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Opinion

On functional groups and forest dynamics

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Functional trait variation measured on continuous scales has helped ecologists to unravel important ecological processes. However, forest ecologists have recently moved back toward using functional groups. There are pragmatic and biological rationales for focusing on functional groups. Both of these approaches have inherent limitations including binning clearly continuous distributions, poor trait-group matching, and narrow conceptual frameworks for why groups exist and how they evolved. We believe the pragmatic use of functional groups due to data deficiencies will eventually erode. Conversely, we argue that existing conceptual frameworks for why a limited number of tree functional groups may exist is a useful, but flawed, starting point for modeling forests that can be improved through the consideration of unmeasured axes of functional variation.

Highlights

The binning of species into categorical and artificial functional groups has often been used in ecology to overcome data deficiencies with the expectation that these deficiencies and, therefore, groups will fade.

Other influential work has argued that functional groups naturally arise in tree communities due to a diffuse competitive environment and a largely uniform abiotic environment leading to functional convergence.

The pragmatic usage and biological arguments for functional groups have clear limitations that may make them dubious.

The development of public functional trait repositories and future trait collection campaigns in undersampled regions will reduce some reliance on functional groups, but the conceptual framework underlying functional groups related to shade tolerance could be modified to include additional complexity relating to pest and pathogen interactions to result in more realistic and defendable insights into the generation and maintenance of tree biodiversity.

A brief overview of functional groups, traits, and forest dynamics

Forest dynamics have played a central role in debates surrounding the relative importance of stochastic and deterministic processes. This literature provides clear evidence of functionally nonrandom tree community dynamics [1,2], the ubiquity of conspecific negative density dependence [3], and evidence for a handful of fundamental life-history trade-offs [4–6]. In sum, determinism and continuous phenotypic variation are key for understanding forest dynamics. It may, therefore, be surprising that there is a renewed interest in cataloging the composition of forests into groups of functionally similar species. For example, recent influential work has distilled continuous demographic variation from hundreds of trees species around the world into a handful of groups [4,5]. Additional work has reduced the dimensionality of **functional trait** (see Glossary) data sets to investigate the importance of priority effects [7], intra-group neutrality [8], or 'clusters' of species in trait space [9,10]. A focus on categorizing species into groups would appear to be a step away from an embrace of continuous functional variation [11,12] and back toward the use of **functional groups**. Functional groups have been traditionally used for pragmatic purposes (e.g., when constructing dynamic global vegetation models [13]) or as biologically relevant emergent properties of selective environments (e.g., Hubbell and Foster's [14] **guild**-based version of neutrality). Whether recent attempts to categorize tree species into functional groups is for pragmatic or biological reasons or a hybrid of these two is not always clear, thereby limiting progress toward our understanding and modeling of forest dynamics. The goals of this article are to discuss the transition in forest ecology from functional groups to functional traits and back to groups, to consider the fundamental limitations of functional groups in forest ecology, and to provide an opinion on where functional groups may be useful in the future of forest ecology.

From groups to traits and back again

Continuous phenotypic variation within and between species should be key for understanding forest dynamics [1,2,6,11,15]. Due to their widespread use and standardized measurement protocols across species and forest types, functional traits have provided a continuous common currency that holds the potential to lead to significant advances in forest ecology. Despite the potential importance of this continuous variation, global syntheses of functional trait data have

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uncovered a few essential global trait syndromes (e.g., [12]) while additional research focusing on community structure and dynamics has proposed the utility of clustering of plant species into a handful of functional groups. The use of a functional group framework in forest ecology has gained renewed interest as quantitative methods are allowing ecologists to capture and model relevant forest processes [16]. These functional groups have provided some insights into tree communities in tropical forests [6,8] and represent an interesting reversal from a push toward incorporating continuous functional variation into forest ecology.

The foundations of functional groups can be linked to the concept of a guilds [17]. Early work on guilds was typically focused on animal assemblages where species were grouped according to their resource use [18–21]. The use of guilds in plant ecology, generally, and forest ecology, specifically, has been limited due to the difficulty in quantifying resources use and resource partitioning in these assemblages [22]. Thus, classical approaches for assigning plant species to functional groups have been based upon phenological differences (e.g., deciduous vs. evergreen) or rough approximations of shade tolerance [14]. Perhaps one of the best-known examples of this in the study of forest dynamics is the functional guild- or group-based neutral model proposed by Hubbell and Foster [14]. In this original work and subsequent work by Hubbell [23,24], Hubbell has argued that the high dissimilarity in heterospecific neighborhoods from one conspecific individual to the next leads to a diffuse biotic selection landscape, which combined with spatially common shaded and spatially rare high-light habitats has resulted in convergence into a few shade-tolerance guilds and the co-occurrence of many functionally equivalent species (Box 1). Thus, the aforementioned work on zoological guilds and in Hubbell and Foster's guild-base neutral model has both implied or argued that these categories are meaningful biological phenomena and not just an analytical convenience.

The lumping tree species into functional guilds or groups has also been extensively used in models of forest vegetation where the thousands of tree species found in a region such as the Amazon are categorized into just a few groups [13,25]. This approach is largely a pragmatic one as quantifying and modeling the inter- and intraspecific functional variation within map grid cells was not feasible. An additional argument may be that the additional information gain provided by measuring and modeling inter- and intraspecific functional variation on fine spatial scale may be relatively minor. This perspective, though, seems unsupported by the plethora of work into trait-based tree community ecology and dynamic global vegetation models that have added additional complexity beyond a few core functional groups [1,2,26–30]. As a result, over the past two decades, there has been a major transition toward continuous traits and away from functional groups. Thus, it may be surprising that an end goal of many recent influential works has been to identify or elucidate functional groups or syndromes. Next, we discuss some of the original conceptual and empirical limitations surrounding the use of functional groups in studying vegetation dynamics.

The inherent challenges of tree functional groups – pragmatical and biological perspectives

Despite the interest of forest ecologists in categorizing plants into groups of similar species, it may be a dubious exercise with respect to both their pragmatic and biological purposes. From a pragmatic standpoint, binning species into functional groups is sensible with respect to constructing global vegetation models. However, an obvious downside of this approach is the, potentially large degree of, functional variation within these groups (Figure 1). Furthermore, the distinction between groups when assessed using continuous functional traits may be slight and binning may appear arbitrary in the light of functional trait data. A less obvious issue that may be as or more important is that these groups do not clearly align with commonly measured functional traits

Glossary

Allopatry: when populations are geographically/physically isolated.
Functional group: a group of species that perform a certain functional role and/or ecosystem function, regardless of their taxonomic relationships, in the community or ecosystem.
Functional traits: a morphological, physiological, or phenological feature which impact plant fitness indirectly via its effects on growth, reproduction, and survival.
Guild: a group of species using the same class or type of resources in a competitive context.
Hidden niche differences: differences in species that are unmodeled or unmeasured that ultimately allow species to coexist.
Limiting similarity: the coexistence of species is limited when species experience niche overlap which may lead to competitive exclusion. Two species cannot coexist when competing for the same limiting resource.

Box 1. Functional group version of the neutral theory

Under the Hubbell and Foster's functional group version of the neutral theory [14], groups of functionally similar species arise due a unimodal, but skewed, light habitat axis. In this model, deterministic processes act at the functional group level, but species within functional groups replace one another stochastically following neutral dynamics (Figure I). Recent simulation models implementing this model [8] demonstrate that it results in a usually large number of species lost from the community. We argue that conspecific negative density dependence, likely due to specialized pest and pathogen pressure, is known to be widespread in tree data sets and should be added to this basic model. The addition of this stabilizing mechanism where an individual has little-to-no chance of replacing a conspecific will lead to more realistic models of forest dynamics. Furthermore, such a model would conceptually align with divergence of species into shade-tolerance groups, but diversification of species within those groups as they undergo allopatry and divergent assemblages of pests, pathogens, and mutualists.

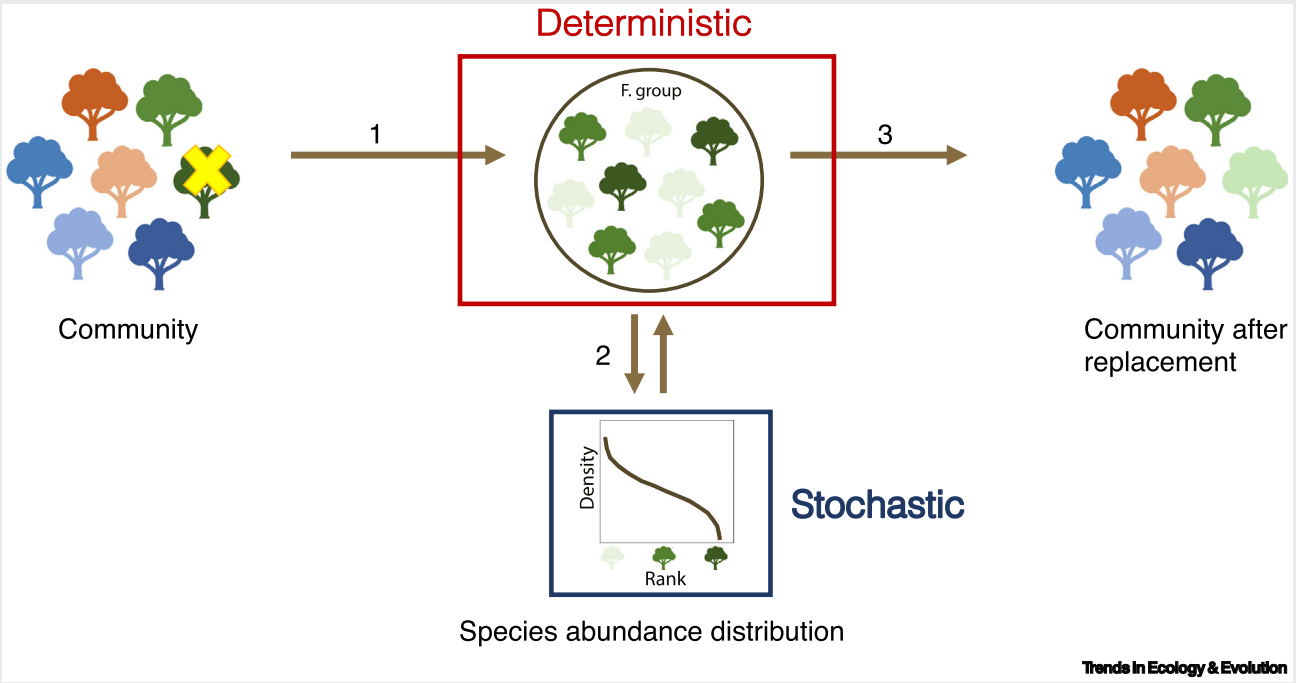

Figure I. Functional group version of the neutral theory. A cartoon depicting the functional group version of Hubbell's neutral theory. The different colors represent different functional groups and different hues within colors represent different species within functional groups. When one individual dies in the community (yellow cross on a tree), a new individual is selected (arrow 1), following a deterministic process, from the species that comprise a functional group (species circled in the F. group). The new individual is selected randomly from the within-group abundance distribution (arrow 2) resulting in a replacement in the community (arrow 3).

that describe fundamental trade-offs [31]. That is, clusters in trait space, if they even exist, may not align with classical functional groups. This has resulted in the argument that a transition to fully continuous trait-based models should be accelerated [13]. In sum, functional groups may be temporary pragmatic placeholders for real functional variation, but their apparent misalignment with commonly measured traits is concerning.

Hubbell's argument that unpredictable tree neighborhoods and selection for functions aligned with, by far, the most common environment (i.e., shade) will inevitably result in exceptional functional convergence is, in our opinion, compelling. Indeed, functional trait distributions in forest plots are often unimodal and skewed with the distribution maximum height often being an exception (i.e., multimodal) [1,2]. The mode of these distributions is, typically, aligned with shade tolerance with few species at the tail of the distribution aligning with shade intolerance. A similar situation can be found in most demographic data where there are many slow growth-low mortality species and few fast growth-high mortality species (e.g., [32]) and recent analyses have shown that this classic dichotomy can be further split by stature groupings [5,9,33,34] as would be

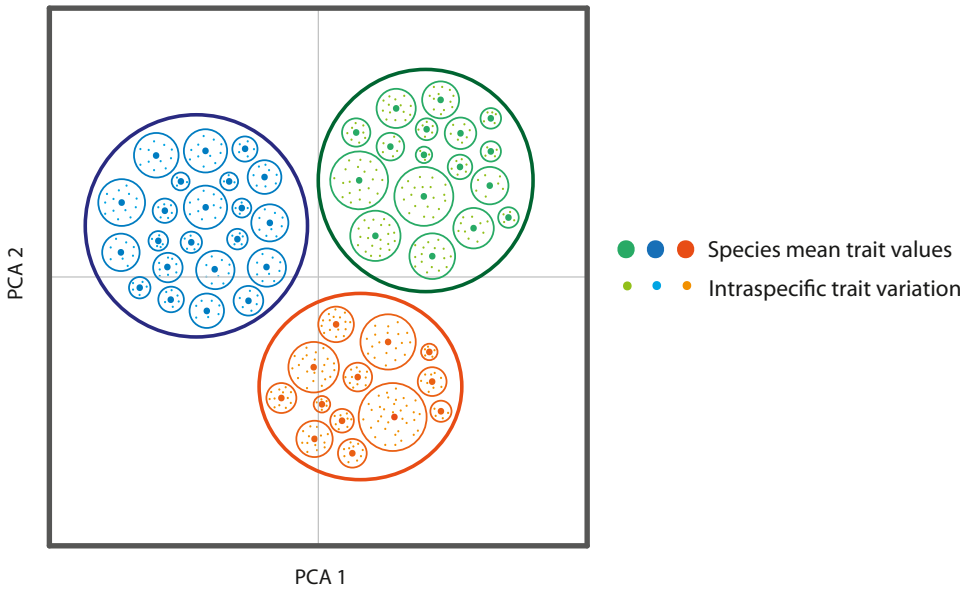

Figure 1. Clustering of functionally similar species in functional trait space. Functional groups (represented in blue, green, and orange) in functional trait space defined by two axes of a principal component analysis (PCA1 and PCA2). Circles within functional groups represent the functional space occupied by intraspecific trait differences, and the centered dot represents the species mean trait value. The integration of intraspecific trait variation into the delineation of functional groups might help to close the gap between continuous trait variation and discrete trait variation occurring when species are clustered in groups.

expected given the typical bi- or multimodal maximum height distributions in forest plots. Despite, this rough support for Hubbell's hypothesis, nearly all these distributions are clearly continuous with one group gradating into another. That is, when they are visualized using either trait or demographic data, the groups are clearly not all distinct. Thus, the evolutionary process has clearly not resulted in just two, four, or eight distinct functional groups in forests.

This raises a second, and more profound, biological issue with functional groups in forest ecology and evolution. A focus on trade-offs relating to shade tolerance generating a few functional groups, while interesting, limits our ability to understand the processes generating and maintaining biodiversity. For example, simulation models of forest dynamics using small numbers of functional groups, and neutrality within these groups, result in unrealistically large amounts of species lost [8] with additional stabilizing factors or spatial processes likely necessary to successfully model forest dynamics (e.g., [33]). Furthermore, the proliferation of species through time almost certainly cannot be explained by such a simple construct. That is, meaningful functional divergence in traits and differentiation of niche axes relating to stabilizing mechanisms (i.e., **hidden niche differences** [10,35,36]; Figure 2) and reproduction should be expected. With an exclusive focus on functional or demographic groups relating to light niche and stature differences, we are unlikely to arrive at meaningful answers to some of the major questions in ecology and evolution (i.e., what determines local coexistence and the generation of diversity?).

Functional groups and their place in modern forest ecology

In the previous section, we outlined clear limitations to the pragmatic and biological usage of functional groups in forest ecology. In the following, we argue that the use of pragmatic grouping of species for large-scale vegetation modeling will and must continue, but it will be gradually eroded

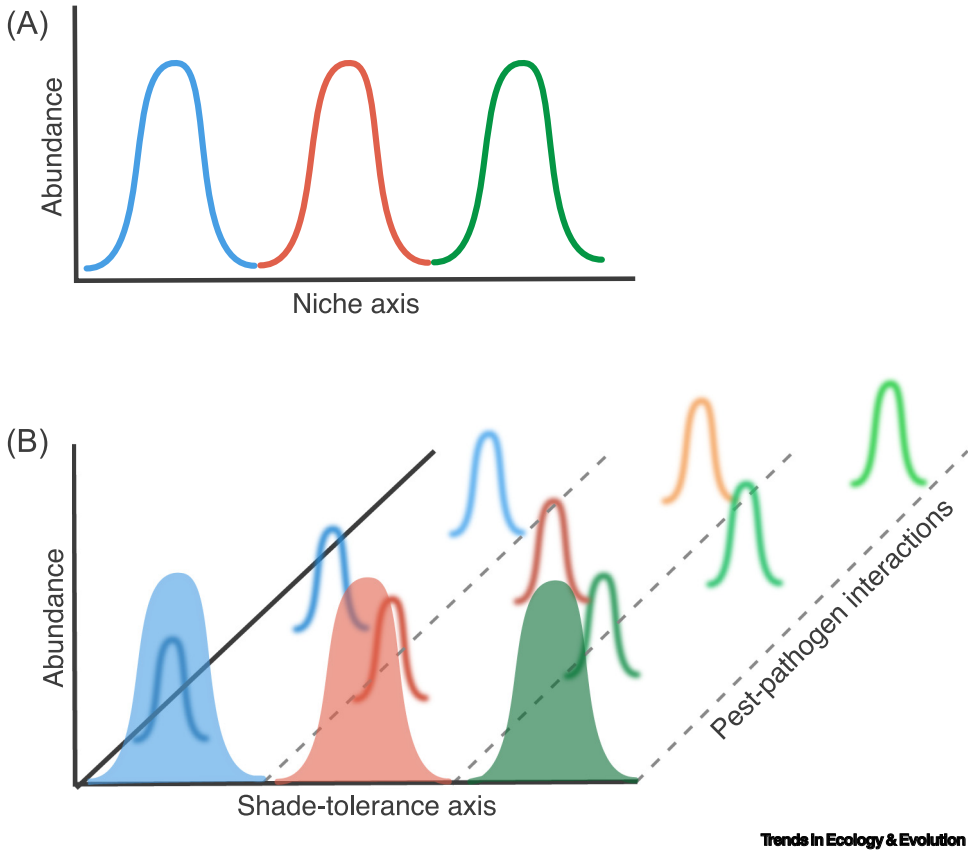

Figure 2. Species clustering in shade-tolerance groups, but differentiating along a pest–pathogen niche axis. (A) Species may be expected to move toward roughly discrete clusters in niche axis (represented in different colors) through evolutionary time. This results in sets of similar species that may co-occur on in assemblages; (B) an unmeasured pest–pathogen interaction dimension (i.e., hidden niche differences) among species within functional groups.

as more trait data are available. By contrast, we argue that there is merit in building off of the conceptual framework for functional groups or guilds introduced by Hubbell and Foster [14] by considering additional functional variation and processes that are not adequately considered in their original framework.

For decades, in the vegetation modeling literature, functional groups have provided a pragmatic approach for modeling forest dynamics and functioning on large spatial scales. Regional scale estimates of functional trait distributions will continue to be limited with respect to the sparseness of global trait matrices and the types of traits in those databases, usually biased toward common species. We see two clear pathways for future improvement beyond simply collecting much more continuous trait data. First, pathways for improving how we define and utilize functional groups are those that incorporate information regarding tree physiology that are, roughly, discrete. This would include the type of mycorrhizal association and N-fixation [37]. Likewise, functional traits that present global low intraspecific variation (i.e., organ-level traits) might be relevant to identify groupings or lumps of species with shared functional information, especially in species-rich communities [38]. Second, as functional trait data may not neatly align with commonly used functional groups [31], we may seek alternative approaches to imputing trait data for gap filling trait databases. For example, many traits exhibit enough phylogenetic signal such that phylogenetic imputation methods can be used [39,40]. However, we caution that some traits of interest

(e.g., leaf traits and height) often have little-to-no phylogenetic signal in woody plant databases leading to imputed trait values with large amounts of associated uncertainty [41].

Interspecific competition and **limiting similarity** have for long been considered the main mechanisms allowing several species to coexist and they, therefore, impact forest dynamics. However, there is clear evidence of convergence in tree species function and the overlap or clustering of species around near-optimal strategies along multiple trait axes [33,35,42–44]. Indeed, the strikingly unimodal and often skewed trait distributions in tree communities indicates the co-occurrence of many functionally similar species. The emergence and co-occurrence of sets of highly similar species has been proposed as an inherent property of competition-driven communities [33,35,36,42–45]. In such communities, important functional differences may be the most obvious at the group level while stochasticity may dominate within groups [7,8,14]. Hubbell has argued these groups are the necessary evolutionary result of the selective environment. Thus, these functional groups may represent broad adaptive zones containing similar species where competitive exclusion is prevented by minimal performance and niche differences [14,23,42,44]. Indeed, recent mathematical and empirical findings suggest that life-history complementarity, where pairs of species maximize their persistence time to avoid exclusion, boosts diversity at local scales [45]. To maximize their persistence time, species tend to cluster into groups that share similar life-history strategies with dominant equalizing mechanisms.

We argue that this framework is useful as a starting point, but not an end point, for both our conceptualization and modeling of the processes underlying forest biodiversity and dynamics. We begin with three key observations. First, simulations of forest dynamics using Hubbell's framework fail to maintain realistic levels of species richness suggesting the need for stabilizing mechanisms [8]. Second, conspecific negative density dependence in forest plot data is nearly ubiquitous. Third, there is substantial functional diversity, frequently relating to pest and pathogen interactions and reproduction, within groups delineated by commonly measured functional traits such that resource-use-related traits are often locally clustered while defense- and reproduction-related traits are typically overdispersed indicating their importance in stabilization (e.g., [46]).

Given these three observations, we propose that there may be an important intersection of the Janzen–Connell mechanism [47,48] and a functional group-based model of neutrality [14] driving forest structure and dynamics. That is, functional groups may naturally arise via broad adaptive zones related to light environments. Diversification of species within these adaptive zones is most likely to occur via **allopatry** where traits related to reproduction and defense diverge due to varying biotic selective environments between allopatric populations – a mechanism supported by the tremendous diversity in reproductive and defense traits in tree lineages that, typically, lacks phylogenetic signal [49,50]. Conversely, the available light habitats are unlikely to be variable between allopatric populations. In the context of forest dynamics, this will result in determinism at the functional group level and density dependence within species (i.e., often measured niche dimensions related to pest–pathogen interactions [46]; Figure 2). This will often reduce or prevent local self-replacement increasing the probability of coexistence of species within functional groups.

Thus, functional groups may be most evident and useful when considering abiotic gradients and key variation within those groups related to pest and pathogen interactions limiting population sizes. Future modeling efforts, therefore, may focus on building simulations of forest dynamics leveraging functional groupings relating to shade-tolerance levels that include varying levels of conspecific density dependence within groups. Surely, this will improve our understanding of how tree functional diversity has evolved, but, more importantly, how groups and variation within those groups can be used for modeling forest dynamics. This, however, will not shed light on the

functions underlying the modeled density dependence. Furthermore, these functions are rarely measured during inventories of tree community functional diversity and more focus should be placed on measuring these hidden dimensions. Specifically, transcriptomic and metabolomics inventories of defense-related genes and metabolites, respectively, would likely yield valuable insights into the ecological and evolutionary processes generating and maintaining the biodiversity in tree assemblages [51–53].

Concluding remarks

Plant ecology has a long history of utilizing functional groups largely for pragmatic, but occasionally for biological, reasons. The past two decades have seen an explosion of studies incorporating continuous functional trait data and a movement away from utilizing discrete characterizations of the functional diversity in assemblages. The pragmatic lumping of species into groups due to a lack of data is an issue that will be resolved as the availability of continuous trait information increases. Thus, the role of functional groups in dynamic global vegetation models may fade. However, we believe Hubbell and Foster's [14] biological argument for why functional groups or guilds of trees exist is an appealing and reasonable starting point from which we should build in complexity relating to conspecific negative density dependence driven by specialized pests and pathogen interactions. This modified framework and addressing key outstanding questions (see Outstanding questions) should help overcome important conceptual and empirical challenges to the original framework that should not only lead to more reliable models of forest dynamics but also a more understanding of the generation and maintenance of tree biodiversity.

Outstanding questions

How much functional diversity occurs within functional groups defined by shade tolerance, particularly with respect to traits related to pest and pathogen interactions?

How closely can temperate and tropical forest dynamics be modeled using functional group-level determinism, intragroup stochasticity, and conspecific negative density dependence?

Are quantitatively clustered functional groups biologically relevant and how sensitive are they to the method and amount of data used?

Given that multiple trait combinations can lead to similar demographic outcomes, are functional groups best defined by functional trait or demographic data and why?

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Declaration of interests

No interests are declared.

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