combined with fungal movement related phenomena. Blue boxes are related to fungal active movement enabled by informed growth. Orange boxes are related to fungal active movement enabled by cytoplasmic transport

2.3.2. Role of active movement in intraspecific and interspecific interactions of fungal communities

Our knowledge of community interactions and assembly in filamentous fungi is still limited, despite the recent advances in this field (1) (196) (197) (198). We argue that this research will benefit from explicit recognition of fungal *active movement* within its ecological context. Below we revisit topics related to fungal intraspecific and interspecific interactions through the lens of movement ecology. Namely mycelial outgrowth as a form of dispersal, mycelial and hyphal foraging, interference competition, and mycelial translocation in clonal subsidizing.

Growth and dispersal

Filamentous fungi can regenerate from small hyphal fragments. This means that any type of growth brings also a potential for dispersal. However, this type of dispersal has rarely been addressed in the context of movement ecology, which we think is a missed opportunity. For instance, since colonization is not only restricted to production and release of spores, then addressing the fundamental movement ecology questions of why the fungus grows in exploration mode (e.g. active avoidance of competitors, search for different resources), how is it able to do it (e.g. changing mycelial architecture or growth rate) and when and where to explore (e.g. what cues determine hyphal direction) would better reflect its colonization ability, and may give us a more detailed insight into traditional mycological topics, such as genet mapping (199) (200). An example of this approach (i.e. how navigation capacity of a foraging fungal individual affects the dispersal on the population level) has been already embodied by Boddy et al (201). Authors decided to tackle dispersal by mycelial outgrowth and the resource capture (foraging) as almost synonymous terms. We imagine that this kind of terminology may leave most of the animal ecologists surprised. However, it follows closely and correctly the biology and movement ecology of filamentous fungi.

Foraging strategies and niche partitioning

Fungal ecologists have long recognized the existence of different foraging strategies while a fungus explores for resources. These include the creation of mycelial cords dedicated to foraging (173), ability to cross an obstacle, or decisions to forage in areas with diverging resource supply (164). Agerer (202) describes up to eight foraging strategies that root mutualistic fungi exhibit. Boddy and Jones (173) pointed to the morphological variability in fungal species, which can be identified as ‘phalanx and guerrilla’ foraging strategy. Studies of hyphal movements at the microscopic scale also show that foraging strategies (*space searching algorithms*) differ between species (203).

Using the movement ecology framework leads to discussing these findings in terms of coexistence. For example, if species differ in foraging related traits such as the effectiveness of exploring different geometry, then this can lead to spatial niche partitioning.

Active movement and fungal interference competition

Interference competition (also known as *fungal combat*) is a well-documented factor of fungal community assembly. We believe the movement ecology framework can offer a new perspective here, since *active movement* plays an important role in two ways: in preemptive competition and in mycelial transport.

Preemptive competition has been identified as one of the main drivers of the fungal interference competition (204). It is known in fungal ecology, that the larger the territory of the mycelium at the moment of contact with the competitor, the higher the likelihood of winning the combat (205) (206) (204) (207) (208). The ability of preempting the available space (i.e. primary resource capture) is given by the growth rate of the mycelium. Just like with the directed hyphal growth, this type of growth can also be seen as active movement: Because the incentive to translocate biomass across the space is not only developmental (growth), but also ecological (to capture territory and nutrients). Hence, it is not only an analogy to animal growth (increasing the biomass), but also to the animal increasing its fitness by gaining and keeping a territory with its resources (biomass translocation). Besides, preemptive growth is also influenced by the navigation capacity of the fungus, and it can be regarded as a trait important in inter-specific variability.

In order for the home range advantage (territory size) to work, the mycelium must not only occupy the resources. Interference competition is resource costly and in an environment with patchy resource distribution the outcomes can depend also on the differences in the ability of the fungus to effectively integrate resources via mycelial transport (171). Perhaps because this is an obvious conclusion to make, and because of technical difficulties to measure (209), mycelial ability to transport has been - to our knowledge - not explicitly taken into account (i.e. not quantified) in fungal combat experiments (but see Lindahl et al (207)). Rather, the size of the territory is usually measured, and the influence of transport on mycelial combat outcome is black-boxed, together with other species traits, such as the ability to produce particular biochemical agents, or morphological fortifications. For example, a recent study by Kolesidis et al. (204), which we believe is a state of the art in fungal interference competition studies, identified six parameters which can predict the combat outcome. Among them the mycelial extension rate and relative size of the combating mycelia (see above: preemptive competition). The ability to translocate resources is involved in these parameters, and the model parameterized without disentangling it as a separate parameter, can still predict the competition outcome. However - as the authors also discuss - this may not be the case in other instances, for example in a natural environment witch patchy resources distribution. Indeed, the experiment was done using a homogenous agar medium. In nature, where resources are patchily distributed across larger spatial scale, interspecific variability in transport capacity can play a major role. The existence of this kind of variability has been already shown in different contexts than the interference competition (169).

In the context of interference competition, the importance of transport ability, although not assessed as a trait value across species, was directly or indirectly shown in several studies. When extra resource was made available to *Hypholoma fasciculare* and *Phanerochaete velutina*, there was no difference in the combative ability related to the position of this resource (which was either distal or proximal to the combat zone) (205). This suggests that the resources from the distal part were readily available in the interference zone. In another study, the resource bases of two species (one saprobic and one mycorrhizal) were separated by a column of soil. Still, the size of the resource base determined the outcome of the interference interaction. The size of the resource also determined the morphology at the interference zone. This is an explicit example of the involvement of mycelial translocations in the outcome of interference competition (207). Transport can also be hypothesized as one of the reasons behind the observation that spatial configuration of mycelia influences the combat outcome, irrespectively of the mycelia size (210).

Given our knowledge about the importance of mycelial transport in interference competition, and our knowledge about the variability in transport abilities from different research context, we can envision studies which track the impact of mycelial transport on interference competition in a more explicit way: With mycelial translocations being quantified as a movement trait value across various species. And with the mycelial translocations seen as active movement phenomena, where questions like when and where to move are central. Hence, in a way similar to how movement ecologists look at the relationship between the movement and competition.

Nutrient translocation in a heterogeneous environment, and clonal subsidizing

As described above, filamentous fungi can use mycelial transport to integrate resources from different patches, but this movement ability (trait) differs among species (169). It is therefore possible that species coexistence can be promoted alongside the trade-off between the ability of resource integration and the faster growth. Similarly, species may differ in the ability to transport metabolites into the parts of mycelium, where their primary production is temporarily not possible due to locally adverse environmental conditions (for possible trade-off in fungal network cost and transport efficiency, see Heaton et al (209)). The ability to transport nutrients and metabolites across the entire mycelium (i.e. genet) in order to support local parts (ramets) is a feature not unique to filamentous fungi. It connects them for example to clonal plants, where the impact of this form of *active movement* has been already studied within the coexistence context (see below and (211)).

2.4. Interdisciplinary opportunities between movement ecology and fungal biology

There are several ways in which we expect our concept to facilitate interdisciplinary collaboration among movement ecologists and fungal biologist, which would be beneficial for the development of both fields. Here, we expand on several specific examples.

Use of common language and concepts to assist data and theory synthesis

Our concept can improve the transfer of knowledge from fungal ecology to movement ecology. As shown above, the concept enables to translate the relevant knowledge in fungal ecology and biology into a form accessible for movement ecologists. We argue that this is needed given the research gaps in movement ecology; Holyoak et al. (212) identified the problem of inconsistent movement terminology among different taxonomic groups and disciplines. Moreover, they admit that their review was probably biased against microorganismal movement. This happened, because during the screening for relevant articles, they had to exclude several keywords often used in the microorganismal movement research (e.g. *chemotaxis*). These keywords proved to be impractical, as using them identified a large number of articles relevant rather for the fields of molecular biology and cell biology. In fungal biology, movement phenomena are often described using specific terminology. For example, the results of the studies about fungal *space searching algorithms* are highly relevant for (fungal) *foraging* topics, however the term *foraging* was not used in the articles which we reviewed (213) (203) (214) (180). Had these researchers discussed their findings within the context of foraging, this work would have reached a broader audience and facilitated knowledge transfer. Similarly, we hope that our concept will inspire a debate among fungal ecologists to discuss fungal nutrient translocation also as a form of *nutrient mobile links*, and to complement the term *fungal highways* by the established ecology term *genetic mobile links*.

The concept of *active movement* based on movement ecology can also have a unifying function within the field of fungal ecology and biology. There are now several research groups which work on topics (potentially) related to the *active movement* of fungi and its relevance for microbial ecosystems. Lynne Boddy pioneered the use of established ecological terminology (e.g. *foraging*) advocated above, but she also went further and conceptualized several *active movement* related phenomena as an important factor in the ecology of wood decomposers (for an interesting example, see (173)). Further, clear links between movement and community assembly are now made by the researchers of *fungal highways,* I. e. fungi as *genetic mobile links* for bacteria, and we already pointed out the potential of the *space searching algorithms* research (see: above). We argue that these and other research lines could acquire an added value, if the results were made comparable by discussing them within our unifying framework.

Finally, movement ecology can develop truly universal concepts and terminology only if it includes all ecologically relevant movement phenomena in all groups of organisms. This is a general aim of the discipline (38). Yet we argue that focusing on animals and propagules of plants leads to sometimes missing this general goal in particular instances. For example, movement ecologists describe the object of their studies as movement of *whole organisms* and *propagules* (38) (212). The adjective *whole* is used to exclude movement types not directly relevant from the ecological perspective, e.g. the movement of appendices, or physiological movements. As we have shown above, this is perhaps too restrictive. Explicitly recognizing the ecologically relevant *active movement* in diverse groups can improve this terminology (see above: Active movement: definition; or Fig. 4 and Fig. 5).

Movement ecology, fungal ecology, and communities of plants

Most movement ecology research is focused on motile unitary animals. For this kind of research, unitary motile microorganisms (bacteria, yeast, protists) will be probably a better model system than filamentous fungi. Fungal movement and interactions with the environment are probably too different to serve as a useful model for studying the ecology and evolution of motile unitary organisms. For the same reason however, the overarching framework provided by movement ecology can be very useful in bringing closer together the research on ecology and evolution of clonal plants and filamentous fungi.

As shown by Boddy and Jones (173), there are clear analogies between the *active movement* (growth) of fungal mycelium and clonal plants. Using common terminology and concepts can facilitate integrating theoretical knowledge from clonal plants research into fungal ecology. Conversely, filamentous fungi with their short generation time, feasibility of laboratory cultivation and accessible genome can prove to be useful models to advance research on movement ecology and evolution of clonal metazoa. Evolutionary experiments in fungi similar to those in plants, with selection pressure on phalanx vs. guerilla foraging could be designed (215). With our current state of knowledge, it is also easy to imagine how fungal ecology could benefit from answering classical questions in clonal plants ecology, as summarized for example by Callaghan et al. (216), or Liu at al. (217): As we already mentioned above (in the context of genet mapping), both fungal and plant ecology are interested in questions around what is the relative contribution of clonal spread vs. dispersal by sexual spores in natural populations, e.g. what is the relative contribution of different dispersal modes in different species and environmental conditions (199) (200) (218) (219)? How does transport of nutrients work in order to increase the likelihood of genet survival? To what extent do ramets collaborate as part of one individual, to what extent do they compete as interconnected individuals, and what is the role of directed growth and transport in this? Further, can clonal integration in fungi decrease species richness by bypassing the niche partitioning options otherwise provided by environmental heterogeneity (211)? Similar to the situation in fungi, in plant ecology there is also limited knowledge about how clonal integration and related movement traits are translated to the community level (217). Experiments with communities of filamentous fungi are less demanding in terms of both space and time, while assaying the analogous experiments in clonal plants can be more straightforward. Hence, experiments on clonal plants and fungi can complement each other. Model organisms would need to be selected taking into account traits related to clonal *active movement* and environmental interactions. For this, our unifying concept and terminology based on movement ecology framework will be useful.

Navigation and motion capacity in fungi and slime molds.

Our movement ecology-based perspective on *active movement* can be applied to all modular organisms. In addition to clonal plants, another notable example is the case of slime molds.
In plasmodial slime molds, navigation and movement capacity has been studied extensively (although not termed this way). What is interesting from the comparative perspective is that these two groups of organisms, however phylogenetically distinct, combine remarkable similarities with important differences.

Both have a clonal and undetermined body plan with hierarchical, transitory biological individuality: The original individual can be separated into several, independently moving individuals, while, unlike in clonal plants, these newly formed individuals can later merge again (220). In terms of movement ecology framework, a perfect intraspecific competition (i.e. isogenic individuals are expected to compete for exactly the same niche space) can be swiftly converted into perfect cooperation, upon the merge of two isogenic individuals into one.

In both groups, navigation capacity occurs without any neural system, or any other processing center. Both filamentous fungi and plasmodial slime molds intertwine the developmental growth function with the foraging movement function (Fig. 4) (221). Foraging is realized either exclusively (fungi) or optionally (slime mold) by the informed growth of the reticulated network of tubes, and it is likely that there are similarities in the mechanism of signal propagation, critical for navigation capacity (222).

In both, the physiological (i.e. homeostasis) function of body fluids (cytoplasmic content) is intertwined with the ecological function of integrating different resource patches (Fig. 4) (221). The network of the mycelium and plasmodium can be remodeled in order to interconnect the resource patches in an efficient way (223) (224) (163) (201).

While most studies about *Physarum polycephalum* did not address the community level, there is one notable exception. Reid et al. (225) studied how slime molds respond to the extracellular secretion (used to mark already explored patches). Its navigation capacity can inform the organism not only about the presence of secretion, but it is also able to distinguish between conspecific and heterospecific secretion. If no fresh patch is available, the slime mold will move into the patch with the heterospecific secretion (after an individual of the same species, there will be fewer resources left). This study clearly demonstrates that not only in animals, movement acts as a factor in community interactions, which can be fully described using the movement ecology framework *sensu* Jeltsch (39). Another important lesson from this and similar studies of *Physarum polycephalum* is that even in microbes, the navigation capacity and its effects on community level is not limited to simple responses to environmental cues (e.g. positive or negative chemotaxis), but involves higher order processing, analogous to “decision making” in animals (see also (226) (221)). In fact, indices exist that filamentous fungi are also able to “make decisions”, which in turn can affect community composition. Boddy and Abdalla showed how mycelia can preferentially colonize (discriminate between) resource patches of different quality in terms of presence/absence of a competitor, or even discriminate between competitors of different species (178). In a study by Holmer and Stendil (206), the cord-forming species *Resinicium bicolor* changed the direction of cords depending on how much resources were available for the combat. In cases when the replacement of the competing *Heterobasidion annosum* was possible, *R.bicolor* oriented its cords towards the competitor. In cases with lower resources availability, *R.bicolor* oriented its cord away from the competitor. It would be interesting to study how the movement related “decision making” of fungi differs between different species, and how this trait affects the community composition.

However, there are important differences between the movement-like phenomena in slime molds and filamentous fungi. First, in fungi, individual hyphae (i.e. a filament) explore microscopic soil structures while forming a potentially macroscopic mycelium. In contrast, in slime molds, the soil microstructures are usually explored by the microscopic (single nucleus, non-plasmodial) amoeba or amoeboflagellate, which is an independent life cycle stage (227). Second, it is true that some fungi are able to recycle their biomass, which in effect can lead to the translocation of entire organisms. However, this always depends on informed growth on one site of the mycelium, and degradation on another. In contrast, plasmodial slime molds are able to use amoebal movement to translocate their entire body, while this movement does not need to be intertwined with the (informed) growth and biomass recycling. In other words, they are able to translocate also in a more “classical”, animal-like way (227).

And finally, while both slime molds and fungi need to avoid foraging in already explored patches, the mechanisms which they apply are rather different. Slime molds use an extracellular secretion (external memory) to mark already explored patches (225). In contrast, fungi use hyphal space searching algorithms (213).

3. MODEL OF INTERACTION BETWEEN HYPHAL MOVEMENT AND MICRO-STRUCTURED ENVIRONMENTS

In the sections above, we outline the possibility of interspecific differences in hyphal movement to generate spatial niche partitioning. In the following section, we explore this in more detail, by developing an agent-based model of hyphal propagation. We describe the concept and technical details of our model, developed to achieve a high degree of structural realism, with multiple parameters derived from structural traits of real mycelia and empirical PDMS research(12,24,45).

3. 1. Agent-based models

Given that application of individual/agent-based modelling (ABM) in fungal ecology lags behind its application in ecology of plants and animals, we provide first a short introduction to its potential and limitations, followed by a detailed description of the model itself, including its code. An advantage of ABMs is that they do not require the individuals and their interactions to be treated as a population-scale, averaged parameters typical of mathematical (analytical) models(161,228). In ABMs, system behavior is an emergent property of interactions between individuals and their environment. Variability among individuals, local environments and their interactions can be maintained, increasing the ecological realism of the system. Thus, ABMs are particularly useful in systems and research questions where individual variability is expected to play a significant role, or where properties of local interactions and local neighbourhoods cannot be meaningfully averaged at a higher spatial scale (161,228). In case of our model, each hyphal tip acts as an individual, independent agent. What follows is that each encounter with microstructure and other hyphae has also its unique outcome, based on spatial variables such as angle of encounter or local density of hyphae.

A disadvantage of ABMs compared to analytical models is that it is not readily evident what are the pathways of emergence, i.e. how exactly the processes at the scale of individual agents lead to the observed patterns at the entire system level. Related to this, ABMs are more complex than analytical models(160,229). To alleviate this downside, the emphasis in publishing the ABMs is on detailed, accessible and transparent descriptions, which in turn should improve the interpretability and reproducibility of the results(160). In following sections, we describe the model in close detail.

3.2. Overview of the model

The purpose of the model is to study whether the species-specific hyphal traits can interact with microstructures to modulate the performance of organism, and lead to the spatial niche partitioning.

The model world is a simulated soil-like 2D arena. This arena is divided into open space and simulation of soil-like particles. Open space is where hyphae can freely propagate forming mycelium (growth starts from a point in the center). Soil-like particles cannot be penetrated by hyphae and must be avoided upon contact, by means described in previous research in PDSM microstructures(45,62,203,214).

The movement processes and distribution of soil-like particles are simulated in continuous space (i.e. the movement and particle geometries are not restricted to the grid/patches – the grid only stores local information to make processes more efficient).

The arena is a square with one side measuring 1 to 25 millimeters and can be filled with 2D particles of varying size (parameter *maximum-grain-diameter* is 5 µm to 500 µm), number and shape. Soil-like particles can be round or rectangular, with their shape being defined by the parameter *roundness*. With increasing size and number of particles, the porosity is decreasing. Porosity reaches values from 1 (i.e. growth of mycelium in open space without obstacles) to approximately 0.35 (most dense environment in our model). The particles are modelled as enclosed spaces delineated by link-type agents (*surface-links*).

Except for the *surface- links* and *patches* (2D squares, basic building blocks of each NetLogo world(229)), all other key agents belong to the mycelium. From the perspective of movement, fungal hypha can be divided into two compartments: the growing hyphal tip and the posterior static part of hypha(230). Hyphal tip realizes the growth (i.e. elongation of hypha) and it is here where mechanisms responsible for space searching algorithms (i.e. movement response to the environment) are located. Thus, in our model, it is represented by a moving agent called *hyphal-tip*. *Hyphal-tip* generates elements of mature hypha alongside its movement track (see below), detects the surrounding surfaces and hyphae and acts accordingly. The posterior parts of hyphae do not grow, but can engage in the formation of the mycelial network through their role in negative autotropism and anastomosis (hyphal fusion)(170,231,232).

In our model, mature hyphae posterior to hyphal tips consist of two static agents; (hyphal) *nodes* and *hyphae* (link-type agents, i.e. edges, connecting *nodes*) (Fig. 6). Hyphal *links* are static structures upon which the *hyphal-tips* react in processes of hyphal autotropism and anastomosis(170,231,232). The *nodes* are static points where the hyphae branch and anastomose.

The following state variables define how the *hyphal-tip* produces hyphae in processes related to its movement, reproduction, anastomosis, respond to other hyphae and *surface-links* of particles: *Propagation-speed* [µm/min], *random-propagation-angle* [°], *lateral-branching-interval* [µm], *lateral-branching-angle* [°], *anastomosis-probability*, *autotropism-strength*, *autotropism-perception-range* [µm], *autotropism-cone-angle* [°], *collision-branching-threshold* [°]. Each state variable is described separately in the table of variables (in which also other model variables related to implementation details can be found) (Supplementary material: Table 1). Here, we briefly describe the processes of the model.

Simulation is initialized as an environment of open spaces and particles delineated by *surface-links.* At the point of initialization, the simulated organism is a point in the middle of the environment, located at open space area. At this point, there are several initial *hyphal-tips* (based on the variable *n-hyphal-tips*, set by the user), connected by *hyphae* links to the single initial hyphal *node*. After initialization, the initial *hyphal-tips* start moving based on the parameters' specification. Each time step, they pass a distance of *propagation-speed* and generate a hyphal *node* (unless frequency is reduced by the user). New hyphal *nodes* connect themselves by *hyphae* links to the previous *node* in their respective hypha, and the newest *node* is connected on one end to the *hyphal-tip* that generated it. *Hyphal-tips* keep track of the distance they passed and at intervals defined by *lateral-branching-interval* [µm] they generate a new *hyphal-tip* that adopts new *heading* in accordance with the value of *lateral-branching-angle* [°]. This new *hyphal-tip* is connected to the parental hypha in a *node*, and after a certain *retention-time*, a new *hyphal-tip* starts growing and producing its own hypha. All hyphal tips grow in straight lines if *random-propagation-angle* [°] equals zero, or hyphal tips wiggle if *random-propagation-angle* [°] is larger than zero.

The above text describes the growth of hyphae in open environment, when no object is detected ahead of the *hyphal-tip* for the given time step. As the *hyphal-tips* move, they interact with two kind of objects: *surface-links* that represent the surface of soil-like particles, and hyphal *links* of other hyphae. If a *surface-link* crosses the movement path, the angle of encounter is calculated. If the angle of encounter is smaller than *collision-branching-threshold* [°], *hyphal-tip* moves towards the surface of the particle and proceeds sliding alongside of it. If angle of encounter exceeds the *collision-branching-threshold* [°], the *hyphal-tip* moves towards the surface, splits into two *hyphal-tips* and these continue sliding in opposite directions.

If a *hypha* is detected ahead of the *hyphal-tip* at a distance smaller than *autotropism-perception-range-micrometers*, the *hyphal-tip* changes its current heading by the value defined by *autotropism-cone-angle* and by *autotropism-strength*. Unless the *autotropism-strength* is set to zero by the user, the *hyphal-tip* changes its heading either towards or away from the closest intersection with the detected hypha (i.e. positive or negative autotropism, respectively). If the detected *hypha* is on collision course with the focal *hyphal-tip*, then anastomosis takes place with the likelihood given by the value of *anastomosis-probability*.

The last variable that defines the deterministic part of behavior is the Boolean called (with a question mark) *memory?*. It determines the behavior of sliding *hyphal-tip* once the obstacle is passed. We will describe the variable *memory?* in more detail in the next section.

Stochasticity is introduced in the growth of mycelium via four variables. *Random-propagation-angle* [°] indicates the degree of random wiggling of a *hyphal-tip* around its *heading*. For *lateral-branching-interval* [µm], *lateral-branching-angle* [°], and *collision-branching-threshold* [°] each *hyphal-tip* grows, moves and reacts with a value that is sampled from the normal distribution around the mean. Both mean value and its standard deviation are set by the user.

3.3. Design concepts and rationale for implementation of model mechanisms

In previous theoretical works, hyphal growth has been conceptualized as a form of ecologically relevant movement(2). This opens the possibility of fungal growth (i.e. *active fungal movement*) to impact the foraging ability and spatial niche partitioning of the organism by means similar to those studied in animal communities(2,40,233). To initially evaluate the model, we test these expectations. Some of the state variables/parameters of fungal behavior, together with their allowable value ranges, were derived directly from empirical research on mycelium architecture, or fungal growth in PDMS microstructures. These include *propagation-speed*, *lateral-branching-interval*, *lateral-branching-angle*, *collision-branching-threshold*, and *memory?.* While the biological relevance and definitions of the first three variables are self-evident, the latter two deserve a closer explanation. *Collision-branching-threshold* is a hyphal trait first identified relatively recently in PDMS microstructures(203,214). In short, species differ in the value of the encounter angle (between hyphal tip and the surface) that decides on whether the tip continues sliding without branching, or it branches apically with two new tips, each exploring opposite directions(203). In general, the lower the collision angle, the more likely the tip will continue sliding without branching. Yet, the exact threshold value is a species-specific trait. Thus, it is one of the traits we explore for their impact on foraging efficiency.

In case the hyphal tip does not branch following collision, once the end of the obstacle is reached two scenarios are available. It can either continue growing in the direction of sliding, or it can resume the original growth direction prior to collision (Fig. 6)(203,214). The former takes place in species without directional memory (represented as Boolean variable, memory? OFF), the latter in species with directional memory (memory? ON). Principally, it would be possible that exactly the same Boolean variable directs the behavior of hyphal tips created at the point of the collision by apical branching. We chose to not implement this, and all hyphal tips created in collision induced branching remain growing in the direction of sliding, without re-assuming the growth direction of the parental hypha. This decision was made based on observation that the Spitzenkörper in hyphal tips is key for existence of directional memory, while during apical branching the Spitzenkörper is degraded and two new ones are created for each hyphal tip(234). This likely leads to the loss of the information about the former growth direction.

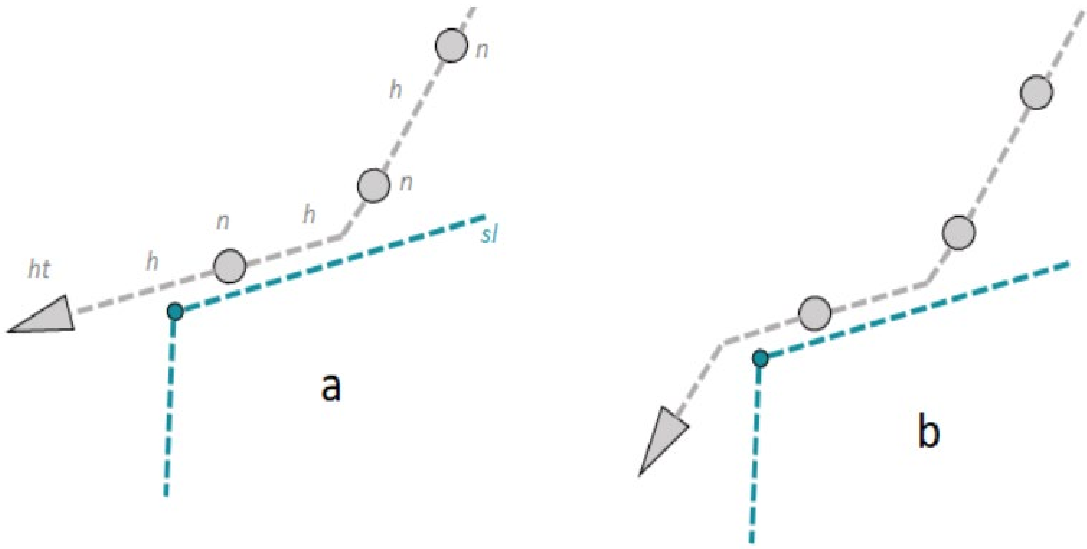

Figure 6. Depiction of hyphal directional memory.

*When the hyphal tip (ht) encounters an obstacle (modelled as surface-link: sl, green), it starts sliding alongside the obstacle until it reaches its edge. Then it will continue with the new heading in fungi without directional memory (**a**). In fungi with directional memory it resumes the heading prior to encounter with the obstacle (**b**). Depicted are also static elements of mature hypha: nodes (n) and the links that interconnected them, called in our model simply hyphae (h).*

During the conceptual development of our model, it became clear that there are several hyphal growth traits that have, to our knowledge, not been studied empirically in any detail that would allow for direct parametrisation of the model. These are the degree of hyphal wiggling, the details about anastomosis and about the negative autotropism. While it is beyond any doubt that these three features of fungal biology influence the growth of the hyphae and mycelial architecture(170,231,232), we did not find any literature attempting to quantify them. Negative autotropism between hyphae of the same mycelium is one of the typical movement- and space-related features in fungi. To our knowledge little is known about the quantitative properties of negative autotropism. For instance, what is the range at which hyphae perceive each other, is the autotropic behavior dependent on spatial parameters of encounter such as angle of approach, or location of hyphae within mycelium? How strong is the autotropic behavior, i.e. to what degree can a hyphal tip be deflected from its original growth trajectory once the other hypha is detected? Given this lack of empirical knowledge, the model interface offers a flexibility in setting up and simulating the properties of negative autotropism. Three autotropism-relevant variables can be manipulated in the interface: *autotropism-strength*, *cone-angle*, and *perception-range-micrometers*. The parameter deciding about the *autotropism-strength* can be set to a wide range of values, both positive to negative. Before simulations, we tested empirically whether the chosen values resulted in a naturally appearing mycelium (see below).

Similarly, although we know that hyphae do not grow in straight lines and the degree of wiggling differs among species, we did not have any exact values with which to parametrize the model. We run multiple simulations, observed the patterns, and chose the interval for simulations that appeared to produce natural mycelia.

The likelihood of anastomosis upon encounter can be set anywhere from zero to one, and in our model, it is not influenced by any additional spatial parameter of encounter (i.e. angle of encounter).

3.4. Details

This section describes details of submodel *go* and other submodels that submodel *go* calls. Together, they define processes that are carried out by each hyphal tip during each time step. Thus, it generates the growth of the hyphae and simulates the way hyphal tips react to the external environment. The growth of the mycelium is therefore an iterative process of multiple runs of *to go* submodels (how many is set by the user). The overview of the relationships between the submodels and the processes they carry out is shown in Figure 7.

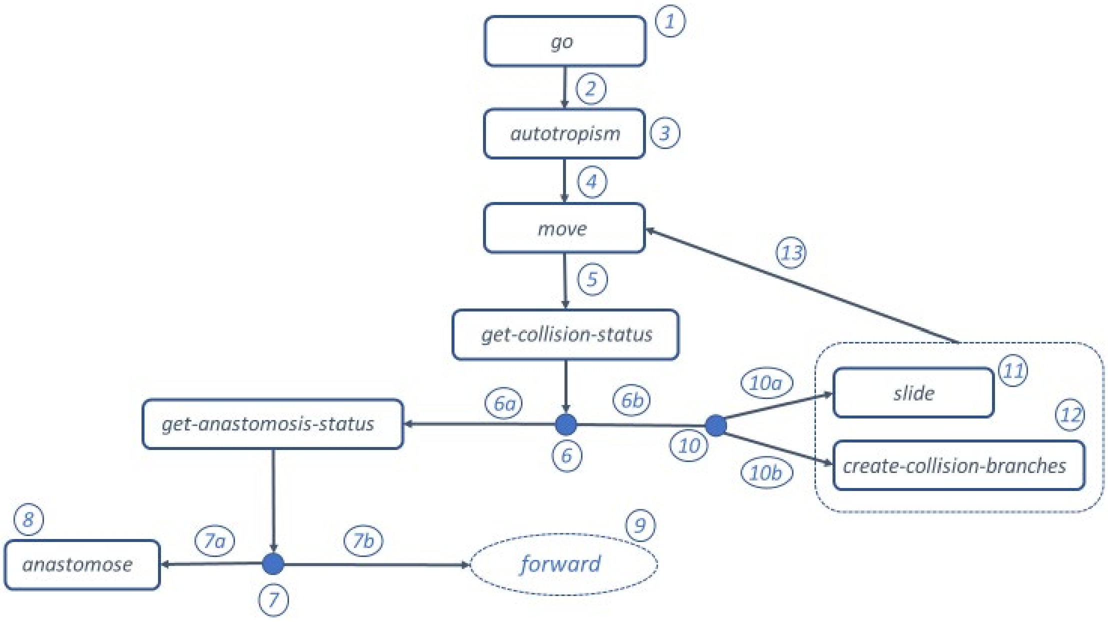

Figure 7. Submodels called by the submodel go.

Submodel go checks the age of the hyphal-tip and if it is greater than retention-time, submodel go produces the node of the hyphal-tip and a link that connects these two agents (1). It then calls submodel autotropism (2), and autotropism adjusts the heading of the hyphal-tip (3). Subsequently, submodel go calls submodel move (4). Submodel move first calls submodel get-collision-status (5). Get-collision-status checks presence of soil-like particle ahead (6). If the result is negative (i.e. no particle ahead), submodel get-anastomosis-status is called (6a). Get-anastomosis-status checks presence of another hyphae ahead of the hyphal-tip (7). If the result is positive (7a), anastomosis may take place by calling submodel anastomosis, which leads to the disappearance of the hyphal tip (8). If the result of (7) is negative, the hyphal-tip moves forward (9). If the result of the submodel get-collision-status is positive (6b), the angle of the collision (i.e. angle between the soil surface and hyphal-tip trajectory) is compared to the collision-branching-threshold (10). If the collision angle is smaller than collision-branching-threshold (10a), the branching is not induced and the hyphal-tip assumes a new heading alongside the soil surface (11). If the collision angle is above the collision-branching-threshold (10b), the branching is induced. The submodel collision-branching-threshold creates two hyphal-tips in place of the original one, and gives each an opposing direction alongside the surface (12). Thus, either following the submodel slide (11), or following submodel create-collision-branches (12), the hyphal-tip(s) will continue alongside the surface, calling the submodel move and other downstream submodels (13).

Submodel go

The submodel *to go* first checks whether the current run (i.e. time step, or *tick*) is the first one in a given simulation. If so (`if ticks = 0`), it calls the submodel *place-initial-nodes*.

Following this, hyphal tips are asked to check their own retention time. Initially, at the moment of tip creation *retention-time* is assigned a negative value that increases with every time step (`set retention-time retention-time + propagation-speed`). The moment the *retention-time* is positive, the hyphal tip can start growing.
Thus, if *retention-time* > 0, the following commands and submodels are run:
The *hyphal-tip* hatches a new *node* (at each time step, or in intervals prescribed by user by *node-frequency* (`if ticks mod node-frequency = 0`).

The new *node* connects itself with the previous *node* (`create-hyphae-with (turtle-set [last-node] of myself)`), asks the parental *hyphal-tip* to cancel its existing links (`ask myself [ask my-links [die]`) , and creates a link with the new *node* (`create-hyphae-with (turtle-set myself)`).

The hyphal tip further inquires whether it is currently sliding. In case it is not (`if sliding-count = 0`), it checks the presence for another *hyphae* that could require it to alter the *heading*, by calling the submodel *autotropism* (`if autotropism-strength != 0 [autotropism]`). Further in case of no sliding, it adjusts the *heading* based on its original *heading*, but with a certain degree of hyphal wiggling (`set heading random-normal heading random-propagation-angle`). In case of sliding, it is the heading of obstacle that gives the *hyphal-tip* its own heading.

The new *heading* is stored as *memory-heading* (`set memory-heading heading`) and initial *momentum* is given the value of *propagation-speed* (`set momentum propagation-speed`). Regardless of the sliding status, the submodel *move* and its own sub-submodels (e.g. get-collision-status) is called (see below).

The *hyphal-tip* asks patches in its vicinity (`ask patches in-radius 2`) to update the agent set *my-nodes* by adding the newly hatched hyphal *node* to it (`set my-nodes (turtle-set my-nodes [last-node] of myself)`). *My-nodes* is used in submodels *get-collision-status*, *get-anastomosis-status* and *autotropism*.

Finally, if the *hyphal-tip* has already travelled the distance larger than the distance between lateral branches, it hatches a new *hyphal-tip* by calling the submodel *create-lateral-branch*:

```
if (dist-travelled * spatial-units-conversion-factor) > lateral-branching-interval-
mean   [create-lateral-branch]
```

Submodel place-initial-nodes

At the start of the growth simulation (`if ticks = 0`), the initial *node* is created by calling the submodel *place-initial-node*. Initial node is created by a randomly selected initial *hyphal-tip* (*hyphal-tips* are already present after the *setup* submodel).

```
ask one-of hyphal-tips [hatch-nodes 1]
```

Once created, the *hyphal-tip* that hatched the initial *node* creates a link to it.

```
create-hyphae-with (turtle-set last-node)
```

Surrounding patches (*in-radius 2*) are asked to update their *my-hyphae* variable by including the newly created *node*.

```
ask myself [set last-node myself]
ask patches in-radius 2[set my-nodes (turtle-set my-nodes [last-node] of myself)]
```

When simulation begins with multiple *hyphal-tip*s, the remaining tips must be also connected to the initial *node*. Thus, all *hyphal-tips* without a link assign status of *last-node* to the existing initial *node*, and subsequently connect to it by a link.

```
ask hyphal-tips with [count my-links = 0]
  [set last-node one-of nodes
   create-hyphae-with (turtle-set last-node)]
```

At this point, the initialized mycelium consists of one *node* and *n* *hyphal-tips* connected to it by *n* links. All these agents still have the same location. In order to rule out an erroneous anastomosis event, the submodel *place-initial-nodes* is finalized by the hyphal tips making a small forward movement away from their initial position.

```
ask hyphal-tips [fd (1 / spatial-units-conversion-factor)]
```

Submodel create-lateral-branch

As the hyphal growth simulation proceeds, each *hyphal-tip* keeps updating the variable of already travelled distance, *dist-travelled*. The submodel *go* is comparing the value of *dist-travelled* with the *lateral-branching-interval*. Once the former is greater than the latter, the *dist-travelled* is reset to zero and the current *hyphal-tip* hatches a new *hyphal-tip* and a new *node*, which are then interconnected by links. That is, a new lateral branch is initiated.

```
if (dist-travelled * spatial-units-conversion-factor)> lateral-branching-interval-
mean [create-lateral-branch]
```

In a deterministic scenario, each *hyphal-tip* would start with exactly zero value of *dist-travelled*. In order to account for stochastic distributions in real mycelia, the actual initial value of *dist-travelled* has zero as its mean value, with *lateral-branching-interval-sd* as the standard deviation around the zero.

```
set dist-travelled random-normal 0 (lateral-branching-interval-sd / spatial-units-
conversion-factor)
```

In addition to setting the initial value of *dist-travelled*, each newly created lateral branch (a *hyphal-tip* at this point) adopts an initial *heading* equal to the *heading* of parental hypha (submodel *go*: `set heading memory-heading`). In submodel *create-lateral-branch*, this initial *heading* is then changed to create branching angle. The hyphae branch randomly on left or right side in open space. In case of an obstacle on one side, it will branch on the opposite (free) side.

```
let lateral-branching-angle random-normal lateral-branching-angle-mean lateral-
branching-angle-sd

ifelse random-float 1 < .5
   [rt lateral-branching-angle
    get-collision-status
    if not empty? collision-status
     [lt 2 * lateral-branching-angle
      set collision-status (list)]]
```

The new hyphal tip needs to be connected to the mycelium (i.e. the model’s network of *nodes* and *hyphae* links). Thus, in *create-lateral-branch* the parental *hyphal-tip* also hatches a new *node*. This new *node* creates a link with the parental *hyphal-tip*, with new *hyphal-tip*, and with the original *last-node* of the parental *hyphal-tip*. It is also assigned the status of the current *last-node* to both *hyphal-tips*, and the link between the former *last-node* and parental *hyphal-tip* is deleted.

```
hatch-nodes 1
  [create-hyphae-with (turtle-set [last-node] of myself)
   ask myself [ask my-links [die]]
   ask myself [set last-node myself]
   create-hyphae-with (turtle-set myself)]
```

And for the new tip in regard of interconnecting the link:

```
hatch-hyphal-tips 1
 create-hyphae-with (turtle-set last-node)
```

In real hyphae, the lateral branches usually start growing at a certain distance posterior to the leading hyphal tip. For this reason, the submodel ends with setting up a negative value of *retention-time* of the new hyphal tip.

```
set retention-time -2
```

Submodel move

In order to limit computational demands, *hyphal-tip*s do not always compute the parameters of possible collision, i.e. *get-collision-status*. Instead, the submodel *move* begins with the *hyphal-tip* determining whether the collision is possible in the next step. That is, whether the patch of its current location is in vicinity of particle's surface. Only if this is true, it will inquire the details of the surface and potential collision.

```
if [soil?] of patch-here [get-collision-status]
```

The variable *soil?* is Boolean that reports true for patches in vicinity of particle's surface, defined in submodel *create-soil-particles*: `ask border-patches [set soil? true]`

The entire rest of the submodel *move* are two alternatives (`ifelse`) based on the result of the *get-collision-status* inquiry.

```
ifelse not empty? collision-status
```

For cases where the vicinity of soil particle actually leads to the collision in the next step, i.e. the *collision-status* list is not empty, the *hyphal-tip* moves towards the collision surface and sets the new momentum.

```
let move-towards-surface (distancexy item 0 collision-status item 1 collision-
status) - (2 / spatial-units-conversion-factor)

set momentum momentum - move-towards-surface
fd move-towards-surface
```

The value of *collision-angle* is calculated from the current growth *heading* and the heading of the surface, and subsequently compared to the value of *collision-branching-threshold* parameter. That results either in sliding of the original tip, or apical (i.e. collision-induced) branching.

```
ifelse (collision-angle < random-normal collision-branching-threshold-mean
collision-branching-threshold-sd)or sliding-count > 0
  [slide]
  [create-collision-branches]
```

An alternative scenario unfolds if the *collision-status* either remains empty or returns empty. The submodel *move* will run with empty *collision-status* if the *hyphal-tip* is not in vicinity of the particle's surface (the *get-collision-status* is not inquired and the *collision-status* remains empty (`set collision-status (list)`). In addition, there can be cases where the vicinity of soil particle does not lead to the collision in the next step, so the *collision-status* is inquired but returns empty.

In either case, the *hyphal-tip* not heading for collision with a surface checks for the presence of other hyphae.

```
  set anastomosis-status (list)
  get-anastomosis-status
```

In case of a sliding tip, the *hyphal-tip* will wiggle in order to detect potential tips sliding alongside of it. If this returns positive, *anastomosis* submodel is called.

```
if not empty? anastomosis-status [
  if random-float 1 < anastomosis-probability [anastomose]]
```

If the *hyphal-tip* has not anastomosed, it is now facing an open space ahead (i.e. there has been no obstacle, or the obstacle has been reached and *hyphal-tip* is sliding with the remaining value of *momentum*). Thus, it moves ahead and updates the value of travelled distance.

```
fd momentum
set dist-travelled dist-travelled + propagation-speed
```

Submodel slide

Before we describe details of the submodel *to slide*, let us first outline how this submodel works within the hierarchy of submodels superior to it, namely *to move* and *to go*. First, in submodel *go* the initial value of *momentum* is set as equal to the value of *propagation-speed*. In other words, at the beginning of each time step, hyphal tip has its entire movement distance per time step, i.e. *propagation-speed* available. Subsequently, the submodel *go* calls the submodel *to move*.

```
set momentum propagation-speed
move
```

In submodel *move*, the first part of the *momentum* is consumed to move towards the sliding surface ahead of the hyphal tip (i.e. through the open space).

```
ifelse not empty? collision-status
```

```
 [set momentum momentum - move-towards-surface
  fd move-towards-surface]
```

Now the current (remaining) value of *momentum* is only a fraction of the original *propagation-speed* and in case the conditions for sliding are met, submodel *move* calls submodel *slide*.

```
ifelse (collision-angle < random-normal collision-branching-threshold-mean
collision-branching-threshold-sd) or sliding-count > 0
  [slide]
  [create-collision-branches]
```

In the submodel *slide*, the *hyphal-tip* establishes the new *heading* (see below, the details of *slide* submodel). Once this and additional operations are run within the scope of the submodel *slide*, the submodel *slide* calls back to the *move* in a loop. Now, the hyphal tip is running again the submodel *move*, and with its new *heading* it checks again the presence of obstacles. Assuming (for simplicity) that this time there is no obstacle ahead (neither a hypha to anastomose with), *hyphal-tip* moves ahead, consuming the remaining fraction of the *momentum*.

```
ifelse not empty? collision-status ;in this scenario, collision-status is empty

fd momentum
```

In summary, above we described how the submodels *go*, *move* and *slide* keep updating the value of *momentum* during one time-step, in order to realise *propagation-speed* no matter if the movement takes place in free space, or in collided and sliding *hyphal-tip*. Analogically, submodels *go* and *move* also communicate with submodels *create-collision-branches* and *anastomose.*

The submodel *slide* itself updates the heading of *hyphal-tip* so it follows the collided surface in the correct direction, it assigns the sliding status to the *hyphal-tip* (`set sliding-count sliding-count + 1`), and updates the *memory-heading* for *hyphal-tip*s without the directional memory, so it is defined by the heading of the obstacle's surface (`if not memory? [set memory-heading heading]`).

Hyphal-tip adopts the heading from the heading of the surface in three steps:

First, the two alternative directions (to the left and to the right, or *dir1* and *dir2*) alongside the surface are defined as either equal to the *heading* (angle) of the collided surface (i.e. `item 2 collision-status`), or as its exact opposite.

```
let dir1 ((item 2 collision-status + 180) mod 360)
let dir2 item 2 collision-status
```

Second, values of *dir1* and *dir2* are used to calculate the angle by which the *hyphal-tip* needs to alter its current *heading* in order to align its growth to the surface.

```
let angle1 subtract-headings dir1 heading
let angle2 subtract-headings dir2 heading
```

Third, select the correct new *heading* (i.e. turn left or right) by comparing the absolute values of turning angle.

```
ifelse abs angle1 < abs angle2
  [set heading dir1]
  [set heading dir2]
```

Submodel create-collision-branches

Analogical to the submodel *slide*, also *create-collision-branches* communicates with its superordinated submodels *go* and *move* in order to correctly update the value of *momentum*. We refer to the description of submodel *slide* for more details about this hierarchical communication. The submodel *create-collision-branches* is called by the submodel *move* when *hyphal-tip* is already at its position next to the collision surface.

First, new growth directions alongside the collision surface (to the left and to the right, or *dir1* and *dir2*) are defined as either equal to the heading (angle) of the collided surface (i.e. `item 2 collision-status`), or as its exact opposite.

```
let dir1 ((item 2 collision-status + 180) mod 360)
let dir2 item 2 collision-status
```

Then the current *hyphal-tip* is asked to hatch a new node that will later become the new *last-node* for both new *hyphal-tips*. This new *node* connects itself to the previous *last-node*.

```
hatch-nodes 1
 [create-hyphae-with (turtle-set [last-node] of myself)]
```

After this, new *hyphal-tips* are hatched by the new *node* and interconnected to it. Each new *hyphal-tip* assigns the status of *last-node* to their parental *node*, and adopt their respective new heading (*dir1* or *dir2*) alongside the surface. Given that directional memory is likely lost after the collision-induced branching, each *hyphal-tip* takes the current sliding *heading* as the value of *memory-heading* (`set memory-heading [heading] of self`). The submodel *to create-collision-branches* assigns the sliding status to each new *hyphal-tip*, and calls back the submodel *move* (see details of this loop in description of submodel *slide*).

```
hatch-nodes 1 [
  hatch-hyphal-tips 1
    [set heading dir1
     set last-node myself
     create-hyphae-with (turtle-set myself)
     set sliding-count 1
     move]
```

Finally, the submodel cancels the original *hyphal-tip* and its links.

Submodel anastomose

Once the *get-anastomosis-status* returns a positive result, the submodel *anastomose* is called. At this point, the result of *get-anastomosis-status* is available as a list of variables with information the *hyphal-tip* needs to anastomose with the hyphal *link* ahead of it. This link is *item 1* of the *anastomosis-status* list.

The agent set *ends* is defined and contains both nodes of the *item 1* link.

```
let ends (turtle-set [end1] of item 1 anastomosis-status [end2] of item
anastomosis-status)
```

Subsequently, *ends* is used to make sure the link detected by *get-anastomosis-status* is not the *hyphal-tip*’s own hypha. This is done by counting how many nodes are left to the item 1 link, once the *last-node* of the hyphal tip is excluded. Only if the resulting number is 2, anastomosis takes place.

```
let anastomosis-nodes count ends with [ who != ([[who] of last-node] of myself)]

if anastomosis-nodes  = 2
```

If so, the *hyphal-tip* hatches a new *node*, and this *node* assumes the position of intersection/anastomosis (where *hyphal-tip*’s path intersects with the link to anastomose with).

Coordinates are imported from *item 0* of the *anastomosis-status* list. The *item 0* itself is a list containing two variables, the x and y coordinate of the intersection point.

```
let is-x (item 0 (item 0 anastomosis-status))
let is-y (item 1 (item 0 anastomosis-status))
hatch-nodes 1
    [setxy is-x is-y
```

The rest of the submodel creates links of this new *node*, and cancels the old links and the *hyphal-tip* (which ceases to exists due to anastomosis).

Thus, the new *node* establishes three links. With the *item 1* nodes (*ends*), and with the *last-node* of the *hyphal-tip*.

```
create-hyphae-with (turtle-set [last-node] of myself)
create-hyphae-with ends
```

Finally, the original link between *ends* and the original *hyphal-tip* are cancelled.

```
ask item 1 anastomosis-status [die]
die
```

Submodel autotropism

Submodel *autotropism* runs several processes analogical or same as submodels *get-collision-status* and *get-anastomosis-status*. For better orientation, please see also Figure 8.
At the start of the submodel, the agent name *active-hyphal-tip* is assigned to the *hyphal-tip* running the submodel. Then it makes a minuscule movement forward, so the possibility of detecting its own hypha is prevented.

```
let the-active-hyphal-tip self
fd (0.0025 / spatial-units-conversion-factor)
```

Further, the variable *angles* is defined as a list of two items: `autotropism-cone-angle/2` and its inverse value (the value of variable `autotropism-cone-angle` is set by user). The variable *min-dists* is defined as a list of two identical variables, *perception-range* and *perception-range*, value of which is set by the user. Together, these two two-item lists, *angles* and *min-dists* define respectively the perimeter and the range at which the presence of other hyphae is checked in two iterations, first for the right side, then for the left side. The key agent that checks this presence is a *probe* hatched by the *hyphal-tip*.

```
let angles list (autotropism-cone-angle/2) (-1 * autotropism-cone-angle/2)
let repeat-count 0
let min-dists list perception-range perception-range
  repeat 2
  [
    let distance-list (list)
    hatch-probes 1
    [
      rt item repeat-count angles
      fd perception-range
```

Hence, once the *probe* is hatched, it turns right or left (`rt item repeat-count angles`) based on the current iteration and moves forward by the value of *perception-range* (`fd perception-range`).

At its new position, the *probe* check whether it has crossed any *hyphae* while moving from the original position. To do so, it first checks whether the patches in vicinity (`in-radius 2`) of its new location (i.e. *patch-here*) contain any *nodes* (i.e. *my-hyphal-nodes*). These *nodes* of potentially intersecting hyphae are called *the-hyphae-start*, from which the *last-node* of the own *hyphal-tip* is excluded (to prevent the detection of own hypha).

```
let the-hyphae-start [my-nodes] of patch-here
if member? [last-node] of the-active-hyphal-tip the-hyphae-start
[set the-hyphae-start the-hyphae-start with [who != [[who] of last-node] of the-
active-hyphal-tip]]
```

In the next step, the agent set containing links of all *nodes* in vicinity (except for the own *last-node*) is defined. These are potentially intersecting links.

```
let potential-IS-links link-set [my-out-links] of the-hyphae-start
```

If there are any potentially intersecting links, it is checked whether the intersection actually takes place. The *probe* creates a link to its parental *hyphal-tip* and then it is checked whether this *probe-link* intersect with any of the *potential-IS-links*.

```
if count potential-IS-links > 0
  [create-probe-link-to myself
    [ask potential-IS-links
      [let is intersection self myself
```

If the intersection exists (`if not empty? is`), then the list *distance-list* is updated. *Distance-list* is empty if this is first iteration, but might be already filled if this is the second iteration. In updating, the distance from the *hyphal-tip* to the intersection is added to it.

```
if not empty? is

[ask the-active-hyphal-tip [set distance-list lput distancexy item 0 is item 1 is
distance-list]]
```

Once the *distance-list* is updated following intersection event (`if not empty? distance-list`), the list *min-dists* is update as well. While originally it contained two equal values of *perception-range*, now one of them is being replaced by the distance to the nearest intersection.

```
if not empty? distance-list [set min-dists replace-item repeat-count min-dists min
distance-list]
```

The iterative part of submodel ends with the *probe* dying and updating the *repeat-count*. The *hyphal-tip* returns to its original position, and a new variable *anastomosis-heading* is defined with an original value zero.

```
fd (-0.0025 / spatial-units-conversion-factor)

let anastomosis-heading 0
```

The zero value of *anastomosis-heading* is maintained in two situations. Either there has been no intersection within the perception range and perception perimeter, or there has been an intersection but on both sides of the perimeter the distance to the intersecting hypha is equal. That is, there is no space to deflect the growth, and in both cases the *hyphal-tip* continues growing with its original *heading*.

In case there has been an intersection and there is a possibility to deflect towards the side with either further distance towards the intersecting hypha or no intersecting hypha, the *hyphal-tip* will be given a new value of *anastomosis-heading* and deflect by the value based on *anastomosis-heading* and *autotropism-strength*.

```
if min min-dists != max min-dists

[set anastomosis-heading item position min min-dists min-dists angles]

rt autotropism-strength * anastomosis-heading
```

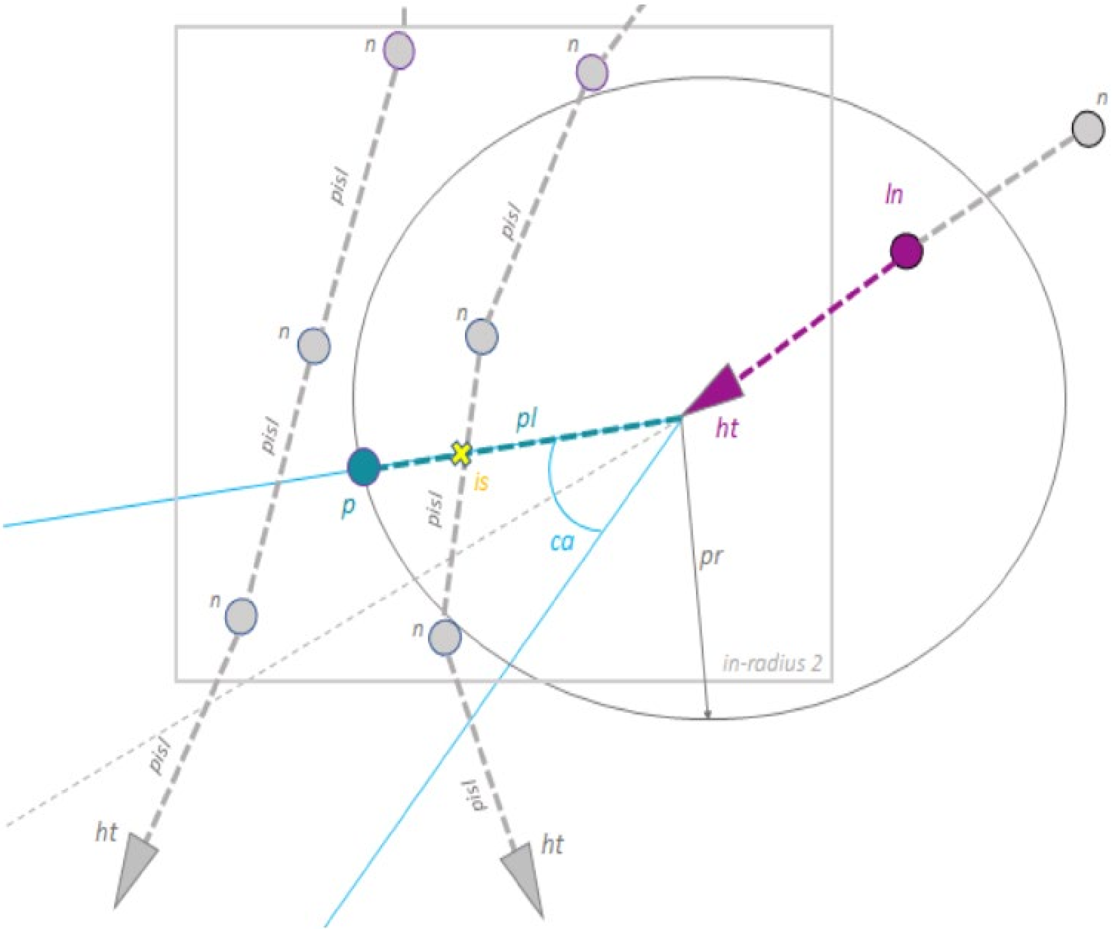

Figure 8. Depiction of processes, variables and agents of submodel autotropism, involved in detection of hyphal links ahead by the focal hyphal tip (ht, purple). If hyphal nodes (n) are present in vicinity of current location (in-radius 2), focal hyphal tip hatches a probe (p, green) which travels to the point defined by the variables perception-range (pr) and cone-angle (ca, cyan). The probe creates a probing link between itself and the focal hyphal tip (pl, green). If this one intersects with a potential intersection link (pisl), an intersection (is) is calculated. The last-node of the focal hyphal tip is depicted in purple (ln). Similar agents and processes are involved in submodels get-anastomosis-status, and get-collision-status.

Submodel get-anastomosis-status

In analogy to submodels *get-collision-status* and *autotropism*, *get-anastomosis-status* starts by defining its output as a list (empty at the beginning) and assigning the agent name *active-hyphal-tip* to the *hyphal-tip* running the submodel.

```
  let result (list)
  let the-active-hyphal-tip self
```

The *hyphal-tip* makes a minuscule movement forward, so the possibility of detecting its own hypha is prevented.

```
  fd (0.0025 / spatial-units-conversion-factor)
```

In order to detect potential hyphae ahead, a *probe* is hatched that runs the operations necessary for detection.

These operations are first analogical to those in *to autotropism*. The probe moves by the distance which the hyphal tip can move in current time step.

```
hatch-probes 1
  [fd [momentum] of myself
```

At its new position, the *probe* check whether it has crossed any hyphae while moving from the original position. To do so, it first checks whether the patches in vicinity (`in-radius 2`) of its new location (i.e. *patch-here*) contain any *nodes* (i.e. *my-hyphal-nodes*). These *nodes* of potentially intersecting hyphae are called *the-hyphae-start*, from which the *last-node* of the focal *hyphal-tip* is excluded (to prevent the detection of its own hypha).

```
         let the-hyphae-start [my-hypha-nodes] of patch-here
         if member? [last-node] of the-active-hyphal-tip the-hyphae-start
         [set the-hyphae-start the-hyphae-start with [who != [[who] of last-node]
         of the-active-hyphal-tip]]
```

In the next step, the agent set containing links of all *nodes* in vicinity (except for the own *last-node*) is defined. These are potentially intersecting links.

```
let potential-IS-links link-set [my-out-links] of the-hyphae-start
```

If there are any potentially intersecting links, it is checked whether the intersection actually takes place. The probe creates a link to its parental *hyphal-tip* and then it is checked whether this *probe-link* intersect with any of the *potential-IS-links*.

```
if count potential-IS-links > 0
  [create-probe-link-to myself
    [ask potential-IS-links
      [let is intersection self myself
```

If the intersection is detected (`if not empty? is`), the *result* list will be updated. The *result* list will carry the information on *x* and *y* coordinates of the intersection point (that is *item 0* and *item 1* of *is* list) and the intersected link *potential-IS-links*.

The submodel must ensure that in case of multiple intersections detected for given time step, the *hyphal-tip* anastomoses with the nearest one and ignores the distant ones. Thus, if the *result* list is still empty at the moment of detecting the intersection, it is simply filled with intersection coordinates and intersected link (`[set result (list is self)]`).

If the *result* list is already filled at this point, the *hyphal-tip* is first asked to compare distances to two intersection points and the nearest one is chosen to fill the *result* list.

```
ask the-active-hyphal-tip

[if distancexy item 0 item 0 result item 1 item 0 result > distancexy item 0 is
item 1 is [set result (list is myself)]]].
```

At the end of the submodel, the probe is cancelled, the *result* list is renamed to *anastomosis-status* list, and the hyphal tip moves back to its original position.

```
      die
    ]
  ]
  set anastomosis-status result
  fd (-0.0025 / spatial-units-conversion-factor)
```

Submodel get-collision-status

The submodel *get-collision-status* is highly analogical to *get-anastomosis-status*. It also hatches a probe, detects the intersection and fills the result list. The only two differences are:

1) While in *get-anastomosis-status* the potentially intersected links are hyphae in the vicinity of the

current *probe*’s patch, in *get-collision-status* the potentially intersected links are those that create surfaces of soil particles.

```
let potential-IS-links [link-set [my-links] of my-surfaces] of patch-here
```

2) The result of *get-collision-status* is a list of three items: The coordinates x and y of intersection point, and the angle (*heading*) of *potential-IS-links* (that is the heading of the *surface-link* to collide with).

```
 [set result is]
 if length result = 2 [set result lput [link-angle] of self result]
```

3.5. Simulations

We simulated multifactorial experiments in environments with five different degrees of porosity: Without spatial constrains (i.e. simulation of growth on plain agar), and with low, intermediate, high and very high porosity. For respective five degrees of soil porosity, the following number of *soil-particles* was generated: 0, 100, 200, 800, 1200. The experimental arena was 7.5 x 7.5 mm large, simulation time was 1000 minutes. The following soil parameters were chosen: *maximum-grain-diameter* was 250, and *roundness* of particles 20.

In total, 800 different parameter sets were simulated with 10 repeats each. The following model parameters (i.e. simulated fungal traits) were kept constant for all 8,000 simulations: *n-hyphal-tips* (i.e. number of initial hyphal tips at the start of the simulation), *propagation-speed-micrometers*, *lateral-branching-interval*, *anastomosis-probability*, and all three parameters that define negative autotropism. Below we provide the reasoning for the particular values we chose for these parameters.

Each simulation starts with nine initial hyphal tips. Although actual spores often germinate as a single conidial anastomosis tube (CAT), the initial CAT can branch frequently at an early stage, which can be then approximated as multiple hyphae spreading from nearly a single point(235). In addition, multiple initial hyphal tips reduce the stochasticity in outcomes based on random spatial constellation of initialized mycelia. For instance, a higher number of initial tips reduces the chances of some areas being unexplored. The mycelia are thus growing in a more symmetrical fashion. That in turn makes mycelia more comparable and it becomes easier to observe the influence of studied growth parameters.

For all simulations, *propagation-speed* was kept at the value of three micrometers per minute. This is within the range of growth rate in the fungal kingdom, while we do not expect the growth rate to have an impact on the relative ranking of different space-searching algorithms(62,236).
The branching frequency (*lateral-branching-interval*) was kept constant in order to minimize the effect of different number of hyphal tips in different mycelia on results and interpretations of our simulations. The value was normally distributed around the mean of 100 µm (M = 100 µm, SD = 50 µm), thus comparable to natural mycelia(12).

We kept the likelihood of anastomosis at the value one, so each time a hyphal tip encounters a hypha, it is either deflected from it by negative autotropism, or it anastomoses. On the one hand, this may not always happen in natural mycelia (a fraction of hyphal tips that are not deflected will cross the hypha without anastomosing). On the other hand, in natural mycelia a proportion of hyphal tips could be suppressed in their growth by other means, so the higher anastomosis likelihood can compensate for the lack of this function in our model. Indeed, the simulated mycelia have appearance closest to the natural mycelia when the values of anastomosis likelihood are high.

Autotropism parameters were kept constant at a low negative value. This enables negative autotropism typical for hyphae, but also does not prevent the parallel growth of hyphae in narrow channels, observed in natural mycelia (autotropism-strength: – 0.05; cone-angle: 20°; perception-range-micrometers: 40 µm).

The following growth parameters were studied for their impact on foraging capacity in different porosities: *random-propagation-angle*, *lateral-branching-angle*, *collision-branching-threshold*, and the presence or absence of spatial memory in hyphal tips.

The parameter *random-propagation-angle* is one of those for which we do not have direct empirical data. When *random-propagation-angle* is set to zero, the hyphae grow as straight lines. When too high (three degrees and above), the resulting mycelium does not appear natural either, with many hyphal growth trajectories collapsing back to the colony center and to the sides. Following observations of multiple morphologies of real and simulated mycelia, we decided to keep the *random-propagation-angle* at the values of 0.5°, 1°, 1.5° and 2° for our simulations.

Lateral-branching-angle and *collision-branching-threshold* were kept within ranges comparable to empirical data, with mean values of 25°, 40, 55°, 70°, and 85° for lateral-branching-angle(237), and mean values of 45°, 60°, 75° and 80° for *collision-branching-threshold*(203,214). Standard deviation for all values of both *lateral-branching-angle* and *collision-branching-threshold* was 10°.
Directional memory is a Boolean, in simulations hyphal tip either expresses it or not.

3.6. Analysis of the model output

We processed the NetLogo output in R to calculate the maximum distance reached by the hyphae from the colony center. For each parameter set, we run ten simulations and calculated the mean value of all ten repeats.

To visualize the results, we chose a heat map. The maximum distance reached (area covered) defined the 100% foraging efficiency (yellow, see Fig. 9). Darker colors on the scale represent the respective fractions of this maximum foraging efficiency.

3.7. Initial evaluation of the model

Figure 9. Visualization of the foraging capacity in simulated microstructures.
In general, presence of directional memory (above) resulted in better foraging capacity (i.e. area covered relative to maximum), as compared to fungi without the directional memory (below). This effect was more pronounced for environments with lower porosity (i.e. higher number of soil particles, columns on the right side).

Our initial results strongly indicate that the porosity itself, before its effect on other vital environmental variables (i.e. oxygenation or water holding capacity) can be studied as a driver of fungal community assembly. In environments with no obstacles (zero particles), the presence of directional memory after collision did not alter the foraging capacity. This is fully expected, as the trait is only activated by contact with surfaces. Similarly, the trait collision branching threshold had no impact in open space environment. In line with expectations, increasing the hyphal wiggling in open space had an overall negative impact on foraging capacity (i.e. the closer the hyphae are to straight lines, the further they reach). The effect of hyphal wiggling was slightly modulated by the value of branching angle.

Overall, increasing hyphal wiggling has a negative impact on foraging capacity in all environments, regardless of porosity. This is unsurprising as in our model, the increased wiggling does not improve navigational capacity of hyphal tip. That is, by investing into a less straightforward growth, in our model the hypha does not collect additional information about its immediate surroundings. In real hyphae this may be different and the trait may have more pronounced and more positive effects on foraging capacity. What is surprising that in spite of the overall pattern described above, for some particular trait value and porosity combinations, increased wiggling actually improved foraging capacity. For instance, at low porosity (1200 particles) the hyphae without directional memory with high branching angle (85°) and a high collision branching threshold angle (75°) perform better at moderately higher wiggling (random propagation angle 1° as compared to 0.5°).

In line with previous research in PDMS microstructures, the directional memory increases the foraging capacity of mycelia across all porosities(24,238). It interferes with the collision branching threshold in an expected manner. The smaller the collision branching threshold, the less successful directional memory becomes in navigating hyphae through obstacles. The memory can only work if the hyphae slide without branching upon encountering the obstacle, but it is lost if the obstacle encounter triggers a branching event. This can be observed as decreasing foraging capacity as the value of collision branching is decreasing in hyphae with memory. The pattern is most pronounced for higher porosities. Surprisingly, the combination of directional memory with a high collision branching threshold (and to some degree with lower branching angle) can result in high foraging capacity being maintained even in low porosity environment. Thus, it is possible that species with directional memory living in high density soils might be selected towards high collision branching thresholds and low branching angles. In species without the directional memory the lower branching threshold allowed for higher foraging capacity in higher porosities.

Interestingly, outside of the general patterns described above, there are multiple unexpected and not easily interpretable combinations of traits and porosities in which hyphal foraging performed well, indicating further opportunities for degree of porosity acting as an axis of niche partitioning between species of filamentous fungi. For instance, in case of the presence of directional memory, random-propagation-angle = 1°, and collision-branching-threshold = 85° the performance in environment with 800 particles was best for branching-angle = 40°. When the porosity decreased, in environment with 1200 particles the branching-angle = 25° performed better.

CONCLUDING REMARKS

Two parallel trends can be recognized in microbial community ecology. It is the growing appreciation of spatial processes in microbial community assembly(2,49,95,239). And technological advances enabling us to study these processes at all relevant spatial scales(62,238). Yet, given the specifics of fungal biology and ecology, generating mechanistic insight into processes of fungal community assembly remains challenging(3). Here, we show that two macro-organismal theoretical frameworks can be useful to alleviate these challenges. Namely modern coexistence theory and movement ecology, as both provide insight into spatial processes of community assembly(4,27,40,233).

We developed the concepts of *unit of community interaction* and *fungal active movement*. In doing so, we integrated fungal community ecology into the established frameworks of spatial coexistence theory and movement ecology.

We believe that close integration between fungal community ecology and established macro-organismal theory can be beneficial for both disciplines. We showed that *modern coexistence theory*, in spite of its arcane reputation(5), can be a very practical framework for navigating empirical research in fungal community ecology, in several highly relevant ways. It provides insight into which spatial scales are meaningful to study. It places competitive interactions into a wider, holistic framework and elucidates natural history gaps. We used the theory to define a practical concept of *unit of community interaction* (*UCI*). 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 that are of secondary interest. We argue that this is an essential step in designing feasible research for life forms as complex as filamentous fungi.

Further, we reviewed studies in fungal biology and ecology through the lens of movement ecology, and proposed an inclusive definition of *active movement*. This definition covers all movement types which organisms from diverse groups can employ in order to interact with their environment. In the case of filamentous fungi, these movement types are informed growth and morphology, directed translocation of substances within the mycelial network, and translocation of entire cytoplasmic contents within hyphae.

Although studies on various forms of biomass translocation in filamentous fungi are rarely framed in a community ecology context, the *active movement* of fungi is likely important for fungal (microbial) community dynamics. Active movement abilities are variable across species and at the same time crucial for the response of the fungus to environmental challenges(163,201,238). That is, they can be viewed as an important fungal movement trait. We showed that fungal studies with different research aims, using diverse techniques, studying diverse scales of organization, movement phenomena, and fungal species, can be all organized under the same umbrella of movement ecology. We argue that formalizing what represents ecologically significant movement in fungi can jump start interdisciplinary collaboration between movement ecology and ecology of fungi and other modular organisms. Movement ecology can more efficiently tap into the data gathered by fungal research, and improve the universality of its terminology and framework. Fungal ecology can benefit from the theoretical developments in the field of movement ecology.

We have now rapidly developing technical options for studying fungal network properties, translocations, and hyphal growth on the one hand(234,238). On the other hand, movement ecology provides the theoretical background and terminology for thinking about fungal translocations as movement traits important in intraspecific and interspecific interactions(2,40,233). Armed with theory, technical tools, and knowledge from previous fungal ecology research, we can now study fungal translocations with the aim of improving our understanding of fungal ecology and community development.

Especially in soil microbial habitats, the concepts proposed here can help answer the recent call by several authors to further pursue the research of microbial communities at the microscale, while taking into account the traits related to this highly heterogeneous and complex environment (46,239–241). Finally, we demonstrated the opportunities for future research on *fungal active movement* by developing an agent-based model of hyphal growth in microstructures. In the model environment, we were able to show that interspecific variability in hyphal movement traits can indeed lead to spatial niche partitioning. We believe our model can be used to facilitate broader research on interactions between fungi and micro-structured environments. Setting up a PDMS *in vitro* experiment comes with considerable costs. Our model provides an opportunity to simulate experiments before their implementation in PDMS environments. This can not only decrease the costs, but also improve the crosstalk between empirical research and broader theory. In the future, we hope to upgrade our network-based model to include other spatial processes, namely transport of nutrients across the mycelium.

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SUPPLEMENTARY MATERIAL:

Table S1. *Agents, objects and variables of the model*

NAME OF VARIABLE, AGENT, OR ANOTHER OBJECT	AGENT OR OBJECT TO WHICH THE VARIABLE BELONGS. (AGENRS AND OBJECTS MARKED WITH N/A)	TYPE OF VARIABLE	DESCRIPTION
anastomosis-heading	hyphal-tip	continuous	Pertains only to the procedure autotropism. It informs about the side on which the detected hypha is located, and the value in degrees by which the hyphal tip is deflected from this side in case of negative autotropism.
anastomosis-nodes	hyphal-tip	integer	Pertains only to the procedure anastomose. Number of agents (ends) connected by the link with which the hyphal tip is about to anastomose. Under the condition that the number of these agents equals 2 (end1 and end2 of this link), the anastomosis procedure will proceed. It is implemented to ensure that the hyphal tip does not anastomose with its own immediate hypha.
anastomosis-probability	hyphal-tip	continuous	Set by user, probability that the hyphal tip will actually anastomose, if the opportunity for that is detected (i.e. a hypha is ahead). When set to 1, hyphal tips always anastomose with the hypha that intersect their path.
anastomosis-status	hyphal-tip	list	Result of the procedure get-anastomosis-status. List remains empty, if no hypha is detected on the "collision course". In case of positive result of the get-anastomosis-status procedure, the list contains two items: Item "is", and item "potential-IS-link". Item "is" is the intersection (anastomosis) point and contains two variables, the x and y coordinate of the intersection (anastomosis) point. Item "potential-IS-link" is an agent, an intersection link. That is, the link with whom the hyphal tip is about to anastomose.
autotropism-cone-angle	hyphal-tip	continuous	Value in degrees, set by user. Defines the extend of perimeter ahead of the hyphal tip, which the given hyphal tip is to scan for presence of other hyphae.
autotropism-strength	hyphal-tip	continuous	Defines the intensity by which the hyphal tip will change its current heading towards or away from another hypha ahead of it. If the value is negative, the hyphal tip will deflect its growth from the detected hypha (i.e. negative autotropism). If the value is

			positive, it will lean its growth towards the detected hypha (i.e. positive autotropism).
collision-angle	hyphal-tip	continuous	The angle between the heading of the hyphal tip and the surface with which it is about to collide.
collision-branching-threshold	hyphal-tip	continuous	A value in degrees set by the user. It is compared to collision-angle. If collision-angle is smaller than collision-branching-threshold
collision-status	hyphal-tip	list	Result of the procedure get-collision-status. List remains empty, if no particle surface is detected on the "collision course". In case of positive result of the get-collision-status procedure, the list contains three items: x and y coordinates of the point at which hyphal tip will collide with the surface, and the heading of the trajectory of the hyphal tip (angle of the intersecting probe link).
dir1 , dir2	hyphal-tip	continuous	Values dir1 and dir2 are given in degrees and indicate two alternative, opposite directions for sliding alongside the particle surface.
distance-list	hyphal-tip	list	Collects the distances to all hyphae in perimeter of autotropism. The collected values are compared, and the lowest value is used to assign the value of min-dists.
dist-travelled	hyphal-tip	continuous	Updated every time step, maintains information about the distance which hyphal tip passed since its creation. Used to trigger the lateral branching event once the dist-travelled is larger than lateral-branching-interval.
is	hyphal-tip	list	List that contains two variables: x and y coordinate of the intersection point between the trajectory of the hyphal tip and the hyphal link this tip is to anastomose with.
last-node	N/A	agent	The node to which the hyphal tip is immediately connected by the link, i.e. the node hyphal tip hatched as the last.
lateral-branching-angle	hyphal-tip	continuous	Set by user, the angle at which the lateral branches grow from their parental hypha. Set as a mean value and its standard deviation.
maximum-grain-diameter	helper	continuous	Set by user, the diameter of largest particles in the environment.
memory?	hyphal-tip	Boolean	Set by the user. Informs the hyphal tip about its behavior after the sliding period, when the edge of the surface is reached. At this point, hyphal tip either resumes the original heading before

			sliding (memory? ON), or maintains the new heading equal to the direction of sliding (memory? OFF).
min-dists	hyphal-tip	continuous	Informs the hyphal tip about the nearest hypha ahead of it and within the autotropism perimeter. Enables to select this hypha to be acted upon.
momentum	hyphal-tip	continuous	It is the fraction of the distance the hyphal tip can still move in given time step, which is transported between procedures. At the beginning of each time step, it equals the distance of propagation-speed (set by the user). If for instance only half of this distance is "used" before encountering the sliding surface, other half is transported to the procedure slide as momentum.
move-towards-surface	hyphal-tip	continuous	Because of the technical reasons inherent to NetLogo language, hyphal tips colliding with the particle surface do not touch this surface. Instead, they approximate their position to its very close vicinity, maintaining a margin *M*. Move-towards-surface is the real distance between the hyphal tip and the surface, minus the value *M*.
my-hyphal-nodes	patch	agent set	The nodes which lie on the surface of the given patch, and of all patches in its neighborhood (in-radius 2). It is used to save computational requirements of the procedure get-anastomosis-status. The probes and probing links will be only hatched in case the value of my-hyphal-nodes is larger than zero.
my-surfaces	patch	agent set	In procedure get-collision-status, the function of this variable is analogical to the function of my-hyphal-nodes in procedure get-anastomosis-status. Only if the value is positive, the procedure will hatch probes and probing links. If there are no surfaces, this step will be skipped to save computational requirements.
node	N/A	agent	Each time step, or after predefined (by user) number of time steps, the hyphal tip hatches a node. These agents are interconnected by hyphal links, and together with them they create the hyphal. Their additional functions are described in particular procedures.
node-frequency	hyphal-tip	integer	Set by the user, frequency of time steps at which the node is hatched by the hyphal tip. Hatching the node every time step increases the resolution, but also the computational requirements.
parental-momentum	hyphal-tip	continuous	Residual momentum (see variable: momentum) specific to the branches created by the collision induced branches.

perception-range	hyphal-tip	continuous	Distance at which a hyphal tip may perceive other hyphae in the context of autotropism. Set by the user.
potential-IS-links	patch	agent set	Hyphal links in vicinity of the hyphal-tip that is scanning environment for potential anastomosis.
probe	N/A	agent	Probe hatched by the hyphal tips in procedures get-anastomosis-status, get-collision-status, autotropism. The probe moves to the position where hyphal tip is about to move and creates a link back to its parental hyphal tip.
probe-link	N/A	agent	The link between the probe and its parental hyphal tip. In case this link intersects with another one (surface link, or hyphal tip), their intersection coordinates are used to update the results of the given procedures.
propagation-speed	hyphal-tip	continuous	Set by the user, distance hyphal tip passes during each time step.
random-propagation-angle	hyphal-tip	continuous	Set by the user, the degree of hyphal wiggling, or to what degree the trajectory of hyphal tip deviates from a straight line. The hyphae grow as straight lines, in case the variable random-propagation-angle is set to zero.
retention-time	hyphal-tip	continuous	After the lateral branch is hatched in form of a hyphal tip, it does not start growing immediately (which would make it an apical branch). It waits for a value of time steps defined by retention-time.
roundness	particles	continuous	Set by the user, defines the degree to which the particle surface is smooth (round), or not (sharper angles).
sliding-count	hyphal-tip	integer	Formally it is an integer, increases every time step the hyphal tip finds itself in the sliding status. For the purposes of procedures, it behaves as a Boolean: When equal zero, it informs the procedure the hyphal tip is not sliding. When larger than zero, it is sliding.
surface-link	N/A	agent	Links that form the surface of particles.
the-hyphae-start	patch	agent set	The nodes in vicinity of the hyphal tip. The agent set includes my-hyphal-nodes, but excludes the last-node of the given hyphal-tip. The function of distinguishing between these two agent sets (the-hyphae-start vs. my-hyphal-nodes) is to prevent the identification of hyphal-tip’s own link as a link to anastomose with or to react upon through autotropism.