

The return of the variance: intraspecific variability in community ecology

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Despite being recognized as a promoter of diversity and a condition for local coexistence decades ago, the importance of intraspecific variance has been neglected over time in community ecology. Recently, there has been a new emphasis on intraspecific variability. Indeed, recent developments in trait-based community ecology have underlined the need to integrate variation at both the intraspecific as well as interspecific level. We introduce new T-statistics ('T' for trait), based on the comparison of intraspecific and interspecific variances of functional traits across organizational levels, to operationally incorporate intraspecific variability into community ecology theory. We show that a focus on the distribution of traits at local and regional scales combined with original analytical tools can provide unique insights into the primary forces structuring communities.

The importance of variance has been neglected in community ecology

Community ecologists are interested in documenting and predicting the structure and dynamics of assemblages of organisms that co-occur within a local place and time [1]. The most probable conditions that allow for such coexistence of species were worked out long ago through classical niche-based coexistence theory [2,3]. MacArthur and Levins [2] highlighted the importance of the quotient of the interspecific differences in niche means, d , and intraspecific niche widths, σ . This ratio was seen as the central quantity to resolve the paradox of Gause's Principle which states that two species cannot share the same niche [4]. How small the value of d/σ could be while still maintaining species coexistence was termed 'limiting similarity' (see Glossary) [3,5,6]. Thus, from the beginning of coexistence theory both interspecific species means and intraspecific variance have theoretically been important for the study of coexistence.

Since the work of MacArthur and Levins [2], numerous coexistence studies have invoked the difference between

species niche means, d , as a key promoter of diversity [7,8]. This assumption follows from the mindset of the common mathematical tool of mean field theory (the study of the behavior of the mean while ignoring variance). Interestingly, the role of MacArthur and Levins' σ in coexistence has received diminished attention through the 1980s and 1990s despite the existence of potentially wide within-population variation being widely recognized in ecology and evolutionary biology [9–11]. The dominant theories in ecology in recent years support our claim that intraspecific variation is no longer considered in the study of communities. For instance, community assembly theories, and related assembly rules [12], have focused on interspecific differences between co-occurring species. Furthermore, in the emerging field of community phylogenetics, where community assembly is studied from a phylogenetic perspective [13], within-species variation is largely ignored.

The mean field theory has been widely adopted in trait-based community ecology [12,14] where the focus is on trait differences between co-occurring species. Indeed, McGill *et al.* [14] stated that 'to be useful to community ecology, traits should vary more between than within species'. This statement has been a key assumption guiding the development of functional ecology [15] and has been further

Glossary

Assembly rules: rules that aim to explain the assemblage and relative abundances of species in a given community (or guild) from the regional pool potentially containing many more species [87]. These rules are largely hypothetical and controversial at present.

External filter: all assembly processes that operate at a larger spatial scale than the scale of the community, including climate, soil and possible non species-specific agents such as generalist predators (Box 1).

Functional trait: any trait affecting, directly or indirectly, individual performance and fitness of species [14,89].

Internal filter: all assembly processes internal to the community, including competition, parasitism and microenvironmental heterogeneity (Box 1).

Limiting similarity: an ecological concept that refers to the level of niche overlap between two species above which coexistence is not possible. It was originally defined as the ratio of the distance between species niche means (d) to their niche widths (σ) [2,3].

Trait: any morphological, physiological, phenological or behavioral feature measurable at the individual level [89].

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amplified in community ecology by the use of species mean trait values extracted from global databases [16]. In support of these theoretical and pragmatic assumptions, several studies have reported low intraspecific variation for both organismal traits [17] and population-level parameters [18]. However, several recent studies have challenged the findings that intraspecific variation is necessarily low by measuring trait values either for all individuals within a community [19] or for a large number of populations along environmental gradients [20].

The gap between theoretical assumptions that the mean captures a majority of the important dynamics and empirical results suggesting that there is significant intraspecific variation, indicates a fundamental issue in the theoretical foundation of community ecology. Indeed, recent papers [19,21–39] have demonstrated the importance of intraspecific variability for the maintenance of species coexistence and the dynamics of communities. Specifically, the question is whether community ecology should be based on the ecology of species or individuals [10,37]. Because interactions with the biotic and abiotic environment are ultimately based at the level of the individual, it makes sense to build a theory of community ecology starting with individuals.

Here we review the limitations of the mean field approach in community ecology and present a framework for incorporating ‘both’ intraspecific (σ) and interspecific (d) trait variability into community ecology theory. Our approach builds on the F -statistics familiar from population ecology. Specifically, we propose a renaissance of the study of MacArthur and Levins’ ratio d/σ to more quantitatively predict the assembly, structure and dynamics of communities and to further disentangle several competing theories of species coexistence.

Limitations of the mean field approach in community ecology

The ubiquitous presence of individuals within populations that differ from each other was the central independent

observation made by both Darwin and Wallace that laid the foundation for the theory of evolution by natural selection. Variation between individuals has also been widely discussed in ecology, as emphasized by the concepts of ‘niche variation’ [40–42], ‘individual specialization’ [10,43–45], ‘individual heterogeneity’ [9,25,36,46] and ‘intraspecific polymorphism’ [23,47]. These theories state that some individuals within the population have a more specialized behavior to forage for alternative resources or prey (i.e. behavior specialization) or to select alternative habitats (i.e. habitat specialization) [10,43,45], allowing the population to release intra- and interspecific competition or predation [10,43–45]. Below we use the generic term of ‘individual variation’ (see also Figure 3c) to refer to the possibility for individuals within a local population to exhibit different ecological strategies. This idea is reinforced by the fact that a given organism can respond to the presence of direct neighbors via phenotypic plasticity (i.e. trait adjustment) [48–50]. The immediate neighbors are the ones directly involved in species interactions [29,51]. As such, niche complementarity, that is ‘the tendency for phenotypically divergent individuals (or species) to compete less strongly’ [21], most probably occurs primarily at this neighborhood scale [29,48,51,52]. This partly explains why intraspecific (genetic and phenotypic) variation usually coincides with greater coexistence and resource use among species [24,31,34,36,37].

Considering traits as mean values per species (i.e. mean field approach) then underestimates the ability of a species to endure the presence of others in a community [48], misrepresents the fraction of resources that the population can use [10], and ultimately underestimates the degree of niche and trait overlap between species [39] (Figure 1). In short, using mean traits will have consequences for the predictive ability of community ecology and can lead to critical misinterpretations. First, in order to understand the mechanisms promoting species coexistence, the use of the mean field approach is not appropriate due to the direct

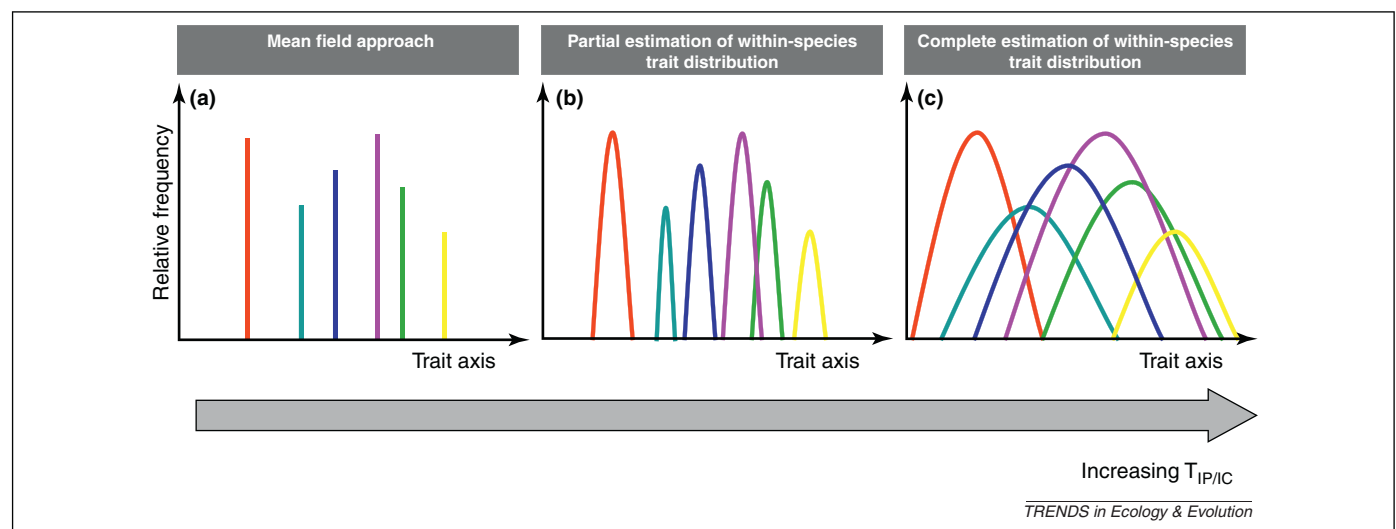


Figure 1. The mean field approach to community structure overemphasizes significant differences between species. In the mean field approach, the traits of species are described by single mean values (a). Each stick is the trait value for a given species. The trait frequency can be different between species if the abundance of species is taken into account (in this case, the trait value of a species is weighed by its relative abundance in the community; [89]). When accounting for intraspecific trait variation, the trait distributions of species in the community can overlap (b,c). The level of differentiation between species can be assessed by the $T_{IP/IC}$ -statistic (Box 2). Note that a partial sampling of intraspecific variation (e.g. in the case of measurements of plant functional traits, standardized protocols minimizing intraspecific variation are used; [67]) can underestimate the degree of overlap between species (b).

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