TRAIT-BASED COMMUNITY AND INVASION ECOLOGY OF TERRESTRIAL ARTHROPODS

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ABSTRACT

The search for general rules that predict the form, function and fate of biodiversity is an enduring goal in Ecology. Traits which impact the interactions and fitness of organisms have emerged as useful common currency with which to formulate general and predictive rules about ecological processes. A trait-based framework of community assembly will help to elucidate how ubiquitous processes such as interspecific competition shape and maintain biodiversity, and to predict the impacts of environmental change such as invasions by non-native species. Advances in both areas are needed to explain and address recent widespread changes in the diversity of terrestrial arthropods, organisms representing a massive and functionally significant portion of life on Earth.

In this thesis I first review the burgeoning field of terrestrial arthropod trait-based ecology (Chapter 2). Studying ant assemblages in subtropical Asia, I then use trait-based approaches to investigate the mechanistic causes and functional consequences of assembly processes such as interspecific competition, within the context of invasions by non-native species. I find that invasion leads to a functional homogenization across the landscape which, notably, is unmet by comparable changes in taxonomic diversity (Chapter 3). To investigate underlying processes, I test whether differences in ant species' morphological traits predict their fine-scale spatial associations in ways consistent with theories on interspecific competition (Chapter 4). At the assemblage level, I then show that two opposing mechanisms of competitive exclusion act varyingly on separate morphological, physiological and behavioural traits, causing the invasion to drive contrasting patterns in functional structure (Chapter 5). Addressing a key limitation of trait-based research, I also demonstrate empirically that decisions to exclude

intraspecific trait variability from functional diversity assessments can distort the patterns observed, even overturning the conclusions drawn (Chapter 6).

My work strengthens the foundations for a predictive trait-based ecology of animals in general. It makes specific empirical and methodological contributions to the use of traits for understanding community assembly and the competitive mechanisms determining the impacts of invasions on functional diversity. Building on the work described in this thesis, studies investigating how individual and multidimensional traits determine niche and competitive differences between species will further steer Ecology towards general rules for a predictive understanding of biodiversity and associated ecosystem functions.

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patience and prayers. I love you. Finally, glory be to God for all that has passed and all that is to come in this beautiful life. *Dominus illuminatio mea* (Psalm 27).

FORMAT OF CHAPTERS

The work presented constitutes an integrated thesis. Each of the five chapters below comprises a free-standing paper which has either been published as or prepared for an article in an academic journal. The journals, article types, and publication status of the chapters at the time of writing are:

Chapter 2: *Biological Reviews* (Article) – Published
Chapter 3: *Oikos* (Research Paper) – Published
Chapter 4: *Ecography* (Original Research Paper) – Accepted
Chapter 5: *Ecology Letters* (Letter) – In Preparation
Chapter 6: *Methods in Ecology and Evolution* (Research Article) – Major Revisions

Chapters that have been published are presented as original journal articles. Unpublished chapters are presented as manuscripts formatted to the requirements of the journals for which they have been intended. As free-standing papers, there is inevitably some degree of overlap and repetition between the chapters. The four data chapters, Chapters 3 to 6, used data on ant assemblages which the author sampled systematically via pitfall traps in grasslands in Hong Kong. Chapter 5 focused on a subset of the ant assemblages: the 'ground-foraging' species which were observed recruiting to baits (see Chapter 5). Supplementary material for each chapter may be found in the appendices.

STATEMENT OF AUTHORSHIP

In all chapters, I served as the first and corresponding author. Except where stated otherwise, I designed the study, conducted the fieldwork, data collection and analyses, and led the writing of the manuscript. Statements further detailing authorship are provided at the beginning of each chapter.

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1

GENERAL INTRODUCTION

Human activity is swiftly altering the form, function, and fate of biodiversity (Vitousek et al., 1997; Chapin et al., 2000). There is thus an urgent need to understand how biodiversity is maintained, how populations and communities respond to changes in the environment, and what the consequences for ecosystem functions will be. Though Ecology has made headways in many areas (e.g. Real & Brown, 2001), this predictive understanding of the maintenance, responses and effects of biodiversity remains elusive.

Community assembly and the ecological Holy Grail of form and function

Ecological communities are the building blocks of biodiversity. Their composition results from the interactions of species with and within the environment, under the influence of assembly processes such as dispersal, environmental filtering, competition and other interspecific interactions (Keddy, 1992; but see Kraft et al., 2015; Münkemüller et al., 2020). Since ecological interactions are intrinsic properties of communities, assembly processes also influence ecosystem functions downstream (Bannar-Martin et al., 2018).

So crucial are assembly processes in shaping the form of biodiversity and its functions in ecosystems that general rules for predicting the composition of ecological communities from observable properties of organisms across environments and spatiotemporal scales have been likened to the ‘Holy Grail’ of Ecology (Lavorel & Garnier, 2002). If attained, these general rules can provide crucial predictions about the responses and effects of biodiversity amidst environmental change. Although ecologists have broadly identified the main processes involved in community assembly (outlined above), general, predictive rules have mostly remained out of grasp (Lawton, 1999). One reason for this has been the lack of an operational ‘common currency’ for mechanistically linking the processes operating across various ecological and spatiotemporal scales (Levin, 1992) as well as the patterns observed in different taxonomic assemblages.

Traits as common currency for linking the responses and effects of biodiversity

The sheer diversity of phenotypic traits among organisms has long captivated biologists (e.g. Darwin & Wallace, 1858). Nonetheless, only in the past two decades has an emphasis on the phenotypic traits of organisms over their taxonomic affiliations emerged as a conventional means to study community ecology (McGill et al., 2006). This 'trait-based approach' uses traits which impact the ecological interactions and fitness – the 'functions' – of organisms as common currency for characterizing and connecting multiple scales of biodiversity; from individuals to populations, communities and ecosystems (McGill et al., 2006; Violle et al., 2014). Traits therefore provide the framework for predicting and aggregating – across taxonomic, ecological and spatiotemporal scales – the responses of biodiversity to environmental change, as well as the associated effects on ecosystem functions. Studies on plants, for instance, have scaled up the interactions of species' leaf traits to explain how tree diversity is maintained in tropical forests (Kraft et al., 2008), as well as to predict carbon fluxes at macroscales (Enquist et al., 2007) and the responses of tree diversity to forecasted climate change (Bjorkman et al., 2018). In sum, trait-based ecology provides the operational framework needed for attaining general and mechanistic rules for predicting community assembly.

The enigma of competition

Nonetheless, the ways by which assembly processes act precisely on species' traits to mould community structure are not fully resolved. The role of interspecific competition in structuring communities is particularly enigmatic. The classical perspective of Niche

Theory takes competitive exclusion to occur via limiting similarity (MacArthur & Levins, 1967), generating assemblages comprised of species with dissimilar ecological niches and traits (Schoener, 1974). More recent theory (e.g. Modern Coexistence Theory; Chesson, 2000) as well as empirical observations, however, call into question the effects of ecological differences on the nature and outcome of competition between species. For example, studies on plant assemblages have shown that instead of promoting resource (niche) partitioning, differences in the traits of species can actually determine their competitive abilities for the same resources, causing competitive exclusion to occur along a hierarchy of competitive ability (Goldberg & Landa, 1991; Shipley & Keddy, 1994; Kunstler et al., 2012;2016). This other mechanism of competitive exclusion has very different consequences for community structure relative to limiting similarity (Mayfield & Levine, 2010; D'Andrea & Ostling, 2016).

There have been few empirical investigations on the different mechanisms of competitive exclusion in natural assemblages of taxa other than plants (Mayfield & Levine, 2010; Mittelbach & McGill, 2019; Münkemüller et al., 2020). Most studies are not designed to address these questions from the outset (Münkemüller et al., 2020); doing so requires the rigorous characterization of assemblages and their traits at the fine spatial scales at which competition unfolds (Swenson et al., 2007). Yet, recent work suggests that the different mechanisms of competitive exclusion, acting through species' traits, can alter the trait structure or 'functional diversity' (Tilman et al., 1997) of communities and consequently their ecosystem functions to a large degree (Godoy et al., 2020).

The ecological causes and functional consequences of biological invasions

Invasions by non-native species are top drivers of species extinctions and biodiversity change globally (Pyšek et al., 2020). Non-native species can even penetrate intact systems and reorganize native communities at speeds unmatched by the effects of climate change and other abiotic factors (Mooney & Cleland, 2001; Sanders et al., 2003). Why is this so? One likely reason is that the ecological mechanisms driving biotic invasions and their impacts are distinct from those involved in the abiotic drivers of biodiversity change. For example, interspecific interactions such as competition, predation, and mutualism often ensue from the arrival of non-native species (Vila & Weiner, 2004; Traveset & Richardson, 2006; Doherty et al., 2016). In this regard, invasions by non-native species in ecological communities provide novel 'natural experiments' in which to observe and understand interspecific interactions such as competition and their consequences for community structure directly. Invasions essentially make ideal testbeds for theoretical predictions about assembly processes (Shea & Chesson, 2002).

Many studies have examined how invasions impact species richness (Mollot et al., 2017). Ecosystem functions and stability, however, may be more strongly determined by the nature of ecological interactions than by species richness *per se* (Gagic et al., 2015). Since these ecological interactions are modulated intricately by the traits of organisms, studies distilling biodiversity into functional diversity are needed to further understand how invasions and other disturbances impact ecological interactions and ecosystem functions. Research on plant and vertebrate communities undergoing invasion by exotic species found declines in functional diversity and a tendency for functional homogenization (i.e., an increased similarity in trait values between communities) (Villéger et al., 2014; Castro-Díez et al., 2016). Crucially, invasion-driven changes in functional structure were also linked to altered ecosystem functions (Castro-Díez et al., 2016). In comparison, the impacts of invasions by arthropod species on native functional diversity and ecosystem functions are less understood.

The need for a trait-based community and invasion ecology of terrestrial arthropods

Arthropods are integral components of the biodiversity and ecological functions of terrestrial systems (Didham et al., 1996; Basset et al., 2011). However, their numbers are also declining in multiple areas worldwide (Van Klink et al., 2020). Though specific drivers of these changes are not well understood, they likely involve compounded effects from habitat loss and alteration, climate change, pesticides and invasive species (Harvey et al., 2020; Wagner, 2020). The multifaceted ecological interactions of arthropods mean that the effects of changes in their diversity will reverberate through the green and brown webs of ecosystems (encompassing organisms and interactions involved in primary production and decomposition, respectively; Zou et al., 2016), altering the form and function of multitrophic communities (Slade et al., 2007; Tylianakis et al., 2007; Lewis & Gripenberg, 2008; Bagchi et al., 2014; Visakorpi et al., 2018).

The promise of the trait-based approach to reveal mechanisms determining the responses and effects of biodiversity has attracted strong research interests across many taxonomic groups (Floeter et al., 2017; Funk et al., 2017; Zanne et al., 2019) including terrestrial arthropods. As the burgeoning studies (e.g., Schmitz, 2009; Gerisch et al., 2012; Deraison et al., 2015; Gagic et al., 2015; Gámez-Virués et al., 2015; Bishop et al., 2016; Aguirre-Gutiérrez et al., 2017) vary extensively across scales, processes and arthropod taxa, a general consolidation of the concepts, assumptions, limitations, evidence base and research prospects of ‘terrestrial arthropod trait-based ecology’ is needed to steer the development of this novel field.

In addition to the conceptual synthesis, empirical trait-based investigations of assembly processes such as competition which shape arthropod assemblages will be important for explaining how their diversity and associated ecosystem functions are maintained, and for predicting how these respond to environmental change. In particular, the likely crucial and yet poorly understood role of invasions in contemporary arthropod declines (Goulson, 2019; Wagner, 2020) highlights a need to investigate the ecological mechanisms that underlie invasions of arthropod assemblages, as well as their consequences for functional diversity.

Structure of the thesis

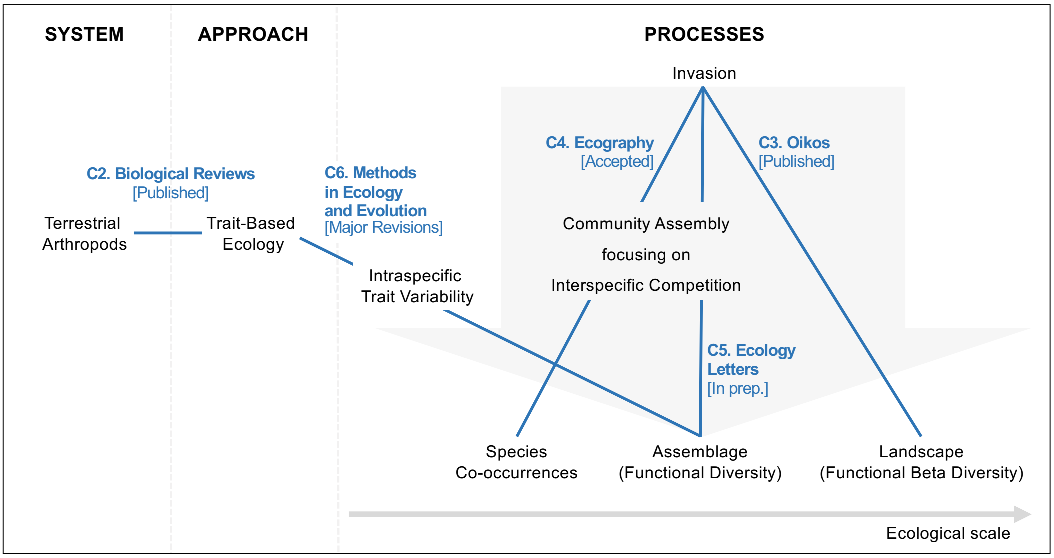
In this thesis I synthesise the trait-based ecology of terrestrial arthropods and use novel approaches to advance empirical understanding of their community and invasion ecology. In Chapter 2 I review terrestrial arthropod trait-based ecology, focusing on its foundations, the state of knowledge, key limitations, and prospects for future work. This review also identifies crucial but less explored areas in the current research, which I address with the empirical studies performed in Chapters 3 to 6.

My empirical studies mainly focus on interspecific competition and the effects of invasions by non-native species, as well as unexamined assumptions of trait-based approaches. They exploit new model systems for studying competition and invasion in terrestrial arthropods: ant (Hymenoptera: Formicidae) assemblages in subtropical Asia (Fig. 1). I focus on ants not only because they are diverse and ubiquitous (Hölldobler &

Wilson, 1990) but also in light of the specific questions asked in the thesis, for which ants possess several key merits as model systems: their traits are accessible for measurement and associated with a variety of ecosystem functions (Parr et al., 2017; Elizalde et al., 2020); interspecific competition often plays an important role in determining their assembly (Parr & Gibb, 2010); and invasions by non-native species are common and well-studied (Holway et al., 2002).

Figure 1. Images of the focal system in Chapters 3 to 6 (leftmost and centre), which investigated the ecology of ant assemblages within subtropical grasslands in Hong Kong. Some of the assemblages contained non-native species such as the Red Imported Fire Ant, *Solenopsis invicta* (top right). Interactions of and among ant species influence a variety of ecosystem processes, such as resource exploitation (bottom right). Aerial image of Lok Ma Chau from wikipedia.org; image of *S. invicta* courtesy of Francois Brassard.

In Chapter 3, I perform the first study on the impacts of an ant invasion on the functional diversity of ant assemblages at local and landscape scales. In Chapter 4, I explore the degree to which spatial associations between ant species are explained by different mechanisms of interspecific competition acting on their morphological traits. In Chapter 5, I sample traits of ant species spanning the multidimensional phenotype and test whether the opposing mechanisms of competitive exclusion predict the causes of an invasion as well as its consequences for functional structure at the assemblage level. Finally, in Chapter 6, I investigate the extent to which excluding intraspecific trait variability from functional diversity assessments – a common practice in empirical studies – alters inferences of ecological processes in both ant and plant assemblages, and provide solutions for addressing these key limitations in trait-based research. A conceptual summary of the thesis and its main questions, outlining the study system, approaches, and processes investigated across a spectrum of ecological scale is provided in Fig. 2.



BROAD QUESTIONS

Why, how and where to apply trait-based approaches on terrestrial arthropods? – **Chapter 2**

How do invasions affect functional diversity from local to landscape scales? – **Chapter 3**

How do species' trait differences determine their co-occurrences? – **Chapter 4**

How do invasions affect assemblage composition and structure through interspecific competition? – **Chapter 5**

How does intraspecific trait variability affect observations of functional diversity; how can these effects be accounted for? – **Chapter 6**

Figure 2. Conceptual summary of the thesis, outlining the research questions investigated in each of five chapters (Chapters 2-6), as well as their placement within a wider framework connecting the study system, approaches, and processes of interest across a spectrum of ecological scale. The publication status of individual chapters in relevant journals are also indicated.

2

Trait-based ecology of terrestrial arthropods

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Author contributions

MKLW conceived the research with inputs from BG and OTL, conducted the review and wrote the first draft of the manuscript. All authors contributed to subsequent revisions.

ABSTRACT

In focusing on how organisms' generalizable functional properties (traits) mechanistically interact with environments across spatial scales and levels of biological organization, trait-based approaches provide a powerful framework for attaining synthesis, generality and prediction. Trait-based research has considerably improved understanding of the assembly, structure and functioning of plant communities. Further advances in ecology may be achieved by exploring the trait-environment relationships of non-sessile, heterotrophic organisms such as terrestrial arthropods, which are geographically ubiquitous, ecologically diverse, and often important functional components of ecosystems. Trait-based studies and trait databases have recently been compiled for groups such as ants, bees, beetles, butterflies, spiders and many others; however, the explicit justification, conceptual framework, and primary evidence base for the burgeoning field of 'terrestrial arthropod trait-based ecology' have not been well established. Consequently, there is some confusion over the scope and relevance of this field, as well as a tendency for studies to overlook important assumptions of the trait-based approach. Here we aim to provide a broad and accessible overview of the trait-based ecology of terrestrial arthropods. We first define and illustrate foundational concepts in trait-based ecology with respect to terrestrial arthropods, and justify the application of trait-based approaches to the study of their ecology. Next, we review studies in community ecology where trait-based approaches have been used to elucidate how assembly processes for terrestrial arthropod communities are influenced by niche filtering along environmental gradients (e.g., climatic, structural, and land use gradients) and by abiotic and biotic disturbances (e.g., fire, floods, and biological invasions). We also review studies in ecosystem ecology where trait-based approaches have been used to investigate biodiversity-ecosystem function relationships: how the functional diversity of arthropod communities relates to a host of ecosystem functions and services that they mediate, such as decomposition, pollination and predation. We then suggest how future work can address fundamental assumptions and limitations by investigating trait functionality and the effects of intraspecific variation, assessing the potential for sampling methods to bias the traits and trait values observed, and enhancing the quality and consolidation of trait information in databases. A roadmap to guide observational trait-based studies is also presented. Lastly, we highlight new areas where trait-based studies on terrestrial arthropods are well-positioned to advance ecological understanding and application. These include examining the roles of competitive, non-competitive and (multi-)trophic interactions in shaping coexistence, and macro-scaling trait-environment relationships to explain and predict patterns in biodiversity and ecosystem functions across space and time. We hope this review will spur and guide future applications of the trait-based framework to advance ecological insights from the most diverse eukaryotic organisms on Earth.

Keywords

Functional trait, functional diversity, community assembly, ecosystem function, insect, invertebrate, ant, bee, beetle, butterfly, spider, review

INTRODUCTION

Biodiversity is often described exclusively in terms of the distinct taxonomic entities (species) which it contains, and measured in terms of its taxonomic component, taxonomic diversity (e.g., species richness). Taxonomic approaches, however, offer limited insight into the evolutionary and mechanistic underpinnings of ecological phenomena; these have recently been studied using alternative approaches for describing biodiversity. For instance, phylogenetic approaches emphasize organisms' evolutionary affiliations, and measure the phylogenetic component of biodiversity, phylogenetic diversity (Cadotte et al., 2010). In contrast, functional trait-based approaches (henceforth 'trait-based approaches') emphasize the values of organisms' phenotypic traits, whose interactions with biotic and abiotic environments affect organism fitness – hence the term 'functional' (McGill et al., 2006; Violle et al., 2007). In measuring the diversity of traits and trait values (the values of traits at specific points along environmental gradients), trait-based approaches measure the functional component of biodiversity, functional diversity (Díaz & Cabido 2001; Petchey & Gaston 2006; Violle et al., 2007).

Studies using trait-based approaches to investigate ecological relationships have proliferated over the past decade (McGill 2015). The rapid rise of 'trait-based ecology' has been propelled by its promise of synthesis, generality and prediction (see "What is trait-based ecology?" below, and Shipley et al., 2016). Most progress has been witnessed in plant ecology (reviewed in Funk et al., 2017), where trait-based approaches are now widely employed to investigate the processes underlying patterns of species coexistence (Cornwell & Ackerly 2009; Kunstler et al., 2016) and Biodiversity and Ecosystem Function (BEF) relationships (Cadotte, Carscadden & Mirotchnick 2011; Faucon, Houben & Lambers 2017). Extensive databases of plant traits (Kattge et al., 2011) are also available to ecologists.

Trait-based approaches were introduced to plant ecology in a series of highly-cited papers published during the first decade of the 21st century (e.g., Díaz & Cabido 2001; Lavorel & Garnier 2002; Díaz et al., 2004; McGill et al., 2006; Petchey & Gaston 2006; Violle et al., 2007), but can be traced to earlier work (e.g., Weiher & Keddy 1995a,b). Soon, they were incorporated in research on microbes (Green, Bohannan & Whitaker 2008; Krause et al., 2014), and animals including vertebrates (Luck et al., 2012), aquatic invertebrates (Poff et al., 2006), and terrestrial arthropods such as ants, bees, beetles, butterflies, and spiders (Pey et al., 2014; Moretti et al., 2017; Perović et al., 2018; Brousseau et al., 2018a). Researchers working on these groups have recently established protocols for selecting and measuring traits (Fountain-Jones et al., 2014; Moretti et al., 2017), extensive databases consolidating trait information (Homburg et al., 2014; Parr et al., 2017), and guidelines for using trait-based approaches to enhance biological control services in managed landscapes (Perović et al., 2018; Gardarin et al., 2018). Recently, Brousseau et al. (2018a) also reviewed trait-based studies on terrestrial arthropods to identify the traits that were used, and how these related to the studied ecological filters (*sensu* Keddy 1992). Evidently, considerable efforts are underway to navigate the technicalities – the 'hows' – of using trait-based approaches in both empirical and applied studies on terrestrial arthropods. However, the explicit justification, conceptual framework, and primary evidence base for the burgeoning field of 'terrestrial arthropod trait-based ecology' have not been well established. Consequently, there is some confusion over the scope and relevance of this field, as well as a tendency for studies to overlook important assumptions of the trait-based approach (Didham, Leather & Basset 2016).

Here we provide a broad and, we hope, accessible overview of trait-based ecology as applied to terrestrial arthropods. We define and justify this field, summarise existing knowledge, suggest how future work can address current limitations, and highlight new areas of research that will have most impact. Specifically, our review addresses the following questions: What is a trait and what is trait-based ecology? Why are trait-based approaches relevant to the study of terrestrial arthropod ecology? What areas in ecology have been explored in current trait-based studies on terrestrial arthropods? What are the assumptions and limitations of trait-based studies, and how can these be addressed? What new areas in ecology should be explored in future trait-based studies on terrestrial arthropods?

As trait-based studies encompass multiple subdisciplines of ecology, and considering the spectacular diversity of terrestrial arthropods (estimated at 7 million species globally; Stork 2017), it is impossible to cover all relevant material within this review. Although our discussion draws primarily from research on commonly studied groups (ants, bees, beetles, butterflies and spiders), the underlying framework as well as the opportunities and challenges of trait-based research presented here should be relevant to similar work on the majority of terrestrial arthropods. We hope this review will establish a preliminary knowledge base for the exciting field of terrestrial arthropod trait-based ecology, and guide future applications of the trait-based framework to advance ecological insights from the most diverse eukaryotic organisms on Earth.

Defining a trait

Technical applications of trait-based approaches vary among fields and are shaped by new developments, but studies of both plants and animals agree on the general properties of traits (by 'traits' we mean functional traits). These are twofold: (i) traits are phenotypic entities that are strictly measured on individual organisms, and (ii) traits are functional, in the sense that their interactions with biotic and abiotic environments affect performance, and consequently organism fitness (McGill et al., 2006; Violle et al., 2007) – we term this 'fitness-functionality'. For the many trait-based studies investigating BEF relationships, traits should also be functional in the sense that they impact or regulate higher-level ecological processes and patterns (Mlambo 2014; Schmitz et al., 2015) – we term this 'ecosystem-functionality'. Importantly, and as highlighted by previous authors (Pey et al., 2014; Middleton-Welling et al., 2018), several studies incorrectly labelled as 'traits' environmental properties associated with species occurrences. Some examples we encountered include 'habitat openness' (Eskildsen et al., 2015) and 'moisture preference' (Pakeman & Stockan 2014). While the former is a measure of vegetation, the latter is based on occurrence distributions of multiple individuals of a species along an environmental gradient. Since these properties are not measured on individual organisms, they should be distinguished from traits. They might more appropriately be termed 'ecological preferences' (Pey et al., 2014).

To facilitate comparisons across studies, traits are often broadly categorized according to the particular aspects of phenotype that they describe. Moretti et al. (2017) proposed five categories of traits for terrestrial invertebrates: morphology (body size, eye number, etc.), feeding (ingestion rate, biting force, etc.), life history (ontogeny, clutch size, etc.), physiology (resting metabolic rate, relative growth rate, etc.), and behaviour (activity time, sociality, etc.). An extensive list of the traits across these five categories as used in existing trait-based studies on terrestrial arthropods was recently made available (see Table S2, Brousseau et al., 2018a). Depending on the specific ecological question at hand, however, individual studies may further distinguish traits based on the impacts of their interactions. Two common examples – which are not mutually exclusive – are the response-effect paradigm (Lavorel & Garnier 2002; Suding et al., 2008), and the performance paradigm (Violle et al., 2007).

The response-effect paradigm (Lavorel & Garnier 2002; Suding et al., 2008) considers the impacts of trait interactions with the environment. Here, traits may be identified as 'response traits' – the attributes of which vary in their responses to environmental conditions (e.g., in lepidopterans, larval diet specialization determines responses to changes in habitat composition; Aguirre-Gutiérrez et al., 2016); or 'effect traits' – the attributes of which vary in their effects on ecosystem properties (e.g., in dung beetles, body size affects the efficiency of dung removal and seed burial; Slade et al., 2007). In general, effect traits influence the performance of ecosystem functions, whereas response traits influence their resilience (Lavorel & Garnier 2002; Violle et al., 2007; Wright, Ames & Mitchell 2016). Response traits and effect traits can be interlinked; for instance, body sizes of bees and dung beetles are informative as both response traits and effect traits (Larsen, Williams & Kremen 2005). Studies on plants have established links between response and effect traits that facilitate predictions about the effects of environmental changes on community dynamics (responses) and the ecosystem functions mediated by these communities (effects) (Suding & Goldstein 2008; Fortunel et al., 2009); similar work has emerged in studies on terrestrial arthropods (see "Investigating biodiversity-ecosystem function relationships" below).

The hierarchical performance paradigm (Violle et al., 2007) identifies traits that essentially describe individual performance in growth, reproduction and survival – the three components of individual fitness (Arnold 1983), and distinguishes these ‘performance traits’ from other functional traits that are ‘lower’ on the performance hierarchy, which only impact fitness indirectly through their influence on growth, reproduction and survival. For instance, the three plant performance traits – vegetative biomass, reproductive output, and plant survival – are distinguished from other functional traits such as leaf morphology and wood density (Violle et al., 2007). To the best of our knowledge, the performance paradigm has not been explicitly incorporated in trait-based studies on terrestrial arthropods; often, data on traits describing performance (e.g., clutch size) are combined with data on other functional traits that indirectly affect performance (e.g., wingspan). However, employing the performance paradigm to link lower traits to performance (and fitness) may contribute to addressing the fundamental assumption of fitness-functionality in observational studies where this is often a challenge (see “Trait functionality in observational studies” below). The performance paradigm may also be relevant to future trait-based studies investigating competition and coexistence, where it may be useful to distinguish performance traits that potentially provide competitive advantages, or which directly impact growth rates, from other traits that may otherwise contribute to stabilization (see “Competition and coexistence” below).

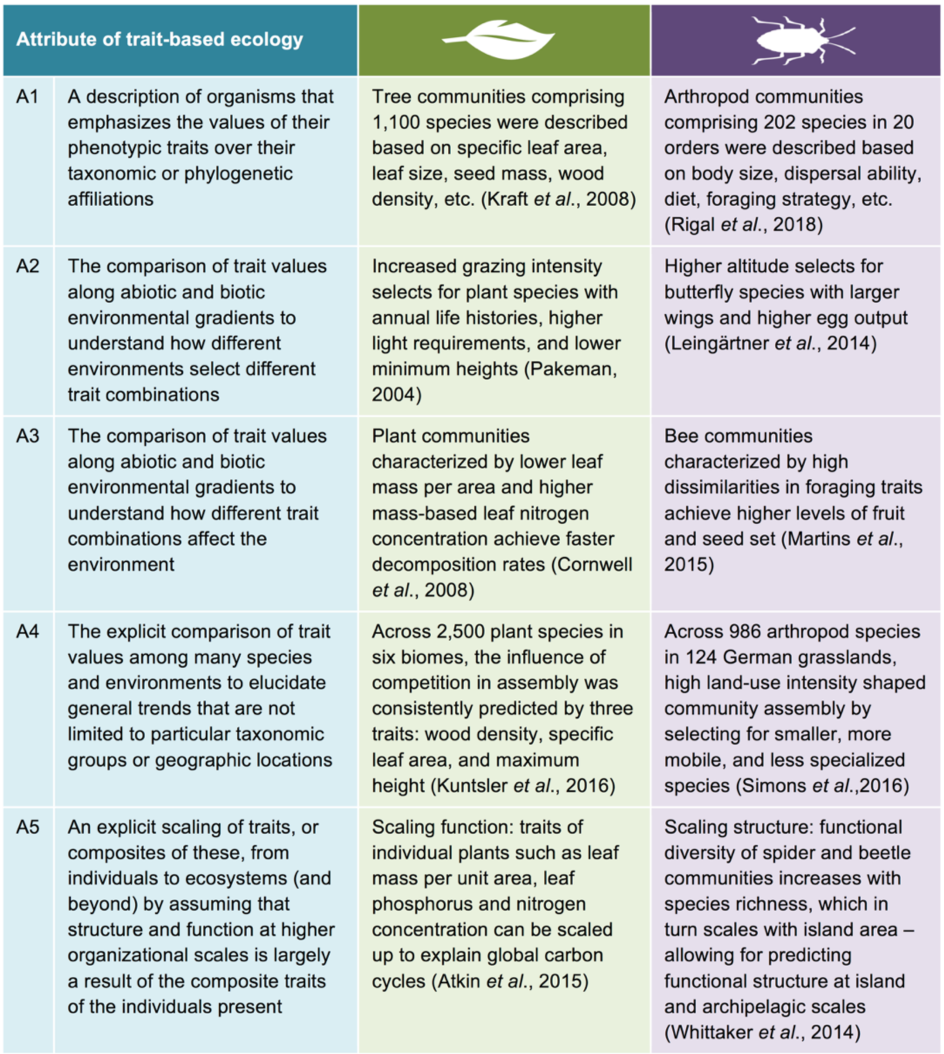
What is trait-based ecology?

Trait-based ecology is the study of how the generalizable, functional properties of individual organisms – their traits – interact with abiotic and biotic environments across different levels of biological organization. Here, it is organisms’ traits – and not their species identities – that are viewed as the common currency across biological organizational levels and taxonomic groups (Violle et al., 2014). Trait-based approaches facilitate the testing of hypotheses to reveal the ecological mechanisms which determine how individual traits interact with abiotic and biotic environments via their responses and effects. This makes it possible to aggregate and integrate different traits to explain structure and functioning mechanistically across different scales of organization (i.e., populations, communities, ecosystems, biomes, and beyond) (Violle et al., 2014). In this way, trait-based ecology facilitates the synthesis of generalizable (i.e., comparable; independent of geographical location or taxonomic assemblage) and predictive (i.e., based on knowledge of mechanisms) explanations for multiple ecological phenomena. Together with the increasing availability of trait values in the literature – epitomized in massive trait databases (e.g., Kattge et al., 2011) – this promise of generality, synthesis, and predictive ability accounts for the burgeoning prominence of trait-based ecological research (Shipley et al., 2016).

As ecology is the study of organisms and their interactions, and as all organisms have traits, there is unsurprisingly some confusion over the types of studies that constitute trait-based ecology. Clarification was recently provided by Shipley et al. (2016): trait-based ecology is not defined by the ecological phenomena that it studies, or the organizational scale at which it is studied (as for subdisciplines such as ‘population ecology’, ‘community ecology’ and ‘ecosystem ecology’), but rather by the *way* that it studies them. In Figure 1 we list several defining attributes of trait-based studies (after Shipley et al., 2016) and provide examples for plants as well as terrestrial arthropods.

It should be emphasized that trait-based approaches are not (and should not be) constrained to examining one particular ecological theory or question; the predictive value of trait-based approaches essentially stems from their versatile potential to test different ecological theories empirically, and reveal mechanisms across different organizational scales. Much of the existing research on terrestrial arthropods has applied trait-based approaches to investigate community assembly within the context of ecological filters (Keddy 1992; Shipley, Vile & Garnier 2006; see examples in the section “Elucidating community assembly”, below, and Brousseau et al., 2018a); although only a minority (19%) of these clearly postulated hypotheses linking traits, their functions, and the studied environmental filters (Brousseau et al., 2018a). Other such studies are limited to describing correlations between trait values and environmental properties (Bousseau et al., 2018a). While purely descriptive studies on trait-environment relationships do contribute some information about ecological structure, the dearth of theory-driven investigations represents lost opportunities for elucidating specific ecological mechanisms underlying observed patterns, effectively undermining the predictive value of trait-based research. In addition to the current scope of trait-based research on terrestrial arthropods, more theory-driven applications are possible (some examples are given in the “New frontiers for terrestrial arthropod trait-based ecology” section, below) and further such work will be required to facilitate synthesis and generality.

Trait-based studies often measure functional diversity – the diversity of traits and trait values – so as to describe the diversity of forms and functions within a particular study unit. Functional diversity is comprised of three main aspects: functional richness, the volume of multidimensional trait space that is occupied; functional evenness, the distribution of abundance in multidimensional trait space; and functional divergence, the degree to which the distribution of abundance in multidimensional trait space maximises differences in trait values (Mason et al., 2005; Villéger et al., 2008). These aspects of functional diversity can be measured using a variety of metrics such as Functional Richness (FRic), Rao's quadratic entropy (*Q*), Functional Divergence (FDiv), and Functional Eveness (FEve); see Mouchet et al. (2010) for a review and discussion on the use of different functional diversity metrics.



Attribute of trait-based ecology		🍃	🪲
A1	A description of organisms that emphasizes the values of their phenotypic traits over their taxonomic or phylogenetic affiliations	Tree communities comprising 1,100 species were described based on specific leaf area, leaf size, seed mass, wood density, etc. (Kraft *et al.*, 2008)	Arthropod communities comprising 202 species in 20 orders were described based on body size, dispersal ability, diet, foraging strategy, etc. (Rigal *et al.*, 2018)
A2	The comparison of trait values along abiotic and biotic environmental gradients to understand how different environments select different trait combinations	Increased grazing intensity selects for plant species with annual life histories, higher light requirements, and lower minimum heights (Pakeman, 2004)	Higher altitude selects for butterfly species with larger wings and higher egg output (Leingärtner *et al.*, 2014)
A3	The comparison of trait values along abiotic and biotic environmental gradients to understand how different trait combinations affect the environment	Plant communities characterized by lower leaf mass per area and higher mass-based leaf nitrogen concentration achieve faster decomposition rates (Cornwell *et al.*, 2008)	Bee communities characterized by high dissimilarities in foraging traits achieve higher levels of fruit and seed set (Martins *et al.*, 2015)
A4	The explicit comparison of trait values among many species and environments to elucidate general trends that are not limited to particular taxonomic groups or geographic locations	Across 2,500 plant species in six biomes, the influence of competition in assembly was consistently predicted by three traits: wood density, specific leaf area, and maximum height (Kuntsler *et al.*, 2016)	Across 986 arthropod species in 124 German grasslands, high land-use intensity shaped community assembly by selecting for smaller, more mobile, and less specialized species (Simons *et al.*,2016)
A5	An explicit scaling of traits, or composites of these, from individuals to ecosystems (and beyond) by assuming that structure and function at higher organizational scales is largely a result of the composite traits of the individuals present	Scaling function: traits of individual plants such as leaf mass per unit area, leaf phosphorus and nitrogen concentration can be scaled up to explain global carbon cycles (Atkin *et al.*, 2015)	Scaling structure: functional diversity of spider and beetle communities increases with species richness, which in turn scales with island area – allowing for predicting functional structure at island and archipelagic scales (Whittaker *et al.*, 2014)

Figure 1. Attributes of trait-based ecology (modified after Shipley et al., 2016)

Five defining attributes of trait-based ecology (A1-5) are listed, with examples from studies on plants and terrestrial arthropods. These attributes distinguish studies using trait-based approaches from those using other approaches (e.g., taxonomy and phylogenetics). Not all trait-based studies display all attributes, but at minimum they should display A1; thereafter, depending on the specific ecological question, studies may display one or a combination of the other attributes (A2-5). Note that trait-based research is not constrained to a particular organizational scale or set of ecological phenomena; for instance, studies displaying A2 may investigate community ecology, studies displaying A3 may investigate ecosystem ecology, and studies displaying A5 may investigate macroecology.

Why a trait-based ecology of terrestrial arthropods?

In addition to the notable contributions of trait-based studies on plants, trait-based research on other taxa has considerable potential to improve ecological theory and practice. We suggest that terrestrial arthropods represent an ideal group for such work because their taxonomic and ecological diversity is unmatched. Most eukaryotic species on Earth are terrestrial arthropods (Zhang 2011; Stork 2017); they are ubiquitous throughout the terrestrial biosphere, and the biomass of groups such as ants and termites commonly exceeds that of larger vertebrate animals (Fittkau & Klinge 1973). Hence, trait-based research on terrestrial arthropods can contribute generalizable, mechanistic explanations for the processes generating and maintaining the diversity of non-sessile, heterotrophic organisms across a variety of habitats, environmental gradients, and spatial scales. Trait-based research on terrestrial arthropods will also advance understanding and prediction of numerous ecosystem processes and services (Losey & Vaughan 2006) that are still poorly understood, and for which terrestrial arthropods are major contributors in their diverse roles as herbivores, fungivores, granivores, detritivores, predators, and parasites. For instance, as ecosystem engineers, ants and termites extensively modify soil properties, disproportionately affecting the fitness of other organisms (Lavelle et al., 2006); spiders consume insects at globally significant levels (Nyfeller & Birkhofer 2017), in turn altering plant diversity and productivity (Schmitz 2003); and many Hymenoptera, Diptera and Lepidoptera are important pollinators (Potts et al., 2010).

To facilitate trait-based research on terrestrial arthropods, there is an abundance of information in the literature and extensive physical and digital collections (Short, Dikow & Moreau 2018). The trait-based approach is also an avenue for overcoming the many taxonomic impediments that have long plagued ecological research on terrestrial arthropods. These impediments include: the great majority of species remaining undescribed – and even more understudied ecologically (Cardoso et al., 2011; Hortal et al., 2015); the sheer diversity and abundance of cryptic species, even in common, functionally important taxa (Molbo et al., 2003; Murray et al., 2008); and poor standards of taxonomic treatment in most ecological studies, undermining validation and reproducibility (Packer et al., 2018). To this end, we envision that ecological studies incorporating a focus on traits and their interactions (and thus not being constrained to taxonomic affiliations) will cut to the mechanistic bases of ecological relationships; however taxonomic excellence is still crucial for macroecological trait-based research integrating data from multiple studies, and for the development and maintenance of trait databases (see the section "Limitation: source, structure and consolidation of trait information" below). Together, trait-based studies across the diversity of terrestrial arthropod taxa and habitats could provide a broad, comparative framework (with traits as standard properties) for investigating fundamental and applied ecological questions. This is particularly important for expediting understanding of the ecology and functioning of threatened systems such as tropical forests, which support – and are in turn supported by – high levels of arthropod diversity (Basset et al., 2012).

How novel are trait-based studies of terrestrial arthropods?

It should be noted that a focus on terrestrial arthropods' traits and their relationships to environmental gradients is not entirely new. For instance, many earlier studies on Bergmann's rule in insects (e.g., Park 1949; Masaki 1967; Hawkins & Lawton 1995) investigated trait-environment relationships, although these may not have been stated explicitly (in earlier studies traits were often referred to as 'characters'). Nevertheless, the latest wave of trait-based studies on terrestrial arthropods – those incorporating the trait-based framework outlined in plant studies from the first decade of the 21st century (examples cited above) – do represent a distinct shift from the previous era where terrestrial arthropod functional ecology was predominantly investigated via a functional group approach akin to that used in plants (e.g., Tilman et al., 1997). This involved assigning species to different functional groups *a priori*, based on their observed or assumed biotic and abiotic interactions (functions); the number of groups within a particular scale of biological organization determined its functional diversity. Examples of widely used functional groupings include those for ants and termites, based on taxonomic relationships and diet specialization (Andersen 1995; Donovan et al., 2001); and dung beetles, based on method of dung removal (Doube 1990). However, the functional group approach is problematic for a number of reasons (Villéger, Mason & Mouillot 2008). For instance, groupings impose a discrete structure on functional differences that are usually continuous, resulting in a loss of information (Gitay & Noble 1997); relationships observed are dependent on the specific functional grouping selected from an often wide variety of options (Wright et al., 2006); functional groups fail at accounting for the effects of abundance (Díaz & Cabido 2001); and functional groups fail on their promise of generality because they were developed based on few assemblages in specific locations (Bourguignon et al., 2011). Hence, in addition to the relative success of trait-based plant ecology, significant limitations of the functional group approach lent impetus to the current ascent of terrestrial arthropod trait-based ecology.

CURRENT TRAIT-BASED STUDIES ON TERRESTRIAL ARTHROPODS

In this section we review knowledge in two broad and related areas of ecology that have received the most attention from existing trait-based studies on terrestrial arthropods. The first area is the study of community assembly based on patterns in community functional structure. Most such studies investigate deterministic assembly mechanisms, in particular the influence of niche filtering along environmental gradients, while others investigate how abiotic and biotic disturbances influence assembly processes and shape community functional structure. The second area investigates how community functional structure affects the performance of ecosystem functions, that is, BEF relationships.

Elucidating community assembly

The community refers to a set of species with shared ecological characteristics that coexist in the same area (Chesson 2000). Community assembly, the processes by which species from a regional pool colonize and coexist in the same area (HilleRisLambers et al., 2012), may occur deterministically through niche-based mechanisms, as well as stochastically through niche-independent processes, such as dispersal, colonization and extinction (Chase & Myers 2011). Here the niche comprises both a species' responses to and its effects on the abiotic and biotic environmental properties required for its survival and reproduction (Chase & Leibold 2003). Since species' interactions with abiotic and biotic environments occur through their traits, the particular composition and distribution of traits and trait values among species in a community (i.e., the community's functional structure or functional diversity) may be interpreted as the pattern of niche occupation by species in that community (McGill et al., 2006). Community functional structure provides limited insight into stochastic processes because these are niche-independent (Funk et al., 2017); however, if deterministic mechanisms have influenced community assembly, these should generate non-random community functional structure – comprising only traits that successfully exploit available niches. For instance, the strength of deterministic mechanisms in the assembly of ant communities in rubber plantations (Liu et al., 2016) was inferred from patterns of functional diversity significantly deviating from null-modelled expectations of random structure. By contrast, random-like patterns in morphological traits of ant communities in Brazilian Atlantic forests suggested that deterministic mechanisms (relating to the niches represented by those traits) had little influence on their assembly (Silva & Brandão 2014).

In addition to establishing the overall deterministic nature of the assembly process, trait-based approaches can be used to reveal how specific niche-based mechanisms operate in community assembly. Thus far, trait-based studies on terrestrial arthropods have predominantly investigated how the mechanism of niche filtering influences community assembly along various environmental gradients (below). Later in the review we discuss the potential for future work to investigate how other niche-based mechanisms such as competition and interspecific interactions influence community assembly (see the section "New frontiers for terrestrial arthropod trait-based ecology" below).

Niche filtering along environmental gradients

Niche filtering (or environmental filtering) occurs when the abiotic or biotic environment imposes barriers to establishment and/or survival, thus favouring the co-occurrence of individuals with similar traits. It then follows that the typical signature of niche filtering is a non-random pattern of clustering among trait values (functional clustering) in the emergent community (Weiher & Keddy 1995a; Maire et al., 2012). However, other niche-based mechanisms may also produce a similar pattern (Mayfield & Levine 2010). Functional clustering may be revealed by comparing the observed dispersion in trait values – calculated from functional diversity metrics (reviewed in Mouchet et al., 2010) such as Rao's entropy and Functional Dispersion (FDis) – to random expectations from a null model (Villéger et al., 2008; Cadotte & Tucker 2017). The effect of niche filtering may also be inferred from a shift in the community-level weighted mean (CWM) – the mean of trait values in a community, weighted by the relative abundance of taxa bearing each trait value (Ricotta & Moretti 2011). Below we summarise the effects of niche filtering observed along commonly studied environmental gradients, and highlight the response traits found to be indicative of the niche filtering process.

(i) Climatic, altitudinal, and latitudinal gradients. Given that thermoregulation is important for activity and survival in ectotherms (Heinrich 1996), temperature is likely an important niche filtering mechanism for terrestrial arthropod communities. Initial findings from trait-based studies examining climatic, altitudinal and latitudinal gradients generally support this notion. Especially among communities of social insects such as ants and bees, where thermoregulatory and thermophilic behaviours are widely documented (e.g., Stabentheiner & Kovac 2014; Shi et al., 2015), a trait-based approach has shown that niche filtering along temperature gradients (correlated with altitude) is driven by a selection on physiological response traits measuring performance (survival), such as species' upper and lower thermal limits, which were higher in warmer environments and lower in colder environments, respectively (Peters et al., 2016; Bishop et al., 2017; but see Nowrouzi et al., 2018). The relationships between species' thermal tolerances and their altitudinal ranges were also employed to test predictions of the climatic variability hypothesis (Janzen 1967), with contrasting results (see Bishop et al., 2017; Nowrouzi et al., 2018). Likewise, studies examining altitudinal and latitudinal patterns in the morphological and behavioural response traits of similar communities suggest that increased demands for thermoregulation in colder climates at higher altitudes or latitudes could explain the observed functional clustering of species with larger body sizes and increased pilosity (Bishop et al., 2016; Osorio-Canadas et al., 2016; Peters et al., 2016; Costa et al., 2017), darker colour (Bishop et al., 2016), as well as ground-nesting habits and higher sociality (Hoiss et al., 2012; Reymond et al., 2013; but see Purcell 2011). Few studies have investigated the potential for gradients in aridity to structure communities, although Wiescher et al. (2012) observed that ant communities from environments of contrasting aridity did not differ significantly in desiccation resistance (but see Hood & Tschinkel 1990). In general, trait-based studies on terrestrial arthropod communities distributed along climatic, altitudinal and latitudinal gradients often identify body size as a response trait that is indicative of niche filtering; however the direction of the relationship varies both within and between taxonomic groups (e.g., Leingärtner, Krauss & Steffan-Dewenter 2014; Gibb et al., 2015; Osorio-Canadas et al., 2016; Classen et al., 2017; Costa et al., 2017). Crucially, not all the above investigations of trait-environment relationships were necessarily theory-driven (thus failing to reveal ecological mechanisms and limiting the predictive value of the results); the exception being body size-temperature relationships, which were often compared with the theoretical expectations of Bergmann's rule (Osorio-Canadas et al., 2016; Peters et al., 2016; Costa et al.,, 2017). Notably, Classen et al. (2017) also tested whether intraspecific and interspecific variances in the body sizes of bees along altitudinal clines conformed to contrasting theoretical expectations of body size-temperature relationships under 'physiological constraints hypotheses' such as Bergmann's rule, and 'energy constraints hypotheses' which focus on how resources are allocated in size-structured communities (Brown & Maurer 1989). It should also be emphasized that environmental variation along climatic, altitudinal and latitudinal gradients is multidimensional (e.g., variation in temperature, aridity, habitat structure, resources). Hence, studies investigating the mechanisms driving coexistence along these gradients should not only be grounded in theory, but also aim to quantify multidimensional environmental variation, and prioritize the measurement of relevant performance traits (e.g., thermal and desiccation performance and/or tolerance). Notably, other studies have used community phylogenetics to show evidence for niche filtering with increasing elevation (e.g., Brehm et al., 2013; Smith et al., 2014). Unlike trait-based approaches, however, such methods cannot yield information on the precise ecological mechanisms by which niche filtering occurs. Furthermore, studies using 'phylogenetic-patterns-as-proxy' approaches tend to overlook the potential for evolution to have varying impacts on traits across the phylogeny, and as such are prone to accepting unsubstantiated assumptions (Gerhold et al., 2015; Cadotte, Davies & Peres-Neto 2017; but see Tucker et al., 2018). For example, phylogenetic niche conservatism is often implicitly assumed, though it may not be supported (Münkemüller et al., 2015).

(ii) Gradients in habitat structure. Several studies have measured the structural attributes of habitats such as vegetation height, aboveground plant biomass, canopy cover and landscape heterogeneity to investigate whether gradients in habitat structure could act as niche filters. Most focused on flying insects, under the assumption that habitat structure could potentially impact their dispersal and foraging niches, as well as others associated with flight (e.g., exposure to predators). Studies on European Lepidoptera report equivocal results. Some found evidence for functional clustering in homogenous habitats with shorter vegetation, where species with higher mobility, growth and fecundity were selected for (Aguirre-Gutiérrez et al., 2017; Halder et al., 2017); however Hanspach et al. (2015) observed an opposite relationship where similar traits were selected for in more heterogeneous habitats, and Scalercio et al. (2012) did not observe significant effects of habitat structure on functional diversity. In a unique attempt to distinguish between community responses to compositional landscape heterogeneity (the diversity of habitat types) and configurational landscape heterogeneity (the number, size and arrangement of habitat patches), Perović et al. (2015) found that taxonomic diversity increased with compositional heterogeneity, but only high configurational heterogeneity selected for lepidopterans of larger body size and lower mobility. Habitat complexity has been suggested to impact the specific foraging niches of different arthropods. Complex habitats in tropical forests selected for larger bees that could potentially travel greater distances to locate trophic resources, but did not affect the functional structure of moth communities that may have had immediate access to abundant trophic resources (Costa et al., 2017). Similarly, reduced complexity (decreased ground cover) selected for ants possessing longer legs, which were conceivably advantageous for movement and resource discovery in simpler environments (Wiescher et al., 2012).

(iii) Anthropogenic land use gradients. There are many studies investigating whether increasing land use intensity functions as a niche filtering mechanism for terrestrial arthropod communities. Perović et al. (2018) recently reviewed some of these studies in detail from the perspective of landscape management; here our discussion focuses on broad trends. It appears that high intensities of land use in simplified, less heterogeneous habitats such as grasslands, pastures and farmlands can produce broad effects of niche filtering, creating functionally-clustered communities with taxa of smaller body size, higher mobility or dispersal, and reduced ecological specialization (e.g., more generalist diets and nesting strategies). These effects have been observed across numerous taxa with diverse ecologies and spanning multiple trophic levels such as bees, beetles, butterflies, hemipterans, orthopterans, spiders (Börschig et al., 2013; Rader et al., 2014; Forrest et al., 2015; Gámez-Virués et al., 2015; Mazzia et al., 2015; Simons, Weisser & Gossner 2016; De Palma et al., 2017; Hanson et al., 2017; but see Perovic et al., 2015; Le Provost et al., 2017; Ng et al., 2018), and soil-dwelling arthropods in dozens of orders (Birkhofer et al., 2017; Rigal et al., 2017). By contrast, the effects of high-intensity land use on the functional structures of arthropod communities may be buffered by landscape heterogeneity in relatively complex habitats such as forests (Edwards et al., 2014; Gossner et al., 2013; Gámez-Virués et al., 2015; Perovic et al., 2015; Birkhofer et al., 2017; Gómez-Cifuentes et al., 2017; Murray et al., 2017; Salas-Lopez et al., 2018; but see Martello et al., 2018). It is important to note that most studies were conducted in temperate regions; additional studies incorporating varying landscapes and land use practices (grazing, logging etc.) in the tropics are needed to explore the generality (or contingency) of land use intensity as a niche filtering mechanism for terrestrial arthropods. Global meta-analyses on individual groups have made progress towards prediction by identifying response traits (e.g., bee nesting location and sociality; ant body size) that were broadly predictive of communities' functional responses to increasing land use intensity across different land use types and climates (Williams et al., 2010; Gibb et al., 2017; da Encarnação Coutinho et al., 2018; but see Bartomeus et al., 2018). Finally, that functional diversity responded to land use in the absence of similar responses in taxonomic diversity (e.g., Forrest et al., 2015; De Palma et al., 2017) suggests taxonomic approaches alone cannot fully account for anthropogenic impacts on biodiversity – this highlights the value of trait-based approaches to research and conservation.

While the influence of niche filtering has been demonstrated in experimentally-assembled plant communities (e.g., Weiher & Keddy 1995b), the majority of trait-based studies investigating niche filtering in terrestrial arthropod communities were observational. This is noteworthy because observational studies have limited potential for distinguishing the effects of niche filtering from those of other niche-based mechanisms such as dispersal limitation and competition (Mayfield & Levine 2010; HilleRisLambers et al., 2012). Still, observation-based inferences of niche filtering may be strengthened if these are supported by three independent lines of evidence (Cadotte & Tucker 2017). First, evidence of functional clustering should be demonstrated, such as by showing that the standardized effect sizes of trait distances, in relation to an appropriate null expectation, are significantly less than zero. Second, the functional clustering must be shown to be associated with an environmental gradient; this requires the measurement environmental properties and statistically relating these to observed functional clustering. Finally, there should be evidence of a direct link between community structure and potential environmental drivers; this may be achieved by demonstrating that the environmental conditions where species are found, or where they attain maximal abundance, are nonrandomly related to species traits. A small number of terrestrial arthropod trait-based studies investigating niche filtering do not provide robust evidence for the latter two criteria. In particular, environmental gradients were not measured; instead they were either assumed (e.g., assuming that temperature gradients directly correlate with altitudinal gradients) or qualitatively described (e.g., “low”, “medium” and “high” categories for land use). Consequently, efforts to demonstrate direct links between functional structure and environmental drivers were hindered. As the pitfalls of observational studies on niche filtering were only recently highlighted (Mayfield & Levine 2010; Cadotte & Tucker 2017), we foresee that future trait-based studies on terrestrial arthropods will be better designed to address current limitations. For instance, novel approaches to improve the quantification of environmental gradients have begun to emerge, such as the measurement of functional diversity of the local plant community – a possible alternative to qualitative descriptors of resource gradients (Pellissier et al., 2013; Pakeman & Stockan 2014).

Effects of disturbances on assembly and community structure

Disturbances are abiotic or biotic forces or processes that result in perturbations, where ecosystems deviate – that is, are changed – from their reference states (Rykiel 1985). Below we highlight trait-based studies that have revealed how the assembly and functional structures of terrestrial arthropod communities are shaped by various abiotic and biotic disturbances, often in ways that would not be deciphered by taxonomic approaches alone.

(i) Fire. In line with theoretical expectations (Swengel 2001; Schowalter 2012), trait-based studies have shown that fire generally shapes the assembly of terrestrial arthropod communities by causing local extinction of their original populations, and enabling rapid colonization by species that have high dispersal ability, which are able to tolerate the altered microclimate (e.g., open, less shady) and exploit the altered diversity of resources (e.g., food and reproduction substrates) in the post-fire environment (Moretti et al., 2010; Heikkala et al., 2016). Positive effects of fire on functional diversity are reported for communities of ants, bees and saproxylic beetles (Moretti et al., 2010; Arnan et al., 2013; Lazarina et al., 2016; but see Heikkala et al., 2016). In ants and bees, fire functioned as a niche-filtering mechanism, where species with ground-nesting colonies and ecological plasticity (e.g., polymorphism, polylecty) were selected for in fire-prone habitats (Arnan et al., 2013; Lazarina et al., 2016). By contrast, fire reshaped the functional structure of saproxylic beetle communities through contrasting mechanisms acting on different niches. While altered climatic conditions functioned as a niche filtering mechanism that selected for species with narrow climatic requirements (Moretti et al., 2010; Heikkala et al., 2016), the simultaneous release of diverse food sources in post-fire conditions increased resource opportunities, which shifted average trait values and expanded trophic niche space (Moretti et al., 2010). Comparative studies have also demonstrated the contrasting effects of fire on the functional structures of bee communities in the Mediterranean (unchanged) and temperate regions (high functional replacement); here, an assessment of functional structure was crucial as the communities' responses in species diversity were similar (Moretti et al., 2009). In general, one might expect the effects of fire on the functional structure of arthropod communities to differ between biomes where it is frequent and natural (e.g., many grasslands) and those where it is relatively infrequent (e.g., tropical rainforests).

(ii) Floods. Like fire, flood events generally act as strong niche filtering mechanisms across multiple taxonomic groups (Dziock et al., 2011; Gerisch 2011; Gerisch et al., 2012; Gerisch 2014; Fournier et al., 2015); although it must be noted that as these studies were conducted in temperate floodplains, the relationships are not generalizable to other arthropod communities experiencing different flood pulses (e.g., Amazonian floodplains; Adis 1997). While relationships vary among taxa, most of the above studies observed that small-bodied and highly-mobile (especially flying) species were selected for in areas experiencing regular floods, highlighting the importance of dispersal ability in the re-colonization of previously flooded areas (Dziock et al., 2011; Gerisch et al., 2012; Fournier et al., 2015). Trait values promoting rapid population recovery after re-colonization such as adult overwintering and high fecundity (ovariole number) were also selected for in some instances (Dziock et al., 2011; Gerisch et al., 2012). Trait-based approaches have also been useful for revealing contrasts between communities' taxonomic and functional responses, where regular flooding was associated with highest taxonomic diversity, but lowest functional diversity (due to strong filtering on species with similar traits mentioned above) (Gerisch et al., 2012). Few trait-based studies have explored the interactive effects of regular and stochastic disturbances on the functional structures of terrestrial arthropod communities, but floodplains may represent model systems for such work. For instance, sampling during regular and stochastic flood events, Gerisch (2014) hypothesized that the high functional redundancy (proportion of species sharing similar functions) of ground beetle communities shaped by regular disturbances (i.e., many species with high propensities for dispersal and population recovery) would be a stabilizing force during a stochastic disturbance. Following a rare extreme flood event, these communities indeed recovered their original levels of functional diversity quicker than less functionally-redundant communities shaped by irregular flood regimes (Gerisch 2014).

(iii) Biological invasions. Few studies have used trait-based approaches to investigate the functional responses of terrestrial arthropod communities to biotic disturbances. Within the context of biological invasions, studies generally observed that invasive plants altered the functional structures of arthropod communities through effecting dietary and habitat shifts (Schirmel & Buchholz 2013; Grass, Berens & Farwig 2014; Gomes, Carvalho & Gomes 2018). However, in contrast to the sweeping effects of abiotic disturbances such as fires and floods, which can wipe out existing arthropod assemblages and generate subsequent filtering of the new colonizers, the precise effects of plant invasions vary considerably with habitat, arthropod community, and ecological characteristics of the invader. For instance, moss invasions on coastal dunes selected for larger-bodied spiders and beetles, and led to the loss of some species of phytophagous beetles and web-building spiders dependent on native vegetation for food and habitat – yet this produced contrasting effects on the functional diversity of the two groups (Schirmel & Buchholz 2013). Additionally, while invasions by exotic plants produced the typical effects of niche filtering on flower visitors – favouring smaller-sized species and reducing functional diversity (Grass et al., 2014) – in other cases, exotic plant invasions actually reduced the strength of niche filtering. For instance, Gomes et al. (2018) observed that invasions by *Acacia longifolia* on dunes mitigated the otherwise extreme environmental conditions, resulting in more functionally-diverse spider communities, as xerophilic specialists were replaced by generalists possessing a wider variety of traits. We are not aware of trait-based studies investigating the functional responses of terrestrial arthropod communities to closely related invaders of the same trophic level, though some studies have attempted to address these questions with community phylogenetics (e.g., Lessard et al., 2009). Thus, there is much scope for using trait-based approaches to test various invasion hypotheses (see MacDougall, Gilbert & Levine 2009) and to advance current understanding of the mechanistic processes that underpin biological invasions – many of which involve terrestrial arthropods (Lowe et al., 2000).

Investigating biodiversity-ecosystem function relationships

Knowledge of the effects of biodiversity on ecosystem functions (BEF relationships) is integral to safeguarding Earth systems and human wellbeing (Hooper et al., 2005). The value of trait-based approaches for revealing the mechanistic bases of BEF relationships and improving their prediction has long been acknowledged in plant studies (Díaz et al., 2004; Lavorel & Garnier 2002). However, only recently have comparable trait-based studies on terrestrial arthropods and their associated ecosystem functions begun to emerge (Fründ et al., 2013; Barnes et al., 2014; Gagic et al., 2015). Several hypotheses describe how community functional structure may influence ecosystem function; these can be tested by the extent to which different distance metrics of functional diversity predict ecosystem function. First, if functional differences among species are unimportant, then the overall numerical or biomass abundance of organisms in a community might better predict ecosystem function than any trait-based measure (Null Hypothesis). Second, if a single trait value is strongly linked to an ecosystem function, then the abundance of this trait value in the community – the CWM – may best predict ecosystem function (Functional Identity or Mass Ratio Hypothesis; Grime 1998). Third, ecosystem functions may depend on the complementarity of different trait values in the community (Functional Complementarity Hypothesis; Díaz & Cabido 2001; Tilman et al., 2001); here, the condition of complementarity may be fulfilled solely by the presence of trait value combinations – predicted by functional richness (FRic) or functional dispersion (FDis), or it may also be dependent on the relative abundance of trait values in combination – predicted by functional evenness (FEve), functional divergence (FDiv) or weighted FDis (Gagic et al., 2015).

Terrestrial arthropods are mediators of numerous ecosystem functions (Yang & Gratton 2014; Noriega et al., 2018), but only a minority of these have been investigated in trait-based studies on BEF relationships (Table 1). Across the studies, each hypothesis linking biodiversity to ecosystem functioning found support at least once (Table 1), and in some cases ecosystem functions were best predicted by both functional identity and functional complementarity, which are not mutually exclusive (see Loreau & Hector 2001). This lack of consensus among the studies is likely attributed to their inherent differences in several key aspects. First, the extent of phylogenetic-relatedness among species in a community varies considerably; while some studies use closely related communities (e.g., ants, Retana, Arnan & Cerdá 2015), others use distantly related communities (e.g., isopods and millipedes, Coulis et al., 2015). Second, the types of interactions that constitute the focal ecosystem functions are dissimilar; for instance, predation and herbivory involve trophic interactions, but seed burial and seed dispersal may involve non-trophic interactions. Third, important methodological differences among studies stem from both the overall study design (e.g., experimental manipulations of functional diversity versus observational studies), as well as the specific techniques used (e.g., different ways of measuring the same ecosystem function). Spatial scale is another vital factor to consider and may explain interaction effects between functional identity and functional complementarity. For instance, research on plant communities suggests that functional identity better predicts BEF relationships at larger spatial scales, where niche filtering along environmental gradients leads to the clustering of trait values that in turn dominate communities and ecosystem functions (Grime 1998; Lavorel & Garnier 2002;

Díaz et al., 2004; Laughlin 2014), whereas the importance of trait differences and their combinations (functional complementarity) should increase at smaller spatial scales, where competitive interactions shape local diversity patterns and promote functional dispersion (Cadotte et al., 2011; Laughlin 2014; Cadotte 2017). Essentially, such arguments allude to the influence of community dynamics on ecosystem functions – a relatively unexplored area in terrestrial arthropod trait-based studies of BEF relationships.

Table 1. Examples of trait-based BEF studies on a variety of terrestrial arthropods and ecosystem functions, and support for four different hypotheses describing how community functional structure influences ecosystem function: organisms' abundance (Null), Functional Identity (FI), Functional Complementarity by presence of trait values only (FC), and Functional Complementarity by presence and abundance of trait values (FCa). *Indicates a study that experimentally manipulated functional diversity.

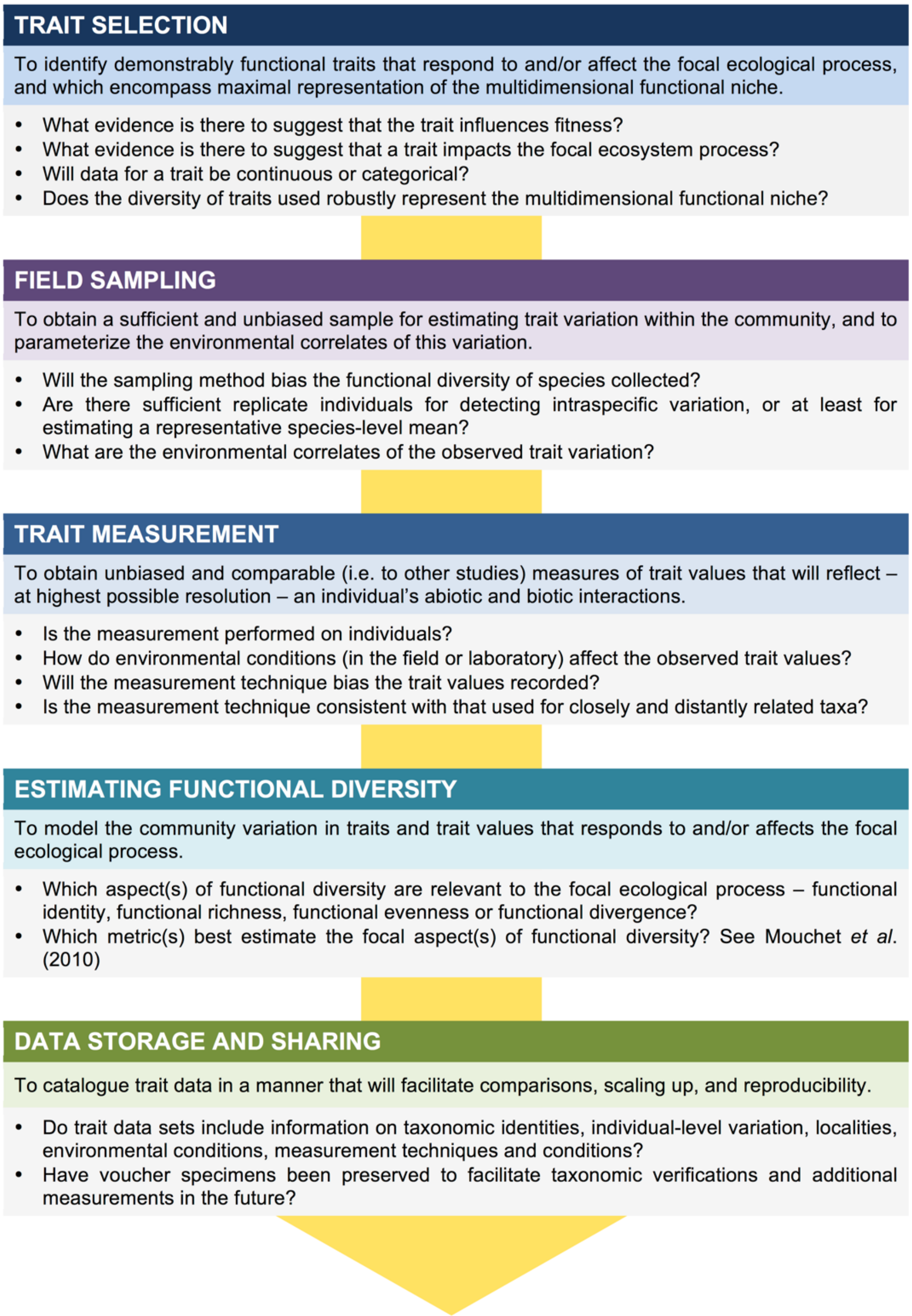
Taxa	**Ecosystem Function(s)**	**BEF hypotheses supported**				**Reference**
		Null	**FI**	**FC**	**FCa**	
Ants	Resource exploitation			✓		Retana, Arnan & Cerdá 2015
Ants	Resource exploitation		✓	✓		Salas-Lopez et al., 2017
Bees*	Pollination			✓		Fründ et al., 2013
Bees	Pollination		✓		✓	Gagic et al., 2015
Bees	Pollination			✓		Garbaldi et al., 2015
Bees	Pollination			✓		Martins, Gonzalez & Lechowicz 2015
Beetles	Dung removal		✓			Barnes et al., 2014
Beetles	Dung removal, seed burial		✓		✓	Gagic et al., 2015

Beetles	Seed predation		✓		✓	Gagic et al., 2015
Beetles*	Seed dispersal, seed burial			✓	✓	Griffiths et al., 2015
Grasshoppers	Herbivory		✓		✓	Moretti et al., 2013
Grasshoppers	Herbivory			✓		Deraison et al., 2015
Isopods*	Decomposition		✓		✓	Bílá et al., 2014
Isopods and millipedes*	Decomposition			✓		Coulis et al., 2015
Multi-taxa (leaf litter invertebrates)	Energy fluxes	✓				Barnes et al., 2016
Spiders*	Plant primary production (through top-down control of herbivory)		✓			Schmitz 2009
Spiders and beetles	Predation		✓			Rusch et al., 2015

The response-effect framework (Lavorel & Garnier 2002; Suding et al., 2008) is useful for conceptualizing the effects of community dynamics on ecosystem functions. Specifically, it aims to predict the effects of environmental change on ecosystem functions by explicitly identifying linkages between response traits that determine community responses to environmental changes, and effect traits that determine the effects of those changes on ecosystem functions. Surprisingly few terrestrial arthropod trait-based studies have embraced this framework in its entirety; many studies investigated responses (examples in section on niche filtering above), and others examined effects (Table 1), but studies attempting to identify linkages between responses and effects are currently scarce. However, preliminary findings suggest that the identification of these linkages can improve the prediction of terrestrial arthropod BEF relationships. For instance, Barnes et al. (2014) observed that the assembly of dung beetle communities along a restoration gradient was mediated through a selection on the response traits of dispersal ability and body size; subsequently, the functional identity (CWM) of body size in these communities was predictive of the rate of dung removal. Many ecosystem functions, however, ultimately rely on interactions between organisms of different trophic levels (e.g., predation, herbivory) (Reiss et al., 2009). To improve predictions for such ecosystem functions, Lavorel et al. (2013) expanded the response-effect framework by incorporating a multi-trophic perspective and interaction networks. Applying the new framework, Moretti et al. (2013) showed that ecosystem function (biomass production) was predicted by effect traits of both producers (plants) and consumers (grasshoppers), as well as the interactions between them; these effect traits were in turn related to response traits that were selected across an environmental gradient of land use. The new framework was also recently modified to address top-down processes such as biological control (Perovíc et al., 2018). However, in spite of these significant conceptual advances, a shortage of information on effect traits and their relationships to ecosystem functions remains a fundamental challenge to understanding terrestrial arthropod BEF relationships (Moretti et al., 2013). Experimental studies manipulating functional diversity across multiple traits and tracing the corresponding impacts on ecosystem functions (e.g., Deraison et al., 2015) will likely be most effective at identifying effect traits and quantifying their effects. Along with more standardized measures of ecosystem functions, such basic gaps will need to be filled before the explanatory and predictive potential of conceptual frameworks (e.g., Suding et al., 2008; Lavorel et al., 2013) can be realised.

HOW CAN TRAIT-BASED STUDIES ADDRESS OUTSTANDING ASSUMPTIONS AND LIMITATIONS?

Here we highlight outstanding assumptions and limitations that presently impede research on terrestrial arthropods from realizing trait-based ecology's ultimate promise of synthesis, generality and prediction (Shipley et al., 2016), and discuss how future research can address these issues. As the majority of trait-based studies on terrestrial arthropods will likely remain observational, we also present guidelines for future work in this area (Figure 2).



TRAIT SELECTION

To identify demonstrably functional traits that respond to and/or affect the focal ecological process, and which encompass maximal representation of the multidimensional functional niche.

- What evidence is there to suggest that the trait influences fitness?
- What evidence is there to suggest that a trait impacts the focal ecosystem process?
- Will data for a trait be continuous or categorical?
- Does the diversity of traits used robustly represent the multidimensional functional niche?

FIELD SAMPLING

To obtain a sufficient and unbiased sample for estimating trait variation within the community, and to parameterize the environmental correlates of this variation.

- Will the sampling method bias the functional diversity of species collected?
- Are there sufficient replicate individuals for detecting intraspecific variation, or at least for estimating a representative species-level mean?
- What are the environmental correlates of the observed trait variation?

TRAIT MEASUREMENT

To obtain unbiased and comparable (i.e. to other studies) measures of trait values that will reflect – at highest possible resolution – an individual's abiotic and biotic interactions.

- Is the measurement performed on individuals?
- How do environmental conditions (in the field or laboratory) affect the observed trait values?
- Will the measurement technique bias the trait values recorded?
- Is the measurement technique consistent with that used for closely and distantly related taxa?

ESTIMATING FUNCTIONAL DIVERSITY

To model the community variation in traits and trait values that responds to and/or affects the focal ecological process.

- Which aspect(s) of functional diversity are relevant to the focal ecological process – functional identity, functional richness, functional evenness or functional divergence?
- Which metric(s) best estimate the focal aspect(s) of functional diversity? See Mouchet *et al.* (2010)

DATA STORAGE AND SHARING

To catalogue trait data in a manner that will facilitate comparisons, scaling up, and reproducibility.

- Do trait data sets include information on taxonomic identities, individual-level variation, localities, environmental conditions, measurement techniques and conditions?
- Have voucher specimens been preserved to facilitate taxonomic verifications and additional measurements in the future?

Figure 2. Roadmap for observational trait-based studies on terrestrial arthropod communities

The majority of trait-based studies on terrestrial arthropod communities rely on observational data. To provide accurate explanations for ecological phenomena and high-quality trait data for further use, it is crucial that observational studies are robustly designed to address commonly overlooked assumptions and limitations. Here, objectives and relevant considerations for important stages of trait-based research are suggested.

Assumption: functional traits are functional

A fundamental assumption of the trait-based approach is trait functionality; all studies should use traits that possess fitness-functionality, and where BEF studies are concerned, those traits should also possess ecosystem-functionality. However, these assumptions of trait functionality have not been explicitly tested for the overwhelming majority of terrestrial arthropods, and the problem is further compounded by the diversity of traits recorded for each species. For instance, some studies used multiple morphological measurements with limited evidence for the functionality of these separate 'traits' (Wiescher et al., 2012; Mickaël et al., 2015). It is not uncommon for morphological traits to be included on the basis of their accessibility to measurement – but this is an incorrect approach. There is evidence to suggest that some traits do not predict growth, reproduction nor survival (Yang, Cao & Swenson 2018); that some traits do not actually respond to or impact ecosystem processes (Mlambo 2014; Bartomeus et al., 2017); and that trait expression can be flexible (Schmitz et al., 2015). Using traits when there is no evidence for their functionality runs the risk of attributing patterns in community functional structure to false mechanisms. The important task of establishing the fitness-functionality of traits (the fundamental criterion) will be challenging because fitness-functionality is essentially a complex dynamic outcome, influenced by the interaction of traits in multidimensional trait space as well as the environment. That is, within the individual organism, the contribution of one trait to fitness is influenced by the contributions of other traits to fitness, and the nature of these interactions (termed 'trade-offs'; Lavorel & Garnier 2002) change along environmental gradients (Laughlin & Messier 2015). Identifying predictable patterns (e.g., trade-offs and correlations) along major axes of trait variation in multidimensional trait space can significantly enhance the process of trait selection if they allow for the use of a few, easily measurable traits to represent species' relative positions along different axes (Westoby et al., 2002), thereby achieving a more robust and efficient characterization of their multidimensional niches. General patterns of multidimensional trait variation are relatively well established in plants (e.g., the leaf-economics spectrum; Wright et al., 2004), and similar attempts to identify such patterns in terrestrial arthropods recently emerged (Ellers et al., 2018).

Experiments to determine trait functionality

To investigate the fitness-functionality of terrestrial arthropod traits rigorously, assessments of trait-fitness relationships along environmental gradients are needed. For instance, by measuring the traits of 66 tree species grown in controlled conditions, Kramer-Walter et al. (2016) identified trade-offs among multidimensional root and leaf traits, and their corresponding impacts on fitness (i.e., growth) along a gradient of soil fertility. Similar experiments have been performed with well-studied insect models, such as in *Drosophila*, where thermal reaction norms for multiple morphological traits were assessed along a thermal gradient (Liefting, Hoffmann & Ellers 2009). Such work can provide a framework for investigations on other terrestrial arthropods amenable to field and laboratory mesocosm experiments, where the direct effects of trait variation on fitness can be estimated by measuring performance in terms of growth, reproduction and survival. Here, it will be essential to select traits on theoretical bases of their functionality so that the results contribute to elucidating mechanisms. It will also be crucial that assessments of trait-fitness relationships are assessed along measured environmental gradients, and that a 'Trait × Environment' interaction term is factored in to explain fitness; leaving this out would imply that some set of trait values can confer fitness in all environments – an over-simplistic and impossible scenario (Laughlin & Messier 2015). In determining the fitness-functionality of traits along environmental gradients, investigators may simultaneously adopt the response-effect framework (Lavorel & Garnier 2002; Suding et al., 2008) to measure the ecosystem processes regulated by the organisms' performance along these gradients; this approach would be advantageous, as it would allow investigators to explicitly establish the ecosystem-functionality of traits or trait sets in relation to fitness and the environment. Experimentally-obtained information on the fitness- and ecosystem-functionality of individual traits and trait sets, trends in trade-offs and correlations, and the environmental correlates of trait interactions may also improve *a priori* trait selection in observational studies on similar taxa.

Trait functionality in observational research

Naturally, experiments involving performance measures along environmental gradients can only be undertaken for a fraction of terrestrial arthropods. However, standards for observational trait-based studies can still be raised so as to enhance their potential for synthesis, generality and prediction. First, investigators should strive to justify explicitly the functionality of the traits used. In the absence of evidence, traits should at the very least be selected on the theoretical bases of their functionality – that is, how their abiotic or biotic interactions may impact specific fitness components (growth, reproduction or survival) and relevant ecosystem processes. Selecting traits in this manner will better facilitate a mechanistic understanding of observed empirical patterns (i.e., trait-environment relationships) to generate good predictions. Essentially, only traits with demonstrable indirect or direct links to performance should be selected, while also balancing this with the important objective of maximising the functional niche represented (achieved by sampling traits from different functional dimensions) (Laughlin 2014; Kraft, Godoy & Levine 2015). One approach for positing fitness-functionality might be to establish links between traits from different levels of the performance hierarchy. If lower traits that are more accessible to measurement (e.g., pilosity, cuticle thickness) can predict interactions between the environment and higher traits (e.g., foraging activity) or performance (e.g., thermal tolerance, survival); then there may be some grounds for using the lower traits as proxies (within those environmental parameters). In ants, some morphological traits were found to be associated with trophic position, and these associations persisted after correcting for phylogeny (Gibb et al., 2015). Likewise, morphological traits were recently shown to predict nesting behaviours and activity periods in dung beetles (Raine et al., 2018). However in most cases morphological traits were used without evidence of any associations between morphological traits and higher traits, let alone their effects on performance. As previously mentioned, the ecosystem-functionality of putative effect traits may be explored in pilot studies assessing how different values of these traits impact ecosystem functions (e.g., Deraison et al., 2015).

Second, investigators should quantify the environmental gradients that correspond to the observed variation in trait values. While many studies examined community functional structures across varying environments, only a minority linked this trait variation to a demonstrable (i.e., quantified) environmental gradient (e.g., Gerisch et al., 2012; Peters et al., 2016; Aguirre-Gutiérrez et al., 2017). The inferred-but-unquantified environmental effects across many studies make the comparison of observed functional relationships impossible (hindering generality and synthesis). Such studies also have limited potential for predicting the responses of terrestrial arthropod communities to environmental changes, both in terms of their functional structure and effects on ecosystem processes.

Assumption: effects of intraspecific variation can be ignored

Intraspecific variation in phenotypic traits within a species may be generated through mechanisms such as local adaptation, parental conditions, ontogenesis and phenotypic plasticity (Des Roches et al., 2018). In studies on ecological relationships at, and above, the community level, the ecological consequences of intraspecific variation are often implicitly assumed to be negligible, or at least subservient to those of interspecific variation; most analyses are performed using only species-level means (Violle et al., 2012; Didham et al., 2016). However, recent theoretical and empirical studies, spanning diverse taxa and multiple trophic levels, propose that because intraspecific effects are often comparable to, and sometimes stronger than, species effects (Siefert et al., 2015; Des Roches et al., 2018), they may influence species coexistence (Violle et al., 2012; Hart, Schreiber & Levine 2016) and ecosystem functions (Johnson et al., 2012), and also determine ecological responses to global change (Moran, Hartig & Bell 2016; Wright et al., 2016). Such notions have found support in trait-based research on fungi (e.g., Hazard et al., 2017) and plants (e.g., Bennett et al., 2016), as well as animals (e.g., Ross et al., 2017) including terrestrial arthropods. Studies on wild bee communities have shown that intraspecific variation in body size may shape assembly along climatic gradients (Classen et al., 2017), and mediate the effects of habitat fragmentation on community structure and the ecosystem function of pollination (Warzecha et al., 2016). Similarly, intraspecific variation in the foraging and web-building behaviours of several spiders has been shown to drive their community dynamics and responses to environmental change (Pruitt &

Ferrari 2011; Pruitt & Modlmeier 2015; Dahirel et al., 2017), as well as changes in the structure of prey communities (Royauté & Pruitt 2015).

The ecological consequences of intraspecific variation in most terrestrial arthropods remain unexplored (Didham et al., 2016). Yet trait-based studies using only species-level means will fail to detect the effects of intraspecific variation on community structure and dynamics (reviewed in Bolnick et al., 2011). Few studies have sought to investigate the ‘stable species hierarchy’ hypothesis, which predicts that trait variation is higher at the interspecific level than at the intraspecific level (but see Bonfanti et al., 2018). Intraspecific variation is reported to be high among particular traits of some arthropods (e.g., colouration in the ladybird beetle *Harmonia axyridis*, Koch 2003; diet breadth of the fire ant *Solenopsis invicta*, Roeder & Kaspari 2017); but low in others (e.g., morphology of dung beetles; Griffiths et al., 2016). Moving forward, investigators should explore the effects of intraspecific variation in terrestrial arthropods, such as by determining how individual differences in multidimensional trait space and in trade-offs between traits influence performance along environmental gradients. Following this, the higher goal would then be to investigate how trade-offs within species differ from trade-offs among species, as this would improve understanding of functional trait evolution and the sorting of phenotypes across environmental gradients (Laughlin & Messier 2015). To complement such work, which would likely be limited to experimental communities consisting of few species, the many observational studies investigating the assembly, dynamics and ecosystem functions of diverse species communities should move away from a total reliance on species-level means, and instead strive to model the effects of intraspecific variation on community functional structure. For such purposes, a variety of analytical tools that compare intraspecific to interspecific trait variability (e.g., ‘T-statistics', Violle et al., 2012) and which incorporate intraspecific variation into the calculation of functional diversity metrics should prove useful (e.g., de Bello et al., 2011; Laughlin et al., 2012; Carmona et al., 2016). Here, a foreseeable challenge will be collecting and measuring sufficient individuals to provide a representative sample for each species. Previous studies measured between one to over 2000 individuals per species (Griffiths et al., 2016; Warzecha et al., 2016; Classen et al., 2017). Griffiths et al. (2016) recommend measuring "at least 30 individuals [per species] when working with invertebrate traits that are likely to display high levels of phenotypic plasticity"; however they did not account for the effects of multidimensional trait covariances in their estimate. While 30 individuals per species may suffice when estimating a 1D normal trait distribution with 90% accuracy, at least 50 individuals per species are required to estimate a 3D trait distribution with 90% accuracy, and the minimum number of replicates increases with increasing trait dimensionality and with departure from normality (Laughlin & Messier 2015). Such high demands for replicates underscore the importance of curating individual-level trait information in multi-species trait databases (discussed further below).

Limitation: sampling methods as trait filters

Most if not all sampling methods bias detection towards particular species and away from others. When sampling methods consistently fail to detect certain species because of their particular traits or trait values (detection filtering), the effects on observed trait-environment relationships may be substantial (Pakeman 2014; Roth et al., 2018). Under-sampling bias is especially pervasive for terrestrial arthropods, which are a difficult group to sample, and for which a wide variety of sampling methods have been developed (Coddington et al., 2009). However the potential effects of under-sampling bias and detection filtering on the observed functional diversity of terrestrial arthropod assemblages are neither acknowledged nor addressed in most trait-based studies. It is conceivable that detection filtering could operate on traits such as body size (e.g., pitfall traps are more effective at capturing larger-sized ants, Olson 1991), mobility (when fast-moving species escape sweep nets), diet (if baits are used in collections), seasonality and activity time (when sampling is conducted during a specific season and time of day), and many others. Notably, these traits are commonly used in trait-based studies on terrestrial arthropods. Moving forward, studies investigating the direction and strength of detection filtering by widely used sampling methods for terrestrial arthropods will contribute practical information to guide method selection in trait-based work. One approach to reduce under-sampling bias may be to incorporate a greater variety of sampling methods in the protocol (Bestelmeyer et al., 2000); however this may also impede efforts to standardize sampling across studies, which is crucial for the comparison of results and the integration of trait data. While it is seldom possible to remove all biases from the sampling process, it remains imperative that investigators recognise – and also report – how these may affect the trait-environment relationships and patterns of functional diversity observed.

Limitation: source, structure and consolidation of trait information

Information on traits may be obtained from the primary source – that is, through observation and measurement on organisms encountered during the study – or from secondary sources such as the literature and data repositories. The structure of trait data may be in continuous form (e.g., body size in mm, clutch size) or categorical form (e.g., colour, diet). The particular source and structure of trait information used will affect the quality of results obtained. Where possible, investigators should prioritize the collection of primary data on traits, and in continuous form. Primary data on traits measured in situ will be most representative of the ecological relationships investigated, since these are the traits directly undergoing selection by, or affecting, the studied environment. Continuous data will better reflect changes in the intensities of a trait's interactions than discrete categorical data (Lavorel & Garnier 2002). Using primary and continuous data will also be important if potential effects of intraspecific variation are to be addressed. However, across the studies presently reviewed, the use of trait data from secondary sources and in categorical form was very common. As one example, among studies on lepidopterans, 'larval diet breadth' was often estimated via a ranked variable, which recorded whether the larvae of a species fed on "(1) one plant species; (2) two plant species; (3) three plant species, etc." (Diamond et al., 2011), or alternatively "(1) one plant species, (2) more than one species from the same genus, (3) more than one genus from the same family, (4) more than one family from the same order, etc." (Graça et al., 2016; 2017). This information was either obtained from the literature (e.g., Hardy et al., 2007) or databases (e.g., Janzen & Hallwachs 2009); and where information was absent for a particular species, information from a congeneric was used in its place (Graça et al., 2016; 2017).

Of course, it will not always be feasible to collect primary data on traits. There is a general lack of knowledge on species' traits, ecological functions and interactions (see the 'Raunkiearan' and 'Eltonian' shortfalls; Hortal et al., 2015). Furthermore, acquiring trait information is especially difficult in studies investigating relationships at global and regional scales where primary sampling may be impractical, as well as studies on rare and endangered species where collecting specimens may be difficult or prohibited (although phylogeny based imputation may be one way to reconcile missing trait data; see Penone et al., 2014). In this regard, the value of consolidating high-quality trait data in comprehensive and organized data repositories cannot be overstated. Several of these already exist for terrestrial arthropods such as ants (e.g., GLAD, Parr et al., 2017), ground beetles (e.g., Carabids.org, Homburg et al., 2014) and soil invertebrates (BETSI, Hedde et al., 2012; Edaphobase, Burkhardt et al., 2014); there are likely to be many more databases that are unpublished. Previous authors have provided recommendations for managing the eco-informatics of trait databases (Schneider et al., 2018), including those for terrestrial arthropods (Pey et al., 2014). Below we propose seven additional recommendations for the development of terrestrial arthropod trait databases, focusing on the collection of trait information.

First, maintaining accurate taxonomic identifications and updates for species' trait data is paramount, as these are the primary means for identifying and comparing trait information. This will be a significant challenge as substantial taxonomic inaccuracies are prevalent in most biological databases (Goodwin et al., 2015; Maldonado et al., 2015) – and especially so for the terrestrial arthropods, where research is hampered by many taxonomic impediments (discussed above). Thus, while data on the traits of terrestrial arthropods could accumulate relatively easily, advances in taxonomic research will be important for effectively curating (including depositing and updating) these trait data in databases. One approach may be to tag trait data from the same individual with a DNA barcode or other genetic identifiers. Second, standardising the measurement of traits is essential for facilitating comparisons among studies from different regions and localities; this potential for generality is a primary merit of the trait-based approach (Moretti et al., 2017). Inconsistencies in trait information will be compounded when data from studies using different sampling methodologies and measurement techniques are compiled (e.g., in macroecological research). Third, prioritizing continuous data over discrete categorical trait data will improve the resolution of trait information and its potential to reflect intensities in trait interactions (Lavorel & Garnier 2002). Fourth, prioritizing information on individual-level trait variation will facilitate much-needed research on intraspecific trait variation. This may be especially important for species with wide geographic distributions. Fifth, depositing information on sampling and measurement methodology, as well as the environmental correlates of observed trait values will be important for clarifying inconsistencies and also enhancing potential for reproducibility. Sixth, even if specimens used in ecological studies are not taxonomically identified, storing vouchers – and also their linked genetic sequence data, if possible – will facilitate the verification of trait information and reproducibility in the long term (Turney et al., 2015; Packer et al., 2018). Finally, incorporating trait data from digital and physical collections of museums, which are vast, will be especially useful for temporal and spatial comparisons.

NEW FRONTIERS FOR TERRESTRIAL ARTHROPOD TRAIT-BASED ECOLOGY

In this section we highlight several areas that represent promising avenues for future trait-based research on terrestrial arthropods. The research proposed here is especially well suited to investigations in terrestrial arthropod systems, likely to advance understanding of broad ecological phenomena, and should also enhance real world practice in ecological management and conservation.

Idiosyncratic traits of terrestrial arthropods

The sheer biological diversity of terrestrial arthropods affords new and exciting opportunities for exploring the ecological effects of distinct phenotypes that are absent from other organisms. Many of these idiosyncratic traits have not been investigated in trait-based studies thus far. Especially relevant to intraspecific variation are traits that reflect ‘personality’: temporally consistent individual differences in behaviour along one or more behavioural axes (Modlmeier et al., 2015). Several studies on predator-prey and pollination networks suggest that variation in personality traits relating to foraging, resource use, and responses to predators can impact community structure and/or ecosystem functions through interspecific interactions (Hawlena, Hughes & Schmitz 2011; Pruitt & Ferrari 2011; Pruitt & Modlmeier 2015; Royauté & Pruitt 2015; Venjakob et al., 2016). However there remain numerous arthropod species varying in personalities and behavioural repertoires (e.g., circadian activity, territoriality, sexual interactions, sociality) – for which the effects on community structure, dynamics and ecosystem functions remain unexplored. Extended phenotypes may also potentially be considered functional traits if they influence interactions and individual fitness (Violle et al., 2014); for instance, in plants, phyllosphere bacterial diversity plays a key role in plant functioning (Kembel et al., 2014). How the diversity of extended phenotypes among terrestrial arthropods – such as the structural diversity of galls of gall-making insects, webs of spiders, and nests of social insects – relates to their individual fitness, and interacts with the environment is relatively unexamined (but see Stone & Cook 1998; Dahirel et al., 2017). Given the substantial biomass of these taxa in many environments, trait-based research focusing on extended phenotypes may be the key to understanding a variety of important ecosystem functions (e.g., predation by spiders, biogeochemical processes of termite and ant nests). Other interesting questions may be explored by examining chemical traits (e.g., how do different defensive chemical compounds influence survival among communities of herbivorous insects? See Zvereva & Kozlov 2016) as well as traits across life stages (e.g., in holometabolous insects, are the traits of larval and pupal stages indicative of niches and fitness of adults?). Importantly, future research in any of these areas should not assume but rather test explicitly the functionality of the focal traits; this will facilitate the scaling of trait interactions from individuals to ecosystems.

Competition and coexistence

The biotic force of competition has traditionally been thought to shape community assembly by preventing individuals with very similar niches from coexisting (MacArthur & Levins 1967). Consequently, it has been posited that the intensity of competition decreases as two species diverge in trait values (trait dissimilarity) (MacArthur & Levins 1967), and that competition produces a non-random pattern of dispersion among trait values (functional overdispersion) in the community (Weiher & Keddy 1995a; Maire et al., 2012). Accordingly, a few studies on ants, bees and spider communities have cited patterns of trait dissimilarities or functional overdispersion – mainly in feeding traits – as evidence for the influence of competition in assembly (Houadria et al., 2015; Michalko & Pekár 2015; Litchenberg et al., 2017).

However, modern coexistence theory (Chesson 2000; HilleRisLambers et al., 2012; Barabás, Andrea & Stump 2018) proposes that relationships between competition and coexistence are more complex, and not solely dependent on species' dissimilarities in their niches (and traits). Rather, coexistence occurs when invasion growth rates are positive, resulting from a balance between the effects of stabilizing mechanisms (stabilization, A) (e.g., storage effects and relative nonlinearities) mediated by species' niche differences, and the effects of differences in competitive abilities (competitive advantages, f_i) that favour particular species over others in the absence of stabilization

(Barabás et al., 2018). In line with this theory, experiments on plant communities show that competition may actually result in functional clustering among community members if the traits in question are associated with competitive dominance (Narwani et al., 2013; Godoy, Kraft & Levine 2014), and that particular trait values may confer competitive advantages independently from trait dissimilarity (Mayfield & Levine 2010; Kraft et al., 2015). At the global scale, traits that consistently influenced competitive interactions in plant communities were also identified (Kunstler et al., 2016).

Integrating modern coexistence theory with trait-based ecology may provide a powerful paradigm for tackling the fundamental question of coexistence (Kraft et al., 2015). However most empirical applications have been constrained to plant research. Trait-based studies on terrestrial arthropods by and large have not investigated their community ecology from the perspective of modern coexistence theory. Often, traits which may conceivably contribute to f_i (e.g., body size, aggression) as well as performance traits which may conceivably directly impact growth rates (e.g., fecundity) are not distinguished from traits that are assumed to reflect niche differences, which potentially contribute to A.

Future trait-based studies investigating the relative magnitudes and roles of A and f_i in determining coexistence in terrestrial arthropod communities may advance understanding of how their diversity is shaped and maintained. In addition, the effects of competition and coexistence on ecosystem functions may also be explored. For instance, how do ecosystem functions vary between communities that are robust (small f_i, large A), dynamic (large f_i, large A), unstable (large f_i, small A) and quasi-neutral (small f_i, small A) (Adler, HilleRisLambers & Levine 2007; Mayfield & Levine 2010)? Such questions will have direct implications for the management of biodiversity and ecosystem services under changing environments. However, there are at least two obstacles and one caveat to the application of modern coexistence theory to empirical studies on terrestrial arthropods. The first obstacle will be identifying an appropriate spatial scale – one at which competition could potentially occur. Most resources that terrestrial arthropods compete for (e.g., plants, prey, nest sites) vary locally and across fine spatial scales, hence the many studies examining variation in community structure across broad environmental gradients (e.g., altitude) are not suited for detecting the influence of competition in assembly (Swenson et al., 2007). The second obstacle will be identifying the traits (or trait sets) that contribute to A and f_i in terrestrial arthropod communities, which are largely unknown at present. Elucidating these traits may require experiments that assemble communities of species in varying densities, and measuring multiple traits as well as growth rates for each species in each community (e.g., Kraft et al., 2015). Finally, as a caveat, modern coexistence theory may fail to explain coexistence in more diverse and complex arthropod communities because the theory assumes the absence of complex dynamics, the stability of the resident community, and the presence of only a few limiting factors – or at least fewer limiting factors than there are species in the community (see Barabás et al., 2018).

Structure and function across trophic levels in ecological communities

Competition between species within a trophic level does not always account for species coexistence at this level; nor does it explain the biodiversity of the ecological community, defined as all organisms living in the specified place and time (*sensu* Vellend 2016). To do so requires understanding the wider array of non-competitive interspecific interactions (including mutualism, facilitation, predation and parasitism), which may occur both within and across trophic levels (Levine et al., 2017). How these manifold interactions shape community dynamics and structure is poorly understood (Godoy et al., 2018). Terrestrial arthropods, which encompass diverse trophic levels and ecological strategies, are excellent systems for investigating such questions. Recent studies have successfully employed trait-based approaches to elucidate the mechanistic bases of non-competitive interactions, as well as their effects on community structure. For instance, a focus on traits revealed a strong role for Müllerian mimicry (in wing patterns) in shaping coexistence of butterfly species along altitudinal gradients (Chazot et al., 2014); while in a non-trophic facilitative interaction, the functional diversity of cavity-producing wood-boring beetles influenced the body sizes of cavity-nesting bees (Sydenham et al., 2016). Similarly, the functional diversity of socially parasitic rove beetles was shown to be driven by the abundance of their ant hosts (Psomas, Holdsworth & Eggerton 2018). Recently, the identification of traits mediating trophic linkages between adjacent trophic levels (trait-matching) has been useful for characterising the structures of predator-prey (Brousseau et al., 2018b), plant-herbivore (Le Provost et al., 2017) and pollination (Garibaldi et al., 2015; Bartomeus et al., 2016) networks. Identifying trophic linkages via trait-matching also have facilitated assessments of the impact of environmental changes on multiple trophic levels (e.g., impact of landscape simplification on plant and herbivore functional diversity, Le Provost et al., 2017), as well as predictions on BEF relationships (e.g., in pollination networks, predictions of fruit set were enhanced by matching the body sizes and mouthpart lengths of flower visitors with the nectar accessibility of flowers; Garibaldi et al., 2015).

Moving forward, terrestrial arthropod trait-based studies may take advantage of recent theoretical and conceptual advances to predict structure and function across multiple trophic levels. For instance, conceptual models using traits as the basic properties to integrate the structural components of ecological network research (e.g., trait-matching and modular trophic units for interacting species) with the functional components of BEF research (e.g., species' responses to and effects on their environments) have been proposed to improve prediction of the many ecosystem functions encompassing multi-trophic interactions (Schleuning, Fründ & García 2015; Schmitz et al., 2015). Recently, Godoy et al. (2018) also presented a theoretical framework integrating niche and network theories to explain coexistence at multiple trophic levels, which explicitly considers the effects of stabilizing mechanisms as well as differences in competitive abilities. Future terrestrial arthropod trait-based studies adopting these integrative frameworks may make important advances in explaining and predicting the emergent properties (structure and function) of complex ecological communities, and thus produce more accurate models of natural systems. Additionally, such research may also provide new insights into the BEF relationships of interspecific interactions such as mutualism (Schleuning et al., 2015) and parasitism (Frainer et al., 2018).

Functional biogeography of terrestrial arthropods

The emerging field of functional biogeography investigates the patterns, causes, and consequences of the geographic distribution of trait diversity (Violle et al., 2014). Trait-based approaches are integral to this new field, which aims to (i) describe the distribution of traits along environmental gradients and across spatial scales; then, using this information (ii) explain the geographic distribution of organisms, biodiversity patterns, and ecosystem processes, and (iii) predict responses to environmental changes using trait-based predictive functions and models (Violle et al., 2014). Some of these aims have already been realized through the rapid progress of trait-based plant ecology; for instance, high-resolution world maps of plant trait variation were recently produced (Butler et al., 2017). The prospects for a functional biogeography of terrestrial arthropods are likewise promising. Applying trait-based approaches to test hypotheses from the theory of island biogeography, Whittaker et al. (2014) showed that functional diversity-area relationships for spider and beetle communities scaled in a manner similar to species richness-area relationships across local, island and archipelagic scales. Basic questions of how terrestrial arthropod functional diversity and ecosystem functions scale with environment and area are presently unaddressed, and will likely be a core focus of future trait-based research. Functional biogeography may also complement community ecology (and vice versa), by providing insights into the spatial scaling of assembly processes (e.g., species interactions) across broad gradients (Violle et al., 2014). We envisage that developing a functional biogeography of terrestrial arthropods will first entail extensive efforts to model trait-environment relationships at local and regional scales; importantly, these studies need to be comparable, and address current limitations (see previous section). This foundational work may then be integrated with species distribution models (e.g., GABI, Guénard et al., 2017), trait databases (e.g., GLAD, Parr et al., 2017) and statistical tools for scaling functional diversity (Carmona et al., 2016) to describe, explain and predict geographical distributions of terrestrial arthropod form and function. Finally, novel studies on trait-environment relationships across both space and time may usher in an exciting new field: ‘functional historical biogeography’ (Sukumaran & Knowles 2018). For instance, might the geographic distributions and the traits of fossilised individuals, populations and communities reveal their relationships with prehistoric environments?

CONCLUSIONS

(1) By focussing on the functional properties of individual organisms, trait-based ecology provides a broad, mechanistic framework for synthesising, explaining and predicting structure and function across different levels of biological organization.

(2) The time is ripe for a trait-based ecology of terrestrial arthropods. Such work will improve understanding of the processes underlying patterns of diversity for complex ecological communities encompassing multiple trophic levels, and provide mechanistic insights to the functioning of essential ecosystem services such as pollination, biological control and nutrient cycling. For many terrestrial arthropods, taxonomic impediments have limited ecological research, and a focus on traits will be particularly useful for expediting understanding some of the interactions and functions of these taxa. The growing volume of data on the traits of terrestrial arthropods in databases and the wider literature, as well as physical and digital collections, will facilitate work on the generality of functional relationships across geographic regions and spatial scales.

(3) Findings from pioneering studies on the trait-based ecology of terrestrial arthropods attest to the value of this burgeoning field. Here, trait-based approaches have been especially useful for elucidating the specific mechanisms driving the deterministic assembly of diverse communities across different environmental gradients, as well as their responses to disturbances – often revealing distinct patterns in functional diversity not detected by taxonomic and phylogenetic approaches. Preliminary work investigating terrestrial arthropod-mediated ecosystem functions did not observe a consistent relationship between functional diversity and ecosystem function, although comparisons are strictly limited by differences among studies in terms of the focal scale, community characteristics and methods used.

(4) New studies expanding the scope of terrestrial arthropod trait-based research will advance knowledge in longstanding as well as emerging areas in ecology. As previous studies mainly focused on the interactions between traits and abiotic environments, one immediate avenue for future work will be to explore how biotic interactions – including various competitive, non-competitive, and multi-trophic interactions between species – shape structure and function across different environmental gradients and spatial scales. At the same time, novel research on the functional biogeography of terrestrial arthropods may succeed in mapping global distributions of their functional diversity, thereby enhancing ecological forecasting and the management of ecosystem services in the face of climate change and the spread of invasive species. Importantly, such efforts will be undermined if trait functionality is not rigorously tested, if the effects of intraspecific variation are not accounted for, and if the collection of trait information is biased or inconsistent. The predictive value of future work also rests upon the willingness of researchers to go beyond describing patterns to identify mechanisms – that is, by undertaking hypotheses-driven investigations grounded in ecological theory. Future studies in terrestrial arthropod trait-based ecology should thus explicitly address these aspects in the critical stages of study design, trait selection, sampling and measurement, as well as in the treatment and consolidation of trait data.

(5) Realizing trait-based ecology's higher goal of synthesis, generality and prediction also demands taxonomic excellence – to safeguard the accuracy and coherence of trait data. Thus it is important to recognize that functional approaches to describing biodiversity are ultimately complements, and not substitutes to taxonomic ones. While a focus on traits can help to overcome significant taxonomic impediments to the understanding of ecology, trait-based research faces an even greater impediment

– the lack of information on the form and functionality of organisms. Especially in the hyper-diverse terrestrial arthropods, basic data are lacking on diet, physiology, phenology and behaviour – let alone information on how these vary intraspecifically along environmental gradients. In conclusion, we propose that reconciling contemporary trait-based research with the long-established study of taxonomy and natural history will pave the way for a more robust understanding of the mechanisms structuring arthropod diversity across space and time.

3

The cryptic impacts of invasion: functional homogenization of tropical ant communities by invasive fire ants

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MKLW, BG and OTL designed the study. MKLW conducted fieldwork, analysed the data and wrote the first draft of the manuscript. All authors contributed substantially to manuscript revisions.

ABSTRACT

The diversity and distribution of traits in an ecological community shapes its responses to change and the ecosystem processes it modulates. This ‘functional diversity’, however, is not necessarily a direct outcome of taxonomic diversity. Invasions by exotic insects occur in ecosystems worldwide, but there is limited understanding of how they impact functional diversity. We present the first comprehensive trait-based investigation of the impacts of an ant invasion, and the first incorporating intraspecific polymorphisms in species-level functional diversity. The fire ant *Solenopsis invicta* is an invasive species with a global distribution. Focusing on invaded and uninvaded plots in tropical grasslands of Hong Kong, we investigated how the presence of *S. invicta* affects the diversity and distribution of ant species and traits within and across communities, the functional identities of communities, and functionally unique species. Using trait probability density functions, we built trait spaces for 29 different species, and scaled up these components to calculate functional diversity at community and landscape levels. We found that invasion had limited effects on species and functional richness but pronounced effects on functional composition. Specifically, invaded communities had fewer functionally-unique individuals, and were characterized by species with narrower heads and bodies and shorter mandibles. Moreover, invaded communities showed substantially higher levels of functional redundancy (+56%) due to a clustering of trait values. Consequently, across the landscape, invaded communities displayed 23% less functional turnover than uninvaded communities despite showing comparable levels of taxonomic turnover – a result confirming theoretical predictions of the effects of high local functional redundancy. In sum, the presence of *S. invicta* alters the functional properties of multiple local communities selectively, resulting in functional homogenization across the landscape. The disparities between taxonomic and functional impacts of invasion highlight the need to consider how trait diversity across ecological scales shapes biodiversity and its responses to change.

Keywords

Beta diversity, functional diversity, functional trait, functional rarity, insect, intraspecific, invasive species, turnover

INTRODUCTION

Invasions by exotic species are not only the second most common cause of extinctions (Bellard, Cassey and Blackburn, 2016) but also drive cascading impacts on ecosystems, cause economic damage and undermine human health (Pyšek and Richardson, 2010). As with many ecological phenomena, invasions have long been studied by summarising ecological communities using metrics based on species' taxonomic identities: abundance, richness and diversity. Changes in these metrics, however, may provide only limited insight into the specific mechanisms underlying the causes of invasions (MacDougall, Gilbert and Levine, 2009). Furthermore, subsequent effects of invasion on ecosystem processes are more likely to depend on the ecological interactions of species, than on species numbers and identities *per se* (Gagic et al., 2015). To this end, summarising biodiversity in terms of the traits that directly impact organisms' ecological interactions (Functional Diversity) (McGill et al., 2006) may advance understanding of the causes and consequences of invasions.

Traits are the phenotypic properties of organisms which modulate their ecological interactions. The ecological interactions modulated by key 'functional traits' influence organism fitness and may also contribute to ecosystem functions (Wong, Guénard and Lewis, 2019). Thus, changes in the diversity of functional traits in an ecological community can simultaneously reveal how biodiversity and ecosystem processes are impacted by disturbances such as invasive species. For instance, trait-based research on plant and vertebrate communities undergoing invasion by exotic species reveal declines in functional richness (the variety of trait values in individual communities) and a tendency for functional homogenization (i.e., an increased similarity in trait values between communities) (Villéger, Grenouillet and Brosse, 2014; Castro-Díez et al., 2016).

Crucially, invasion-driven changes in functional structure are further linked to altered ecosystem functions (Castro-Díez et al., 2016).

One general limitation of most trait-based analyses is the exclusive use of mean trait values for species to estimate community functional diversity. This approach underestimates intraspecific trait variation, which can strongly influence community dynamics and ecosystem processes (Des Roches et al., 2018). Intraspecific trait variation is also implicated in the success of some invasive species (González-Suárez, Bacher, and Jeschke, 2015). Recently-developed statistical tools such as the Trait Probability Density (TPD) framework can incorporate intraspecific trait variation into estimates of functional diversity (Carmona et al., 2016, 2019), but few studies have explored this within the context of invasions. Additionally, although trait-based research is advancing the understanding of invasions by plants and vertebrates, there is a shortage of similar work on invasive insect species (Wong et al., 2019), despite their ubiquity and widespread impacts on biodiversity and ecosystem services (Bradshaw et al., 2016).

Several ants, for instance, are contenders for the world's most harmful invasive species (Lowe et al., 2000). Documented impacts of ant invasions on native ant communities include declines in species richness, taxonomic homogenization, and phylogenetic clustering (reviewed in Lessard et al., 2009). Invasive ant species were also observed to alter the ecosystem functions performed by native ant species (Ness et al., 2004). However, the consequences of ant invasions for the functional diversity of individual communities (functional alpha diversity) and patterns across multiple communities (functional beta diversity) are relatively unexplored. This is in spite of substantial progress in the understanding of ant communities' trait-environment relationships (Bihn, Gebauer and Brandl, 2010; Arnan et al., 2014; Retana et al., 2015).

To our knowledge, no trait-based studies on ants, and few for insects in general include intraspecific trait variation in estimates of community functional diversity (Wong et al., 2019). Intraspecific trait variation is expected to be high in polymorphic species, and it may influence how such species respond to or effect ecological change. Some ant species display marked variation in the body size and morphology of their worker caste (worker polymorphism), a feature which may contribute to colony fitness and ecological success (Tschinkel, 1988; Wilson, 2003). While the adaptive benefits of worker polymorphisms remain unclear (Wills et al., 2018), polymorphic ant species are known to surpass monomorphic ones in their abilities to collect resources varying in size and to access environments varying in rugosity (Farji-Brener, Barrantes and Ruggiero, 2004). That is, polymorphic species may access a wider variety of niches than monomorphic species. Thus, a basic yet apparently untested assumption is that polymorphic species have higher functional (trait) richness than monomorphic species.

The Red Imported Fire Ant, *Solenopsis invicta* Buren, 1972, is native to South America, but has spread globally to four other continents (Ascunce et al., 2011; Guénard et al., 2017), with vast areas throughout the tropics and subtropics susceptible to future invasion (Morrison et al., 2004). The species is a pervasive ecological problem in North America owing to its strong impacts on biodiversity at multiple trophic levels – including native ants (e.g., Gotellia and Arnett, 2002) – and the subsequent cascading effects on ecosystems (Porter and Savignano, 1990; Vinson, 1997). *Solenopsis invicta* are dietary generalists and mature colonies contain a polymorphic worker caste, factors which, alongside their strong interspecific aggression, may contribute to the success of invasive populations (Tschinkel, 1988; 2006). In Asia, *Solenopsis invicta* was first reported from Taiwan in 2003, and from continental China in 2005 (Ascunce et al., 2011). There is limited ecological research on *S. invicta* in Asia; nonetheless declines in the species richness of arthropod communities in agrosystems in China were recently attributed to the presence of this exotic species (Wang et al., 2018).

Here we investigate the impacts of the invasion of *S. invicta* on taxonomic and functional diversity within (alpha diversity) and between (beta diversity) native ant communities in Hong Kong. This is the first comprehensive trait-based study of an ant invasion's impact on the functional facet of biodiversity, as well as the first to incorporate polymorphisms in calculations of functional diversity at the species level.

At the scale of the local community, we examine how invasion by *S. invicta* affects (i) species and functional richness, (ii) abundance-weighted indices of multidimensional functional diversity, and (iii) functional identity, the dominant value of a trait in the community. We predict lower species and functional richness as well as altered functional identities in communities invaded by *S. invicta* (Porter and Savignano, 1990; Castro-Díez et al., 2016).

At the multi-community (landscape) scale, we investigate how *S. invicta* invasion affects taxonomic and functional beta diversity (the dissimilarities in species and traits between communities). We predict that invasion by *S. invicta* will lead to taxonomic homogenization (Lessard et al., 2009), which will be associated with functional homogenization, as observed in other species introductions (Villéger et al., 2014). Using measures of species-level functional diversity, we also calculate species' functional uniqueness in terms of the extents to which they possess unique traits in the regional species pool as well as in uninvaded and invaded local communities (Violle et al., 2017). Lastly, we measure and compare the functional richness of different species, with the prediction that the functional richness of polymorphic species such as *S. invicta* will exceed that of monomorphic species.

MATERIAL AND METHODS

Study area and sampling design

Our study sites are two (<4 km apart) wetland reserves in northern Hong Kong: Lok Ma Chau (22.512°N, 114.063°E) and Mai Po (22.485°N, 114.036°E). Both reserves encompass abandoned fish farms that have since been conserved for >35 years as habitats for migratory birds. Each contains a network of bunds (width ≤5 m) which separate individual ponds (Appendix A: Fig. S1). The habitat is relatively homogeneous and comprises exposed grasslands with native tree species interspersed throughout. Ant communities in this landscape are comprised mostly of native species but pilot surveys from 2015 to 2017 revealed that colonies of *S. invicta* are present at high densities at multiple locations. We marked these locations, and in 2018 selected a total of 61 plots, each a 4 × 4 m quadrat, to reflect two ant community types: communities with *S. invicta* absent (uninvaded; 37 plots), and those with *S. invicta* present (invaded; 24 plots) (Appendix A: Fig. S1). A minimum distance of 20 m between individual plots facilitated independent observations since most ant species in the region forage no further than 5 m from their nests (Eguchi, Bui and Yamane, 2004) and *S. invicta* forage within 4 m of their nests (Weeks, Wilson and Vinson, 2004). Given the homogeneity of the landscape we assumed that any community differences observed between uninvaded and invaded plots would primarily be a consequence of invasion by *S. invicta*; environmental data collected at fine spatial resolutions were used to test this assumption (see below).

Sampling was conducted from April to September 2018. At each plot, six pitfall traps (55 mm in diameter) were installed to sample the ant community over 48 hours (Appendix A: Fig. S2). The maximum distance between any two traps in each plot was 5.65 m; this sampling density (i.e., traps / m^2) was comparable to (if not higher than) previous studies characterizing ant communities which placed adjacent pitfall traps at distances of 5–10 m in individual plots (Sanders, Moss and Wagner, 2003; Parr, 2008), thus allowing better characterization of fine scale communities. All specimens were sorted into morphospecies and subsequently most were identified to species using taxonomic keys.

Environmental data

We used local GIS models (Morgan and Guénard, 2019) to obtain high-resolution data (30 × 30 m rasters) for three environmental variables corresponding to each plot: Normalized Difference Vegetation Index (NDVI), mean annual temperature, and mean annual precipitation.

Assembling the individual-level trait dataset

Here we aimed to obtain values of functional diversity that incorporated intraspecific trait variation, including the variation arising from worker polymorphisms. We assembled an individual-level trait dataset comprising data for seven morphological traits that influence ant physiology and behaviour and that are hypothesized to impact performance and fitness (see Table 1). Using mounted specimens from the pitfall traps and a Leica M165c stereo microscope paired with Leica Application Suite software, we recorded high-resolution images and performed trait measurements on at least 10 individual workers of every species (N=319). For dimorphic species of *Camponotus* and *Pheidole* where workers comprise two distinct sub-castes (minors and majors), we included trait data for individuals of both sub-castes based on caste-ratios documented in natural colonies in previous studies (in both genera majors comprise ≤10% of all workers; Passera, 1984; Wilson, 2003). The invader *S. invicta* has a polymorphic worker caste, and Tschinkel (1988) showed that this polymorphism is mainly expressed in the morphological variation displayed by the 'majors' (head width >0.7 mm), which are present only in mature colonies where they comprise 35% of the worker population ('minors' of head width <0.7 mm comprise the remaining 65%); juvenile colonies consist only of minors. We observed that majors were present in all invaded plots, indicating the presence of mature colonies; thus, our trait data for *S. invicta* (n=20) included both minors (65% of individuals) and majors (35% of individuals).

Table 1. The seven traits measured on each individual, and each trait's hypothesized links to the performance and fitness of ants. All measurements are consistent with those used in the *GlobalAnts* trait database (Parr et al., 2017).

Trait	**Measurement**	**Hypothesized link to performance and fitness**
body size	Weber's length: diagonal length of mesosoma	Modulates vital and physiological rates, determines physical constraints and exposure to predators, influences resource type and acquisition efficiency (Silva and Brandão, 2010).

head width	Width of head including eyes	Determines the size of gaps through which an individual can pass (Schofield, Bishop and Parr, 2016) and the volume of muscles powering the mandibles during foraging (Richter et al., 2019).
eye width	Width of left eye	Determines ability in navigation, foraging, predator and prey detection, and indicative of activity times (Silva and Brandão, 2010).
mandible length	Length of left mandible	Responds to selection on diet type and specialization (Silva and Brandão, 2010).
scape length	Length of scape of left antenna	Responds to selection on navigation and sensory abilities (Silva and Brandão, 2010).
pronotum width	Width of pronotum	Determines volume of muscles for head-support and load-bearing (Keller et al., 2014).
leg length	Combined length of femur and tibia of left hind leg	Determines mobility; leg length influences running speed, which affects success in foraging or escape from predators (Grevé et al., 2019).

Compressing trait variation

Prior to all statistical analyses, we applied size-correction to six traits (*head width*, *eye width, mandible length*, *scape length*, *pronotum width* and *leg length*) by dividing their values by *body size* (measured as Webers' Length; see Table 1). With the new trait dataset containing values of *body size* and the six size-corrected traits, we then applied log-transformations to reduce the influence of extreme values, and standardized trait values to have mean of zero and unit variance. Next, we used Principal Components Analysis (PCA) to synthesize the major axes of variation in multidimensional trait space and to reduce the number of dimensions used to calculate functional diversity indices. We performed the PCA using the mean trait values of each species and subsequently predicted the values of the PCA components for all individuals in the dataset. We used species means instead of individual trait values in the PCA because using the latter could bias the analysis if some species had disproportionately large numbers of individuals in the dataset. We retained the first two principal components, which had eigenvalues greater than unity and which also satisfied the broken-stick criterion (Peres-Neto et al., 2003). The first principal component explained 55.1% of the variation and was negatively correlated with *head width* and *pronotum width* and positively correlated with *leg length.* The second principal component explained 21.6% of the variation and was strongly negatively correlated with *eye width* and positively correlated with *body size.* We predicted the values of these two components for every individual in the trait dataset and used these new 'traits' to calculate functional diversity indices.

Functional diversity from species to communities

All functional diversity indices were calculated using the Trait Probability Density framework which incorporates intraspecific variation, the multidimensional nature of traits, species abundances, and probabilistic trait distributions (see Carmona et al., 2016, 2019). First, we used multidimensional probability density functions to calculate trait probability distributions (which reflect the probabilities of observing different trait values) at the level of individual species (TPDsp) (Appendix A: Fig. S3). Next, we scaled up TPDsp to local community levels (TPDcom) by summing the TPDsp of all species in each local ant community (i.e., plot), weighted by their frequencies of occurrence (i.e., the proportion of the six pitfall traps capturing each species). Here, we estimated species' relative abundances in each local community using their frequencies of occurrence instead of the numbers of individual workers in the pitfall traps because the latter could overestimate the relative abundances of species with large colonies (Gotelli et al., 2011).

Five different indices for functional diversity were calculated using each community's TPDcom. The indices were Functional Richness (FRic), the volume of functional space occupied by the community; Functional Evenness (FEve), the regularity of the distribution of abundance in functional space; Functional Divergence (FDiv), a measure of how abundances tend to be on the outer margins of the functional space while controlling for functional richness; Rao, the abundance-weighted dispersion of individuals (or species) in functional space; and Functional Redundancy (FRed), the degree to which trait values are represented by multiple species in the community (Carmona et al., 2019). We used this multi-index approach to measure functional diversity because no one index can encapsulate the independent components of functional diversity (Mouchet et al., 2010).

In addition to calculating the observed values of the functional diversity indices, we calculated Standardized Effect Size (SES) values for all indices so as to estimate community-level functional diversity that had been corrected for potential effects of species richness (Swenson, 2014). SES values were calculated by comparing the observed values to values generated from 999 constrained null models randomizing the community data matrix using the "Independent Swap" algorithm. The formula for calculating SES is:

$\text{SES} = (\text{Mean}_{\text{observed}} - \text{Mean}_{\text{null}})/\text{s.d.}_{\text{null}}$

Functional identity

To estimate functional identity, we calculated the community-weighted mean (CWM) for each trait in every local ant community. A CWM reflects the dominant value of a given trait in a given community (Swenson, 2014). We calculated CWMs using mean trait values of species weighted according to their frequencies in the different communities. Size-correction was applied to all traits except *body size* (see above).

Taxonomic and functional beta diversity

We calculated six pairwise measures of taxonomic and functional beta diversity for all possible pairs of local ant communities. We followed the framework of Baselga (2010) to calculate pairwise Taxonomic Dissimilarity (Sørensen dissimilarity), and to further partition this into components of Taxonomic Turnover and Taxonomic Nestedness, which reflect species replacement and the loss of species between sites, respectively. We calculated the Functional Dissimilarity between paired communities using their TPDcom, and further decomposed this into Functional Turnover (dissimilarities in the trait values between communities), and Functional Nestedness (dissimilarities in the relative abundances of trait values shared between communities); for details, see Carmona et al. (2019).

In addition to observed values, we calculated SES values (from comparisons with 999 constrained null models using the “Independent Swap” algorithm) for all components of functional beta diversity. Although the “Independent Swap” algorithm may not be optimal for generating null models of beta diversity patterns shaped by dispersal limitation (Swenson, 2014), this is unlikely to be a problem for the present study because all species disperse by flying alates that can travel distances exceeding the scale of the study landscape (the maximum distance between any two plots was 4 km).

Species’ functional richness and functional uniqueness

We calculated functional richness and functional uniqueness values for all species. Functional richness was calculated based on each species’ trait probability distribution (TPDsp) (Carmona et al., 2019). Species’ functional uniqueness values were calculated relative to individual local communities, based on the degree to which a species’ functional space (TPDsp) did not overlap with a local community’s functional space (TPDcom) (Carmona et al., 2019). We calculated each species’ ‘relative uniqueness’ with respect to the different uninvaded and invaded communities, as well as its ‘objective uniqueness’ in the species pool (using a hypothetical community containing all species at equal abundance).

Statistical analysis

Taxonomic and functional alpha diversity, CWMs, and environmental variation

We used separate linear mixed-effects models with maximum likelihood estimation to assess whether the values of alpha taxonomic diversity, functional diversity indices (including observed and SES values) and CWMs differed significantly between uninvaded and invaded local ant communities, while including a random effect of environmental variation that was captured in the first component of a PCA for the three environmental variables, which explained 91% of the variation and had eigenvalues greater than unity. Using generalized linear models, we tested for environmental heterogeneity between invaded and uninvaded communities after using a Levene’s test to test for homogeneity of variance within each group. We also tested for the effects of variation in the three environmental variables on alpha taxonomic diversity, functional diversity (including observed and SES values) and CWMs.

Taxonomic and functional beta diversity

We used non-metric multidimensional scaling (NMDS) to scrutinize the relationships between and among invaded and uninvaded local ant communities in multidimensional space (Fig. S4). We used PERMANOVA (9,999 permutations) to quantify dissimilarity, turnover and nestedness between the observed taxonomic and functional compositions of uninvaded and invaded communities. We used permutation tests for multivariate dispersions to assess whether the levels of taxonomic and functional beta diversity (in three components) observed among uninvaded communities differed from those observed among invaded communities. We also used nonparametric Mann-Whitney U tests to compare SES values of the three functional beta diversity components between uninvaded and invaded communities.

Functional uniqueness of individual species

We calculated each species' average relative uniqueness to uninvaded and invaded local communities, and regressed these against its objective uniqueness in the species pool in a linear model.

Software

We used the following packages in R software version 3.3.3 (R Core Team, 2017): *TPD* (Carmona, 2018) for calculating trait probability distributions, functional diversity indices, functional dissimilarity and functional uniqueness measures; *FD* (Laliberté, Legendre and Shipley, 2014) for calculating CWMs, *betapart* (Baselga et al., 2018) for beta diversity analyses; *lme4* (Bates et al., 2015) for linear mixed-effects models; *MASS* (Venables and Ripley, 2002) for NMDS; and *ggplot2* (Wickham, 2009) for graphics.

RESULTS

Community composition and species richness

A total of 29 ant species (including *S. invicta*) were collected from 366 pitfall traps in 37 uninvaded plots and 24 invaded plots (Appendix A: Table S1). The species composition across invaded and uninvaded communities was similar overall, with 27 of the 28 native species occurring in both community types, and only one species not found in invaded communities. On average, the species richness of invaded communities was marginally and non-significantly lower (by 13%) than that of uninvaded communities (Table 2; Fig. 1).

Functional diversity, functional identity, and environmental variation

Uninvaded and invaded communities had similar levels of FRic and FEve for both observed and SES values. However, in linear mixed-effects models, the observed FDiv and Rao of invaded communities were significantly lower than those of uninvaded communities by 11% and 7% respectively, and the FRed of invaded communities was significantly higher than that of uninvaded communities by 56% (Table 2; Fig. 1); similar relationships were observed for SES values. Community-weighted means for the traits *body size*, *scape length*, *eye width* and *leg length* did not differ significantly between uninvaded and invaded communities. By contrast, the CWMs for *head width*, *pronotum width* and *mandible length* were significantly smaller (by 4–7%) in the invaded communities (Table 2; Fig. 2). In generalized linear models, no significant differences were found between the environmental variables of invaded and uninvaded communities, and no environmental variables significantly predicted the taxonomic and functional diversity or CWMs of local communities.

Table 2. Summary statistics for response variables in separate linear mixed-effects models with community type (uninvaded vs. invaded) as fixed effects and environmental variation as a random effect.

Index	**Uninvaded (mean ± SE)**	**Invaded (mean ± SE)**	χ^2	**df**	***P***
Species Richness	8.97 ± 0.42	7.80 ± 0.67	3.06	1	0.08
FRic	14.1 ± 0.61	12.9 ± 0.97	1.59	1	0.21
FRic.SES	-0.008 ± 0.15	0.22 ± 0.24	0.86	1	0.35
FEve	0.60 ± 0.007	0.59 ± 0.01	0.24	1	0.62
FEve.SES	0.14 ± 0.16	-0.09 ± 0.26	0.83	1	0.36
FDiv	0.73 ± 0.01	0.65 ± 0.02	17.8	1	<0.001***
FDiv.SES	0.61 ± 0.15	-0.46 ± 0.24	20.7	1	<0.001***
Rao	0.82 ± 0.01	0.76 ± 0.02	7.97	1	<0.01**
Rao.SES	0.44 ± 0.13	-0.42 ± 0.2	18.0	1	<0.001***
FRed	0.34 ± 0.05	0.53 ± 0.07	13.8	1	<0.01**
FRed.SES	-0.48 ± 0.13	0.55 ± 0.21	23.9	1	<0.001***
CWM*head.width*	0.76 ± 0.005	0.72 ± 0.007	23.7	1	<0.001***
CWM*pronotum.width*	0.52 ± 0.003	0.48 ± 0.004	85.8	1	<0.001***
CWM*mandible.length*	0.42 ± 0.003	0.40 ± 0.005	10.1	1	<0.01**

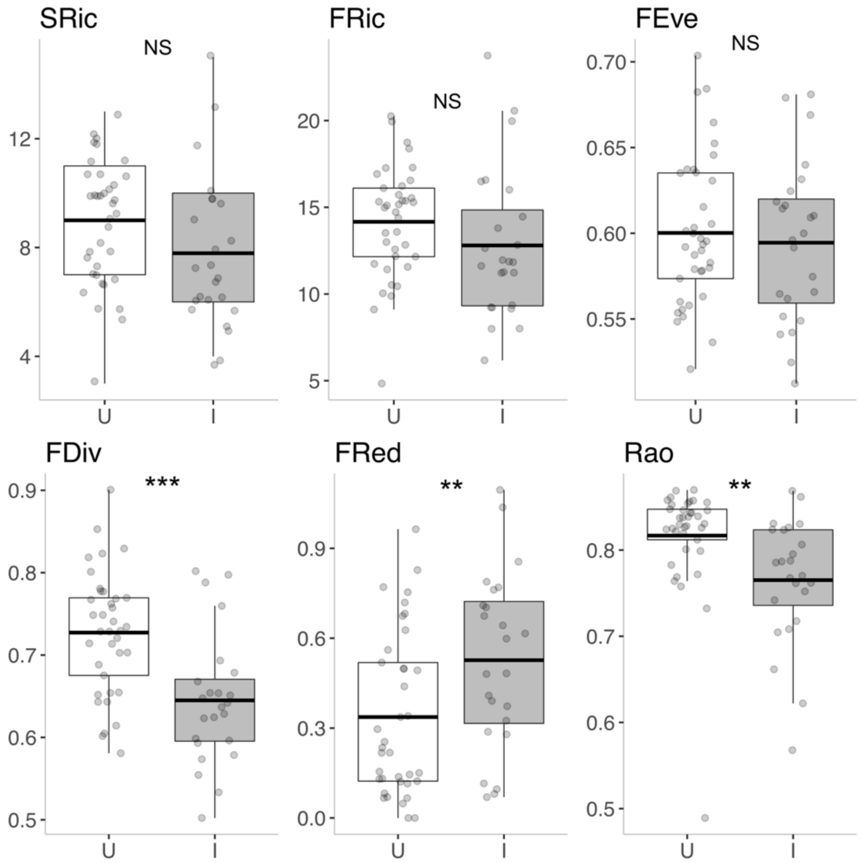

Figure 1. Boxplots showing species richness (SRic) and observed values of five functional diversity indices – Functional Richness (FRic), Functional Evenness (FEve), Functional Divergence (FDiv), Functional Redundancy (FRed) and Rao – in 37 uninvaded and 24 invaded local communities. Dots show values of individual communities, thick bars show means, boxes show inter-quartile range and vertical lines extend to maximum and minimum values (excluding outliers). Asterisks indicate statistical significance (*** *P*<0.001, ** *P*<0.01, * *P*<0.05, NS, not significant).

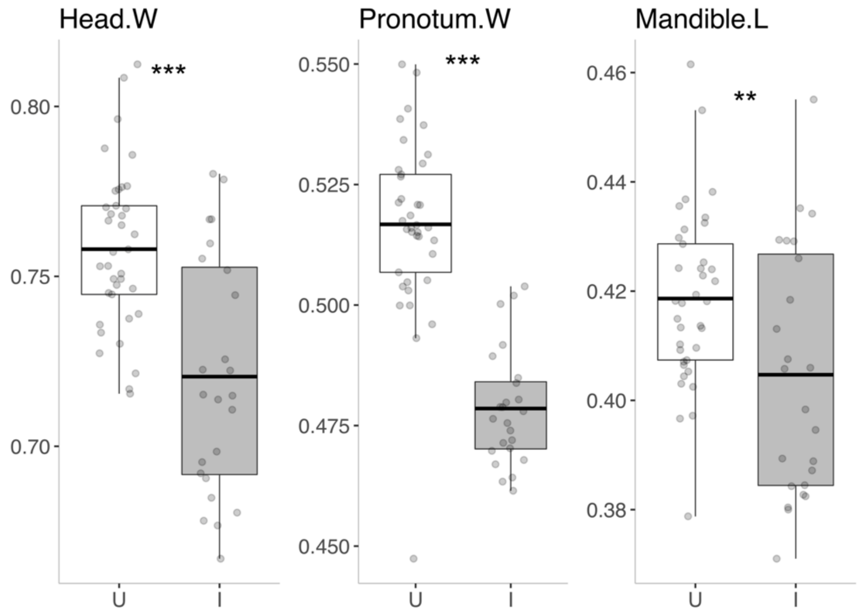

Figure 2. Boxplots displaying community-weighted mean values for size-corrected *head width*, *pronotum width* and *mandible length* in 37 uninvaded and 24 invaded communities. Dots show values of individual local communities, thick bars show mean values, box edges show standard deviations, and vertical lines extend towards minimum and maximum values. Asterisks indicate statistical significance (*** $P<0.001$, ** $P<0.01$).

Taxonomic and functional beta diversity

Uninvaded and invaded communities were significantly dissimilar in both taxonomic and functional composition, and these dissimilarities were driven by turnover in species as well as trait values (Table 3; Fig. 3). The observed levels of total taxonomic and functional dissimilarities among both uninvaded and invaded communities were comparable (Table 4), but SES values revealed that total functional dissimilarity was lower among invaded communities when corrected for species richness (Mann-Whitney U test: $P < 0.001$) (Fig. 3). Invaded communities had significantly lower levels of functional turnover (by 23%) and higher functional nestedness (by 20%) in observed values; these relationships were maintained in SES values (Mann-Whitney U tests: $P < 0.001$) (Table 4). Likewise, invaded communities were significantly more taxonomically nested than uninvaded communities (by 42%, Table 4; Fig. 3). That is, in comparison to uninvaded communities, relatively greater proportions of the total taxonomic and functional dissimilarities among invaded communities were driven by losses of species than by replacements of species, and by changes in the abundances of trait values than by changes in the trait values themselves, respectively.

Table 3. Results of PERMANOVA tests for dissimilarities between uninvaded and invaded communities in their observed taxonomic and functional compositions.

Beta diversity	**Component**	**F**	**R^2**	***P***
Taxonomic	Total Dissimilarity	22.4	0.28	<0.001***
	Turnover	31.9	0.35	<0.001***
	Nestedness	13.6	0.31	1.0
Functional	Total Dissimilarity	33.1	0.36	<0.001***
	Turnover	32.7	0.36	<0.001***
	Nestedness	14.7	0.33	1.0

Table 4. Permutation tests for multivariate dispersions, with calculations based on the average distances to centroids of uninvaded and invaded communities for different components of taxonomic and functional beta diversity. These tests compare the levels of

beta diversity observed among uninvaded communities to those observed among invaded communities.

Beta diversity	**Component**	**Uninvaded**	**Invaded**	**F**	***P***
Taxonomic	Total Dissimilarity	0.35	0.36	0.10	0.77
	Turnover	0.29	0.28	0.20	0.66
	Nestedness	0.07	0.10	5.89	0.02*
Functional	Total Dissimilarity	0.32	0.31	0.01	0.91
	Turnover	0.30	0.23	5.01	0.03*
	Nestedness	0.41	0.49	7.37	<0.01**

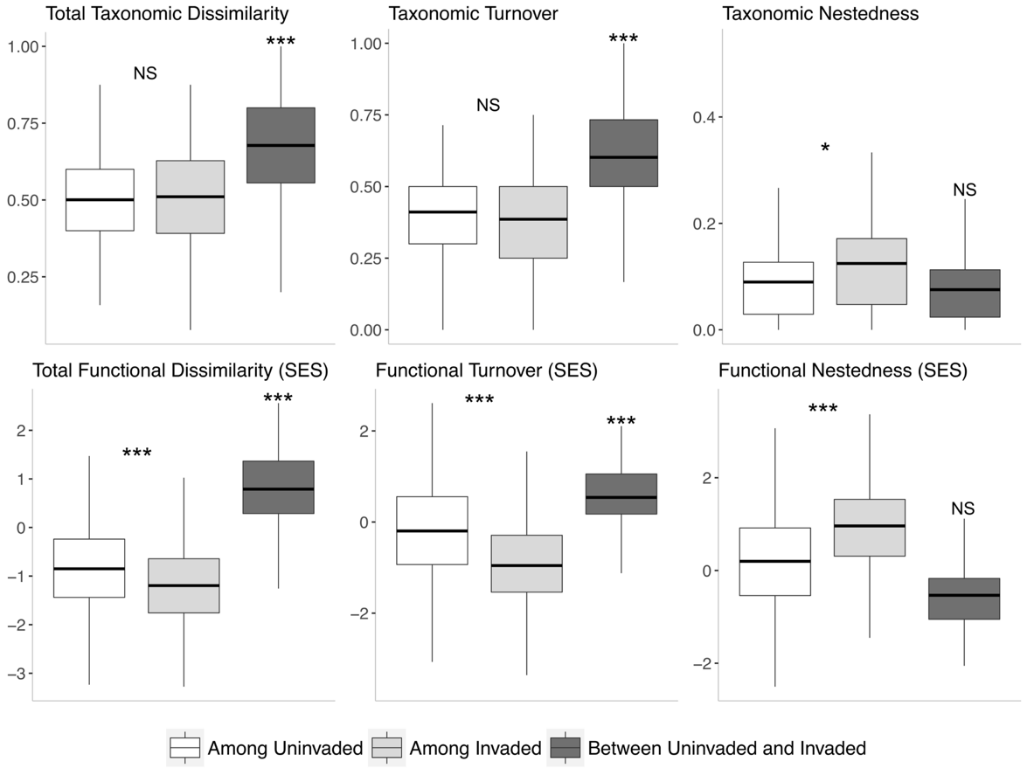

Figure 3. Observed levels of taxonomic beta diversity and functional beta diversity corrected for species-richness (SES values) in three measures of dissimilarity (Total, Turnover, and Nestedness). Boxplots show values among uninvaded communities,

among invaded communities, and between uninvaded and invaded communities. Asterisks indicate statistical significance (*** $P<0.001$, * $P<0.05$, NS, not significant).

Species' functional richness and functional uniqueness

Functional richness varied over four-fold among species (Min. = 0.86, Max. = 3.61) (Fig. 4). The four most functionally-rich species were two dimorphic species of *Camponotus*, another dimorphic species, *Pheidole nodus*, followed by the polymorphic invader *S. invicta*. In separate linear regressions, species' relative uniqueness to both uninvaded and invaded communities increased with their objective uniqueness in the species pool (Fig. 5). However, there was relatively more overlap between the functional spaces of objectively less unique species and the functional spaces of invaded communities ($\text{Intercept}_{\text{Invaded}} = -0.15$; $\text{Intercept}_{\text{Uninvaded}} = 0.45$). Furthermore, the relative uniqueness of species to invaded communities increased more steeply with an increase in objective uniqueness ($\text{Slope}_{\text{Invaded}} = 1.17$; $\text{Slope}_{\text{Uninvaded}} = 0.52$), such that very unique species in the species pool were more unique to invaded communities than to uninvaded communities (Fig. 5).

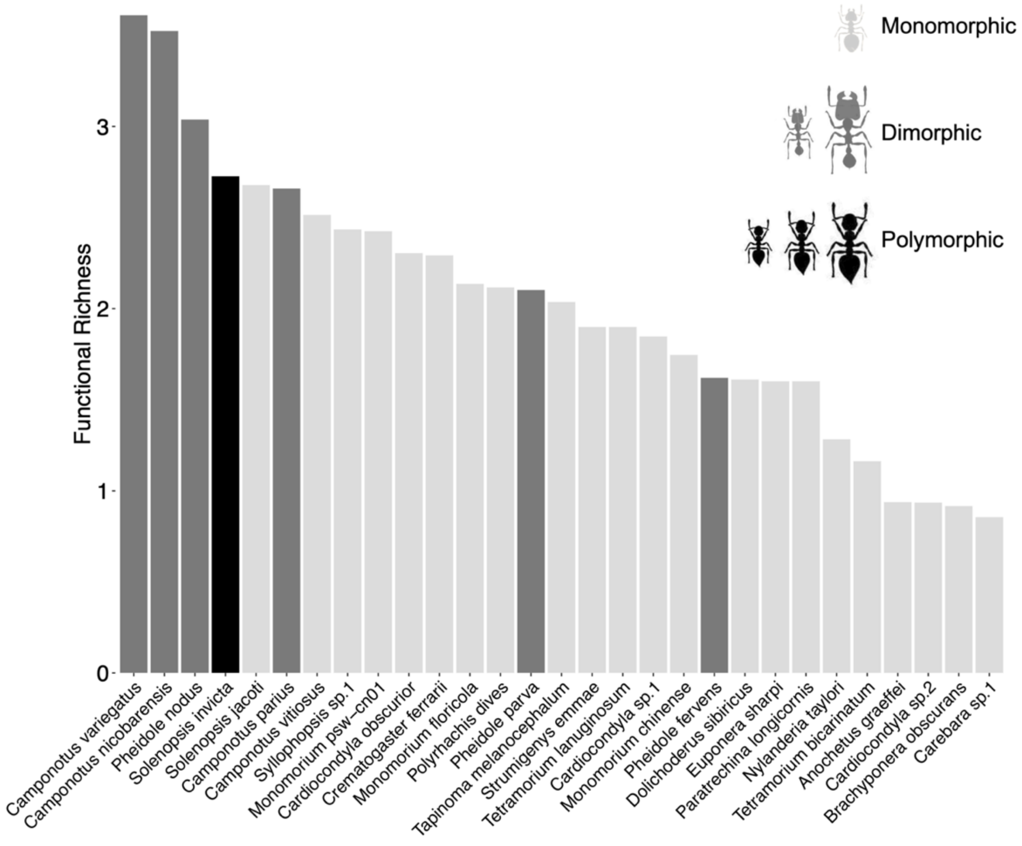

Figure 4. Functional richness of ant species with three different degrees of polymorphism. Bars show values for 22 monomorphic species (light grey), six dimorphic species (dark grey), and the polymorphic species *S. invicta* (black). Images of monomorphic, dimorphic and polymorphic species are shown in Fig. S6.

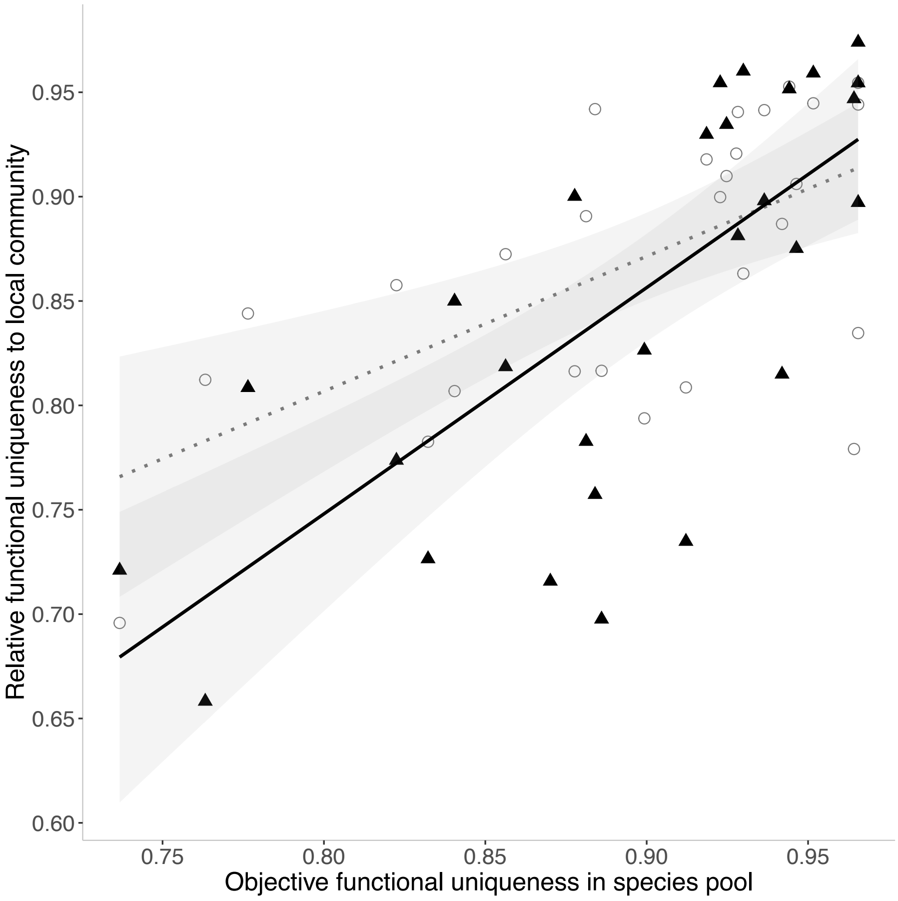

Figure 5. Species' relative functional uniqueness to local communities that were uninvaded (grey dotted line; circles) and invaded (black solid line; triangles) plotted against their objective functional uniqueness in the regional species pool.

DISCUSSION

Multiple lines of evidence suggest that the *S. invicta* invasion has had significant impacts on the ant community in Hong Kong, and that these impacts are still unfolding. At local scales, the most striking differences between uninvaded and invaded ant communities are the abundance distributions of their trait values. These are mainly evidenced by (i) the community-weighted means – i.e., the abundance-weighted functional identities of the communities – which differ significantly (Fig. 2), and (ii) multiple abundance-weighted functional diversity indices (Fig. 1: FDiv, Rao and FRed), which show a general pattern of species' abundances converging towards particular trait values in invaded communities, or 'functional clustering'. While the precise mechanisms driving these directional changes in the abundance distributions of trait values are unknown (possible explanations are discussed further below), the patterns indicate that invasions by *S. invicta* exert a non-random selection (*sensu* Vellend, 2016) on local ant communities, determined largely by the trait values of individuals.

At the same time, marginal differences in the taxonomic and functional richness of uninvaded and invaded communities (Fig. 1) also suggest that the impacts of the *S. invicta* invasion on the diversity of local communities are still unravelling. That is, the invasion has led to reduced abundances of a select group of species with particular 'vulnerable' trait values, but these effects have not (yet) culminated in local extinctions that would substantially change total species richness or functional richness (Mouillot et al., 2013). Our hypothesis is further supported by the fact that two thirds of all native ant species have lower relative abundances in *S. invicta*-invaded communities (Appendix A: Fig. S5), despite similar levels of taxonomic richness.

If decreases in the abundances of native species are indeed driven deterministically by the invasion of *S. invicta* and acting through some trait-based mechanism, then future resampling of the same sites should eventually reveal (i) significantly lower species richness in invaded communities, and (ii) the complete loss of the trait values which are uncommon in the invaded communities at present, independent of the identities of resident species that eventually become locally extinct, or of species that newly enter the communities. Notably, the former condition is often documented in longitudinal studies of ant invasions (Sanders et al., 2001; Hoffmann and Parr, 2008). The latter condition remains unexplored.

Invasion alters functional identity and drives functional clustering

The presence of *S. invicta* in individual communities selected for individuals with narrower heads and pronotums and shorter mandibles (Fig. 2: 4-7% decrease in community-weighted means for size-corrected *head width*, *pronotum width* and *mandible length*), significantly altering the functional identities of those communities. One hypothesis is that the observed patterns relate to mobility. The width of an ant's head and pronotum determine the size of gaps through which it can pass (Schofield et al., 2016). Narrower heads and pronotums of ants in invaded communities may thus reflect demands for moving through tighter spaces to avoid the behaviourally-dominant *S. invicta* during foraging (Tschinkel, 2006) or to exploit resources in less accessible locations. In invasions by Argentine ants, *Linepithema humile*, native species specialised to forage in soil increase in relative abundance and are relatively unaffected as compared to surface-dwelling species (Ward, 1987; Menke, Ward and Holway, 2018). Likewise, smaller-bodied native ant species appear to be less impacted than larger-bodied ones during ant invasions (Holway and Suarez, 2006), possibly because narrower nest entrances are more resistant to raiding by invasive species (LeBrun, Abbott and Gilbert, 2013).

An alternative hypothesis relates to diet. In ants, long mandibles of many predatory species are specialized adaptations for prey capture (Silva and Brandão, 2010). Selection for relatively shorter mandibles in *S. invicta*-invaded communities may be associated with a decline in the abundance of ant species that are specialized predators (e.g., Fig. S5: species of *Anochetus* and *Strumigenys* have lower abundances in invaded communities).

This would occur if particular arthropod prey were at lower abundance at invaded sites due to an overall depletion of the arthropod community by *S. invicta* (Tschinkel, 2006). By contrast, generalist ant species would be favoured for their abilities to exploit a variety of resources opportunistically. Separately, although we did not observe any clear environmental gradients or environmental effects on diversity, microclimates or biotic factors varying at finer scales could still influence the assembly of the communities.

That ant communities invaded by *S. invicta* tend towards functional clustering (Fig. 2: FDiv: -11%, Rao: -7%, FRed: +56%) is particularly interesting, and consistent with patterns of phylogenetic clustering observed in other ant invasions (Lessard et al., 2009). The latter has been attributed to the effect of invasive species acting as “strong environmental filters” which “prune the phylogenetic tree of native species in a non-random manner” (Lessard et al., 2009, p.2664). Still, this fails to address why, in the first instance, invasive species should impact a subset of species distributed non-randomly across the phylogeny or in trait space.

Theory holds that patterns of functional or phylogenetic clustering emerge in communities when their assembly is driven primarily by environmental filtering, or alternatively by competitive hierarchies (Mayfield and Levine, 2010; Herben and Goldberg, 2014). We found no evidence for strong environmental gradients spanning from uninvaded to invaded sites. We suspect that communities invaded by *S. invicta* may be structured by competitive hierarchies (Savolainen and Vepsäläinen, 1988), where species with trait values linked to high competitive abilities dominate, decreasing the abundances of other species through competitive exclusion associated with specific trait values (Gross et al., 2015).

Notably, King and Tschinkel (2006) showed that experimental suppression of *S. invicta* abundance over two years did not significantly change the diversity of co-occurring ant species, suggesting an absence of a competitive hierarchy. However their study examined ant communities 50 years post-invasion, so weaker competitor species may have been excluded long before the start of the experiment. Further, even if the *S. invicta* suppression facilitated the re-establishment of these other species, their colonies may not have reached sizes or densities sufficient for detection within two years. By contrast, both distribution records (Ascunce et al., 2011) and our findings of unfolding impacts indicate that the *S. invicta* invasion in Hong Kong is far younger. Future work could thus pair suppression or addition experiments with trait-based approaches to investigate the potential competitive advantages associated with the head, pronotum and mandible morphology of ants in this system.

Uniform selection promotes functional homogenization

As discussed above, the direct impacts of the *S. invicta* invasion mainly unfold at local scales. However, their synergistic effects also significantly alter ant diversity at the landscape scale. Because a selection based on specific trait values has repeated uniformly over separate communities invaded by *S. invicta*, functional beta diversity patterns across multiple ant communities show a trend towards functional homogenization. This is evident from the significantly lower functional dissimilarity among communities where *S. invicta* is present (Fig. 3).

Contrary to our hypothesis, functional turnover did not track taxonomic turnover. In other words, changes in the species found in different *S. invicta*-invaded communities were not matched proportionately by changes in those communities' trait values. The invaded communities actually retained similar levels of taxonomic turnover to uninvaded communities (Fig. 3). However, the former displayed significantly less functional turnover in observed structure (by 23%; Table 4), as well as in SES values of functional beta diversity corrected for the effects of species richness (Fig. 3).

Simulation analyses show that patterns of low functional turnover amid higher taxonomic turnover emerge most frequently when there are high levels of functional redundancy in individual communities (Baiser and Lockwood, 2011). Given that communities invaded by *S. invicta* show 56% more functional redundancy than uninvaded communities (Fig. 1), our observations in an invasion context provide empirical support for previous theoretical predictions (Baiser and Lockwood, 2011).

Ordinary winners and unique losers of invasion

Examining the responses of functionally unique species may help predict the impacts of invasions (Flynn et al., 2009). Previous studies have used trait patterns of aggregated communities or regional species pools to define functionally unique groups or species (e.g., Coetzee and Chown, 2016); these can be deemed 'objective' measures of uniqueness. A species' functional uniqueness, however, is also a relative property – it depends on the values and abundances of other traits present within the same community (Violle et al., 2017).

Using both objective and relative measures of functional uniqueness, we found that objectively unique species were on the whole more unique than others across different uninvaded and invaded communities (Fig. 5: positive linear relationships for both lines).

Next, we found that the functional spaces of objectively non-unique (i.e. ordinary) species constituted more of the functional spaces of invaded communities than uninvaded communities (Fig. 5: lower intercept of the ‘invaded’ line). Furthermore, the functional spaces of objectively very-unique species constituted less of the functional spaces of invaded communities than uninvaded communities (Fig. 5: steeper slope of the ‘invaded’ line).

Collectively, the findings suggest that the *S. invicta* invasion leads to multiple communities becoming more comprised of a subset of species (winners) sharing trait values which are common in the species pool, and less comprised of other species (losers) with trait values that are rare in the species pool. These patterns mirror the trend for functionally unique species to decline before functionally redundant species that has been observed in other disturbances (Flynn et al., 2009).

Implications for ecosystem function

The effects of *S. invicta* invasion on various ant-modulated ecosystem functions such as predation, nutrient cycling and bioturbation is a pertinent question to tackle in future research. If such ecosystem functions mainly respond to the functional identities of the ant communities (i.e., selection effects), we can expect that they will be impacted most by the shift in the dominant trait values in the communities. For instance, a shift in the most common foraging mode or dietary specialization in the community – as indicated by a change in the dominant head, pronotum and mandible morphology – could alter rates of predation.

On the other hand, functional homogenization and the decline of functionally unique species in invaded communities could impact ecosystem functions driven by functional complementarity and optimized by trait value diversity. For instance, decomposition may jointly depend on individuals which break down carcasses as well as others which move small pieces into the soil. Such a process would slow down if either group became increasingly rare in the community, as indicated by the loss of specific morphological trait values.

On the subject of functional complementarity, future work would also benefit from investigating the extent to which the high trait variation within polymorphic species (Fig. 4) translates into a wider array of ecological interactions undertaken by these species. For instance, dimorphic species of *Camponotus* and *Pheidole* whose colonies contain large and powerful majors as well as lightweight and fast-moving minors (Appendix A: Fig. S6), do appear to excel at the two complementary tasks involved in decomposition as discussed above. Investigating whether functional richness predicts niche variety or specialisation across polymorphic and monomorphic species could thus further our understanding of how species and ecosystem processes respond to ecological change.

Mitigating the cryptic impacts of global species exchange

We have shown that a single invasive species alters the functional diversity of native communities in a selective, non-random manner. Crucially, our findings further indicate that such impacts may unfold in the absence of similar changes in both taxonomic and functional richness. Thus, investigations exclusively using taxonomic measures of diversity, or indices that only describe trait variety, may fail to detect various consequences of invasions for the structure and function of ecological communities.

Cryptic impacts of invasion, such as functional clustering and homogenization, can be uncovered by investigating patterns in the diversity and distribution of traits at the species, community, and landscape scales. While our study targeted a well-known invasive species, similar approaches may be used to identify potentially overlooked exotic species that likewise impact native biodiversity beyond the taxonomic dimension.

4

Trait-similarity and trait-hierarchy jointly determine fine-scale spatial associations of resident and invasive ant species

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Author contributions

MKLW and TPNT conceived the study with inputs from BG and OTL. MKLW conducted fieldwork, collected trait data and built probability density functions. TPNT performed the statistical analyses. MKLW and TPNT wrote the first draft of the manuscript. All authors contributed significantly to revisions.

ABSTRACT

Interspecific competition, a dominant process structuring ecological communities, is influenced by species' phenotypic differences. Limiting similarity theory holds that species with similar traits should compete intensely ("trait-similarity"). In contrast, competing theories including modern coexistence theory emphasize that species with traits conferring competitive advantages should outcompete others ("trait-hierarchy"). Either or both of these mechanisms may drive competitive exclusion, but their relative importance and interacting effects are rarely studied. Here, we explore empirically whether trait-similarity and trait-hierarchy can explain fine-scale spatial associations observed between invasive and native ant species in a tropical assemblage. We find that pairwise co-occurrences between the invasive Red Imported Fire Ant, *Solenopsis invicta*, and 28 other species across relatively homogenous grasslands can be explained largely by an interaction of trait-similarity and trait-hierarchy in a single morphological trait, pronotum width. Specifically, higher trait-hierarchy values are associated with negative co-occurrences; however, these effects are counteracted when species are increasingly dissimilar in their trait ranges. These findings are consistent with the notion that limiting similarity and competitive hierarchies are interactive rather than discrete mechanisms driving competitive exclusion.

Keywords

Assembly, coexistence, competition, exclusion, functional trait, invasion, limiting similarity, niche

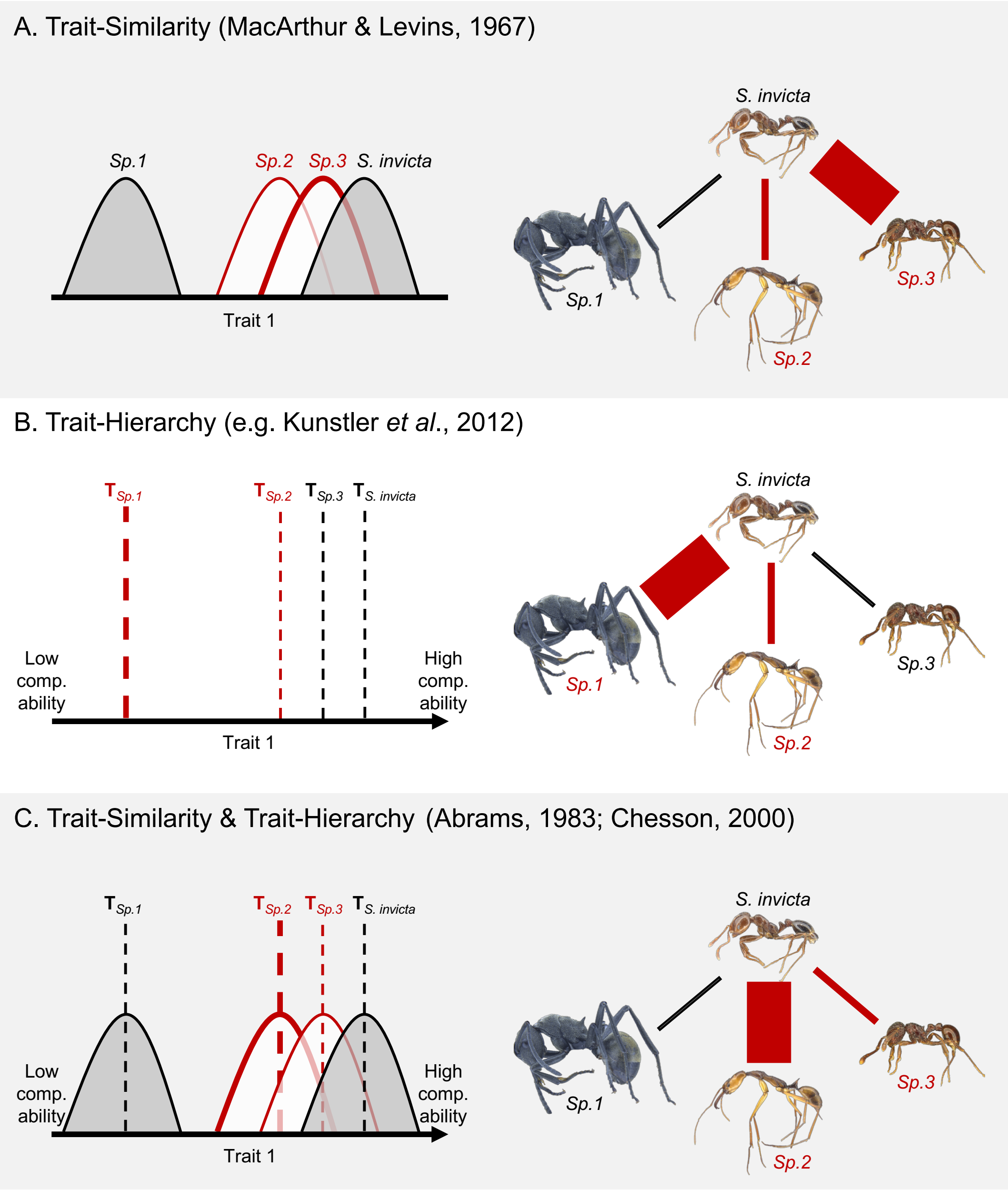
INTRODUCTION

Interspecific competition, a primary driver of community assembly and biodiversity patterns, is a process that is both well-known and yet stubbornly enigmatic. While patterns consistent with competitive interactions have been widely documented in a variety of ecological communities (Schoener, 1974; Calatayud et al., 2020), precisely how phenotypic differences between species determine the nature of competitive exclusion has remained highly contested (D'Andrea & Ostling, 2016). Limiting similarity theory (MacArthur & Levins, 1967) holds that species of similar niches compete more intensely, with competitive exclusion eventually leading to co-occurring species displaying dissimilar niches. Studies investigating limiting similarity have measured resource overlap (Schoener, 1974) and phylogenetic distances (Mayfield & Levine, 2010) between species as proxies for their niche dissimilarity. Recent work has emphasized functional traits (D'Andrea & Ostling, 2016). These are useful for understanding and predicting ecological mechanisms in that they are both mechanistic (i.e., tied to physical, chemical and biological processes) and general (i.e., quantifiable and comparable across taxa) (McGill et al., 2006). One trait-based proxy for the niche dissimilarity between two species is a non-directional or 'absolute' measure of their dissimilarity in trait space (Fig. 1A) (Carmona et al., 2019a). Accordingly, the *trait-similarity hypothesis* predicts that the likelihood of co-occurrence will always decrease with increasing overlap in trait space, such that co-occurring species display 'overdispersion': high absolute dissimilarity in trait space (Fig. 1A).

In contrast to limiting similarity, more recent theories on interspecific competition such as modern coexistence theory (Chesson, 2000) as well as colonization-competition (Tilman, 1994) and tolerance-fecundity (Muller-Landau, 2010) trade-off models emphasize that species' niche dissimilarities are not the only factors determining competitive outcomes. Common to these theories is the notion that species can be organized along competitive hierarchies (D'Andrea & Ostling, 2016), where differences in competitive ability drive the exclusion of weaker competitors (e.g., Kunstler et al., 2012). Directional measures of trait differences, such as the 'hierarchical difference' in species' mean trait values, provide a proxy for differences in competitive ability (Fig. 1B) (Kunstler et al., 2012). Contrary to the trait-similarity hypothesis, the *trait-hierarchy hypothesis* predicts that the likelihood of co-occurrence will decrease with increasing hierarchical difference (and dissimilarity), while decreasing hierarchical difference promotes 'clustering': the co-occurrence of similar species (Fig. 1B).

Despite a lasting focus on limiting similarity theory, empirical support for the trait-similarity hypothesis has been mixed (Mayfield & Levine, 2010). Some studies have documented patterns of trait overdispersion consistent with limiting similarity (Wilson, 2007), but others have found patterns of trait clustering consistent with competitive hierarchies (Kunstler et al., 2012; Herben & Goldberg, 2014). Furthermore, recent studies applying modern coexistence theory show that the outcomes of competition between plant species can be predicted by hierarchical differences in traits governing resource acquisition (e.g., leaf area for light interception, Kraft, Godoy & Levine, 2015; Kunstler et al., 2016; Perez-Ramos et al., 2019). The majority of such studies have focused on plants, and have used experimentally-assembled communities (Grainger et al., 2019), which may not adequately represent the dynamics of natural communities (Carpenter, 1996). Most observational studies investigating the role of competition in structuring communities, however, measure only trait dissimilarities and test for overdispersion

(D'Andrea & Ostling, 2016; Münkemüller et al., 2020). The potential for species' trait differences to reflect competitive ability differences may therefore be underestimated.


A. Trait-Similarity (MacArthur & Levins, 1967)

B. Trait-Hierarchy (e.g. Kunstler *et al.*, 2012)

C. Trait-Similarity & Trait-Hierarchy (Abrams, 1983; Chesson, 2000)

Figure 1. The trait-similarity and trait-hierarchy hypotheses of competition predict different outcomes for species co-occurrences separately and in combination. Panels show hypothetical relationships between three ant species and the invader *S. invicta* for one trait (left) and the corresponding pairwise co-occurrences (right) as predicted under

specific hypotheses. In each panel, species in red experience competitive exclusion and negative co-occurrence with *S. invicta* (i.e., they are not found in the same plots), with thicker lines indicating stronger relationships; species in black can co-occur with *S. invicta* in the same plots. **A**: If competitive exclusion is driven entirely by trait-similarity for all pairs of species (MacArthur & Levins, 1967), decreasing absolute dissimilarity (i.e. increasing overlap) between a species' range of trait values and that of *S. invicta* increases the strength of the negative co-occurrence, while increasing absolute dissimilarity (decreasing overlap) promotes co-occurrence. **B**: If competitive exclusion is driven only by trait-hierarchy (e.g., Kunstler et al., 2012) and species' mean trait values (T) correspond to their competitive abilities along a directional axis, then a larger hierarchical difference (T1-T2) between a species and *S. invicta* increases the strength of the negative co-occurrence, while a smaller hierarchical difference promotes co-occurrence. **C:** Trait-similarity and trait-hierarchy may jointly determine co-occurrences because niche dissimilarities and competitive hierarchies interact to determine competitive outcomes across different species pairs (Abrams, 1983; Chesson, 2000). The likelihood of competitive exclusion (and strength of the negative co-occurrence) between a species and *S. invicta* increases with increasing hierarchical difference in competitive ability; however, this competitive effect can also be counteracted and overcome by a large absolute dissimilarity in trait space, promoting co-occurrence.

Inferences of assembly processes from patterns in community structure are ubiquitous in the literature (Münkemüller et al., 2020). However, this approach assumes that all species within a community are subject to the same 'dominant' assembly process (Siepielski & McPeek, 2010). Rather than assuming that competition acts uniformly across all species at the community level, it can be informative to investigate whether and how competitive exclusion occurs for individual pairs of species. At this finer scale, competitive outcomes should be driven by an interaction between trait-similarity and trait-hierarchy (Chesson, 2000). That is, competitive exclusion will only occur for pairs of species which are insufficiently dissimilar in niches relative to their differences in competitive abilities (Fig. 1C; Mayfield & Levine, 2010). This interplay of trait-similarity and trait-hierarchy in determining competitive outcomes between species pairs is relatively unexplored. Nonetheless, it was anticipated by Abrams (1983): "What is needed instead is a broader definition of limiting similarity. The concept should be represented as a relationship between the difference in competitive ability and the maximum similarity that will permit coexistence. Such a relationship has the potential to be different for every different pair of species."

Biological invasions, which often lead to intense competitive interactions, are choice settings for investigating competition (Shea & Chesson, 2002). Moreover, many classical invasion hypotheses (empty niche, enemy escape, novel weapons, etc.) essentially attribute invasion outcomes to niche dissimilarities and competitive ability differences between invader and native species (MacDougall et al., 2009). This framework of modern coexistence theory has been used to identify the trait values conferring competitive advantages and promoting the success of invasive plant species (Gross et al., 2015) – but its potential to explain invasions in other taxa is untapped. Ecological literature on the ants (Hymenoptera: Formicidae) is replete with studies identifying competition as a strong driver of community structure (e.g., Fayle et al., 2015) as well as reports of competitive exclusion by exotic species (e.g., Holway et al., 2002). In the presence of invasive ant species, many ant communities show patterns of phylogenetic clustering

(Lessard et al., 2009), which could arise as a result of either environmental filtering or competitive hierarchies. It is difficult to distinguish these two processes solely on the basis of phylogenetic relationships (Cadotte & Tucker, 2017), but a focus on species' traits, which govern their abiotic and biotic interactions in real time, can help resolve their importance (McGill et al., 2006).

Both theory and experimental evidence suggest that ecological interactions may affect patterns of species co-occurrence. However, observed patterns of species co-occurrences can be poor proxies for ecological interactions (reviewed in Blanchet et al., 2020). Rather than treating species co-occurrences as standalone proxies of interactions, co-occurrence analysis can be one component in an integrative approach for detecting the effects of ecological mechanisms. Approaches emphasizing traits over taxonomic identities are well-suited to detecting mechanisms (McGill et al., 2006). Thus, integrating information on species' traits with observed co-occurrences may improve inferences of underlying mechanisms (Veech, 2014; Morales-Castilla et al., 2015). Recent studies have integrated pairwise co-occurrence and trait-similarity analyses to investigate the relative importance of limiting similarity and environmental filtering in community assembly (Kohli et al., 2018; He & Biswas, 2019). However, the potential influence of competitive ability differences, which can be reflected by hierarchical differences in trait values (Kunstler et al., 2012), has not been explored.

Here, we test trait-based hypotheses from limiting similarity theory and modern coexistence theory. We focus on the invasion of the non-native Red Imported Fire Ant (*Solenopsis invicta*) in grassland ant communities in Hong Kong (reported in Wong, Guénard & Lewis, 2020). In these relatively homogenous landscapes, communities are more likely to be structured by competition than by other mechanisms such as environmental filtering (Keddy, 1992). Furthermore, Wong et al. (2020) reported a weak environmental gradient in this system and the occurrences of several ‘tramp’ taxa (e.g. *Tetramorium, Monomorium, Brachyponera*) known for their ecological plasticity (McGlynn, 1999). There is some disagreement as to whether *S. invicta* competes strongly with resident ant species during invasion. While some studies report competitive exclusion by *S. invicta* (Porter & Savignano, 1990; Gotelli & Arnett, 2000), others contend that altered abiotic conditions under anthropogenic disturbances – which happen to favour *S. invicta* – are directly responsible for the decline of resident species (King & Tschinkel, 2008). To this end, trait-based tests for theoretical mechanisms of competition in a system with relatively low levels of environmental variation may clarify the interactions between *S. invicta* and other species.

We integrate trait-based and co-occurrence analyses to investigate whether trait-similarity and/or trait-hierarchy determine how *S. invicta* affect other ant species. There are two advantages to this approach. First, it allows for detecting potentially varying relationships at the fine ecological scales (species pairs) where competition unfolds (Abrams, 1983; Araújo & Rozenfeld, 2014). Second, it allows for testing more specific predictions about assembly processes than would be possible with standalone co-occurrence analyses (Veech, 2014; Morales-Castilla et al., 2015). We first use a network of species’ co-occurrences to reveal the spatial associations between *S. invicta* and other ants across multiple plots. To address some of the limitations of co-occurrence approaches (Blanchet et al., 2020), we sample ant species at fine spatial scales most relevant to biotic interactions, incorporate asymmetric co-occurrence signals into the network with odds ratios, assess observed patterns against null expectations of random co-occurrences, and test for the influence of environmental heterogeneity. Next, for distinct morphological traits that regulate ant physiology and behaviour, we use non-directional and directional measures of species' trait differences as proxies for species' niche dissimilarities (absolute dissimilarity) and competitive ability differences (hierarchical difference) respectively (after Kunstler et al., 2012; Carmona et al., 2019a). We then integrate species' trait differences and co-occurrences to evaluate three hypotheses on the likelihood and nature of pairwise competitive exclusion between *S. invicta* and all resident ant species (Fig. 1).

If competitive exclusion is mainly driven by trait-similarity, absolute dissimilarity will strongly determine species co-occurrences, with decreasing absolute dissimilarity leading to more negative co-occurrence (Fig. 1A). Alternatively, if competitive exclusion is mainly driven by trait-hierarchy, hierarchical difference will strongly determine species co-occurrences, with larger hierarchical difference leading to more negative co-occurrence (Fig. 1B). Finally, if both mechanisms operate, we expect an interaction of absolute dissimilarity and hierarchical difference to determine species co-occurrences. Specifically, we expect absolute dissimilarity to modulate the effect of hierarchical difference, such that hierarchical difference determines species co-occurrences only if absolute dissimilarity is sufficiently low (Fig. 1C).

MATERIAL AND METHODS

Sampling ants at fine spatial scales relevant to biotic interactions

To maximise the likelihood of detecting community patterns reflecting biotic assembly processes such as interspecific competition (de Bello et al., 2012; Blanchet et al., 2020), we characterized ant communities at fine spatial scales in a relatively homogenous landscape (Wong et al., 2020). We selected two reserves in Hong Kong – Lok Ma Chau (22.512°N, 114.063°E) and Mai Po (22.485°N, 114.036°E) – which have been protected for >35 years, and which contain networks of exposed grass bunds (width ≤5 m) separating individual ponds (Wong et al., 2020). These habitats are relatively homogeneous in terms of vegetation, habitats structure and microclimate, and comprise exposed grasslands with native tree species interspersed throughout. The ant communities are comprised mainly of native species in terms of species richness, although exotic species have a high numerical dominance in this system; pilot surveys from 2015 to 2017 revealed that colonies of *S. invicta* are present at high densities at multiple locations (Wong et al., 2020). From April to September 2018, we sampled the local ant community at each plot once in a 4 × 4 m quadrat, using six pitfall traps which were exposed for 48 hours. The maximum distance between any two traps in each plot was 5.65 m (Appendix B: Fig. S1), a higher sampling density (i.e., traps / m^2) than in previous studies characterising ant communities (e.g. Parr, 2008). We intentionally sampled at such fine spatial scales to enhance the detection of species' co-occurrences driven by biotic interactions (Araújo & Rozenfeld, 2014; Blanchet et al., 2020), as most ant species in the region forage within 5 m of their nests (Eguchi, Bui & Yamane, 2004) and *S. invicta* forage within 4 m of their nests (Weeks, Wilson & Vinson, 2004). For the same reasons, a minimum distance of at least 20 m between individual plots facilitated independent observations. All specimens were sorted into morphospecies and subsequently identified to species (Wong et al., 2020). We compiled a matrix of ant species' occurrences (i.e., presence/absence data) across all 61 plots. In addition, we used digital photographs taken in field to estimate the percentage of ground cover at each plot using colour thresholding techniques in ImageJ (Abramoff, 2004). We also obtained data at 30-m resolution on the

NDVI and the mean annual temperature (spanning the past five years including the sampling period) at each plot using recently built local climate models for Hong Kong (described in Morgan & Guénard, 2019). We later used these data to investigate whether environmental heterogeneity influenced species co-occurrences (Blanchet et al., 2020).

Building a co-occurrence network incorporating asymmetric relationships

We built a network documenting all pairwise co-occurrence relationships between all species across all 61 plots. To incorporate signals of asymmetry in species co-occurrences (Araújo et al., 2011; Blanchet et al., 2020) into the network, we summarized the presence and absence of paired species in 2*2 contingency tables and calculated the strength of co-occurrences as their asymmetrical odds ratios (Lane et al., 2014). For example, given paired species A & B, the odds ratio for indication of B by A (OR_{AB}) measures how the probability of B's presence at a plot changes under the presence of A in the same plot, and vice versa for OR_{BA}:

$$OR_{AB} = \frac{\dfrac{N(B = 1\ and\ A = 1) + 0.5}{N(B = 0\ and\ A = 1) + 0.5}}{\dfrac{N(B = 1) + 0.5}{N\ (B = 0) + 0.5}} \qquad OR_{BA} = \frac{\dfrac{N(A = 1\ and\ B = 1) + 0.5}{N(A = 0\ and\ B = 1) + 0.5}}{\dfrac{N(A = 1) + 0.5}{N\ (A = 0) + 0.5}}$$

where N represents the number of plots. We applied Haldane's correction and added 0.5 to all components to avoid odds ratios becoming infinity or undefined (Agresti, 2018). We further log-transformed the odds ratios in subsequent analyses such that they could be compared arithmetically (Agresti, 2018). The co-occurrence network was derived from odds ratios of all possible pairs of species.

Assessing observed species co-occurrences against null models

Since observed patterns could be driven by random co-occurrences (Gotelli, 2000; Blanchet et al., 2020), we used null models to calculate Standardized Effect Sizes (SES), which compared any observed co-occurrence relationships between paired species to random expectation (Appendix B). A co-occurrence relationship was more positive or negative than expected by chance if its SES was greater or less than zero, respectively, and statistically significant when it exceeded 1.96 (Gotelli & Arnett, 2000). We calculated (i) whether each species was on the whole characterized by positive or negative co-occurrences relative to all other species in the network (SES_{all}), and (ii) whether individual resident species were characterized by positive or negative co-occurrences with *S. invicta* (SES_{sinv}). The degree to which the presence of *S. invicta* affected the likelihood that a resident species occurred in the same plots determined its SES_{sinv}.

Measuring traits and trait ranges of species

We measured seven morphological traits (body size, and six size-corrected traits: head width, eye width, mandible length, scape length, pronotum width, leg length) of ≥10 individual workers of every species (N=319 individual ants), including different subcastes (minor and major workers) of polymorphic species such as *S. invicta* (Appendix B: Table S1 and Wong et al., 2020). The selected traits regulate ant physiology and behaviour and are hypothesized to impact performance and fitness (Table 1). For each trait, we built species-level probability density functions (Carmona et al., 2019b) to calculate trait probability distributions (the curves in Fig. 1A). These distributions – or trait ranges – reflect the probabilities of observing different trait values *within* individual species; they were subsequently used to quantify absolute dissimilarities *between* species in trait (niche) space; see below.

Table 1. The seven traits measured on each individual, and each trait's hypothesized links to the performance and fitness of ants. All measurements are consistent with those used in the *GlobalAnts* trait database (Parr et al., 2017). All traits except *body size* were size-corrected prior to analyses.

Trait	**Measurement**	**Hypothesized link to performance and fitness**
body size	Weber's length: diagonal length of mesosoma	Modulates vital and physiological rates, determines physical constraints and exposure to predators, influences resource type and acquisition efficiency (Silva & Brandão, 2010).
head width	Width of head including eyes	Determines the size of gaps through which an individual can pass (Schofield, Bishop & Parr, 2016) and the volume of muscles powering the mandibles during foraging (Richter et al., 2019).
eye width	Width of left eye	Determines ability in navigation, foraging, predator and prey detection, and indicative of activity times (Silva & Brandão, 2010).
mandible length	Length of left mandible	Responds to selection on diet type and specialization (Silva & Brandão, 2010).
scape length	Length of scape of left antenna	Responds to selection on navigation and sensory abilities (Silva & Brandão, 2010).
pronotum width	Width of pronotum	Determines volume of muscles for head-control/support, and load-bearing (Keller et al., 2014). Differentiates species in foraging strategy (Gibb & Parr, 2013).

leg length	Combined length of femur and tibia of left hind leg	Determines mobility; leg length influences running speed, which affects success in foraging or escape from predators (Silva & Brandão, 2010).

Species' dissimilarities in traits, phylogeny, and environmental preferences

For each of the seven traits, we quantified differences between *S. invicta* and each resident ant species with a non-directional measure of niche dissimilarity (Absolute Dissimilarity, AD), and a directional measure of competitive ability difference (Hierarchical Difference, HD). We focused on differences in individual traits, as combining all traits into a composite index requires the assumption that all traits affect interspecific competition uniformly. We measured AD as the proportion of a resident species' trait probability density function which did not overlap with *S. invicta*'s trait probability density function (i.e., the proportion of trait space exclusive to the resident species' trait range) (Carmona et al., 2019b). AD values range from 0 (when a resident species' trait range is identical to that of *S. invicta*) to 1 (no overlap with trait range of *S. invicta*; e.g. *Sp. 1* in Fig. 1A). Our overlap-derived measure of AD was based on the concept of niche overlap under limiting similarity (Abrams, 1983). We measured HD as $T_{Species} - T_{S.\ invicta}$, where T is the mean trait value for the given species (after Kunstler et al., 2012).

To control for the effects of phylogenetic relationships or environmental heterogeneity (Blanchet et al., 2020) in shaping co-occurrences between *S. invicta* and each resident species, we quantified their phylogenetic dissimilarity (as pairwise distances between species in phylogenetic trees) as well as their dissimilarities in environmental preferences in terms of ground cover, NDVI and temperature. We quantified phylogenetic dissimilarity based on the branch length distance between tips within a phylogenetic tree. We used 100 posterior samples of the phylogenetic tree from Economo et al. (2018) to quantify phylogenetic dissimilarities between species. As the ant phylogeny was available only at the genus level, we included phylogenetic uncertainties in creating species-level trees (after Arnan et al., 2018). We randomly generated 100 species-level trees by assigning species into their genus following a Yule (pure-birth) process and removing genera not detected in our study. Phylogenetic trees were generated using the R package *phytools* (Revell, 2012). To incorporate phylogenetic uncertainty, we calculated phylogenetic dissimilarities for 100 randomly-generated trees, using the R package *ape* (Paradis et al., 2019). We quantified dissimilarities in environmental preferences between *S. invicta* and every resident species to investigate whether environmental heterogeneity in (i) ground cover, (ii) NDVI and (iii) mean annual temperature influenced their co-occurrences (Blanchet et al., 2020). We first calculated the 'preference value' of each species for each variable by averaging the values for that variable from all plots where the species was present. Since the locality Lok Ma Chau was sampled more intensively than the locality Mai Po, we averaged the values from each locality prior to further averaging (such that estimates were not biased to Lok Ma Chau). For each of the three variables, environmental-preference dissimilarity between *S. invicta* and every other species was quantified as $|Preference\ value_{Species} - Preference\ value_{S.\ invicta}|$.

Statistical analyses

To investigate whether environmental heterogeneity (Blanchet et al., 2020) and phylogenetic dissimilarity influenced co-occurrences between *S. invicta* and resident species, we built separate models for $\mathrm{SES}_{\mathrm{sinv}}$ with dissimilarities in species' environmental preferences or phylogenetic dissimilarity as predictors. We built one model with phylogenetic dissimilarity as the sole predictor, and three additional models which each included environmental-preference dissimilarity in the form of either NDVI, temperature or ground cover as the sole predictor. Environmental variables and phylogenetic dissimilarity were included in subsequent trait models (see below) as covariates if they were found to be significant. This would allow the models to examine the effects of traits while controlling for environmental heterogeneity and phylogenetic non-independence. We did not conduct p-value corrections for the environmental and phylogenetic models to minimize the risk of falsely classifying their effects as insignificant, which can lead to over-liberal results for the trait models.

To determine whether pairwise co-occurrences between *S. invicta* and resident species were determined by trait-similarity, trait-hierarchy, or both mechanisms, we used multiple linear regression with standardized coefficients to test whether the SES_{sinv} for each species was best predicted by AD, HD, or an interaction of AD and HD. Our objective here was to use species' trait differences to proxy their niche and competitive ability differences, rather than to understand the effect of different traits *per se*. Therefore, rather than using a full model, we built one model for each trait, with AD, HD and a two-way interaction term (AD*HD) as predictors. We used all observed SES_{sinv} values as responses in the models (i.e., not just values meeting the arbitrary $p<0.05$ criterion) because the full range of observed values would be more informative in reflecting the extent of deviations from null models. We excluded the trait Mandible Length where strong correlation between AD and HD (Pearson's $r > 0.7$) suggested their effects could not be separated; AD and HD were not strongly correlated in other traits. As we built separate models for each trait (i.e. six models in total), we conducted Bonferronicorrection on the p-values to minimize type-I error due to multiple comparisons (Appendix B). We also ran the same set of analyses using robust linear regression to ensure our results were not driven by the presence of outliers.

For any trait models (based on multiple regressions) detecting significant effects from the interaction of AD and HD, we also built models without the interaction term, and used chi-square tests, AICc and changes in adjusted-R^2 to assess whether including the interaction term significantly improved model performance. We also used the Johnson-Neyman procedure (Johnson & Neyman, 1936) to calculate the 'zone of significance', that is, the range of values of AD at which HD influenced SES_{sinv} significantly (or *vice versa*). We controlled for false discovery rates using the procedure described in Esarey and Sumner (2017). For traits that were significant in both multiple regressions and robust regressions, we also checked whether these results were invariable to the use of different density-thresholds of *S. invicta* to characterize the occurrence of this species across the plots (Appendix B). Multiple regressions were conducted using generic function in R (R Development Core Team, 2020), while robust regressions were conducted using package *robustbase* (Maechler et al. 2020).

RESULTS

We recorded 29 ant species including *S. invicta* (Fig. 2), which occurred in 39% of the sampled plots. Among these 29 species within the co-occurrence network, *S. invicta* was the species most strongly characterized by negative co-occurrences with other species (SES_{all}=-3.62, Fig. 2A). Four other species were characterized by statistically significant negative (SES_{all}<-1.96) co-occurrences, and two by significant positive (SES_{all}>1.96) co-occurrences (Fig. 2A). Of the 28 resident species, pairwise co-occurrences with *S. invicta* were positive ($SES_{sinv}>0$) for nine species and negative ($SES_{sinv}<0$) for 19 species (Fig. 2B). Of these, one positive and seven negative co-occurrences were statistically significant (Fig. 2B).

We found little evidence to suggest that either trait-similarity or trait-hierarchy solely determined species' co-occurrences. On their own, both AD and HD were poor predictors of co-occurrences between *S. invicta* and the 28 resident species (i.e., SES_{sinv}) in separate models for six traits (Appendix B: Table S2). Rather, an interaction between niche dissimilarities and competitive ability differences best predicted co-occurrences between *S. invicta* and the 28 resident species. Among different models for the six traits (Appendix B: Table S2), the most parsimonious model was that for relative pronotum width incorporating AD, HD and an interaction term (AD*HD), which explained 37% of the variation in SES_{sinv} (Table 2). Here, the interaction term (AD*HD) significantly explained co-occurrences between *S. invicta* and the resident species (Table 2); removing the interaction term and only retaining the main effects of AD and HD significantly reduced model performance, as indicated by a Chi-square test (ΔAICc = 8.04, ΔAdjusted-$R^2 = 0.3$, $p < 0.001$, Fig. S2). A significant interaction between AD and HD was also consistently observed in all other models for relative pronotum width using co-occurrence networks derived from different density-dependent classifications of *S. invicta*'s occurrences across the plots (Appendix B: Table S4). In all relative pronotum width models (Table 2; Fig. 3; Appendix B: Table S4) the significant negative effect of the interaction between AD and HD meant that the positive effect of HD on SES_{sinv} was reinforced when AD was low, and counteracted (or even became negative) when AD was high.

Based on the model, we further estimated the magnitudes of niche dissimilarities (AD) between resident species and *S. invicta* at which competitive ability differences (HD) significantly influenced their co-occurrences. Applying the Johnson-Neyman procedure revealed that co-occurrences between resident species and *S. invicta* were significantly affected by HD when AD<0.37 or AD>0.95. There were 10 species for which AD<0.37 and three species for which AD>0.95 in pronotum width with respect to *S. invicta* (Fig. 3).

In models based on other traits, main effects of AD and HD as well as their interacting effects were not consistently significant predictors among the different regression analyses (Appendix B: Table S2). Phylogenetic and environmental-preference dissimilarities were also not significant predictors in any models (Appendix B: Table S3).

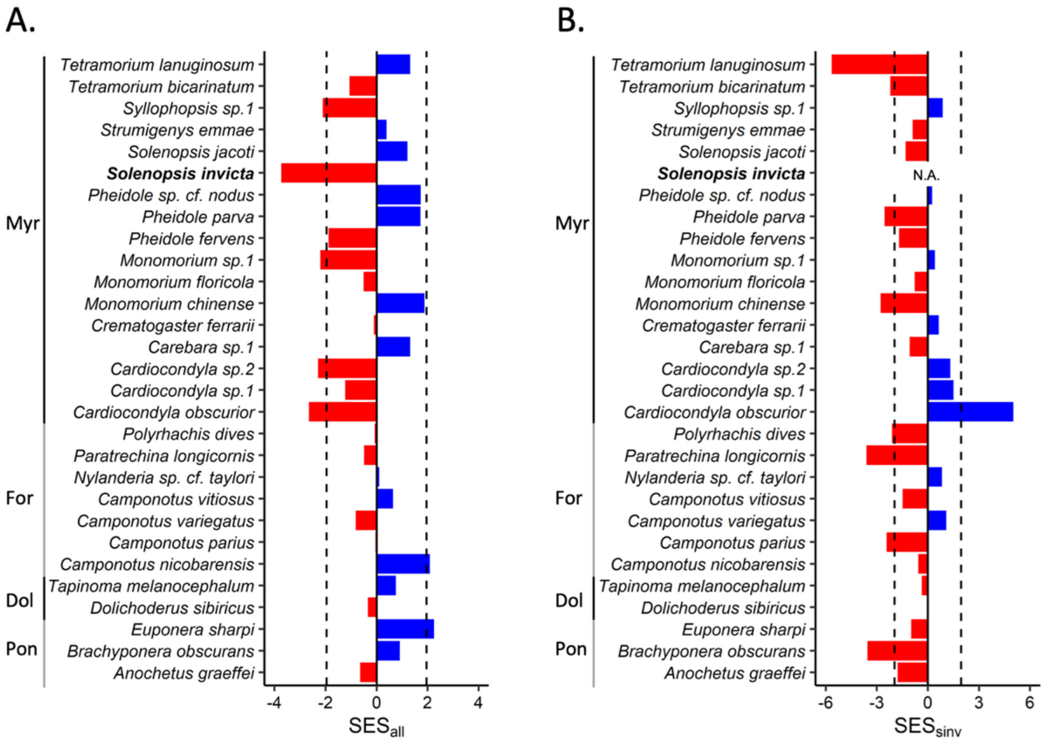


Figure 2. Of the 29 ant species sampled across 61 plots, the invasive ant *S. invicta* is most negatively associated with all other species. Plots show: (A) the degree to which each of the 29 species – including the invader *S. invicta* (in bold) – is characterised by positive (blue) or negative (red) associations within a co-occurrence network containing all species (SES$_{all}$); (B) the degree to which each of the 28 resident species displays positive or negative associations with the invader *S. invicta* (SES$_{sinv}$). Dashed lines indicate critical values for statistical significance of co-occurrence relationships (i.e., SES<-1.96 or >1.96). Ant species are grouped under four subfamilies: Myrmicinae (Myr), Formicinae (For), Dolichoderinae (Dol) and Ponerinae (Pon).

Table 2. Multiple linear regression model for pronotum width. For this trait, a non-directional measure of niche dissimilarity (Absolute Dissimilarity, AD), a directional measure of competitive ability difference (Hierarchical Difference, HD), and their two-way interaction (AD*HD) determine pairwise co-occurrences between the invader *S. invicta* and 28 ant species (Fig. 2B: $\mathrm{SES}_{\mathrm{sinv}}$). Bold value indicates statistical significance ($p<0.05$). 'JN intervals' indicate the range of AD values at which the effects of HD are significant, as identified from the Johnson-Neyman procedure.

Independent variable	β	*P*	JN intervals
AD	-0.47	1	<0.37; >0.95
HD	1.08	0.36	-
*AD*HD*	-1.47	**0.012***	-

$R^2=0.37$

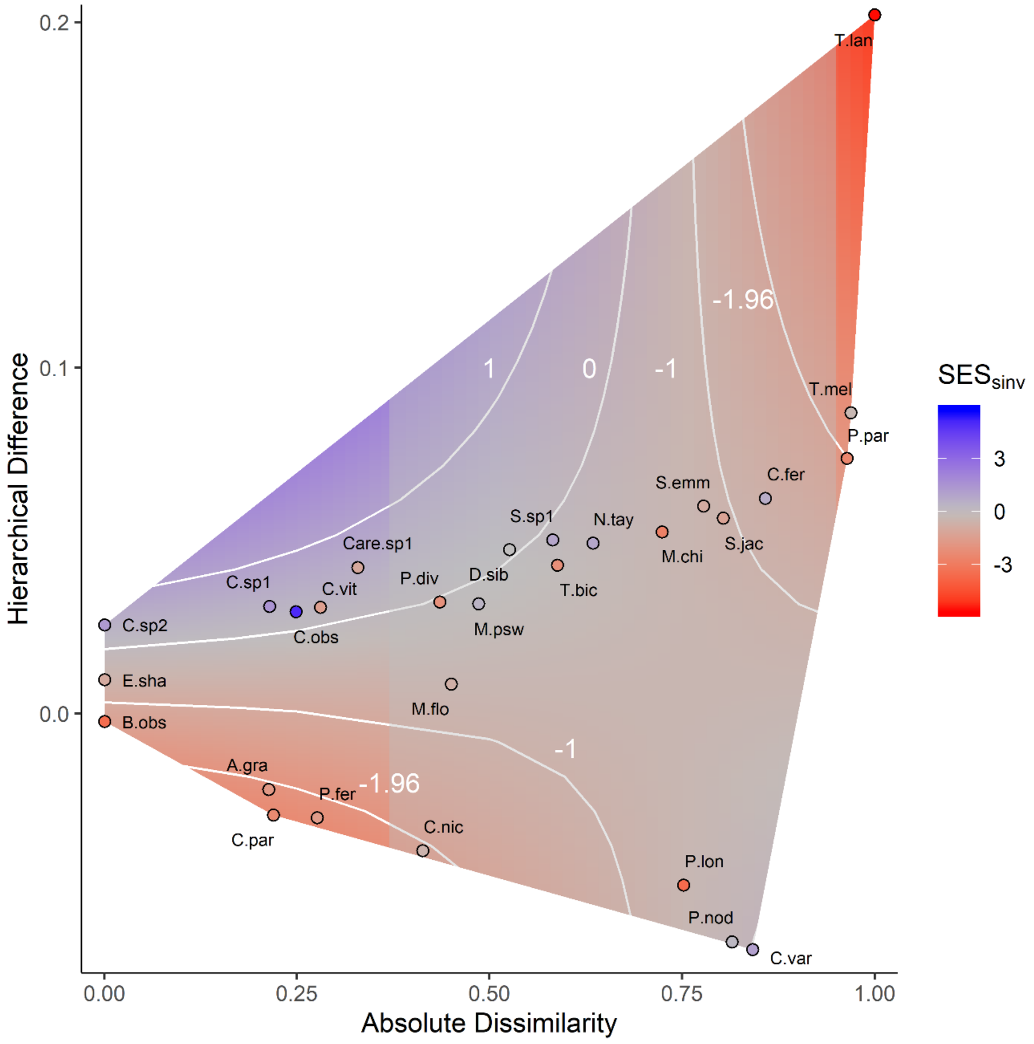


Figure 3. A response-surface showing how niche dissimilarity (Absolute Dissimilarity) modulates the effect of competitive ability difference (Hierarchical Difference) in determining 28 resident ant species' spatial associations with the invader *S. invicta*. The response-surface shows the predicted pairwise co-occurrence between a given ant species and *S. invicta* (SES$_{sinv}$) for the trait pronotum width, based on the multiple linear regression model in Table 2. Pairwise co-occurrences (SES$_{sinv}$) vary from negative (red) to positive (blue), with SES$_{sinv}$<-1.96 and SES$_{sinv}$>1.96 indicating significant negative or positive associations respectively; contour lines illustrate how predicted SES$_{sinv}$ changes across the response-surface. Coloured points on the response-surface show the observed SES$_{sinv}$ for individual resident ant species (N=28) (full names of species shown in Fig. 2).

On the x-axis, increasing values indicate decreasing overlap between a given species' range of pronotum width values and that of *S. invicta.* On the y-axis, a positive or negative value indicates that a given species has a relatively wider or narrower pronotum than *S. invicta*, respectively. The masked area in the centre of the response-surface corresponds to the range of Absolute Dissimilarity (0.37-0.95) where the positive effect of Hierarchical Difference on $\mathrm{SES}_{\mathrm{sinv}}$ is counteracted, as calculated from the Johnson-Neyman procedure.

DISCUSSION

Here, we found that an interaction between trait-similarity and trait-hierarchy could largely explain fine-scale spatial associations between the invasive species *S. invicta* and 28 other ant species. These empirical results are consistent with the notion that limiting similarity and competitive hierarchies are interactive rather than discrete mechanisms driving competitive exclusion (Abrams, 1983). We also found that a model of species co-occurrences, incorporating the interaction of trait-similarity and trait-hierarchy, aligned with predictions of different rules from community assembly theory (discussed further below). These findings underscore the importance of interspecific differences in niches and competitive abilities in determining patterns of species co-occurrences in communities.

The overall pattern of pronounced negative co-occurrences between the abundant *S. invicta* and many other species (Fig. 2) identifies *S. invicta* as an influential component of the community. Abundant species with many negative spatial associations have been inferred to be strong competitors (Calatayud et al., 2020), and previous studies (e.g.

Gotelli & Arnett, 2000) considered *S. invicta* to competitively exclude other ant species on this basis. However, negative spatial associations can arise as a result of other factors, such as environmental heterogeneity (Brazeau & Schamp, 2019). In the absence of significant effects of environmental factors on the co-occurrence patterns, we have little reason to suspect that, at least for the environmental parameters measured, environmental filtering had a strong effect in determining species' spatial associations with *S. invicta*. Furthermore, multiple 'tramp' species showed significant negative co-occurrences with *S. invicta* (see Fig. 2). For this reason, and also considering the general limitations of using co-occurrence approaches in isolation (Blanchet et al., 2020), we explicitly scrutinized spatial associations in light of species' ecological (trait) differences within the context of dominant theories on competition (Fig. 1).

Trait-similarity and trait-hierarchy jointly influence spatial associations between invader and residents

No single mechanism of competition (trait-similarity or trait-hierarchy) was sufficient to explain co-occurrences between *S. invicta* and the 28 resident ant species. However, incorporating the interactive effects of both mechanisms markedly improved explanatory power for a model based on the morphological trait, relative pronotum width (Table 2). The results suggest that competitive outcomes among the ant species may not depend on niche dissimilarities alone, but on the relative magnitudes of these in relation to differences in their competitive abilities (Chesson, 2000). Competitive hierarchies in individual traits are especially known to structure plant communities (e.g., Perez-Ramos et al., 2019) but are unexplored for most taxa. Our finding that ant species' trait differences significantly predict their spatial associations through both trait-similarity and trait-hierarchy (Table 2) highlights the value of assessing *directional* trait differences that may respond to competitive hierarchies among animal species.

In a study of arboreal ant species associated with epiphytic plants, absolute dissimilarities in a single morphological trait, body size, were a strong predictor of spatial associations, as well as the outcomes of antagonistic interactions (Fayle et al., 2015). Hierarchical differences along trait axes (proxying competitive advantages), however, were not explored. Our findings highlight the potential importance of pronotum width – another frequently measured 'functional' trait (Parr et al., 2017) – to competitive interactions among ant species. Keller and colleagues (2014) show that the pronotum of ant workers contain the musculature controlling head movements and powering load-bearing abilities, which are distinct functional innovations underlying the ecological success of ants. Furthermore, Gibb and Parr (2013) demonstrated empirically that species varying in their relative pronotum width have different foraging strategies. Specifically, they found that species with relatively wider pronotums were often first to discover baits, while species with relatively narrower pronotums had reduced discovery abilities but higher interference abilities (Gibb & Parr, 2013). Thus, one testable hypothesis is that the relatively wider pronotum of *S. invicta* may afford a competitive advantage over some ant species (those with low AD and HD and negative co-occurrences with *S. invicta* in Fig. 3) through its more efficient removal and transport of food resources. At the same time, as studies have shown that *S. invicta* have strong interference abilities but not strong resource discovery abilities (Tschinkel, 2006; Calcaterra et al., 2008; Pearce-Duvet & Feener, 2010), we also suspect that other ant species with relatively wider pronotums than *S. invicta* (those with low AD but high HD and non-negative co-occurrences with *S. invicta* in Fig. 3) may reduce their competitive ability differences relative to *S. invicta* through achieving more efficient resource removal and avoiding interference with *S. invicta*. This hypothesis would be consistent with observations that superior discovery ability is important for offsetting inferior fighting abilities and facilitating coexistence in ant communities (reviewed in Cerda et al., 2013). Notably, exploitative interspecific resource competition among ants is especially intense in more homogenous habitats (Gibb, 2005) such as the one studied here. If the patterns we observed do relate to exploitative resource competition between *S. invicta* and the other ant species, this would be consistent with studies on plants, where traits influencing resource acquisition (in contrast to other functions, e.g., structural support) are often closely linked to competitive hierarchies (Herben & Goldberg, 2014; Kraft et al., 2015). The pronotum may also be important to interference competition among ant species, where load-bearing ability likely determines the capacity of workers to lift, manipulate and displace heterospecific individuals.

Nonetheless, links between morphological traits and fitness are not yet well-established for ants, and future studies should assess the load-size selection of ants with different pronotum widths (e.g. Roces & Núñez, 1993). Moreover, we suspect that additional factors influenced interactions between *S. invicta* and the 28 resident species, as the best individual trait model explained 37% of the variance in co-occurrences (Table 2; Appendix B: Table S4). Aside from the traits measured in this study, other traits such as colony size, intra- and interspecific aggression levels, and venom chemistry are likely important for interference competition (Holway et al., 2002). While this study examined differences in morphological traits – which are accessible, basic components of trait-based research in animals (e.g., Parr et al., 2017; Pigot et al, 2020) – additional work investigating absolute dissimilarities and hierarchical differences in physiological and behavioural traits linked closely to performance will probably be most telling. Competitive exclusion may also depend on a net difference in competitive ability across multiple trait axes (Kraft et al., 2015).

How trait differences affect spatial associations: four rules from assembly theory

The trait model incorporating the interaction term reconciled the varying co-occurrences between *S. invicta* and individual ant species to the varying nature of each pair's trait differences (i.e., trait-similarity and trait-hierarchy) (Fig. 3). We note that the distinct ways by which species' trait differences with *S. invicta* determine their co-occurrences, as reflected in the model, are consistent with predictions under different rules from community assembly theory. With reference to Fig. 3, our ecological interpretation of the model identifies four rules that predict the spatial associations between a given ant species and *S. invicta* across the landscape. Each rule is distinguished by the specific magnitudes of niche dissimilarities (AD) and competitive ability differences (HD) between paired species. The rules are: (I) competitive exclusion at $HD<0$ and $AD<0.37$, leading to negative co-occurrence; (II) approximate competitive equivalence and coexistence at $HD>0$ and $AD<0.37$, leading to non-negative co-occurrence; (III) sufficiently large niche dissimilarity and coexistence at $AD=0.37–0.95$, leading to non-negative co-occurrence; and (IV) environmental filtering at $AD>0.95$, leading to negative co-occurrence.

Rules I and II apply to species which are largely similar to *S. invicta* in niches and trait values ($AD<0.37$). Here the model predicts increasingly negative co-occurrence with increasingly negative HD. It suggests that for ant species with similar trait values to *S. invicta*, interspecific competition with *S. invicta* is likely to be intense, such that large differences in species' competitive abilities drive exclusion, causing negative co-occurrence (e.g., Kunstler et al., 2012) (Rule I). However, for some species, small differences in competitive abilities with *S. invicta* may facilitate coexistence in the fashion of neutral-like dynamics (Scheffer & van Nes, 2006) (Rule II). This is evident from the model, which predicts that co-occurrences between *S. invicta* and most similar species (AD<0.37) do not differ significantly from the null expectation (i.e., coexistence is plausible) when HD becomes less negative (Fig. 3: left unmasked area: $-1.96<SES_{sinv}<1.96$).

In contrast to Rules I and II which apply to species sharing high niche similarity with *S. invicta* and potentially competing intensely, Rule III applies to species largely dissimilar (AD=0.37–0.95) from *S. invicta* in niches and trait values – to the extent that niche dissimilarity may mitigate negative effects of competitive imbalances (e.g., individual traits in Perez-Ramos et al., 2019). For these species, differences in competitive abilities do not appear to influence co-occurrences with *S. invicta* significantly (Fig. 3: masked area: SES_{sinv} does not significantly respond to HD). Furthermore, if niche dissimilarities are sufficiently large, coexistence is plausible, and the likelihood of these species occurring with *S. invicta* generally does not differ from null expectations (Fig. 3: masked area: $-1.96<SES_{sinv}<1.96$).

Rules I, II and III above concern interspecific competition, which was predicted to be an important driver of the ant species' spatial associations given the relatively homogeneous landscape. Less anticipated was an additional rule (IV), which likely relates to environmental factors, and applies to species most dissimilar (AD>0.95) from *S. invicta* in niches and trait values (Fig. 3: right unmasked area). The model inherently predicts significant negative co-occurrence (SES_{sinv}<-1.96) between such species and *S. invicta.* The extensive dissimilarities between these species and *S. invicta*, and their low likelihood of co-occurrence, may reflect environmental filtering by unmeasured factors varying across the plots (e.g., ant pronotum widths responded to soil fertility gradients in Fichaux et al., 2019). If such trait-based environmental filtering occurs, directional differences in trait values could further reinforce their deterministic effects, leading to increasingly negative co-occurrence with increasing HD (Fig. 3: right unmasked area).

Not discounting the limitations of a single-trait model (discussed further above), it appears that separate but coherent trait-based rules from community assembly theory can collectively account for spatial associations between the invader *S. invicta* and the 28 resident ant species across the landscape. If different rules do indeed act on different pairs or sets of species, this may explain the context-dependent nature of the impacts of *S. invicta* invasions on native ants observed previously (e.g., competitive exclusion in Porter & Savignano, 1990; Gotelli & Arnett, 2000; environmental filtering in King & Tschinkel, 2008).

Abundant species, ranging from ants and beetles to trees and corals, often display negative and positive spatial associations with many other species (Calatayud et al., 2020). While experimental manipulations and mesocosm studies can be invaluable for understanding the precise mechanisms underlying such community structure, their applicability decreases with increasing ecological, spatial and temporal scales (Levin, 1992). Integrating co-occurrences with species' trait differences within a theoretical framework can provide stronger inferences for the mechanistic bases of observed community patterns than the use of co-occurrence approaches in isolation (Veech et al., 2014; Blanchet et al., 2020). Here, a model encompassing species' trait differences (in terms of trait-similarity, trait-hierarchy, and their interacting effects) (Table 2; Fig. 3) suggests that an abundant, invasive species competes intensely with a subset of similar species, may coexist with species that are sufficiently different, and is further unlikely to co-occur with other species of different environmental requirements. While these findings strictly describe relationships between a single invader and multiple resident species (and not all relationships among all species in the community), they are consistent with the notion that community assembly is a dynamic and multifaceted process acting varyingly on different pairs or sets of species (Abrams, 1983), and not discrete 'filters' acting on the whole community (Cadotte & Tucker, 2017). If so, detailed assessments of interspecific trait differences at fine spatial and organizational scales (e.g., species pairs and guilds) may clarify the contributions of distinct assembly mechanisms to overall community structure. Additional work investigating trait-relationships and associations among the resident ant species will help reveal other processes, such as competition, indirect interactions, and facilitation. These, in combination with the competitive effects of *S. invicta* on many species, will ultimately determine community structure.

5

Opposing effects of competitive exclusion via morphological, physiological, and behavioural traits determine invasion outcomes and structure ant assemblages

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Author contributions

MKLW planned the study with inputs from BG and OTL. MKLW conducted the fieldwork. MKLW, RHL and CML performed trait measurements. MKLW conducted statistical analyses and wrote the first draft of the manuscript. MKLW, BG and OTL contributed substantially to manuscript revisions.

ABSTRACT

In plants, traits can confer competitive advantages promoting the exclusion of weaker competitors in a competition hierarchy, or niche differences fostering the coexistence of dissimilar species by limiting similarity. These variable relationships between traits and the outcomes of interspecific competition, as well as their effects on assemblage structure, are less explored for animals in natural settings. Here we show that the abundance of an invasive ant as well as the composition and structure of native ground-foraging ant assemblages in tropical grasslands are largely attributable to differences between the morphological, physiological and behavioural traits of invasive and native species. Importantly, we detect limiting similarity and hierarchical competition acting varyingly on individual traits, producing contrasting patterns in assemblage functional structure. Our results highlight that different traits across the phenotypic spectrum can distinctly influence niche and competitive differences between animal species, ultimately varying the role and effect of competition in structuring biodiversity.

KEYWORDS

Coexistence, community assembly, competitive ability, fitness difference, functional trait, limiting similarity, niche

INTRODUCTION

Competition between species is a fundamental process which strongly influences both the assembly of communities and their responses to environmental change (Tilman, 1982). An ability to predict the outcomes of competition from ubiquitous and measurable properties of species, such as their traits, will be invaluable for understanding and safeguarding ecosystems (McGill et al., 2006; Díaz et al., 2016; Kunstler et al., 2016; Cadotte, 2017). Nonetheless, the ways in which species' trait differences affect competitive outcomes and structure communities are not straightforward.

Trait differences can have contrasting effects on competitive outcomes between species (Mayfield & Levine, 2010; D'Andrea & Ostling, 2016) (Fig. 1). On the one hand, trait differences which facilitate niche differences, such as the use of different resources or climatic windows, promote coexistence between dissimilar species via limiting similarity (MacArthur & Levins, 1967). Competitive exclusion is therefore driven by *trait similarity* (Kunstler et al., 2012; Herben & Goldberg, 2014). On the other, trait differences which determine differences in species' relative competitive abilities in a competition hierarchy, such as in the exploitation of a shared resource or climatic window, can lead to the exclusion of species which have dissimilar – in this case 'weaker' – trait values. In this case, competitive exclusion is driven by *trait hierarchy* or 'limiting dissimilarity' (Kunstler et al., 2012; Herben & Goldberg, 2014). These two effects of trait differences on interspecific competition produce contrasting patterns in trait structure at the assemblage level. While the positions of species in trait space tend towards overdispersion when trait similarity is at play, they tend towards clustering when trait hierarchy is involved (Mayfield & Levine, 2010; D'Andrea & Ostling, 2016).

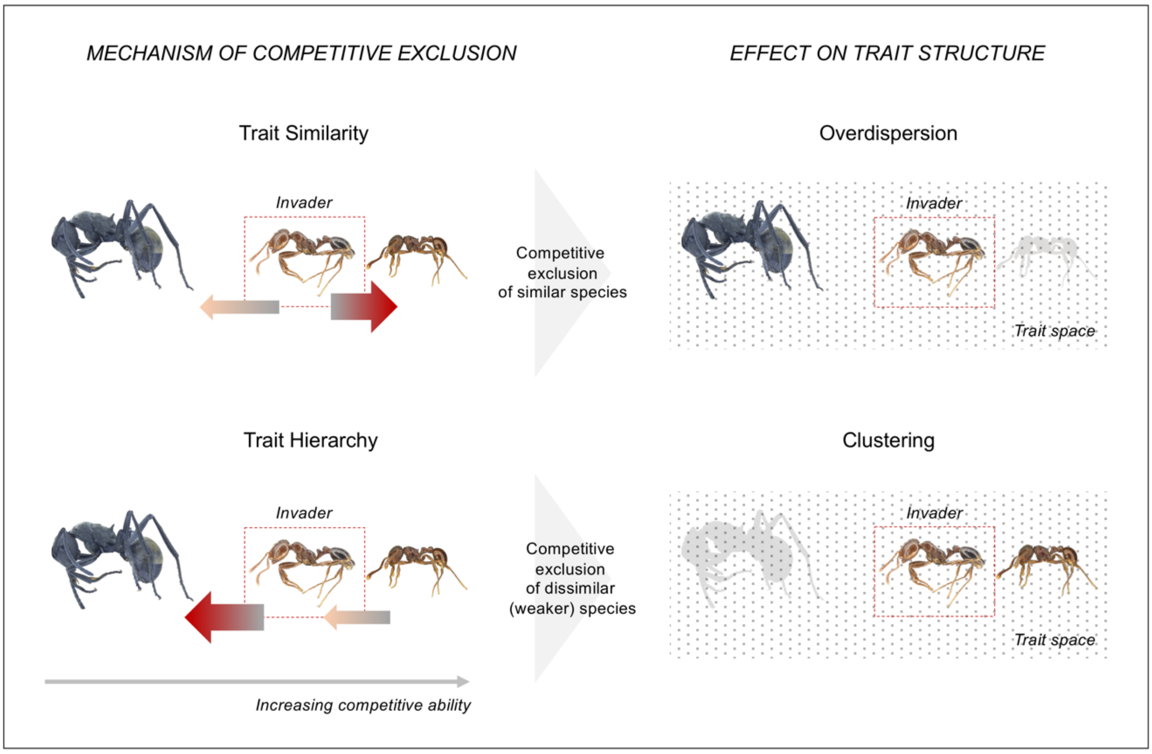

Figure 1. Two opposing mechanisms of competitive exclusion and their contrasting effects on assemblage functional structure. An example for the trait body size is illustrated. **Top:** if competitive exclusion is driven by trait similarity (e.g., if body size determines species' overlap in a niche such as a shared resource), competition is stronger between the invader and species of similar size (strong competitive effect; thick red arrow), but weaker between the invader and species of dissimilar size (weak competitive effect; thin pink arrow). As species similar in size to the invader are excluded, the remaining species observed in the assemblage are dissimilar in size from the invader – either substantially larger or smaller (not shown) – and thus overdispersed in trait space. **Bottom:** Alternatively, if competitive exclusion is driven by trait hierarchy (e.g., if the trait determines species' relative competitive abilities along a competition hierarchy), the impacts of competition are stronger on dissimilar species that have weaker competitive abilities because they are further from the optimal trait value. As dissimilar species are

excluded, the species observed in the assemblage are similar and thus clustered in trait space.

Trait hierarchy is known to be a common driver of competitive exclusion among plant species (Kunstler et al., 2012;2016). Both trait similarity and trait hierarchy may even operate simultaneously in plant assemblages, leading to overdispersion in some traits but clustering in others (Spasojevic & Suding, 2012). Nonetheless, the effects of trait hierarchy tend to be overlooked in studies on other taxa, where the influence of classical niche theory remains strong, with limiting (trait) similarity (MacArthur & Levins, 1967) often implicitly assumed as the only path to competitive exclusion (Münkemüller et al., 2020). This is evidenced by the fact that many studies test only for trait overdispersion when seeking to detect the effects of competition in community assembly (Mittelbach & McGill, 2019; Münkemüller et al., 2020). In addition, while studies on plants distinguish between the effects of morphological and physiological traits in determining species' niche and competitive differences (Pérez-Ramos et al., 2019), these relationships are less explored for animals. Behavioural traits of animals shaping antagonistic interactions are also likely important but seldom considered aspects of assembly in existing trait-based studies (Wong et al., 2019). In short, the potential for traits across the phenotypic spectrum to promote competitive differences instead of niche differences between species is likely underestimated.

Invasions by non-native species represent novel settings for testing assembly rules from community ecology theory (Shea & Chesson, 2002). Consistent with the effects of trait hierarchy, many differences between the traits of invasive and native plant species, especially for performance-related traits such as leaf-area allocation and growth rate, correspond to competitive advantages and not niche differences (Van Kleunen, Weber & Fischer, 2010). However, the extent to which trait differences between invasive and native animal species represent niche and competitive differences, as well as their consequences for the functional structure of animal assemblages – from overdispersion to clustering – are less understood.

In this study we explore whether trait similarity and trait hierarchy can account for the outcomes of an invasion by the Red Imported Fire Ant, *Solenopsis invicta*, and its effects on the functional structure of ground-foraging ant assemblages across plots in a grassland in Hong Kong. Besides being among the first comparative tests of trait similarity and trait hierarchy in an animal assemblage, our work goes further than previous studies by incorporating a diverse suite of traits spanning species' morphology (seven traits), physiology (trophic position and critical thermal maximum) and behaviour (interference ability) – all of which were measured directly from multiple individuals of each species captured in field.

We use a novel comparative approach, focusing not only on the invader's trait differences with the ant assemblage observed in each plot, but also with the species that were missing from each plot (but occurring in the species pool), which we term the 'shadow assemblage'. In using this comparative approach to study the role of competition in assembly, we intentionally chose the simple grassland setting for its low environmental heterogeneity, which naturally minimized the effects of potential environmental filters. Sampling at spatial scales within ant species' dispersal ranges also allowed for minimizing the effects of potential dispersal filters (see Materials and Methods).

Specifically, we investigated the extent to which the density of *S. invicta* across 61 plots (including multiple plots where it was absent) was explained by its trait differences with the assemblage of ant species observed at each plot, and with the shadow assemblage of species missing from each plot. Trait differences were measured to approximate either potential niche or competitive differences (after Kunstler et al., 2012; Kraft et al., 2015; Carmona et al., 2019), and their effects on the relationship between *S. invicta* density and a given assemblage were tested to elucidate the importance of trait-similarity or trait-hierarchy. To further test the effects of these mechanisms in structuring the ant assemblages, we investigated the degree of overdispersion or clustering in individual trait axes as well as in multidimensional trait space. This work advances our understanding of how interspecific differences across the phenotypic spectrum drive competitive outcomes among animal species, and more broadly shows that trait differences can deterministically shape the responses of biodiversity to biotic disturbances.

MATERIALS AND METHODS

Sampling ant assemblages and environmental variables

The study was conducted in two reserves of open grassland in Hong Kong which have been protected for >35 years, and which contain networks of exposed grass bunds (width ≤5 m) separating individual ponds (Wong et al., 2020). Pilot surveys from 2015 to 2017 recorded colonies of *S. invicta* present at high densities at multiple locations (Wong et al., 2020). From April to September 2018, we systematically characterized the ground-foraging ant assemblages at 61 plots (each a 4 x 4 m quadrat; ≥20 m between adjacent plots) using pitfall traps followed by observations at baits. We intentionally sampled at this fine spatial scale to enhance the detection of patterns driven by biotic interactions (Araújo & Rozenfeld, 2014; Blanchet et al., 2020), since *S. invicta* and most ant species in the region forage within 5 m of their nests (Eguchi, Bui & Yamane, 2004; Weeks, Wilson & Vinson, 2004). For the same reasons, the minimum distance of 25 m between adjacent plots facilitated independent observations. The maximum distance between any two plots was 4 km; at this spatial scale, the effects of dispersal limitation were likely minimized as all species disperse via flying alates.

In each plot, six pitfall traps (diameter: 5.5 cm) were installed to sample the ants over a period of 48 hrs. Baits were then installed within 72 hrs from the retrieval of the pitfall traps. Between 1000-1500 hrs, five bait stations were installed in each plot, each comprising a slice of chicken sausage (diameter: 20 mm; height: 2 mm) on a white plastic disc (diameter: 5 cm) flushed with the ground. The sausage bait contained trophic resources required by most ants: proteins, lipids, carbohydrates and sodium (Calcaterra et al., 2010). Each baiting session lasted 40 min, during which photographs were taken with a digital camera in 5 min intervals; these were subsequently used to determine the species recruiting, their abundances, and interspecific interactions (see 'Behavioural trait: interference ability' below). In pilot trials, the 40-min duration allowed for competitive interactions to reach unequivocal outcomes and for baits to be monopolized by single species. After each baiting session, live workers of all species encountered were collected and used for physiological trait measurements in the laboratory (see below). Specimens collected from pitfall traps were used for morphological measurements, confirming species identities, and determining the occurrences of species in plots. While several species collected in pitfall traps were not recorded at baits (but not *vice versa*), many of these were hypogaeic. Given that our study aimed to investigate competition, we focused the analyses on the pool of species recorded at baits as these best represented the ground-foraging ant assemblage sharing common trophic (and other) resources.

At each plot, we also estimated the percentage of ground cover (Ground Cover) by applying colour thresholding techniques in ImageJ (Abramoff, 2004) to digital photographs, and obtained high resolution (30 x 30 m) estimates of mean annual temperature (Temperature) from local climate models (see Morgan & Guénard, 2019). We later used these environmental data to test for the effects of environmental filtering on invasion outcomes and assemblage structure, as these factors were shown to influence ant diversity in other systems (King & Tschinkel, 2008).

Morphological traits

We measured seven morphological traits (Body Size, Head Width, Eye Width, Mandible Length, Scape Length, Pronotum Width, Leg Length) on ≥10 individual workers of every species (N=319) (Appendix C: Table S1). These traits regulate ant physiology and behaviour and are hypothesized to impact performance and fitness (Appendix C: Table S1).

Physiological traits: critical thermal maximum and trophic position

We measured the Critical Thermal Maximum (CT_{max}) of individual ants following established protocols for CT_{max} assays (Diamond et al., 2017). The ants were first acclimated at 25 °C for ≥2 hrs in the laboratory. Individual ants were then placed in 1.5 mL Eppendorf tubes. The entrance of each tube was plugged with dry cotton wool, ensuring that each ant was confined to an area of even temperature distribution. The tubes were then placed in a digital dry bath (BSH1004) connected to an additional thermometer

(UEi Test Instruments DT302 Dual Input IP67) for ensuring temperature accuracy. The assay began at a starting temperature of 36 °C, from which the temperature was increased at a constant rate of 1 °C min^{-1} (Diamond et al., 2017). Every 1 min, each tube was rotated and visually inspected to determine whether the ant had lost muscle coordination (Diamond et al., 2017); the temperature at which this occurred was recorded as the individual's CT_{max}. We measured the CT_{max} of ≥10 individual workers of each species (N=193). Acclimatization at 25°C (the approximate temperature of a nest environment beneath the soil surface and in wood cavities; MKL Wong, unpublished data) was conducted so as to standardize the measurements across specimens collected at different times and environmental temperatures in the field. A starting temperature of 36°C was used because using a low starting temperature would increase the exposure time during the trials, resulting in the measurement of thermal tolerance over time instead of the CT_{max} (Diamond et al., 2017); furthermore, all species measured had CT_{max}>40°C.

The relative trophic positions of different ant species were estimated using stable isotope ratios of Nitrogen ($\delta^{15}N$; henceforth 'N15') with higher ratios of N15 indicating higher trophic position (Tillberg et al., 2006). Live ants collected from the field were killed in a -20 °C freezer. We then rinsed the ants with distilled water, removed their abdomens to avoid contamination by undigested material in the gut (Tillberg et al., 2006), and dried the samples in an oven at 40 °C until a constant mass was reached. Each dried sample comprised 10–40 individuals, depending on the size of the species. The dried samples were transferred into an aluminium capsule weighing 0.3–1 mg (individuals of larger species were first ground and homogenized using a mortar and pestle following Hyodo et al., 2011). We measured the N15 values of each sample using a Nu Perspective Isotope Ratio Mass Spectrometer coupled to an Eurovector Elemental and reported in ‰

(Gebauer & Schulze, 1991). Mineral soil collected from the field was used for baseline calibration. The N15 values of every species were determined using 1–3 dried samples (each comprising 10-40 individuals). While this approach (after Blügthen et al., 2003; Tillberg et al., 2006) mainly quantified interspecific trait differences in N15 (in line with the aims of our study), it should be noted that trophic position can vary intraspecifically in ant species (Roeder & Kaspari, 2017).

Behavioural trait: interference ability

We assessed the interference ability of ant species from observations of interspecific interactions at baits after Le Brun and Feener (2007) (therein termed 'behavioural dominance'). Here, interference ability describes a species' relative success in two types of antagonistic interactions: usurping a resource from heterospecifics (expulsion) and defending an occupied resource from usurping heterospecifics (retention) (Le Brun & Feener, 2007). We recorded the outcomes (win/loss) in expulsion and retention incidents between different ant species at baits. Each species' Interference Ability was then scored using the Colley rating method (after Le Brun & Feener, 2007), which adjusted the value of each win and loss by the interference ability of the competitors that a species interacted with.

Data analysis

Trait selection

For all morphological traits except Body Size, we corrected for the effects of body size by regressing each trait against Body Size and using the residuals as the new values for that trait. We used Principal Components Analysis (PCA) and correlation analysis to select a suite of traits that captured most interspecific variation in multidimensional trait space while minimizing redundancy from trait correlations (Appendix C: Fig. S1). The first principal component, capturing 30% of the variation, was strongly positively associated with Head Width and Mandible Length and strongly negatively associated with Leg Length and Scape Length. The second (28% of the variation) was strongly positively and negatively associated with Interference Ability and Eye Width, respectively. The third (19% of the variation) was strongly positively and negatively associated with Body Size and N15, respectively. The fourth (13% of the variation) was strongly negatively associated with CT_{max}. All subsequent principal components had eigenvalues lesser than unity. Among traits showing strong positive correlations (Appendix C: Fig. S1), we selected those with stronger loadings on principal components. Our final set of traits comprised four morphological, two physiological and one behavioural trait: Body Size, Head Width, Eye Width, Leg Length, N15, CT_{max}, and Interference Ability.

Quantifying two measures of trait differences

For each trait, we quantified two measures of trait differences between the trait value of *S. invicta* ($T_{S.\ invicta}$) and the trait value of every other ant species (T_{Other}) recorded at baits in the study. We calculated Niche Difference as $|T_{S.\ invicta} - T_{Other}|$, a non-directional measure that can indicate the magnitude of niche differences between species. We calculated Competitive Difference as $T_{S.\ invicta} - T_{Other}$, a directional measure that detects for differences in competitive abilities along a competition hierarchy (Kunstler et al., 2012; Kraft et al., 2015).

Modelling invader density as a function of its trait differences with two assemblage types

The total number of *S. invicta* workers collected across the six pitfall traps at each of the 61 plots was used as the response term 'Invader Density'. For each trait, we modelled Invader Density as a function of the average trait differences (including Niche Difference and Competitive Difference as separate terms) between *S. invicta* and the assemblage of ant species observed at each plot. We repeated this process using the average trait differences between *S. invicta* and the shadow assemblage at each plot, which comprised any species missing from the plot but occurring in the species pool. We modelled the relationships using Poisson models with observation-level random effects as well as negative binomial models (prior to selecting the best model), as both of these could address the overdispersion in Invader Density (Harrison, 2014). For each trait, we built a full model which included Niche Difference, Competitive Difference, the quadratic form of Competitive Difference, and the environmental covariates Ground Cover and Temperature. We then selected the best model using a backward-step-wise variable selection procedure based on the Akaike information criterion corrected for small sample size (AICc).

Comparing patterns of trait dispersion between uninvaded and invaded assemblages

To determine whether invaded assemblages were more overdispersed or clustered relative to the uninvaded assemblages, we assessed the weighted dispersion in each trait at the plot level (excluding *S. invicta*) using the 'fdisp' function of the *FD* package in R (R Core Team, 2017), and the ant species' frequencies of occurrence across the six pitfall traps at each plot. To control for potential effects of species richness on trait dispersion, we compared standardized effect sizes (SES) instead of the observed values (Swenson, 2014). We calculated SES by comparing the observed values to values generated from 999 constrained null models randomizing the matrix of species' frequencies of occurrence using the 'Independent Swap' algorithm. The formula for calculating SES is:

$$SES = \frac{Mean_{observed} - Mean_{null}}{Standard\ Deviation_{null}}$$

We then compared the SES values of dispersion in invaded plots to those in uninvaded plots using t-tests or Wilcoxon-Mann-Whitney tests (when sample variances were unequal).

RESULTS AND INTERPRETATION

Weak associations with environment

On their own, the environmental factors of percentage ground cover and mean annual temperature were poor predictors of the density of *S. invicta* across the plots (Table 1). These results imply that environmental filtering, at least in the variables measured and across the grassland studied, did not have a strong effect in determining invasion outcomes.

Competitive advantages and low niche differences underlie exclusion

The density of *S. invicta* across the 61 plots was well explained by its average trait differences with the shadow assemblage of species absent from each plot but occurring in the species pool (Table 1; Fig. 2a-c). These relationships revealed mechanisms accounting for the potential exclusion of particular species from the invaded assemblages (assuming there were few if any barriers to dispersal across the landscape, and given that structural and climatic environmental factors were weakly associated with the invasion). Here, densities of *S. invicta* were high at plots which lacked ant species that had far lower

Interference Ability than *S. invicta* (Table 1; Fig. 2c) and similar Body Size to *S. invicta* (Table 1). These relationships suggest that *S. invicta* may have excluded weaker species in a competition hierarchy based on the takeover and defence of dietary resources, as well as species occupying a similar body size niche. Differences in Interference Ability, in particular, had very strong effects on the density of *S. invicta* across the plots, with the significant negative quadratic term predicting peak densities when competitive differences were almost maximised (Fig. 2c). Densities of *S. invicta* were also high at plots which lacked ant species with thermal tolerances (CT_{max}) that were similar to or lower than that of *S. invicta*, with the latter driving a stronger effect (Table 1; Fig. 2a). This implies that *S. invicta* may have excluded species occupying a similar thermal niche but possessing lower tolerances of high temperatures than itself.

High niche differences and low competitive advantages of invader promote coexistence

The density of *S. invicta* across the 61 plots was also well explained by its average trait differences with the ant species observed in each plot (Table 1; Fig. 2). These relationships revealed mechanisms promoting the abundance of *S. invicta* in the invaded assemblages and the potential coexistence of some ant species with *S. invicta* (or at least their apparent persistence in the presence of the invader). Here, densities of *S. invicta* were high at plots with ant assemblages that had dissimilar (smaller or larger) Body Size from *S. invicta* (Table 1; Fig. 2f), suggesting that ant species occurring amidst *S. invicta* exploited dissimilar niches from the invader. Densities of *S. invicta* were also high at plots where the thermal tolerances (CT_{max}) of the species present were dissimilar from (lower or higher) or simply higher than that of *S. invicta*, with the latter driving a stronger effect (Table 1; Fig. 2d). This implies that the ant species occurring amidst higher densities of *S. invicta* exploited a different thermal niche and/or had a higher thermal tolerance than *S. invicta*.

Replacement along hierarchical dietary and morphological axes

Where it occurred, *S. invicta*, which possessed intermediate values for N15 (trophic position) and Head Width, likely replaced other ant species along hierarchies in both of these trait axes. Species absent from plots with high densities of *S. invicta* had more carnivorous diets and wider heads than *S. invicta* (Table 1; Fig. 2b). In contrast, species occurring in plots with high densities of *S. invicta* had less carnivorous diets and narrower heads than *S. invicta* (Table 1; Fig. 2e). Overall, hierarchical differences in head width showed very strong effects in determining the densities of *S. invicta* across the plots (Table 1).

Opposing effects of competitive exclusion alter assemblage structure

Although total species richness was only marginally lower in the invaded assemblages, competition with *S. invicta* strongly altered their trait structure (Table 2). Invaded assemblages were marginally more clustered in multidimensional trait space (Table 2; Fig. 3a); but these overall patterns also masked important and distinct effects of the invasion on individual traits. In particular, the opposing effects of trait similarity (overdispersion) and trait hierarchy (clustering) were both detected and found to act on separate trait axes (Table 2; Fig. 3). Consistent with the effects of trait hierarchy, the presumed exclusion by *S. invicta* of ant species with weaker interference abilities and wider heads than itself led to significant clustering in these two traits among the species in invaded assemblages (Fig. 3b,d). However, the invaded assemblages were also more overdispersed in CT_{max} than the uninvaded assemblages. Consistent with the effects of trait similarity, this overdispersion arose due to the non-directional exclusion of species with similar CT_{max} as *S. invicta*, as well as the persistence, in the invaded assemblages, of other species possessing a dissimilar CT_{max} (lower or higher) from *S. invicta*, via thermal niche partitioning (Fig. 3c).

Table 1. Results of trait and environmental models for the density of the invasive ant *S. invicta* across 61 plots (which ranged from 0 to 491 workers per six pitfall traps). Trait models explain *S. invicta* density as a function of its average trait differences with either the ant species present in each plot, or the shadow assemblage of ant species absent from each plot (but occurring in the species pool). Two types of trait differences between *S. invicta* and the other ant species were measured: Niche Difference and Competitive Difference. Environmental models were built for the percentage ground cover (Ground Cover) and mean annual temperature (Temperature) at each plot. These variables were also included as covariates in trait models if they improved model performance.

Model Type	**Model Name**	**AICc**	**R^2**	**Terms**	**β**	***P***
Trait Difference: Invader vs. Species Present						
	Head Width	401.6	0.55	Competitive Difference	4.5	<0.001***
				Ground Cover	1.77	<0.05*
	CT_{max}	398.1	0.49	Competitive Difference	-3.32	<0.001***
				Niche Difference	3.02	<0.001***
	N15	409.6	0.47	Competitive Difference	0.84	<0.05*
	Body Size	411.7	0.47	Niche Difference	0.85	<0.05*
Trait Difference: Invader vs. Shadow Assemblage						
	Head Width	409.1	0.56	Competitive Difference	-5.01	<0.001***
				Ground Cover	2.09	<0.05*
	CT_{max}	401	0.51	Competitive Difference	4.18	<0.001***
				Niche Difference	-3.44	<0.001***
	Interference	396.9	0.98	Competitive Difference	3.1	<0.001***
				Competitive Difference^2	-3.17	<0.001***
	Body Size	424.2	0.12	Niche Difference	-2.46	<0.05*
	N15	405.9	0.74	Competitive Difference	-1.29	<0.001***

				Temperature	0.62	0.11
Environment						
	Ground Cover	428.5	0.0004	Ground Cover	0.2	0.79
	Temperature	428.2	0.003	Temperature	0.51	0.54

Table 2. Results of t-tests (*t*) and Wilcoxon Mann-Whitney tests (*w*) comparing uninvaded and invaded ground-foraging ant assemblages in terms of species richness, as well as the SES values of plot-level weighted dispersion (WD) in multidimensional trait space as well as in three individual traits which showed significant differences. The invader *S. invicta* is excluded from the invaded assemblages in these analyses.

Test	**Variable**	**Assemblage**	**Mean**	**SD**	**P**
t	Species Richness	Uninvaded	6.84	1.76	0.02*
		Invaded	5.67	2.01	
w	WD_{SES}: Multidimensional Trait Space	Uninvaded	0.23	0.78	0.06
		Invaded	-0.37	1.19	
t	WD_{SES}: CT_{max}	Uninvaded	-0.35	0.73	<0.001***
		Invaded	1.04	1.02	
w	WD_{SES}: Interference Ability	Uninvaded	0.48	0.62	<0.001***
		Invaded	-0.43	0.79	
t	WD_{SES}: Head Width	Uninvaded	0.47	0.81	<0.001***
		Invaded	-0.82	0.64	

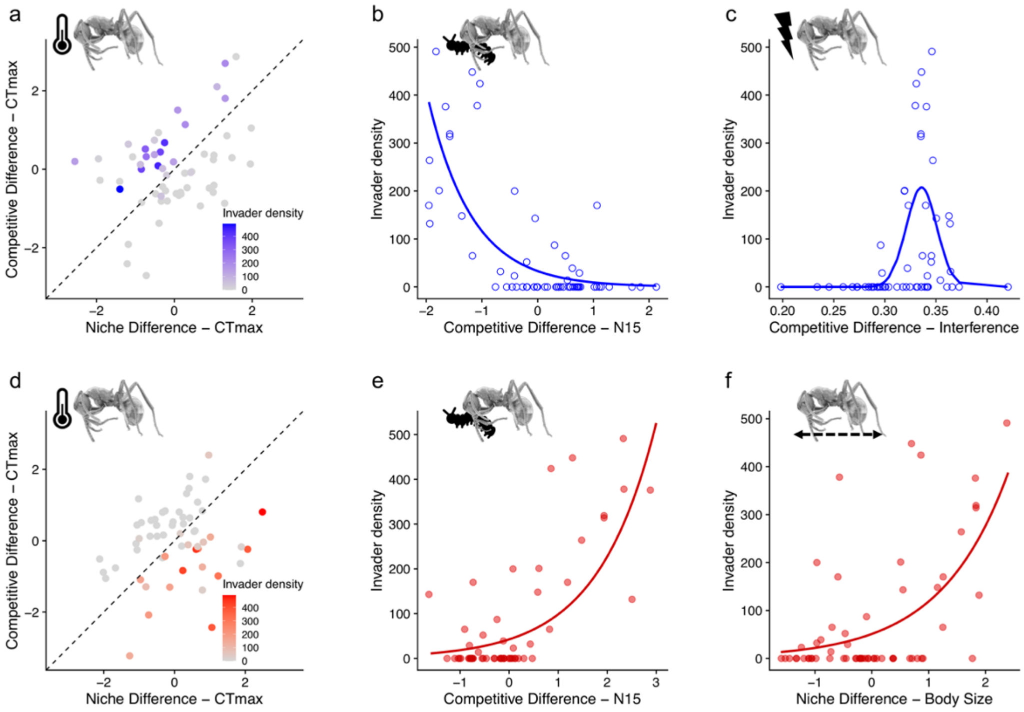

Figure 2. Density of the invasive species *S. invicta* as a function of its average trait differences with the shadow assemblage of the ant species missing from each plot (**a-c**), and with the assemblage of ant species observed at each plot (**d-f**). Against the shadow assemblages, the model for Critical Thermal Maximum (CT$_{max}$) detected significant effects of both Niche Difference and Competitive Difference, and predicted higher densities of *S. invicta* when Competitive Difference exceeded Niche Difference (**a**). The density of *S. invicta* was also significantly higher across plots where the missing species tended to be more carnivorous than *S. invicta* (**b**), and where the missing species had far poorer Interference Ability than *S. invicta* (**c**). Against the observed assemblages, the model for CT$_{max}$ detected significant effects of both Niche Difference and Competitive Difference, and predicted higher densities of *S. invicta* when Niche Difference exceeded Competitive Difference (**d**). The density of *S. invicta* was also significantly higher across plots where the species present were less carnivorous than *S. invicta* (**e**), and where the species present tended to be more dissimilar in Body Size (smaller or larger) from *S. invicta* (**f**).

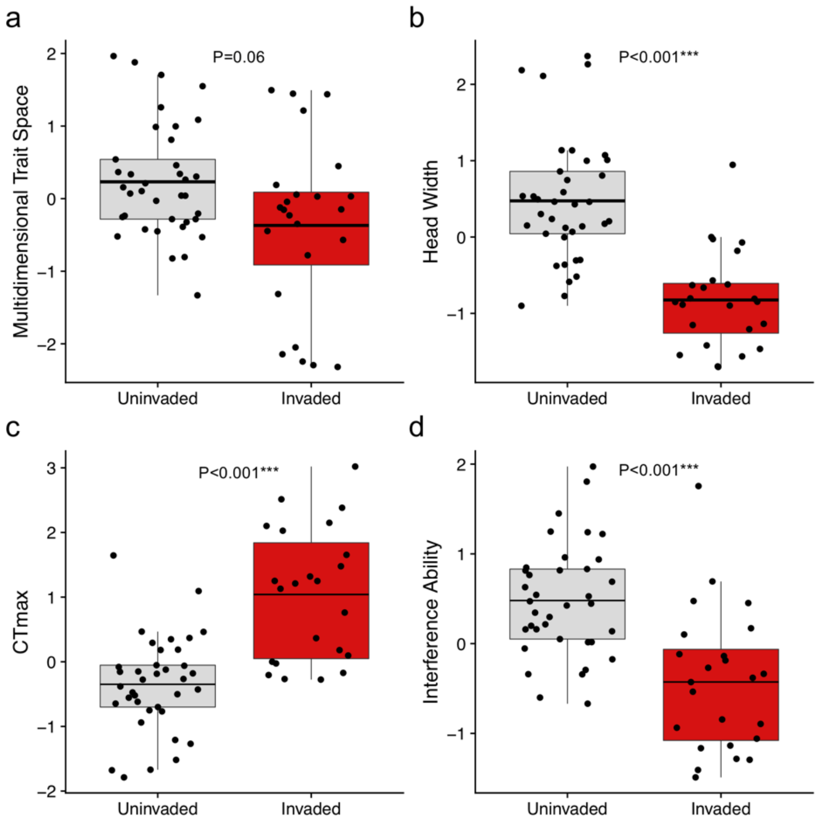

Figure 3. Standardized Effect Sizes (SES) for the weighted dispersion in multidimensional trait space (**a**) and in three traits – Head Width (**b**), Critical Thermal Maximum (**c**), and Interference Ability (**d**) – across uninvaded and invaded ground-foraging ant assemblages. In comparison with the uninvaded assemblages, ants in the invaded assemblages were significantly more overdispersed in Critical Thermal Maximum, but significantly more clustered in Head Width and Interference Ability. NB: the invader *S. invicta* is excluded from these analyses.

DISCUSSION

Trait-based approaches can yield powerful insights into the mechanisms underlying ecological phenomena. Despite this, their potential to do so in areas of community assembly and biodiversity responses is not yet fully realized because empirical studies often disregard the variable roles of traits in interspecific competition. Here, we found that interspecific trait differences largely determined the outcomes of an ant invasion, through opposing mechanisms of competitive exclusion (Mayfield & Levine, 2010). As expected within our design which intentionally attempted to minimize the effects of environment on assembly, invasion outcomes were poorly associated with environmental gradients, with no effects of environmental filtering detected for the ground-foraging ant assemblages across the flat, tropical grassland. Instead, differences between ant species and the invader *S. invicta* in various morphological, physiological and behavioural traits facilitated two distinct mechanisms of competitive exclusion – trait similarity and trait hierarchy (Kunstler et al., 2012). These mechanisms well explained the plausible exclusion of some species and the apparent persistence of the invader and other species. Crucially, the two mechanisms acted separately on different traits across the phenotypic spectrum, and their opposing effects produced contrasting structures among those traits in the invaded assemblages. These findings cast light on the thus far underestimated role of traits in conferring competitive advantages (as opposed to niche opportunities) to animal species, and point to trait hierarchy as an important mechanism for competitive exclusion in natural settings. They also illustrate how multiple, even opposing mechanisms can simultaneously drive assembly processes and structure the functional dimension of biodiversity (Functional Diversity).

That both trait similarity and trait hierarchy played key roles in determining invasion outcomes among ant species suggests that a wider view of competition and coexistence – one extending beyond classical niche theory, incorporating stabilizing and equalizing mechanisms (Chesson, 2000), and which is increasingly well-established for plant assemblages (Kraft et al., 2015; Kunstler et al., 2016) – is applicable to animals too. Consistent with trait similarity, niche differences led to the (non-directional) exclusion of species with similar values to *S. invicta* in traits such as body size (Fig. 2f), indicating that resource overlap promoted exclusion while resource partitioning promoted coexistence between different ant species and the invader. Nonetheless, niche differences alone did not determine competitive outcomes in the invasion (Table 1). Rather, they would more likely contribute to stabilizing mechanisms, which offset the demographic effects of differences in competitive abilities that promoted exclusion via trait hierarchy (Chesson, 2000; Adler, HilleRisLambers & Levine, 2007).

The effects of trait hierarchy were detected: ant species with relatively wider heads and more carnivorous diets than *S. invicta* (e.g., species of *Tetramorium* and *Pheidole*) appeared to be excluded where *S. invicta* occurred, while species with relatively narrow heads and more carbohydrate-rich diets than *S. invicta* (e.g., species of *Camponotus*, *Cardiocondyla,* and *Nylanderia*) were found in its presence. This may have occurred if *S. invicta* depleted arthropod populations and more strongly impacted more carnivorous ant species (as observed in Porter & Savignano, 1990), driving a competition hierarchy in omnivory. Another trait reflecting competitive differences and driving trait hierarchy, as revealed from directional patterns of exclusion (Fig. 2c) and clustering in trait space (Fig. 3d), was interference ability. Competition or 'dominance' hierarchies in resource exploitation among ant species are well documented (Arnan et al., 2018), and it has been proposed that interspecific trade-offs between species' interference abilities and thermal tolerances may facilitate coexistence (Bestelmeyer, 2000). Given that *S. invicta* possessed the strongest interference ability (as well as the strongest ecological dominance, measured as resource monopolization; Supporting Information), and that other ant species in invaded assemblages had dissimilar or higher thermal tolerances than *S. invicta* (Fig. 2d), dominance-tolerance trade-offs may indeed have been at play. Further supporting this hypothesis, individuals of *Cardiocondyla obscurior* – which had higher CT_{max} than *S. invicta* – were observed recruiting to baits abandoned by *S. invicta* when they were naturally exposed to direct sun due to changes in weather (M. K. L. Wong, pers. obs.); *C. obscurior* was also relatively more abundant in invaded than uninvaded assemblages (Appendix C: Figure S2). Such trade-offs would represent equalizing mechanisms which, in addition to stabilizing mechanisms, promoted coexistence among the invader and other ant species by reducing interspecific differences in competitive abilities (Chesson, 2000).

The above findings shed light on potential trait-based stabilizing and equalizing mechanisms that may determine the outcomes of competition among ant species and assemblage structure. Rigorous tests for these coexistence mechanisms would require competition experiments measuring demographic parameters such as invasion growth rates (e.g. Kraft et al., 2015); however such approaches are not readily transferrable to animals (see Terry et al., 2020). In any case, we suggest that the potential for trait differences to reflect niche or competitive differences warrants explicit consideration of both these effects on the structure of empirical assemblages. We therefore agree with recent calls for community assembly studies to test for patterns of clustering in addition to overdispersion as signatures of competition (see D'Andrea & Ostling, 2016;

Münkemüller et al., 2020). However, we also caution against inferences made exclusively from patterns in multidimensional trait space (see further below).

Importantly, our results also show that species' morphology, physiology and behaviour do not necessarily influence interspecific interactions and assembly processes in identical ways. Here, body size, a morphological trait, affected niche differences promoting coexistence among ant species, while interference ability, a behavioural trait, affected competitive differences driving exclusion, and thermal tolerance, a physiological trait, affected both niche and competitive differences. Exactly how interspecific differences in the phenotypic dimensions of morphology, physiology and behaviour affect performance (see Arnold, 1983) and determine coexistence in nature is not well understood (although physiological traits of plants associated more strongly with fitness differences than morphological traits in experiments; Pérez-Ramos et al., 2019). We suspect that these distinct and potentially varying relationships will be as important in animals as they are in plants, if not more so. We thus advocate for the targeted sampling of traits across the phenotypic spectrum in investigations of competition and assembly.

Of particular relevance to observational studies, our findings suggest that inferences about underlying ecological processes from patterns in the multidimensional trait structure of assemblages may be misguided if distinct processes with opposing effects act on different traits simultaneously. Here, an important role of competition in structuring the invaded assemblages was not well detected in multidimensional trait space; the opposing effects of trait hierarchy (clustering) and trait similarity (overdispersion) on separate traits probably counteracted each other. Such effects from multiple interactive and simultaneous assembly processes on functional structure are likely underestimated, especially where trait-hierarchy and trait-similarity are concerned (but see Lasky et al, 2014; Fortunel et al., 2016). Yet these distinct competitive mechanisms have important implications that reach beyond the fundamental understanding of community assembly. For one, they can strongly determine biodiversity-ecosystem function relationships. While niche differences and resource partitioning drive complementarity effects (Godoy et al., 2020), competitive hierarchies are associated with selection effects; these produce vastly different outcomes for ecosystem functions (Loreau & Hector, 2001).

Overall, our study uncovered new insights into the drivers and consequences of an ant invasion, which were consistent with the predictions of coexistence theory. Distinguishing between the contributions of traits to niche and competitive differences among species revealed alternative paths to competitive exclusion by invasion (MacDougall et al., 2009), and potential trait-based stabilizing and equalizing mechanisms structuring invaded assemblages. These specific mechanisms are useful for understanding invasion responses and assembly processes at fine spatial scales. The broader implication for empirical work is to embrace the potential for different traits across the phenotypic spectrum to reflect the varying role and effect of competition in structuring biodiversity.

6

Including intraspecific trait variability to avoid distortion of functional diversity and ecological inference: lessons from natural assemblages

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Author contributions

Both authors designed the research, collected the data and conducted data analyses. MKLW led the writing of the manuscript with substantial contributions by CPC.

ABSTRACT

1. Functional diversity assessments are crucial and increasingly used for understanding ecological processes and managing ecosystems. The functional diversity of a community is assessed by sampling traits at one or more scales (individuals, populations, species) and calculating a summary index of the variation in trait values. However, it remains unclear how the scale at which traits are sampled and the indices used to estimate functional diversity may alter the patterns observed and inferences about ecological processes.
2. For 40 plant and 61 ant communities, we assess functional diversity using six methods – encompassing various mean-based and probabilistic methods – chosen to reflect common scenarios where different levels of detail are available in trait data. We test whether including trait variability at different scales (from individuals to species) alters functional diversity values calculated using volume-based and dissimilarity-based indices, Functional Richness (FRic) and Rao, respectively. We further test whether such effects alter the functional diversity patterns observed across communities and their relationships with environmental drivers such as abiotic gradients and occurrences of invasive species.
3. Intraspecific trait variability strongly determined FRic and Rao. Methods using only species' mean trait values to calculate FRic (convex hulls) and Rao (Gower-based dissimilarity) generally overestimated their levels and distorted the patterns observed as compared to when intraspecific trait variability was considered. These distortions generated Type I and Type II errors for the effects of environmental factors structuring the plant and ant communities. The high sensitivity of FRic to individuals with extreme trait values was revealed in comparisons of different probabilistic methods including among-individual and among-population trait

variability in functional diversity. By contrast, values and ecological patterns in Rao were consistent among methods including different scales of intraspecific trait variability.

4. Decisions about where traits are sampled and how trait variability is included in functional diversity can drastically change the patterns observed and conclusions about ecological processes. We recommend sampling the traits of multiple individuals per species and capturing their intraspecific trait variability using probabilistic methods. We discuss how intraspecific trait variability can be reasonably estimated and included in functional diversity in the common circumstance where only limited trait data are available.

Keywords

Ant, community assembly, competition, environmental filtering, functional richness, functional trait, limiting similarity, Rao

INTRODUCTION

Assessments of the diversity of organisms' functional traits – ‘functional diversity’ – are important for understanding manifold phenomena ranging from macroevolutionary processes (Diaz et al., 2016; Pigot et al., 2020) to community assembly (McGill et al., 2006) and biodiversity-ecosystem function relationships (Gross et al., 2017). Most functional diversity assessments at and above the community level use just a single value for each trait of each species – the species-mean (Villéger et al. 2008, Mouchet et al. 2010). Calculating functional diversity from species-mean trait values lightens demands on trait measurement, especially when diverse ecological communities and large spatial scales are involved. In studies where trait data for species vary in origin or structure (e.g., Díaz et al., 2016; Pigot et al., 2020), the species-mean trait value can also be used directly to achieve uniform representation across species, facilitating interspecific comparisons.

The species-mean trait value, however, overlooks trait variability among conspecific individuals, which may be extensive due to effects from local adaptation, phenotypic plasticity, developmental conditions and ontogeny (Des Roches et al., 2018). This intraspecific trait variability can determine species’ ecological interactions (Des Roches et al., 2018; Carmona et al., 2019a), and contribute substantially to community functional diversity (as shown by Albert et al., 2011; Messier, McGill & Lechowicz, 2010; Siefert et al., 2015). Assessments failing to account for intraspecific trait variability may therefore misestimate the levels of functional diversity in reality. However, the extent to which these effects alter the observed patterns of functional diversity across communities and inferences about ecological processes are less explored in empirical systems.

Intraspecific trait variability mainly occurs at three hierarchical scales (Albert et al., 2011), each varying in its contribution to functional diversity and relevance to different community processes. At the broadest scale is trait variability among separate local populations. This generally increases as species are distributed across heterogeneous environments. Thus, processes such as environmental filtering may be better detected in functional diversity assessments incorporating population-level trait variability than those surveying species-level trait variability only (Gross et al., 2013). At a finer scale, trait variability among individuals within the same populations affects communities through biotic interactions. Simulation-based, field and experimental studies on plant communities show that accounting for such individual-level trait variability can improve the detection of reduced niche overlap (Mason et al., 2011; de Bello et al., 2013) and the prediction of coexistence outcomes between competing species (Carmona et al., 2019a). At the finest scale (and outside the scope of this study), trait variability within an individual may also influence community processes (Westneat, Wright & Dingemanse, 2015). Few empirical studies have compared the effects of individual- to population-level trait variability on functional diversity patterns (but see Messier, McGill & Lechowicz, 2010).

Functional diversity indices summarise the variation in traits at the considered scale. Methods to calculate functional diversity indices can be categorised under two groups. Those in the first group use the trait dissimilarity between species to calculate community functional diversity. Widely used dissimilarity-based indices include Rao's quadratic entropy (Botta-Dukát, 2005), functional dispersion (FDis; Laliberté & Legendre, 2010), mean pairwise distance (MPD; Weiher et al., 1998) and the FD index of Petchey & Gaston (2002). In these, dissimilarity is often calculated based on Gower's distance, which generally does not incorporate intraspecific trait variability because it uses only the mean trait value for each species (but see Cianciaruso et al., 2009). Gower-based dissimilarity is also affected by the species pool considered, as this determines the range of trait values used to standardize Gower's distances (de Bello et al., 2013). As a less context-dependent alternative, one can compute trait dissimilarity based on the overlap between the trait probability density functions (TPD) of different species (Carmona et al., 2016a; 2019b). Unlike Gower-based dissimilarity, overlap-based dissimilarity using TPD includes intraspecific trait variability.

Methods in the second group use the position of entities (i.e., individuals or species) in a multidimensional trait space to characterise the boundaries of a hypervolume encompassing all trait values observed in the community. The various Functional Richness (FRic) indices calculated using convex hulls (Cornwell et al., 2006), n-dimensional hypervolumes (Blonder et al., 2018), or TPD functions (Carmona et al., 2016a; 2019b), are examples of such volume-based indices. Whereas a convex hull is defined by the positions of entities with the most extreme trait values, n-dimensional hypervolume and TPD functions estimate a probabilistic hypervolume in which the frequencies of different trait values are accounted for (Carmona et al., 2016a; 2019b).

The different scales at which traits can be sampled, often with limited resources, and the variety of methods for calculating functional diversity indices make functional diversity assessments logistically challenging to implement (van der Plas et al., 2017). Empiricists thus often have to choose, *a priori*, the scales of trait variability to include (e.g. species-level only, or including population and/or individual levels), the indices used and the methods to calculate them – with the aim of achieving the most unbiased representation of functional diversity patterns. Although dissimilarity- and volume-based functional diversity indices such as Rao and FRic are used widely in empirical studies on functional diversity (Mouchet et al., 2010), there is little information about their sensitivity to different scales of trait variability.

Using data on two ecologically disparate systems – communities of plants in the Mediterranean region and ants in subtropical Asia – we investigate the extent to which excluding different scales of trait variability alter the observed functional diversity patterns and conclusions about the environmental factors driving community structure. We first calculate the FRic and Rao of communities using trait data of the highest available resolution (the greatest number of replicates in the smallest sampling unit, i.e., the plot). These 'HighRes' methods include as many scales of trait variability permitted by the data and use probabilistic distributions (TPD functions) of trait values to calculate indices that should best approximate the functional diversity in reality. The HighRes method for plants includes individual-, population- and species-level trait variability, while that for ants includes individual- and species-level trait variability. We then compare the values of FRic and Rao from HighRes methods to those from other commonly used methods for calculating functional diversity, which include fewer scales of trait variability owing to the lower resolution of the trait data available. Finally, we model the relationships of FRic and Rao against environmental variables, and test whether the patterns captured with HighRes methods are distorted when the other methods are used to calculate functional diversity.

MATERIALS AND METHODS

Community and trait data

The plant community and trait dataset, from Carmona et al. (2015), comprises abundance data for 51 plant species in each of 40 plots distributed along a slope (average inclination: 25%) in central Spain subjected to a Mediterranean climate. Soils towards the upper part of the slope were shallow and with low nutrient and water availability, while soils towards the bottom of the slope were deeper and far more productive. For 10 individuals of each species in each plot, data for two traits – plant height and specific leaf area – were collected, producing a trait dataset encompassing 2540 individuals.

The ant community and trait dataset, from Wong et al. (2020), comprises frequency-of-occurrence data for 29 ant species in each of 61 plots in an open tropical grassland in Hong Kong. One species, present in 24 plots, was the Red Imported Fire Ant (*Solenopsis invicta*), an invasive species known to impact the structure of ant communities (Gotelli & Arnett, 2000). Data for seven morphological traits (summarised in Appendix D: Table S1) were collected for ≥10 individuals (mean=11, max.=20) of every species, producing a trait dataset encompassing 319 individuals. This included data from separate sub-castes of polymorphic species (Wong et al., 2020). As far as possible, the selected individuals of each species were chosen to reflect the range of body sizes encountered across all samples. Digital photographs taken at every plot were used to estimate percentage ground cover via colour thresholding techniques in ImageJ (Abramoff, 2004).

Dimension reduction for ant traits and data preparation

We aimed to synthesize the major independent axes of variation in multidimensional trait space captured by the seven traits in the ant dataset. The trait measurements (except body size) were first size-corrected by dividing by the measurement for body size (Weber's Length). All traits were then log-transformed and standardized to have a mean of 0 and a standard deviation of 1. We performed a Principal Components Analysis (PCA) using the mean trait values of each species and subsequently predicted the values of the PCA components for all individuals in the dataset (after Martello et al., 2018). We retained the first two principal components, which had eigenvalues greater than unity, and predicted the values of these two components for each individual (N=319) in the trait dataset. The values for these two new 'traits' were used for all subsequent assessments of ant functional diversity. Trait data for plants were log-transformed and standardized prior to functional diversity calculations.

Calculating functional diversity indices with different scales of trait variability

We used six different methods to calculate the FRic and Rao of every community (plot) in the plant and ant datasets (Table 1). The methods differ generally in the scales of trait variability included in community functional diversity (Table 1), and specifically in the ways by which trait variability is scaled up to community functional diversity (see descriptions of individual methods below). They encompass a wide array of options available to researchers performing functional diversity analyses, and correspond to different scenarios, across which the required resolution of the trait data varies. The methods are ordered from high resolution (those systematically sampling trait values of individuals within populations and using these values to estimate probabilistic trait distributions of species directly) to low resolution (those using only the mean trait value of each species to calculate functional diversity indices).

Table 1. Methods for assessing functional diversity based on the resolution of trait data. A given method may include up to three hierarchical scales of trait variability: among individuals within the same populations (Individuals), among separate local populations (Populations), and among different species (Species). Methods differ in whether trait variability at each scale has been systematically sampled and included (✓), not systematically sampled but still included (~), or not included entirely (×). All methods estimate functional diversity by combining species' relative abundances in the community with the distributions of their trait values at the finest available scale. At that scale, the distribution of trait values of each species can be estimated directly (using a kernel density function) as a trait probability density function for that species (TPD$_S$) if many conspecific individuals have been measured; if not, the TPD$_S$ can be estimated as a multivariate normal distribution centred in the mean trait value, or the trait distribution can be substituted by the mean trait value entirely. Methods were applied to different taxa. For each taxon, the method using the highest available resolution in the trait data is indicated (*). See main text for full details of individual methods.

Method	**Name**	**Scale of trait variability included**			**Species' trait distributions are…**	**Resolution of trait data used**	**Taxa**
		Individuals	**Populations**	**Species**			
M1	TPD: individuals within populations	✓	✓	✓	estimated as TPD$_S$ directly from values	≥10 values per population	Plants*
M2	TPD: population mean	✓	✓	✓	estimated as TPD$_S$ centred in mean	≥1 value per population	Plants
M3	Classic: population mean	×	✓	✓	substituted by mean	≥1 value per population	Plants
M4	TPD: individuals across populations	~	~	✓	estimated as TPD$_S$ directly from values	≥10 values per species	Plants, Ants*
M5a	TPD: species mean (sd for each species)	~	~	✓	estimated as TPD$_S$ centred in mean	≥1 value per species	Plants, Ants
M5b	TPD: species mean (sd across species)	~	~	✓	estimated as TPD$_S$ centred in mean	≥1 value per species	Ants

M6	Classic: species mean	×	×	✓	substituted by mean	≥1 value per species	Plants, Ants

M1. TPD: individuals within populations

The various trait probability density (TPD) methods all involve generating a trait probability density function for each species – the TPD$_S$ – which probabilistically summarises the distribution of a given species' trait values at a given scale. The TPD$_S$ functions of different species are weighted using species' relative abundances and aggregated to produce the trait probabilistic density function for the community at every plot – the TPD$_C$. Functional diversity indices are then calculated based on properties of the TPD$_C$ (for FRic) as well as the relationships between the TPD$_S$ of different species (for Rao).

M1 includes the intraspecific trait variability among individuals in populations as well as among different populations. It can be used in a scenario where the traits of many individuals within each population have been measured systematically, such that one TPD$_S$ for each population of a species can be estimated directly with a kernel density function and the trait values acquired from that population (Carmona et al., 2016a; 2019b).

To execute M1, we first estimated one TPD$_S$ for each population of a species using kernel density functions and the trait values of conspecific individuals measured in each plot (henceforth we use 'population' in reference to conspecifics within the same plot). In doing so, intraspecific trait variability among individuals in the same population was captured by the TPD$_S$ at a plot, while that among populations was captured by the TPD$_S$

across different plots. We then aggregated the TPD_S of the different species in each plot according to their relative abundances to estimate the TPD_C. We calculated FRic as the volume of the TPD_C, and Rao from the dissimilarity among the TPD_S of the species present. A similar approach has been used in Carmona et al. (2019a).

M2. TPD: population mean

This TPD method includes intraspecific trait variability among different populations. With a smaller degree of precision than M1, it also includes the intraspecific trait variability among individuals within the same population by likewise estimating one TPD_S for every population of a species. However, instead of using a kernel density function to estimate the TPD_S directly from the trait values of individuals (as in M1), M2 uses a variance estimation approach to estimate the TPD_S as a multivariate normal distribution centred in the mean trait value in the population (as proposed by Carmona et al., 2016a). It assigns the same among-individual trait variability to all species occurring within the same plot while doing this. This method is relevant to a scenario where at least one individual from each population (plot) is measured, but the sample size is deemed insufficient for using a kernel density function to estimate TPD_S directly from the trait values acquired (while there are no studies examining the minimum sample sizes for estimating TPD_S with different trait dimensions, Blonder 2016 recommends using at least a number of observations m such that $\log(m) >$ number of dimensions).

To execute M2, we first calculated the mean trait value in each population of each species, using the trait values of conspecific individuals measured in each plot. Then, we estimated the TPD_S using the *TPDsMean* function from the 'TPD' package (Carmona et al., 2019b) and the plug-in bandwidth (variance) selector implemented via the *Hpi.diag* function in the ‘ks’ package (Duong, 2015). The resultant TPD_S for each species in each plot was a multivariate normal distribution centred in the mean trait value among its individuals in that plot, with a standard deviation determined by the estimated bandwidth (across all species in the same plot). Once the TPD_S were estimated, the aggregation of TPD_S to TPD_C at each plot, and the calculation of the FRic and Rao of each community were performed as in M1.

M3. Classic: population mean

The various ‘Classic’ methods disregard the intraspecific trait variability among individuals in the same populations because they assign the same trait value to all conspecific individuals in each plot. Classic methods calculate FRic using convex hulls and Rao using Gower-based dissimilarities. M3 includes intraspecific trait variability among different populations. It can be used in a scenario where at least one individual from each population (plot) is measured for each species (similar to M2).

To execute M3, we first calculated the mean trait value of each population of each species (as in M2). Next, we used those mean trait values of species in populations to calculate the FRic and Rao of the community at each plot directly (i.e., no TPD functions were calculated). We calculated FRic using the convex hull method implemented in the dbFD function from the ‘FD’ package (Laliberté et al., 2014), and Rao with the Gower dissimilarity matrix between populations using the melodic R function (de Bello et al., 2016). A similar approach has been used in Carmona et al. (2015) and Gross et al. (2013).

M4. TPD: individuals across populations

This TPD method includes intraspecific variability among the individuals of each species and treats the trait structure of species and communities in a probabilistic way; however, it does not strictly include the effects of differences between populations on traits. It can be used in a scenario where trait values have not been systematically acquired across the individuals and populations sampled, but the total sample size is nonetheless sufficient for using kernel density functions to directly estimate one TPD_S for the species as a whole (instead of one TPD_S per population as in M1 and M2). For instance, some investigators may arbitrarily measure the traits of many individuals per species, or intentionally measure the traits of the smallest and largest individuals to capture the variability of the species, while ignoring the distribution of those individuals in the plots sampled.

To execute M4 we estimated one TPD_S for each species directly using a kernel density function and the trait values of all its individuals in the dataset. At each plot, the aggregation of TPD_S to TPD_C, and calculation of the FRic and Rao of the community were performed as in M1. A similar approach has been used in Traba et al. (2017).

M5. TPD: species mean

This TPD method includes intraspecific trait variability of a similar structure as that of M4 but forgoes some precision in order to relax demands on sample size. Like M4, M5 estimates one TPD_S for each species only. However, it uses a variance estimator to estimate the TPD_S as a multivariate normal distribution centred in the species' mean trait value (similar to M2). M5 is thus particularly relevant to a scenario where insufficient individuals of each species have been measured to allow for a direct estimation of the TPD_S with a kernel density function.

To execute M5, we first calculated the mean trait value of each species from the trait values of all its individuals in the dataset. We then used the *TPDsMean* function, as in M2 – but here we explored two alternative approaches for assigning the bandwidths (variances). These approaches reflect scenarios researchers encounter frequently.

In the first, **M5a. TPD: species mean (sd for each species)**, the bandwidth used for estimating the TPD_S of each species was the standard deviation of all available trait values of that particular species (after Martello et al., 2018). This approach corresponds to the scenario where multiple trait values are available for each species, but the sample size is insufficient for using a kernel density function to estimate TPD_S directly from those values. Still, this method assigns to each species an amount of intraspecific trait variability that reflects the trait differences between conspecifics observed in reality (Lamanna et al., 2014).

The second approach **M5b. TPD: species (sd across species)** was applied to the ant dataset only. This approach can be used in a scenario where only one trait value is available for each species – a common limitation in studies using trait information from the literature or databases. Here, we followed Lamanna et al. (2014) and estimated the TPD_S of every species using a constant bandwidth value: 0.5 times the standard deviation of the trait values of all species in the dataset. Once the TPD_S of all species were estimated via M5a or M5b, the aggregation of TPD_S to TPD_C at each plot, and the calculation of the FRic and Rao of each community were performed as in M1.

M6. Classic: species mean

This method excludes intraspecific trait variability entirely and includes interspecific trait variability only. It is likely the most widely used approach in functional diversity assessments (Laliberté & Legendre, 2010), as it only requires a single trait value (e.g. the species-mean) for each species and does not involve the estimation of TPD functions.

To execute M6, we first calculated the mean trait value of each species from the trait values of all its individuals in the dataset. We then calculated the FRic and Rao of each community at each plot directly, following the same procedure as in M3.

All methods except M5b were applied to the plant data, while M4–M6 were applied to the ant data because trait measurements of the ants were not associated with specific plots. We designated M1 and M4 as the HighRes models for plants and ants, respectively. All functional diversity analyses were performed in R (R Core Team, 2017); those involving TPD were performed using the 'TPD' package (Carmona et al. 2019b) while those involving convex hull volumes were performed using the 'FD' and 'betapart' (Baselga et al., 2018) packages.

Statistical analyses

To investigate the relationships among different methods, we analysed the Pearson's correlation between the values of each functional diversity index (FRic and Rao) calculated by the different methods with the plant and ant data. This allowed us to identify methods which yielded more similar results to the designated HighRes model overall.

We investigated whether different methods captured the same ecological patterns. For the plant data, we investigated the changes in FRic and Rao in response to changes in water availability (%water content in soil samples taken from each plot) along the slope. For each index and method, we fitted a regression using water availability and its quadratic and cubic terms. For the ant data, we examined the changes in FRic and Rao in response to changes in percentage ground cover, and tested whether these patterns varied depending on the presence of the invasive species, *S. invicta*. For each index and method, we fitted a regression where we considered linear and quadratic terms for percentage ground cover, invasion status (binary variable: invaded/not invaded) and the interaction between them as predictors.

We used the 'MuMIn' package in R (Barton, 2016) to generate all potential subsets of all models, and ranked them using the Akaike information criterion corrected for small sample sizes (AICc). We selected the model from the HighRes method with the lowest AICc value as the one that best reflected the ecological patterns in each dataset. For each of the other candidate methods, we represented the results of the model with the lowest AICc value graphically, and calculated its ΔAICc (difference in AICc score) with respect to the selected HighRes model. An ΔAICc value of 0 indicates that the candidate method leads to a similar ecological interpretation as the HighRes method. Relatively small ΔAICc values (e.g. $\Delta\text{AICc} < 2$) indicate that, while leading to different ecological interpretations, the HighRes model is not deemed as completely implausible under the candidate method. High ΔAICc values (e.g. $\Delta\text{AICc} > 2$) imply that the functional diversity values and patterns produced by the candidate method lead to substantially different ecological interpretations from the results of the HighRes method (Burnham & Anderson, 2002).

RESULTS

Correlations between functional diversity indices calculated by different methods

In analyses for plants, the similarities between the HighRes method (M1) and the other methods (M2-M6) in their calculated FRic and Rao did not show a clear trend with the resolution of trait data and the scales of trait variability included (Fig. 1). Instead, for both indices, the values calculated with M4 were most similar to those calculated with M1 ($\rho_{\text{Fric}} = 0.74$; $\rho_{\text{Rao}} = 0.83$). All other methods largely failed to obtain FRic values similar to those from M1 ($\rho \leq 0.53$) but performed better where Rao was concerned ($\rho \geq 0.73$). In analyses for ants, the similarities between the HighRes method (M4) and the other methods (M5a, M5b, M6) in their FRic and Rao generally decreased with decreasing resolution in trait data and as fewer scales of trait variability were included (Fig. 2); M5a performed best, and especially well for Rao ($\rho_{\text{Fric}} = 0.85$; $\rho_{\text{Rao}} = 0.99$), while M6 performed the worst ($\rho_{\text{Fric}} = 0.82$; $\rho_{\text{Rao}} = 0.66$).

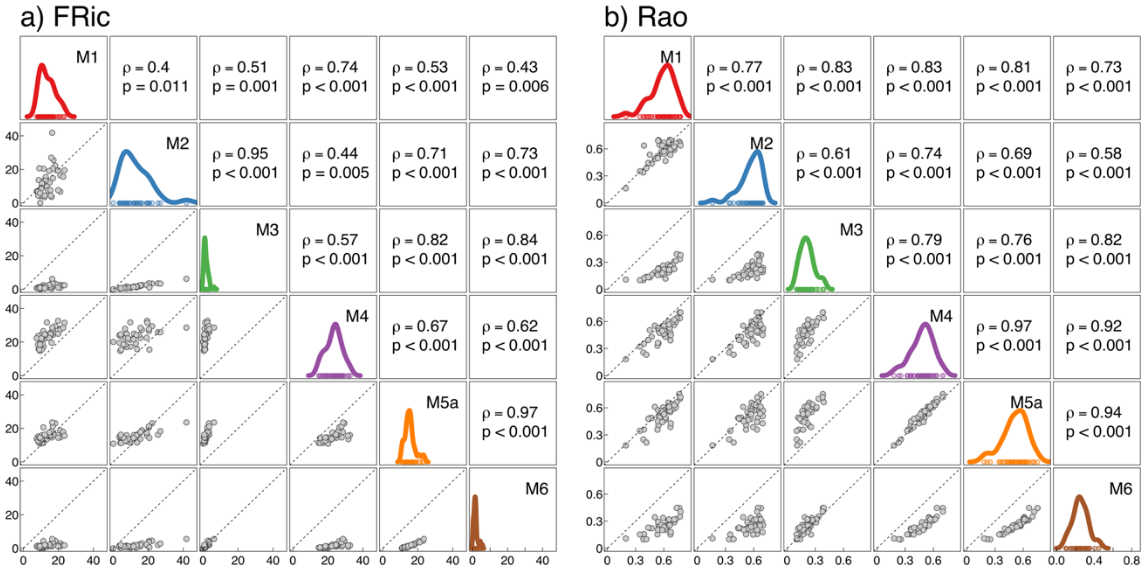

Figure 1. For 40 plant communities, plots show the degree of similarity, as measured by Pearson's correlation (ρ), in values of Functional Richness (FRic) (a) and Rao (b) calculated by different methods. Each method includes a different scale (or scales) of trait variability in functional diversity, based on the resolution of the trait data (see Table 1). Plots along the diagonal depict probability density functions showing the distribution of FRic or Rao values calculated by individual methods.

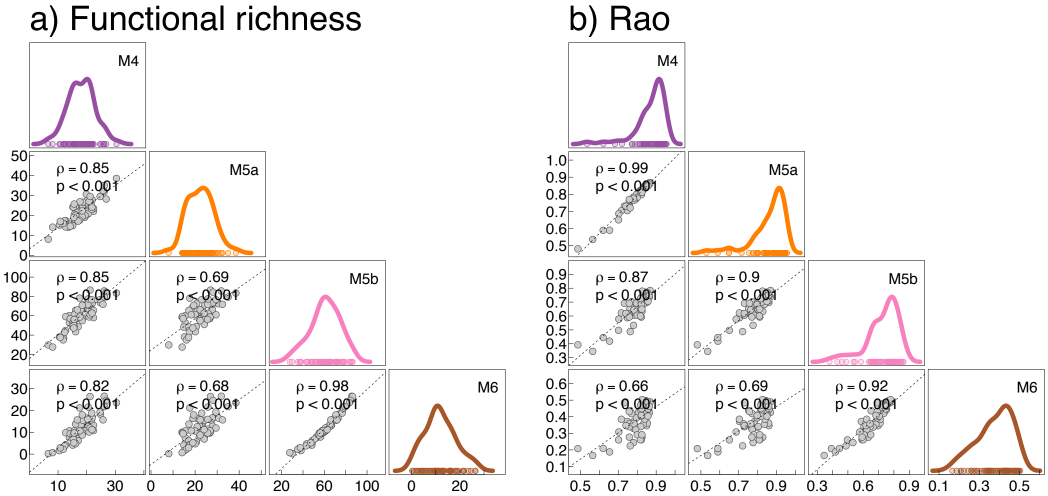

Figure 2. For 61 ant communities, plots show the degree of similarity, as measured by Pearson's correlation (ρ), in values of Functional Richness (FRic) (a) and Rao (b) calculated by different methods. Each method includes a different scale (or scales) of trait variability in functional diversity, based on the resolution of the trait data (see Table 1). Plots along the diagonal depict probability density functions showing the distribution of FRic or Rao values calculated by individual methods.

FRic responds to the exclusion of specific scales of intraspecific trait variability

The FRic patterns detected by the best models of the respective HighRes methods for both the plant and ant data were not likewise detected by the best models of the other methods, which used trait data of lower resolution and which excluded particular scales of intraspecific trait variability. The plant model from the HighRes method (M1) detected a negative linear effect of soil water content on FRic (Fig. 3a). All other methods (M2-M6) led to substantially different ecological interpretations (Fig. 3b-f: ΔAICc > 2). The models from M3, M4 and M6 detected non-linear changes in which FRic peaked at intermediate soil water content (Fig. 3c,d,f), while those from M2 and M5a failed to detect an effect of soil water content on FRic (Fig. 3b,e). The ant model from the HighRes method (M4) detected a significant negative linear effect of ground cover on FRic and a significant effect of invasion (Fig. 4a). No models from the other methods detected an identical ecological pattern (Fig. 4b-d: ΔAICc $\neq 0$). Though the model from M5b reproduced the significant negative linear effect of ground cover (Fig. 4c), it also detected a significant interaction effect between ground cover and invasion. The model from M6 failed to detect the effect of ground cover (Fig. 4d) while that from M5a failed to detect an effect of invasion (Fig. 4b).

Rao responds to the exclusion of intraspecific trait variability in general

The Rao patterns detected by the best models from HighRes methods were accurately reproduced by the best models from a few other methods which included intraspecific trait variability, but not by methods which excluded it entirely. The plant model from the HighRes method (M1) did not detect any significant effect of soil water content on Rao (Fig. 3g). This pattern was accurately reproduced by models from both M2 and M4 (Fig. 3h,j: ΔAICc = 0). In contrast, the model from M5a detected a significant negative linear effect of soil water content on Rao (Fig. 3k). Models from both M3 and M6 detected significant quadratic relationships between Rao and soil water content (Fig. 3i,l), with that from M6 leading to a substantially different ecological interpretation (Fig. 3l: ΔAICc > 2). The ant model from the HighRes method (M4) did not detect any significant effects from ground cover and invasion (Fig. 4e). This pattern was accurately reproduced with M5a only (Fig. 4f: ΔAICc = 0). By contrast, models from M5b and M6 detected significant effects with ground cover and invasion which led to very different ecological interpretations (Fig. 4g,h: 6 < ΔAICc < 20).

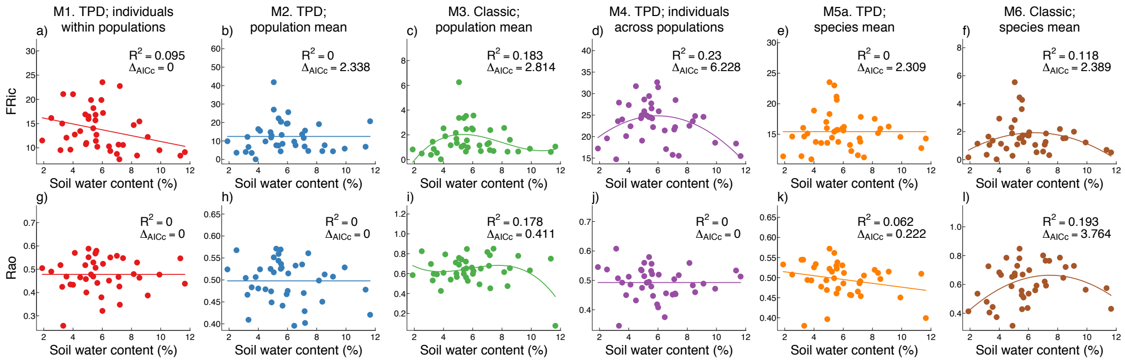

Figure 3. Six models of functional diversity measured in terms of the indices Functional Richness (FRic) (top) and Rao (bottom), in 40 Mediterranean plant communities (dots) distributed along a gradient of soil water content. The models were produced from six different methods for calculating functional diversity, each including a different scale (or scales) of trait variability, based on the resolution of the trait data available (see Table 1). For each index, the congruence of each model from M2-M6 with the model from M1 (which used data of the highest resolution) is summarised by an ΔAICc score, where a value of 0 indicates no distortion of the ecological pattern in the M1 model, and increasing values indicate increasing distortion.

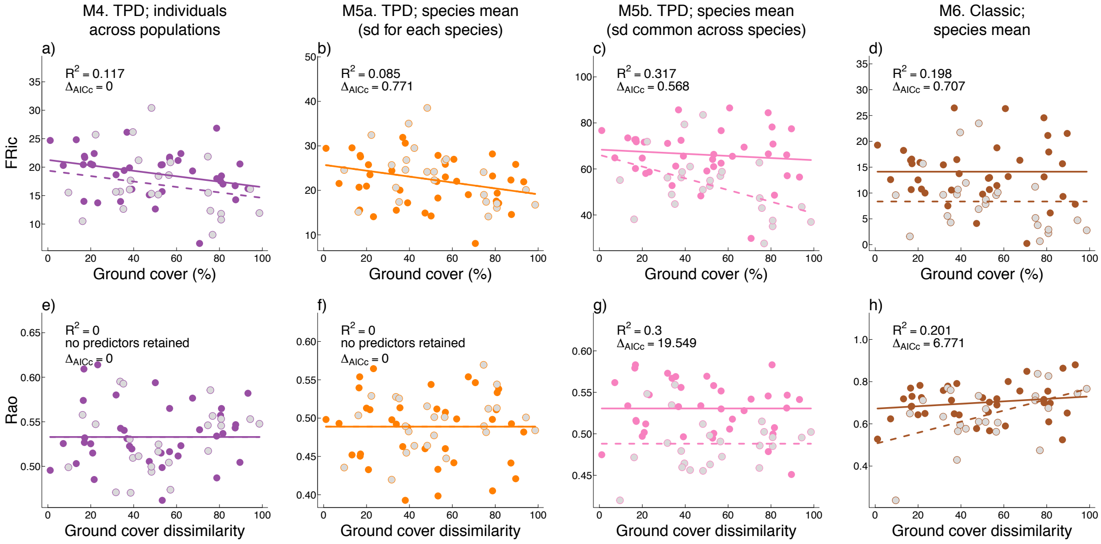

Figure 4. Four models of functional diversity measured in terms of the indices Functional Richness (FRic) (top) and Rao (bottom), in 61 ant communities distributed along a gradient of ground cover, including communities with (coloured dots, solid trend line) and without (grey dots, dotted trend line) an invasive species, *S. invicta.* The models were produced from four different methods for calculating functional diversity, each including a different scale (or scales) of trait variability, based on the resolution of the trait data available (see Table 1). For each index, the congruence of the models from M5a, M5b and M6 with the model from M4 (which used data of the highest resolution) is indicated by an ΔAICc score, where a value of 0 indicates no distortion of the ecological pattern in the M4 model, and increasing values indicate increasing distortion.

DISCUSSION

Our empirical findings in two ecologically disparate systems show that widely used dissimilarity-based and volume-based indices capture different functional diversity patterns, and crucially, that these indices are strongly influenced by the particular scales of trait variability included, as determined by the specific resolution of the trait data available. These results imply that basic decisions in functional diversity assessments – those about whether traits are sampled *in situ*, and if so, from how many and which individuals; which indices are used and how they are calculated – can largely determine the patterns observed and even alter conclusions about ecological processes entirely. As our study examined the morphological traits of plants and ants, further work is needed to explore the effects of intraspecific trait variability on the functional diversity of other taxonomic assemblages and for traits spanning organisms' physiology and behaviour. Nonetheless, in light of the findings, we suggest recommendations and issues to consider in both field-based and data-driven studies on functional diversity.

Use multiple indices to draw inference

Limiting similarity (MacArthur & Levins, 1967) has long been invoked as a powerful driver of community structure, but the extent of its influence across taxonomic groups is less explored with trait-based approaches, which have the advantage of quantifying species' niches in comparable terms (McGill et al., 2006). In our study, volume-based and dissimilarity-based functional diversity indices collectively detected patterns consistent with the effects of limiting similarity in the community structure of ecologically distinct groups such as plants and ants inhabiting different bioregions. Using trait data of the highest resolution, the best models in both groups showed that the total volume occupied by the trait values of all species (FRic) decreased along the respective environmental gradients, suggesting that the total niche space available to all members within the community was reduced (Fig. 3a, Fig. 4a). However, in spite of the shrinking niche space at the community level, the overlap between species within this space – as measured by their trait dissimilarity, Rao – remained constant (Fig. 3g, Fig. 4e). The limiting similarity hypothesis is further supported by evidence that species richness declined along the environmental gradient in both cases (Appendix D). To the best of our knowledge, this is the first study to show the importance of including intraspecific variability at the within-plot scale for detecting the effects of limiting similarity in natural assemblages. It supports previous findings in simulated (de Bello et al., 2013) and experimental conditions (Mason et al., 2011). More broadly, these results demonstrate that using different indices to target distinct facets of functional diversity can enhance inferences about ecological processes. Nonetheless, the relationships were detected using trait data of high resolution, which is not always available. Moreover, we found functional diversity indices to be very sensitive to the particular scales of trait variability included. An understanding of these relationships is therefore crucial for selecting appropriate methods and avoiding misinterpretation in functional diversity research.

Results from mean-based methods may distort patterns and alter inference

In keeping with previous studies (Baraloto et al., 2010; de Bello et al., 2013), we found that calculations solely using the mean trait values of species incorrectly estimated functional diversity (Fig. 1: values from M1 are weakly correlated with those from M6). Our results also go further than previous work, as they empirically show that mean-based methods for calculating functional diversity in general – such as convex hull-based FRic and Gower-based Rao – can distort patterns and alter conclusions about underlying processes. For instance, a negative-linear relationship may be transformed to a quadratic one (Fig. 3a vs. Fig. 3f), a 'false' effect of an invasive species may be detected (Type I error) (Fig. 4e vs. Fig. 4h), and a 'true' effect of an environmental gradient may fail to be detected (Type II error) (Fig. 4a vs. Fig. 4d). Furthermore, even when an effort is made to address among-population trait variability, such as by systematically sampling the traits of conspecific individuals within plots, the resultant functional diversity patterns may still be distorted if the among-population trait variability is derived solely from the mean trait values of populations (Fig. 3: in both FRic and Rao, the model from M3 clearly changes the relationship modelled with M1). Given these apparent limitations of mean-based methods in preserving the integrity of functional diversity estimates and patterns, calls for using probabilistic methods to include intraspecific trait variability into functional diversity (Carmona et al., 2016a; Blonder et al., 2018) should not be understated. Yet, our results show that both the scales of intraspecific trait variability considered (among individuals vs. among populations) and the precise methods with which probabilistic trait distributions are estimated (e.g. M1, M2, M4, M5a, M5b) will strongly influence the functional diversity observed.

Aim to estimate probabilistic trait distributions from trait values of individuals directly

We recommend that ecologists sample traits of multiple individuals per species and use these values to estimate probabilistic trait distributions for each species directly with kernel density functions (e.g. in M4), even when this cannot be done for every population of every species (as in M1). In our study, such an approach sampling at least 10 individuals of each species (M4) achieved values of FRic and Rao that were most similar to those calculated by the method using trait data of the highest resolution, which sampled at least 10 individuals per population of each species (M1) (Fig. 1).

Our results show that FRic is especially sensitive to trait variability among individuals within the same populations. We suggest that assessments of FRic and community niche space can address this scale of trait variability by sampling the traits of conspecific individuals occurring within the same plots. Here, the FRic of plant communities was overestimated by methods which either estimated the trait probability density functions of species (TPD$_S$) from mean values or methods which used only the mean value at the population or species levels (M2, M3 and M6), as compared to methods which estimated TPD$_S$ using the trait values of individuals directly (M4) (Fig. 1a: compare plots for M1 against M2, M3 and M6, with plots for M1 against M4). These relationships imply that each plant community actually occupied a smaller niche space than would be expected if it only included the among-population trait variability in each species, or if it excluded intraspecific trait variability entirely. This reduction in community niche space locally may be driven by environmental filtering or competition hierarchies promoting similarity in the traits of coexisting individuals (Germain et al., 2018; Carmona et al., 2019a). Yet the findings demonstrate that such important assembly processes may fail to be detected if among-individual trait variability is not included in functional diversity assessments.

The low correlation between the FRic values of M1 and M2 (Fig. 1a) was particularly surprising. Both methods capture trait variability at the same spatial and organizational scales (Table 1); the low correlation therefore arose from the different ways by which the TPD$_S$ of populations were estimated. That estimating TPD$_S$ directly using kernel density functions and all sampled values (M1) and estimating them as multivariate normal distributions centred in the mean sampled values (M2) produced distinct results shows that FRic is strongly influenced by the effects of individuals with extreme trait values (in spite of TPD methods theoretically being more robust to such effects than convex hull-based hypervolumes; Carmona et al., 2016a). This sensitivity of FRic to extreme values could be investigated further by testing the effects of setting smaller probability thresholds to the TPD$_S$ (see Blonder, 2016 and Carmona et al. 2016b).

We found that Rao, like FRic, was sensitive to the exclusion of intraspecific trait variability overall (Fig. 1b: M6 vs. M1; Fig. 2b: M6 vs. M4; Fig. 3g vs. 3l; Fig 4e vs. Fig. 4h). Yet, in contrast to the patterns observed for FRic, the methods estimating species' trait probability density functions directly from individual values using kernel density functions (M1, M4) and those estimating them as multivariate normal distributions centred in the mean trait value (M2, M5a) produced similar levels of Rao (Fig. 1b: M1 vs. M2 for plants; Fig. 2b: M4 vs. M5a for ants). Furthermore, Rao calculated by these different methods followed similar trends with environmental gradients (Fig. 3g,h,j and Fig. 4e,f). These results are encouraging – although distinct, the two methods are evidently valid alternatives for calculating trait dissimilarities between populations or species. The results also suggest that estimations of dissimilarities between species (e.g. with Rao) are more robust to methodological choices than estimations of the total functional space occupied by communities (e.g. FRic).

Observed functional diversity will most likely approximate reality when TPD_S are estimated directly using the trait values of multiple individuals per species and information on the spatial structure of their populations across environments (Carmona et al., 2016a). Yet, large samples of trait measurements and spatially detailed trait information are seldom available. Surveys of natural assemblages often encounter many rare species with few individuals are available for trait measurements. With respect to these limitations of empirical studies, our results suggest that even with a lower resolution in trait data, intraspecific trait variability can still be included in dissimilarity-based functional diversity without leading to significant distortion in ecological patterns. This is in agreement with previous results suggesting that trait sampling is more efficient when local (i.e., measured in the corresponding plot) trait values are used, rather than a regional average for each species (Carmona et al., 2015, Gross et al., 2013, Baraloto et al., 2010). In the specific case of the TPD framework, this can be achieved by using variance estimators to estimate the TPD$_S$ of each species as a multivariate normal trait distribution centred in the sampled mean trait value (e.g., M2, M5a).

In estimating the trait distributions of species with variance estimators, however, one should not assume that the same algorithm is valid for estimating the variance in the distributions of trait values of disparate taxa. This is evidenced by our finding that the FRic of ant communities from when TPD$_S$ was estimated assuming a constant variance (following the solution proposed in a plant-based study; Lamanna et al., 2014) (M5b) was over two times higher than their FRic from when TPD$_S$ was estimated using the trait values of all sampled individuals (M4), as well as that from when TPD$_S$ was estimated using the variance in the data (M5a) (Fig. 4a-c). Specifically, this suggests that in comparison to plants, trait variation within ant species may be very low relative to trait variation between species (as reported in Gaudard, Robertson & Bishop, 2019). In any case, these results strongly suggest that decisions about the precise variances used for estimating trait distributions should be grounded in the ecological characteristics of the studied organisms. Caution is therefore advised for multi-taxa analyses, where it may seem temptingly efficient to apply the same estimation procedure across all groups. Further studies on the contribution of intraspecific variability to total trait variability in different taxa (e.g. Siefert et al., 2015) will be useful for navigating these issues.

Conclusion

This study demonstrates the strong influence that trait variability within species can have on our view of functional diversity and underlying ecological processes. It also clarifies when and how intraspecific trait variability can be reasonably included in functional diversity studies with limited trait data. Accounting for this crucial yet overlooked source of functional variability in nature will be key to understanding the responses and effects of biodiversity.

7

GENERAL DISCUSSION

In this thesis I aimed to lay the groundwork for using trait-based approaches to improve understanding of the community ecology of terrestrial arthropods, some of the most diverse and functionally important organisms on Earth. I also sought to attain an empirical understanding of how fundamental community assembly processes, such as interspecific competition, act on traits and species to determine biodiversity responses to environmental change, such as invasions by non-native species. My empirical work is novel for integrating aspects of community, functional and invasion ecology, as well as for targeting areas that have yet to be adequately addressed in trait-based research, such as the effects of intraspecific trait variability on functional diversity. Here, I summarise briefly the main contributions of the thesis and discuss promising directions for additional work.

Summary and integration of key findings

I aimed to strengthen the foundations for the emerging field of trait-based arthropod ecology in Chapter 2. The paper formalised conceptual definitions and reviewed the evidence base, cementing the novelty and value of trait-based research to community and ecosystem ecology. It also discussed in detail the limitations and prospects for future trait-based research on terrestrial arthropods (hence I shall not repeat these here). The majority of the 29 studies citing the published review (Wong et al., 2019) appear to investigate trait-environment relationships and niche filtering of arthropod assemblages within the context of natural gradients (Andriuzzi et al., 2020; Rabl et al., 2020) and disturbances (Carvalho et al., 2020; Sascha et al., 2020) including plant invasions (Garcia et al., 2019; Foster et al., 2020). Several make contributions to topics which the review highlighted as needing further study: quantifying intraspecific trait variability (Bhusal et al., 2019; Mungee et al., 2019), investigating the influence of sampling methods on the functional diversity observed (Lee et al., 2019; Privet et al., 2020), and the ecosystem functionality of traits (deCastro-Arrazola et al., 2020). Still, little attention has been paid to the roles of traits in biotic assembly processes and their consequences for functional diversity (Wong et al., 2019). Given that interspecific competition fundamentally determines community structure and biodiversity patterns, and that invasions are a leading driver of environmental change globally, I conducted empirical studies to advance understanding of these areas.

My empirical research (Chapters 3-6) mainly focused on an invasion by the Red Imported Fire Ant (*Solenopsis invicta*) in grassland ant assemblages in subtropical Asia. Chapter 3 made an important contribution in demonstrating that functional diversity can respond to biotic disturbances in distinct and less detectable ways from taxonomic diversity, across spatial and ecological scales (Wong, Guénard & Lewis, 2020). This adds to a growing literature underscoring the need to address unique and important effects of environmental change on functional diversity (Flynn et al., 2009; Buisson et al., 2013), including functional homogenization (Clavel et al., 2011; Gossner et al., 2016; Fricke & Svenning, 2020), which can cause a loss of ecosystem function (Van der Plas et al., 2016; Hautier et al., 2018). One practical implication of the findings for invasion management is that traits associated with lower abundances in invaded assemblages may be useful for distinguishing species that are susceptible to invasion impacts, thus facilitating intervention before local extinctions occur. More broadly, I contend that an approach linking biodiversity trends to deterministic trait-environment relationships should help clarify the underlying causes of global shifts in arthropod diversity (Van Klink et al., 2020) and predict the effects that environmental change will have on the composition of arthropod communities. While there have been many recent studies reporting temporal trends in abundances and species diversity (Hallmann et al., 2017; Macgregor et al., 2019; Van Klink et al., 2020), few have contextualized these trends with trait-environment relationships.

In Chapter 4 I showed that trait differences explained biodiversity patterns at fine ecological scales (species co-occurrences) in ways consistent with predictions from coexistence theory (Wong, Tsang, Lewis & Guénard, 2020). In contrast to abundance counts that are often difficult to perform, basic data on species' occurrences are collected in most empirical studies of ecological communities. Hence, though they are challenging to interpret and potentially unreliable proxies of ecological interactions on their own (Blanchet et al., 2020), species co-occurrence patterns will likely be a mainstay in ecological research. To this end, Chapter 4 demonstrated how inferences about ecological processes drawn from species co-occurrence patterns may be bolstered by a combination of theory-driven hypothesis-testing and trait-based approaches. One limitation of the study, however, was its exclusive focus on the morphological traits of ant species. While the results do suggest that the relative pronotum width of ant workers may influence interspecific competition – conceivably through resource exploitation, as reported in previous studies (cited in Chapter 4) – they are caveated by the fact that morphological traits on ecological interactions and organismal functions are less direct and inferable (i.e., relative to physiological and behavioural traits which tend to have direct effects on interactions; Arnold, 1983). In general, there is a need for studies on arthropod competition to include a greater diversity of traits representing the multidimensional phenotype (I addressed this in Chapter 5), as well as experiments which determine the functions of different traits to the organisms studied (discussed further below).

While Chapter 4 explored the potential effects of competition and differences in morphological traits on the co-occurrences of ant species, Chapter 5 scaled up the investigation through a substantial expansion of phenotypic coverage (encompassing morphological, physiological and behavioural traits), a focus on relationships between the ‘invader’ and the local assemblages (i.e., a higher ecological scale), and tests to determine the effects of interspecific competition on assemblage functional structure. This work is one of the few studies that simultaneously evaluates the opposing mechanisms of competitive exclusion (trait-similarity and trait-hierarchy) in an animal assemblage. The most prominent finding of the study is the apparent variability among different traits in promoting niche and competitive differences between ant species, the effects of which structured the functional diversity of local assemblages in contrasting ways. The key implication of the findings for community ecology studies in general is that it can be misleading to infer community assembly processes from patterns of trait dispersion (e.g., overdispersion vs. clustering) if one is unaware of the actual functions of specific traits in community assembly (e.g., promoting either niche or competitive differences). While these varying effects of traits on competitive outcomes are well acknowledged in plant ecology, they are overlooked in studies on other taxa, where it is typically assumed that trait differences affect only niche differences and that competition unfolds only via limiting similarity (Mayfield & Levine, 2010). Therefore, extending Chapter 5’s investigation of the opposing trait-based mechanisms of competitive exclusion to a variety of trophic assemblages and ecosystems should prove most fruitful. Nonetheless, while the findings of Chapter 5 do provide intriguing and important evidence for the potential relevance of both mechanisms of competitive exclusion to non-plant taxa, much work remains to be done before these precise mechanisms are demonstrated convincingly. For example, the empirical evidence that trait-hierarchy drives competitive exclusion among plant species is based on numerous studies which quantified the competitive effects of traits on species' fitness in terms of demographic parameters (see Kunstler et al., 2012; Herben & Goldberg, 2014; Kunstler et al., 2016). Some avenues for investigating the opposing mechanisms of competitive exclusion in arthropods are discussed further below.

As demonstrated in the preceding chapters, trait-based approaches can advance insights into the causes and consequences of ecological change. Nevertheless, the effects of intraspecific trait variability – or rather, failing to sample intraspecific trait variability – on investigators' views of functional diversity represent a significant knowledge gap (Violle et al., 2012). In Chapter 6, I demonstrated empirically that decisions to exclude intraspecific trait variability from functional diversity assessments can strongly influence the patterns observed, altering the inferences drawn about ecological processes to a degree where Type I or Type II statistical errors arise (Wong & Carmona, 2020). The takeaway from this work is that assessments of functional diversity should, as far as possible, be designed to account for the potential effects of intraspecific trait variability. To this end, Chapter 6 outlined ways to reasonably include intraspecific trait variability in functional diversity assessments in light of constraints on trait data. These contributions are particularly relevant to studies of arthropod functional diversity, where trait data at the intraspecific level are limited and especially challenging to obtain logistically if the studied assemblages contain high species richness (e.g., 6144 species in <0.5 ha of tropical rainforest; Basset et al., 2012), as well as many rare species (Novotný & Basset, 2000), which are nonetheless important determinants of functional diversity (Violle et al., 2017). From another perspective, the strong effects of intraspecific trait variability on the observed functional structure of the ant assemblages documented in Chapter 6 suggest that intraspecific trait variability may have a substantial influence over assembly processes for arthropod communities (as shown for plants in Jung et al., 2010). When and how intraspecific trait variability in arthropod species influences their dispersal, filtering by environments and local adaptation, as well as competition and coexistence in local communities is largely unexplored empirically (but see Classen et al., 2017).

The research outlined above collectively strengthens the foundations for terrestrial arthropod trait-based ecology, makes progress in addressing general limitations, and contributes understanding to unexplored yet important questions in the areas of community assembly, responses to biological invasions, and functional diversity. The synthesis and conceptual takeaways concerning trait-based approaches in Chapters 2 and 6 are broadly applicable to all studies on terrestrial arthropods, while the specific findings in Chapters 3, 4 and 5 concerning invasion impacts, interspecific competition and its effects on community structure are of direct relevance to studies of ant assemblages as well as other 'horizontal communities' (*sensu* Vellend, 2016) of arthropod species occupying similar trophic levels (communities of grasshoppers, ground beetles and spiders etc.). More broadly, throughout this thesis, an emphasis on traits has facilitated comparative approaches that bridge the patterns observed to theoretical ecological mechanisms (e.g., relating interspecific competitive outcomes to quantifiable trait differences between species, and the functional structure of assemblages to the effects of biotic disturbances). This general and mechanistic framework of trait-based ecology, which views traits instead of species as functional units, will allow future studies on terrestrial arthropods and other groups to build upon the approaches developed and the predictions made in the thesis. This is crucial because the empirical research ultimately focused on a relatively small spatial scale and single trophic level. While the conclusions drawn are broadly consistent with theoretically valid mechanisms determining the structure and responses of the grassland ant assemblages observed, additional work will help clarify the details of the mechanisms and test the generality of the findings.

Future directions

The notion that competitive exclusion is driven by trait-similarity, and that interspecific competition leads to niche partitioning among coexisting species has been invoked in numerous studies on community assembly (Mittelbach & McGill, 2019). In contrast, the effects of traits in influencing species' competitive abilities, and the potential for assemblages to be structured along trait-based competition hierarchies, are less explored. The competition trait-hierarchy hypothesis was formally stated by Kunstler et al. (2012), building on previous studies which documented competition hierarchies among plant species (e.g., Ågren & Fagerström, 1984; Goldberg & Landa, 1991; Shipley & Keddy, 1994). Such hierarchies were determined by consistent differences in species' competitive abilities, which were predictable from differences in traits involved in resource capture (Goldberg & Landa, 1991). More generally, Modern Coexistence Theory Chesson (2000) attributes species coexistence to a balance between the demographic effects of stabilizing mechanisms such as niche partitioning and – crucially – equalizing mechanisms such as differences in competitive abilities.

Given preliminary evidence that trait-hierarchy might influence interspecific competition in ants (Chapters 4 and 5), it is important for empirical studies on community assembly to consider the potential for traits to impact species' competitive abilities (in addition to their niches) across a wider variety of taxa, and in other forms of interspecific interaction besides resource competition (the primary focus in most studies on plant assemblages). I illustrate these two points with the following thought experiment:

Consider an assemblage of fly species, where smaller body size confers a consistent advantage in evading capture by a generalist predator. If apparent competition were a strong driver of assembly, the assemblage could converge towards the clustering of small-sized species as populations of larger (weaker) competitors were excluded. However, this important role of apparent competition in assembly would be overlooked by investigators who assumed trait-similarity to be the only means of competitive exclusion (as this would predict an overdispersion in body size at the assemblage level). The investigators might have even concluded – erroneously – that the clustering in body size was due to the effects of environmental filtering. Yet, while generating the same functional signature as environmental filtering, the ecological mechanisms underlying competitive exclusion by trait hierarchy (or 'limiting dissimilarity') are distinct. For example, larger species could persist in the same environment if smaller ones were removed.

Incorporating Modern Coexistence Theory and trait hierarchy into a framework of community assembly can help advance understanding of the mechanisms structuring arthropod biodiversity. As examples from studies on plants, Kunstler et al. (2016) identified traits which consistently conferred competitive abilities to tree species across different global biomes, and D'Andrea et al. (2020) showed that competition hierarchies for light led to clustered trait structure among trees in a 50-ha plot of tropical forest. Might trait hierarchies in resource, interference, or apparent competition also explain the structure and diversity of natural assemblages of ants, beetles and spiders? Tests for significant clustering in the assemblage structure of individual traits conceivably related to competition (e.g., size, growth rate, aggression) may shed some light on the issue. Importantly, such investigations on trait-based competition must also address potential effects of environmental filtering as well as interactions between environment and competition on trait structure. For instance, it could be that niche partitioning requires a heterogenous environment, while competition hierarchies occur at stressful or resource-poor ends of the gradient (Sapsojevic & Suding, 2012; but see Wilson & Keddy, 1986).

It will remain difficult to draw convincing inferences about assembly processes (environmental filtering, niche partitioning, competition hierarchy, or an interaction of processes) from patterns in the trait structure of arthropod assemblages so long as the fitness-functionality of specific traits as well as trait syndromes and trade-offs are poorly understood. As an example, I attempted to circumvent the issue of trait functionality in Chapter 5 by incorporating physiological and behavioural traits (critical thermal maximum, trophic position, interference ability) for which inferences about function were more intuitive than for morphological traits. Nonetheless, the work did not account for the effects of trade-offs and correlations among different traits on competitive outcomes between ant species and on trait structure at the assemblage level *a priori*. In retrospect, such efforts could have strengthened inferences about the nature of competition between the ant species, as the findings did suggest that a trade-off between critical thermal maximum and interference ability had an important role to play (see discussion in Chapter 5). Elucidating trait syndromes and trade-offs will likely be important to understanding coexistence and competition among arthropod species. In plants, for instance, niche differences were found to be conferred by differences across multiple trait axes only, whereas competitive advantages were conferred by differences in individual traits (Kraft et al., 2015). The next major advances in understanding community assembly in arthropods and their trait-based ecology will likely be driven by studies determining the fitness-functionality of traits, and others characterizing the trait syndromes and trade-offs within and among species. Experiments to address the former were discussed in Chapter 2; the latter can be investigated using macroecological comparisons of many species in global trait space (see Wright et al., 2004; Díaz et al., 2016; Pigot et al., 2020).

Research investigating the effects of arthropods' traits on their niches, competitive abilities, and interactions in general will also advance understanding of biodiversity-ecosystem function relationships and invasion ecology. Key to explaining and predicting ecosystem functions is an understanding of how assembly processes such as interspecific competition structure the functional diversity of arthropod communities (e.g., in Chapter 5). To take a hypothetical example: an assemblage of grasshopper species where coexistence is stabilized by an excess of dissimilarity in dietary niches could see this high niche complementarity cause herbivory (the ecosystem function) to be distributed evenly across a wide variety of plant species; however, an assemblage comprising grasshopper species of similar dietary niche and equivalent competitive abilities in exploiting the same plants would see selection effects drive strong herbivory on a few plant species only. Another interesting area for additional research is the effect of intraspecific trait variability on ecosystem functions. Intraspecific trait variability can be substantial in arthropod species; Chapters 3 and 6 illustrated this with examples of polymorphisms in ant workers (which may influence ecosystem functions such as scavenging and decomposition), however many other factors – for instance variability in the behaviours of predators (Start & Gilbert, 2017) – and their effects on ecosystem functions are relatively unexplored.

Many trait differences between invasive and non-invasive plant species actually promote stronger competitive abilities as opposed to niche opportunities (Van Kleunen et al., 2010; Ferenc & Sheppard, 2020). It is conceivable that some, if not many, trait differences between invasive and native arthropod species promote competitive advantages as opposed to niche differences (e.g., aggression, rapid growth rates, novel chemical and morphological defences against predators). Applying a framework of modern coexistence theory, MacDougall et al. (2009) powerfully unified disparate 'classical' invasion hypotheses (empty niche, enemy escape, novel weapons etc.), showing that these could all be explained in terms of niche and competitive differences between invasive and native species. Future studies adopting this framework may advance understanding on the causes and consequences of arthropod species invasions. For instance, field and experimental studies can be used to quantify the trait differences between invasive and native arthropod species, and link these to their demographic performance (e.g., growth and survival rates) – or otherwise their abundances (as in Chapter 5) or co-occurrence patterns (as in Chapter 4) – so as to understand how differences in individual traits as well as multidimensional trait space influence niche and competitive differences between invasive and native species. Meta-analyses surveying the trait differences between invasive and non-invasive arthropod species, and the effects of these traits on interspecific interactions, will clarify whether different groups of traits in general (e.g., those affecting growth rates, physiological tolerances, resource exploitation or dispersal) are more likely to promote niche opportunities or competitive advantages during competition; these analyses will also help to narrow down the traits selected for investigation in the empirical studies.

Concluding remarks

This thesis contributes to the study and understanding of the community ecology of terrestrial arthropods from a trait-based perspective. It provides new empirical insights into the ecological causes and functional consequences of interspecific competition within the context of invasions by non-native species, across ecological scales spanning species, assemblages, and landscapes. Future studies can build on the findings by investigating the fitness-functionality of arthropod traits, clarifying their contributions to niche and competitive differences between species, and exploring the consequences for interspecific interactions and various community assembly processes. Such efforts will help attain a general, predictive and mechanistic understanding of the form, function and fate of arthropod biodiversity at a time when this is needed most.

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APPENDICES

APPENDIX A. SUPPLEMENTARY MATERIAL FOR CHAPTER 3

Table S1. List of the 29 ant species collected in the study, their presences across uninvaded and invaded plots, and the number of individuals used for trait measurements.

Code	**Genus**	**Species**	**Uninvaded plots (n=37)**	**Invaded plots (n=24)**	**Individuals measured (n=319)**
agra	*Anochetus*	*graeffei*	10	3	10
bobs	*Brachyponera*	*obscurans*	19	4	10
cnic	*Camponotus*	*nicobarensis*	10	5	11
cpar	*Camponotus*	*parius*	6	0	11
cvar	*Camponotus*	*variegatus*	10	12	13
cvit	*Camponotus*	*vitiosus*	6	1	10
cobs	*Cardiocondyla*	*obscurior*	5	19	12
csp1	*Cardiocondyla*	*sp. 1*	2	6	10
csp2	*Cardiocondyla*	*sp. 2*	2	4	10
care	*Carebara*	*sp. 1*	7	2	10
cfer	*Crematogaster*	*ferrarii*	3	4	11
dsib	*Dolichoderus*	*sibiricus*	4	2	10
esha	*Euponera*	*sharpi*	8	2	10
mchi	*Monomorium*	*chinense*	30	10	10
mflo	*Monomorium*	*floricola*	7	4	10
mpsw	*Monomorium*	*sp. psw-cn01*	11	7	10
ntay	*Nylanderia*	*sp. cf. taylori*	26	21	15
plon	*Paratrechina*	*longicornis*	27	8	10
pfer	*Pheidole*	*fervens*	11	4	11
pnod	*Pheidole*	*nodus*	2	2	10
ppar	*Pheidole*	*parva*	25	8	11
pdiv	*Polyrhachis*	*dives*	11	2	10
sinv	*Solenopsis*	*invicta*	0	24	20
sjac	*Solenopsis*	*jacoti*	8	2	10
semm	*Strumigenys*	*emmae*	5	1	10
ssp1	*Syllophopsis*	*sp. 1*	2	4	10
tmel	*Tapinoma*	*melanocephalum*	24	16	14
tbic	*Tetramorium*	*bicarinatum*	16	5	10
tlan	*Tetramorium*	*lanuginosum*	36	5	10

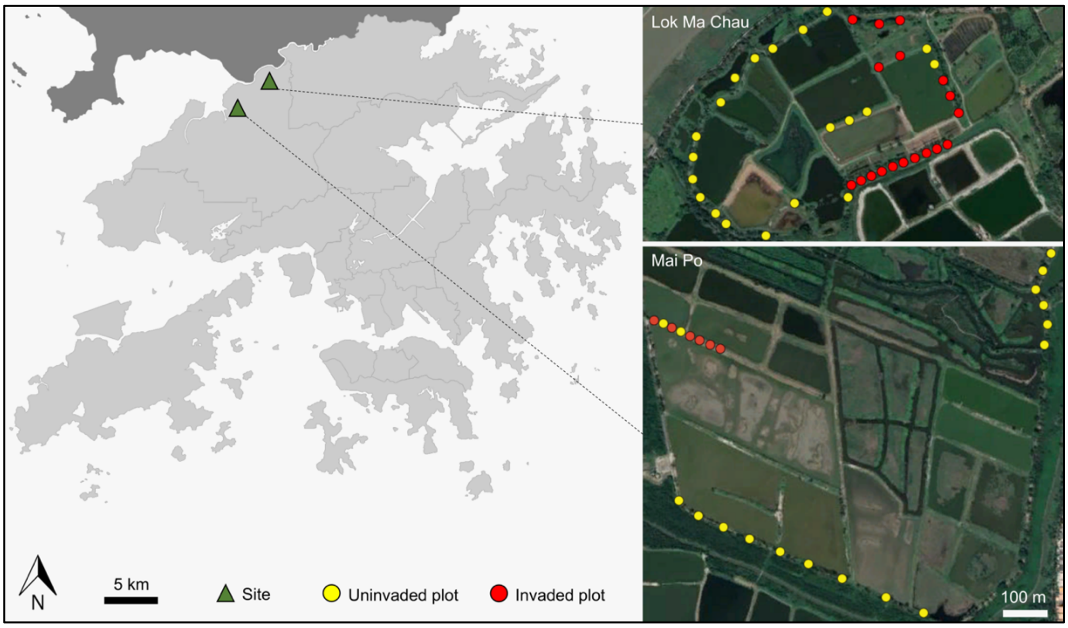

Figure S1. Map of Hong Kong showing the two sites and 61 plots used in the study, which were identified (as either invaded or uninvaded) from 2015–2017 and sampled in 2018. A minimum distance of 20 m between adjacent plots (which exceeded the maximum foraging distances of ant species in the region) facilitated independent observations (see main text).

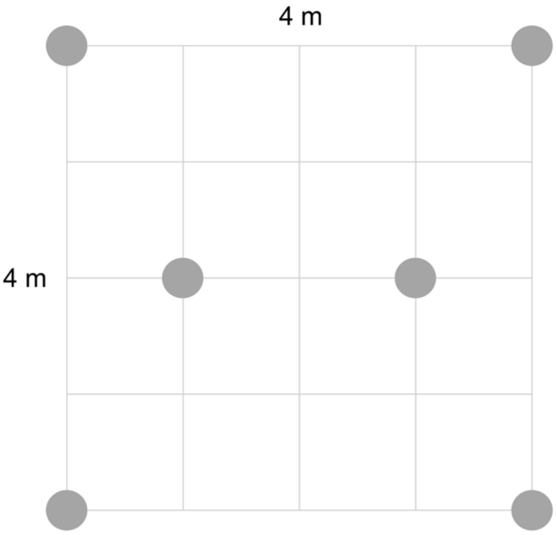

Figure S2. Plot design with grey circles showing the positions of the six pitfall traps.

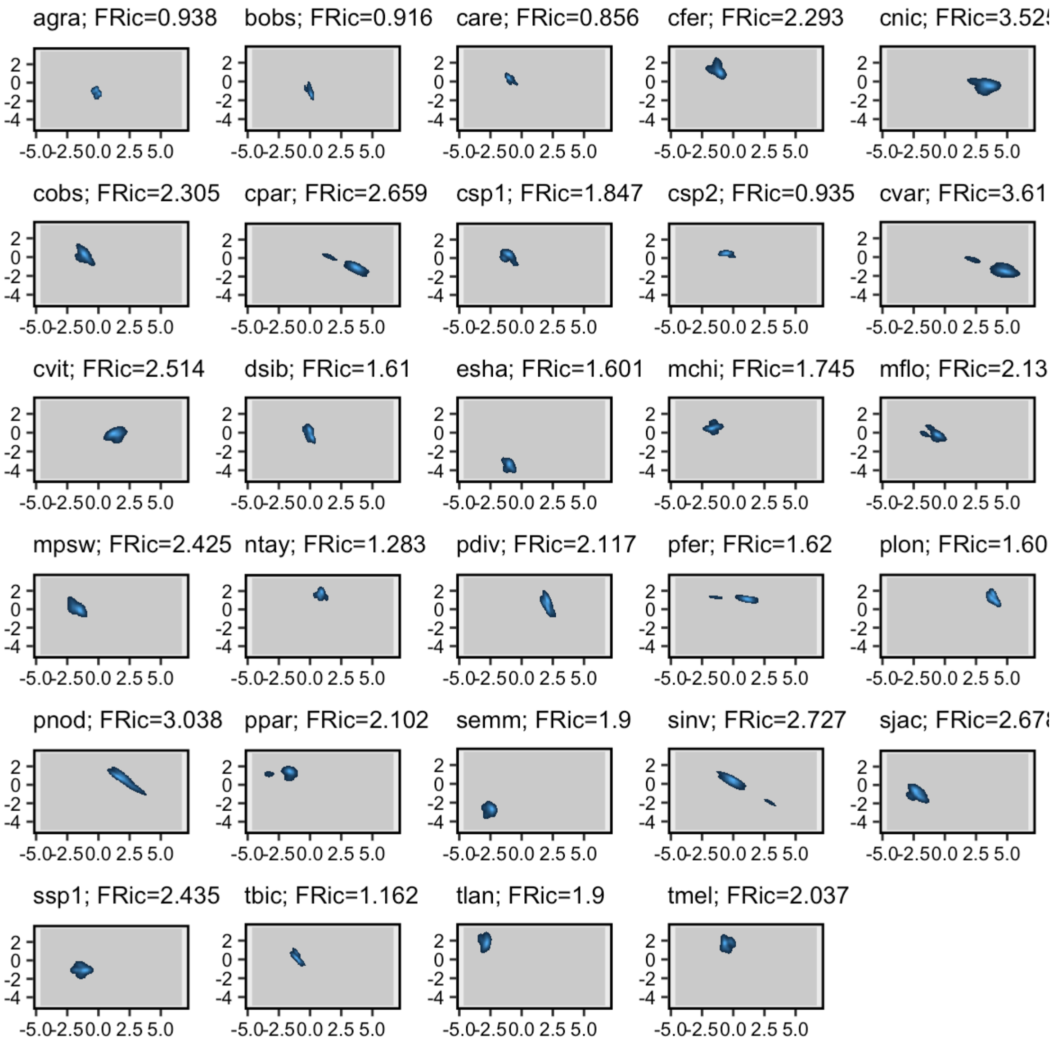

Figure S3. Trait spaces of 29 ant species built from trait probability density functions (see “Material and methods”). Each species’ functional diversity is captured in two-dimensional trait space, with the axes corresponding to the first two components of the PCA, and the relative abundances of various trait values reflected in brightness (i.e., brighter areas indicate higher densities of those trait values in the species sample). Corresponding values of Functional Richness (FRic) are shown next to the species codes, which are explained in Table S1.

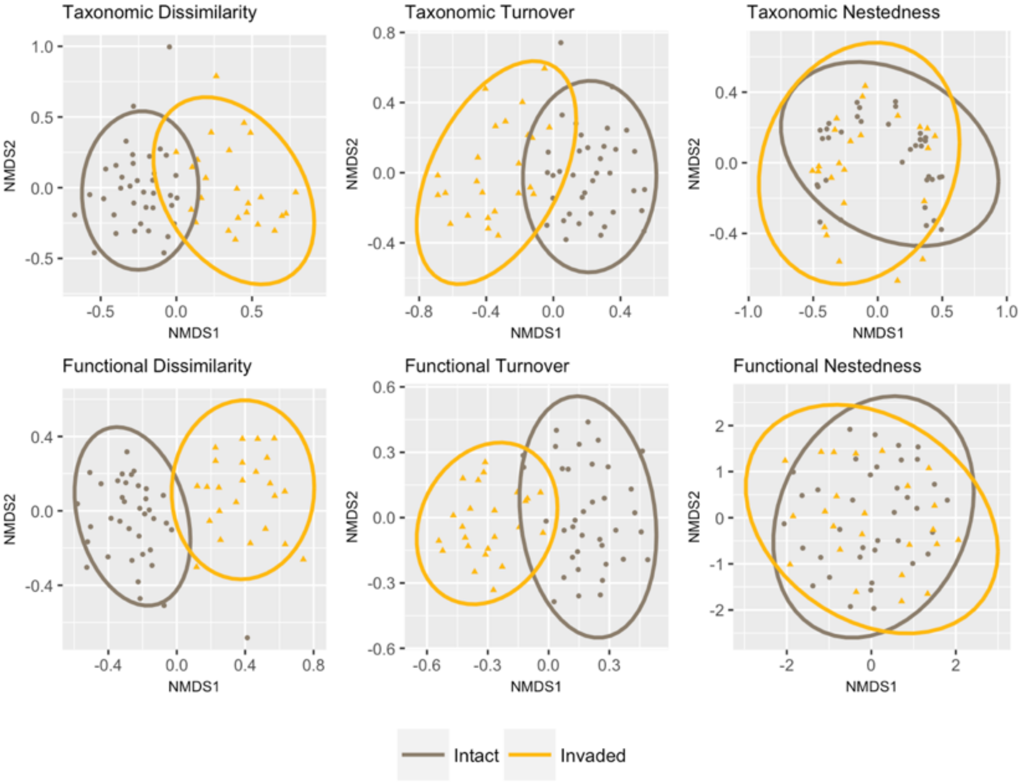

Figure S4. NMDS plots for observed levels of taxonomic and functional beta diversity in three measures of dissimilarity (Total, Turnover, and Nestedness).

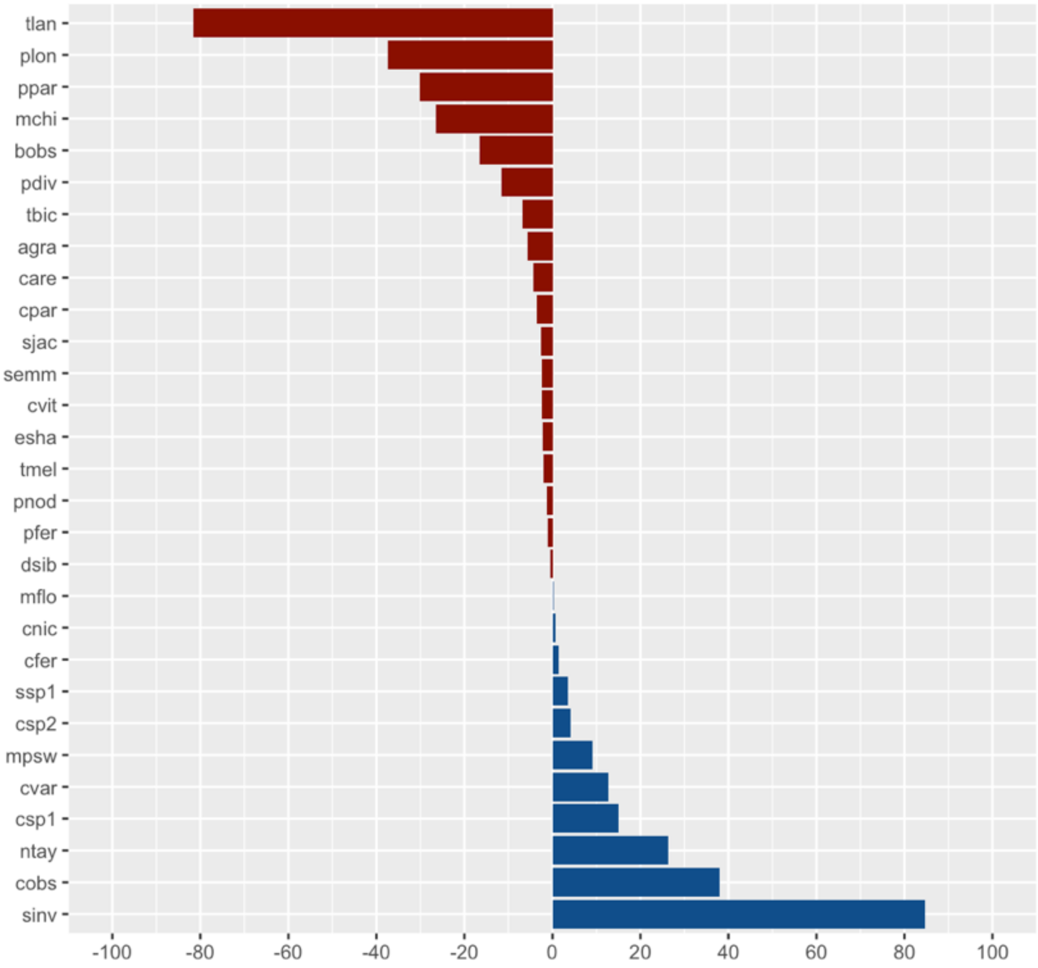

Figure S5. Losers and winners in invaded communities. For each species, bar shows the absolute change in its relative abundance (%) in traps between communities that were uninvaded (N=222) and those that were invaded (N=144). Two thirds of the native species declined in abundance in the invaded communities. NB: *Camponotus parius* (cpar) was absent from invaded communities, and the invader *Solenopsis invicta* (sinv) was absent from uninvaded communities.

Figure S6. Different degrees of polymorphism among various ant species in the study. Individual images show dimorphic species of (A) *Camponotus nicobarensis* (FRic = 3.52) and (B) *Pheidole nodus* (FRic = 3.03), as well as (C) a monomorphic species, *Monomorium chinense* (FRic = 1.75), and (D) the polymorphic invader *Solenopsis invicta* (FRic = 2.73).

APPENDIX B. SUPPLEMENTARY MATERIAL FOR CHAPTER 4

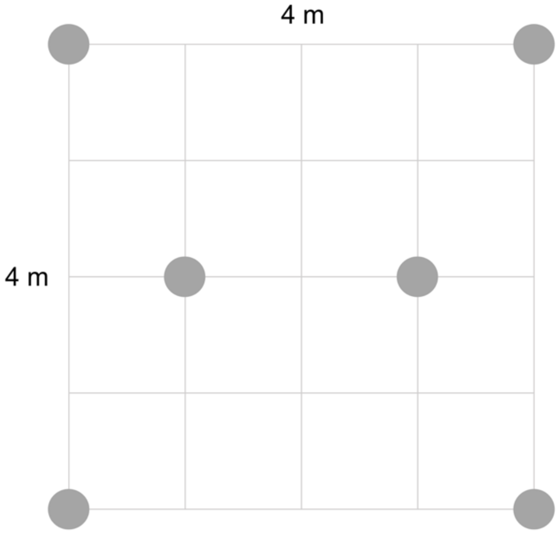

Figure S1. Plot design with grey circles showing the positions of the six pitfall traps.

Table S1. List of the 29 ant species collected in the study, their presences plots where *S. invicta* was absent (Uninvaded) or present (Invaded), and the number of individuals used for trait measurements.

Code	**Genus**	**Species**	**Uninvaded plots (n=37)**	**Invaded plots (n=24)**	**Individuals measured (n=319)**
agra	*Anochetus*	*graeffei*	10	3	10
bobs	*Brachyponera*	*obscurans*	19	4	10
cnic	*Camponotus*	*nicobarensis*	10	5	11
cpar	*Camponotus*	*parius*	6	0	11
cvar	*Camponotus*	*variegatus*	10	12	13
cvit	*Camponotus*	*vitiosus*	6	1	10
cobs	*Cardiocondyla*	*obscurior*	5	19	12
csp1	*Cardiocondyla*	*sp. 1*	2	6	10
csp2	*Cardiocondyla*	*sp. 2*	2	4	10
care	*Carebara*	*sp. 1*	7	2	10
cfer	*Crematogaster*	*ferrarii*	3	4	11
dsib	*Dolichoderus*	*sibiricus*	4	2	10
esha	*Euponera*	*sharpi*	8	2	10
mchi	*Monomorium*	*chinense*	30	10	10
mflo	*Monomorium*	*floricola*	7	4	10

mpsw	*Monomorium*	*sp. psw-cn01*	11	7	10
ntay	*Nylanderia*	*sp. cf. taylori*	26	21	15
plon	*Paratrechina*	*longicornis*	27	8	10
pfer	*Pheidole*	*fervens*	11	4	11
pnod	*Pheidole*	*nodus*	2	2	10
ppar	*Pheidole*	*parva*	25	8	11
pdiv	*Polyrhachis*	*dives*	11	2	10
sinv	*Solenopsis*	*invicta*	0	24	20
sjac	*Solenopsis*	*jacoti*	8	2	10
semm	*Strumigenys*	*emmae*	5	1	10
ssp1	*Syllophopsis*	*sp. 1*	2	4	10
tmel	*Tapinoma*	*melanocephalum*	24	16	14
tbic	*Tetramorium*	*bicarinatum*	16	5	10
tlan	*Tetramorium*	*lanuginosum*	36	5	10

Assessing observed species co-occurrences against null models and calculating Standardized Effect Sizes (SES_{all} and SES_{sinv})

To assess the overall nature (positive/negative) of each of the 29 species' co-occurrences with other species within the network, as well as the specific nature of each of the 28 resident species' co-occurrences with *S. invicta*, we first quantified the weighted degree of each species – the sum of strengths (i.e., log-transformed odds ratios) of all co-occurrence relationships for a given species within the network. For each species, we only considered co-occurrence relationships which indicated how that species affected the odds ratios of other species being present in the same plots. For instance, the weighted degree of species A considered OR_{AB} but not OR_{BA}. Since observed patterns could be driven by random co-occurrences (Gotelli, 2000; Blanchet et al., 2020), we used null models to calculate Standardized Effect Sizes (SES), which compared any observed co-occurrence relationships between paired species to random expectation. Sampling plots were spatially distributed across two general localities – Lok Ma Chau and Mai Po (Wong et al., 2020) – and randomly shuffling species occurrences across the whole matrix could result in unrealistic null communities if the localities had different species pools. Thus, we randomly generated compositional data for each of the two localities, and then combined the two matrices to form one null matrix. To generate random matrices we used the fixed-fixed algorithm "quasiswap" from R-package *vegan*. The algorithm maintains the total occurrences of each species and the species richness of each sampling unit, is robust to Type-I errors, and is suitable for heterogenous compositional data (Gotelli, 2000). We generated 1,000 null matrices, and calculated odds ratios to build null networks. We calculated the Standardized Effect Size for weighted degree (SES_{WD}) (Gurevitch et al., 1992), defined as

$$SES_{WD} = \frac{Observed\ value - Mean_{null\ WD}}{Standard\ deviations_{null\ WD}}$$

SES_{WD} is reported as 'SES_{all}' in the main text, and describes the overall nature (positive/negative) of a given species' co-occurrence relationships with all other species in the network. We also obtained the SES for each of 28 resident species' pairwise co-occurrences with *S. invicta* (SES_{sinv}). Here we considered pairwise co-occurrences which indicated how the presence of species within plots were affected by the presence of *S. invicta*, but not *vice versa*. Co-occurrence relationships (SES_{all} and SES_{sinv}) were more positive or negative than expected by chance when greater or lesser than zero, respectively, and statistically significant when exceeding 1.96 (Gotelli & Arnett, 2000).

Table S2. For six morphological traits, table shows the results of linear and robust linear regressions for the effects of Absolute Dissimilarity (AD), Hierarchical Difference (HD), and their interaction on co-occurrence between *S. invicta* and 28 resident ant species. Significant effects (Bonferroni-corrected $p<0.05$) are in **bold**.

	Linear regression	Robust linear regression

	Estimate	p-value	Estimate	p-value
Body size				
Intercept	-0.90	0.36	-0.84	0.36
HD	-0.13	1	-0.29	1
AD	0.57	1	0.40	1
HD*AD	-0.18	1	0.07	1
	$R^2 = 0.10$		$R^2 = 0.08$	
Pronotum width (size-corrected)				
Intercept	-0.32	1	-0.45	0.96
HD	1.08	0.36	0.83	0.42
AD	-0.47	1	-0.28	1
HD*AD	**-1.47**	**0.01**	**-1.35**	**<0.001**
	$R^2 = 0.37$		$R^2 = 0.38$	
Head width (size-corrected)				
Intercept	-0.47	1	-0.56	1
HD	-1.77	0.18	**-1.60**	**0.04**
AD	-1.28	0.12	**-1.14**	**0.04**
HD*AD	1.56	0.42	1.46	0.42
	$R^2 = 0.23$		$R^2 = 0.21$	
Leg length (size-corrected)				
Intercept	-0.80	0.42	-0.88	0.10
HD	-0.05	1	-0.13	1
AD	0.03	1	-0.08	1
HD*AD	-0.44	1	-0.17	1
	$R^2 = 0.03$		$R^2 = 0.02$	
Eye width (size-corrected)				
Intercept	-1.10	0.12	-1.17	0.12
HD	1.32	1	1.24	0.18
AD	0.04	1	-0.003	1
HD*AD	-1.52	1	-1.45	0.42
	$R^2 = 0.08$		$R^2 = 0.09$	
Scape length (size-corrected)				
Intercept	-0.97	0.28	**-0.99**	**0.02**
HD	-0.70	1	-0.75	0.53
AD	-0.17	1	-0.07	0.88
HD*AD	0.63	1	0.65	0.63
	$R^2 = 0.04$		$R^2 = 0.04$	

Table S3. Results of separate linear and robust linear regressions for the effects of phylogenetic dissimilarity and three measures of dissimilarity in environmental preferences (ground cover, NDVI, and temperature) on co-occurrence between *S. invicta* and 28 resident ant species. For models of phylogenetic dissimilarity, the ranges of all estimated values are reported because 100 phylogenetic trees were used. We did not use adjust p-values here so as to avoid missing important phylogenetic or environmental variables in subsequent trait analyses.

	Linear regression		Robust linear regression	
	Estimate	p-value	Estimate	p-value
Phylogenetic Dissimilarity				
Intercept	-0.15 – 0.47	0.76 – 1	-0.28 – 0.33	0.75 – 0.99
Slope	-0.003 – -0.007	0.38 – 0.56	-0.003 – -0.006	0.24 – 0.43
	R^2 = 0.01 – 0.03		R^2 = 0.01 – 0.03	
Ground cover				
Intercept	-0.90	0.23	-1.05	0.07
Slope	0.005	0.94	0.01	0.75
	R^2 = 0.002		R^2 = 0.002	
NDVI				
Intercept	-0.09	0.90	-0.28	0.65
Slope	-18.84	0.21	-14.89	0.14
	R^2 = 0.06		R^2 = 0.05	
Temperature				
Intercept	-0.95	0.18	-1.31	0.10
Slope	3.78	0.87	14.00	0.51
	R^2 = 0.001		R^2 = 0.02	

Checking for consistency of effects when using varying densities of *S. invicta* to characterise their occurrences across plots

For any trait models (in Table S2) which detected significant effects, we checked whether the results were invariable to the use of different density-thresholds to reclassify *S. invicta*'s occurrences across the plots. We first built four different matrices of ant species' occurrences (i.e., presence/absence data) across all 61 plots. The first matrix ('None') had no density threshold and indicted *S. invicta* as present at a plot when one or more workers were captured in any of the six pitfall traps; the other three matrices indicated this only if the density of captured workers met thresholds reflecting the 25th (‘Low’), 50th (‘Intermediate’) or 75th (‘High’) percentile for densities of *S. invicta* across all plots, which corresponded to densities of 10, 26, or 53 *S. invicta* workers per pitfall trap. We then compared results from the regression models using no threshold of *S. invicta*-presence (None) to results from models using the three different density thresholds (Low, Intermediate, High) (reported in Table S4 below).

Table S4. For three traits which showed significant effects on co-occurrence between *S. invicta* and 28 resident ant species (from Table S2), this table summarises results from comparable linear regressions which used four different density-thresholds to detect the presence of *S. invicta* at plots. Environmental and phylogenetic variables were not added to all models as their effects were not significant. All models were based on standardized predictors. Significant effects (p<0.05) are in **bold**. Note that here all p-values were uncorrected, as for low, intermediate and high abundance thresholds only the model based on relative pronotum width was built. Models of other traits were not built, since their effects were insignificant in both linear regression and robust linear regression when no abundance threshold was applied (see Table S2).

	None		Low		Intermediate		High	
Pronotum width (size-corrected), linear regression								
	Estimate	p-value	Estimate	p-value	Estimate	p-value	Estimate	p-value
HD	1.08	0.06	**1.34**	**0.04**	**1.46**	**0.047**	0.73	0.17
AD	-0.47	0.21	-0.68	0.10	-0.61	0.16	-0.63	0.06
HD*AD	**-1.47**	**0.002**	**-1.94**	**<0.001**	**-1.77**	**0.004**	**-1.07**	**0.01**
	R^2=0.37		R^2=0.46		R^2=0.36		R^2=0.37	
Pronotum width (size-corrected), robust linear regression								
	Estimate	p-value	Estimate	p-value	Estimate	p-value	Estimate	p-value

HD	0.83	0.07	1.25	0.13	1.26	0.09	0.70	0.18
AD	-0.28	0.42	-0.62	0.07	-0.40	0.15	-0.57	0.08
HD*AD	**-1.35**	**<0.001**	**-1.87**	**0.003**	**-1.60**	**0.002**	**-1.02**	**0.01**
	$R^2 = 0.38$		$R^2 = 0.45$		$R^2=0.37$		$R^2=0.34$	

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APPENDIX C. SUPPLEMENTARY MATERIAL FOR CHAPTER 5

Table S1. The seven traits measured on each individual, and each trait's hypothesized links to the performance and fitness of ants.

Trait	**Measurement**	**Hypothesized link to performance and fitness**
size	Weber's length: diagonal length of mesosoma	Modulates vital and physiological rates, determines physical constraints and exposure to predators, influences resource type and acquisition efficiency (Silva and Brandão, 2010).
head width	Width of head including eyes	Determines the size of gaps through which an individual can pass (Schofield, Bishop and Parr, 2016) and the volume of muscles powering the mandibles during foraging (Richter et al., 2019).
eye width	Width of left eye	Determines ability in navigation, foraging, predator and prey detection, and indicative of activity times (Silva and Brandão, 2010).
mandible length	Length of left mandible	Responds to selection on diet type and specialization (Silva and Brandão, 2010).
scape length	Length of scape of left antenna	Responds to selection on navigation and sensory abilities (Silva and Brandão, 2010).
pronotum width	Width of pronotum	Determines volume of muscles for head-support and load-bearing (Keller et al., 2014).
leg length	Combined length of femur and tibia of left hind leg	Determines mobility; leg length influences running speed, which affects success in foraging or escape from predators (Silva and Brandão, 2010).

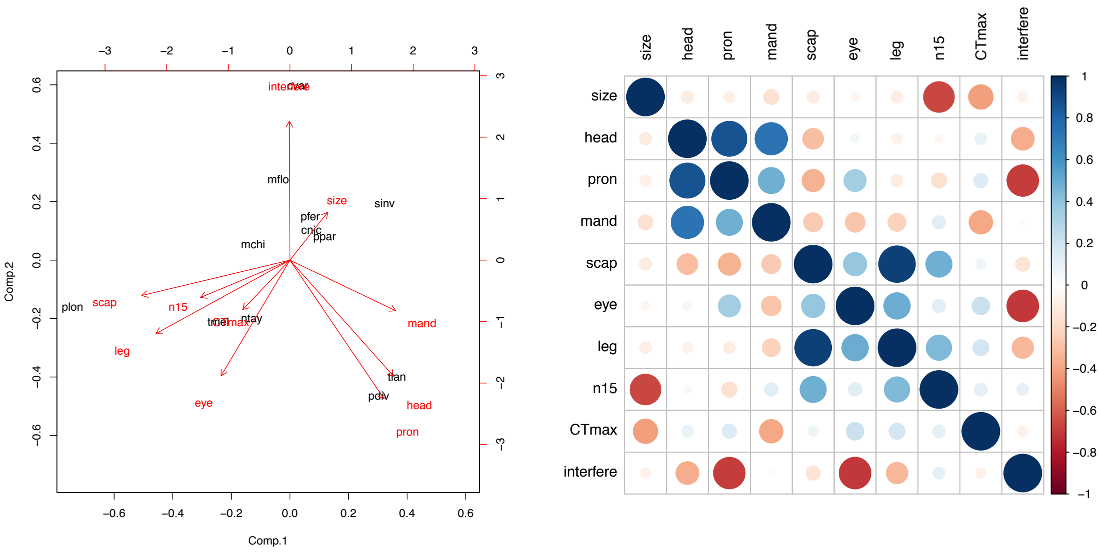

Figure S1. Biplot of first two principal components (left) and plot of trait correlations (right) for ant species' mean values in seven morphological traits (body size, and size-corrected head width, pronotum width, mandible length, scape length, eye length and leg length), two physiological traits (trophic position, proxied by stable isotope ratio of N15; and the Critical Thermal Maximum, CT_{max}), and one behavioural trait (interference ability).

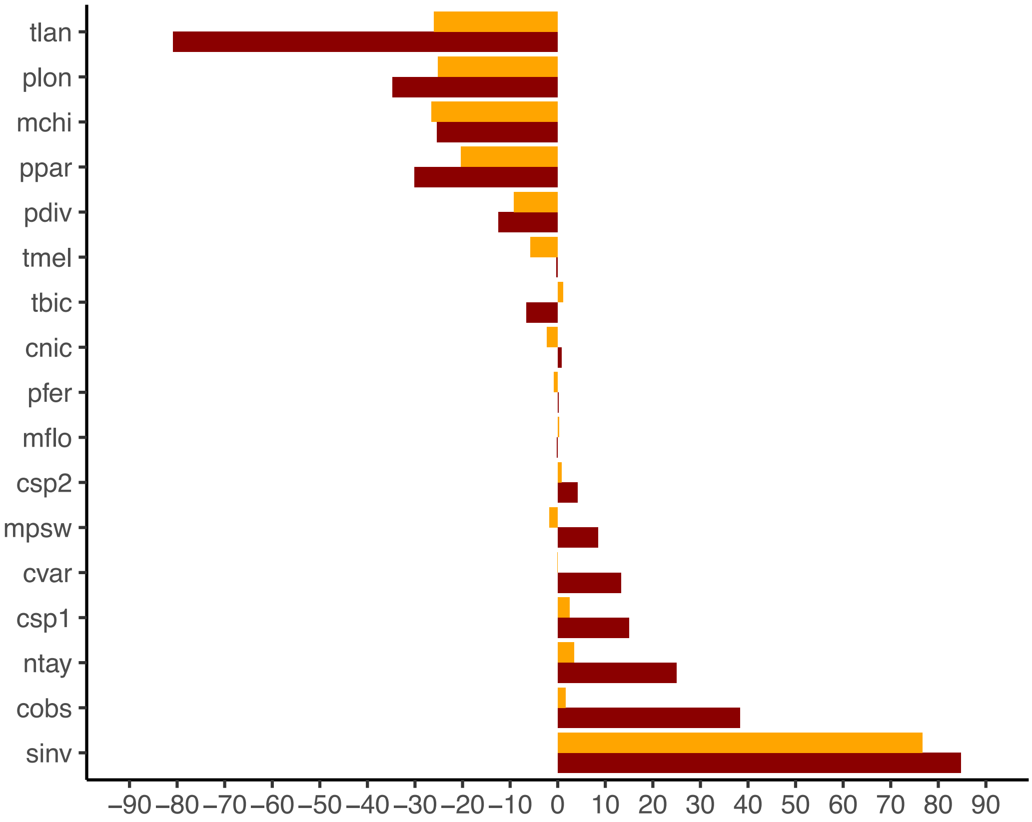

Figure S2. Changes in the total abundance (% pitfall traps; red) and recruitment (% baits; orange) of 17 ant species across plots where the invasive *Solenopsis invicta* (‘sinv’) was absent to plots where it was present. In general, species with bars extending leftwards (e.g., *Tetramorium lanuginosum*, ‘tlan’) were ‘losers’ of the invasion, while those with bars extending rightwards (e.g., *Cardiocondyla obscurior*, ‘cobs’) were ‘winners’ of the invasion.

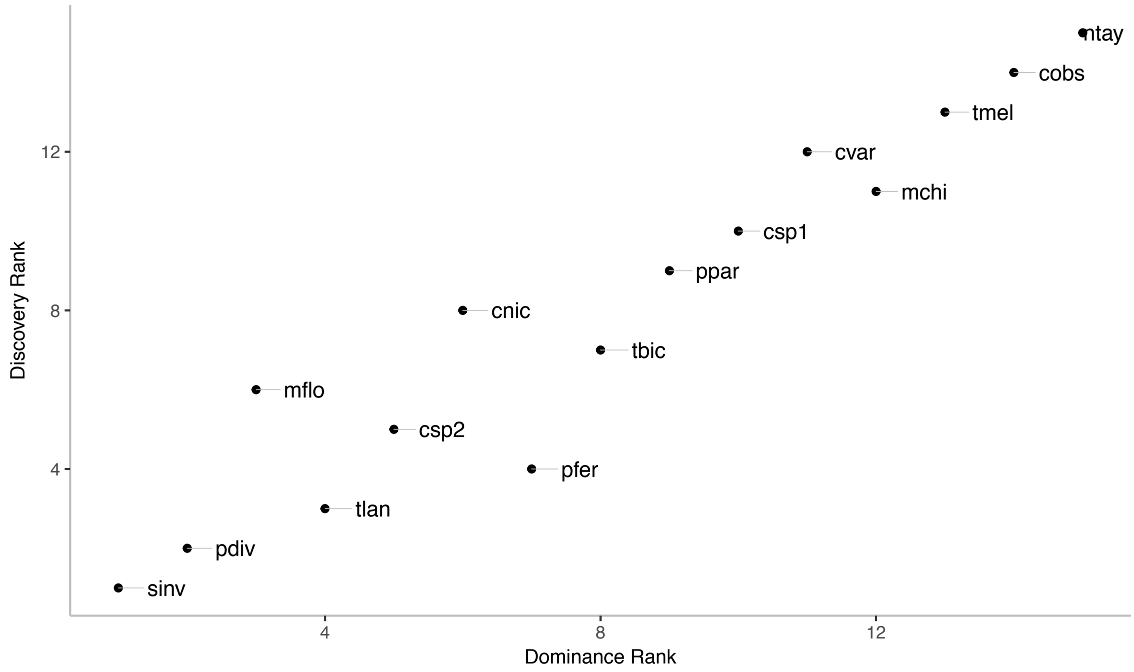

Figure S3. Ant species' abundance-corrected rankings for discovery ability (determined by the proportion of total baits where a given species was first to recruit) and ecological dominance ability (determined by the proportion of total baits monopolized by a given species, after Stuble et al., 2017). Ability rankings have been corrected for species' relative abundances across plots (after LeBrun & Feener, 2007). Lower ranks indicate stronger ability. The invasive species *Solenopsis invicta* displayed both the strongest discovery and ecological dominance abilities across invaded plots.

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APPEDNIX D. SUPPLEMENTARY MATERIAL FOR CHAPTER 6

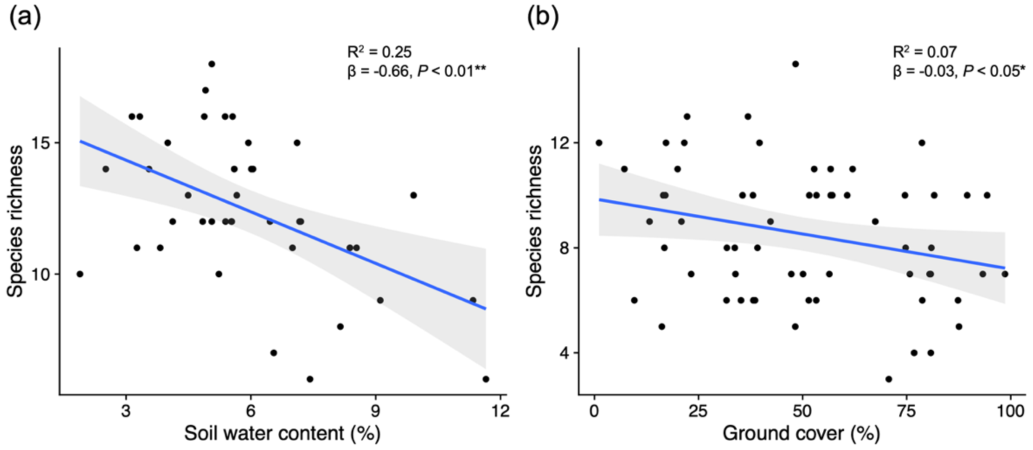

Figure S1. Linear regressions for the species richness of the 40 plant communities along the gradient of percentage water content (a) and for the species richness of the 61 ant communities along the gradient of percentage ground cover (b).

Table S1. The seven traits measured on each individual, and each trait's hypothesized links to the performance and fitness of ants.

Trait	**Measurement**	**Hypothesized link to performance and fitness**
size	Weber's length: diagonal length of mesosoma	Modulates vital and physiological rates, determines physical constraints and exposure to predators, influences resource type and acquisition efficiency (Silva and Brandão, 2010).
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eye width	Width of left eye	Determines ability in navigation, foraging, predator and prey detection, and indicative of activity times (Silva and Brandão, 2010).
mandible length	Length of left mandible	Responds to selection on diet type and specialization (Silva and Brandão, 2010).
scape length	Length of scape of left antenna	Responds to selection on navigation and sensory abilities (Silva and Brandão, 2010).
pronotum width	Width of pronotum	Determines volume of muscles for head-support and load-bearing (Keller et al., 2014).
leg length	Combined length of femur and tibia of left hind leg	Determines mobility; leg length influences running speed, which affects success in foraging or escape from predators (Silva and Brandão, 2010).

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