Review

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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

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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
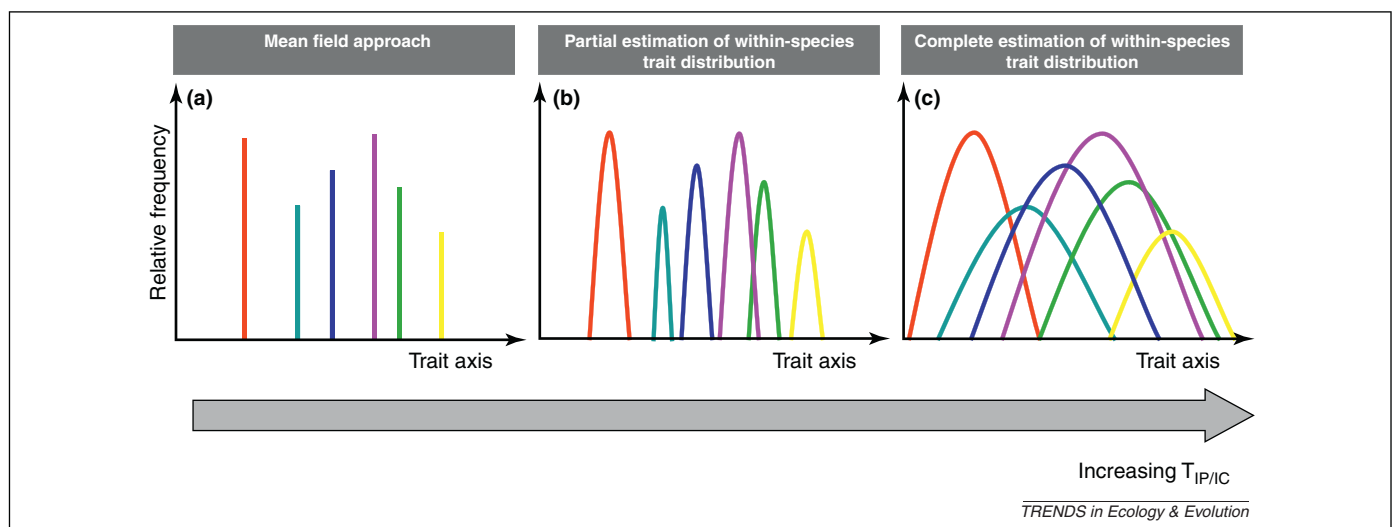

| Mean field approach | Partial estimation of within-species trait distribution | Complete estimation of within-species trait distribution |

Increasing $T_{IP/IC}$

TRENDS in Ecology & Evolution

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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limitations detailed above. Second, to detect nonrandom community assembly mechanisms, adequate null models have been proposed to compare patterns in natural versus randomized communities [53]. Because the mean field approach omits intraspecific variation the use of null models can bias the estimation of coexistence in multispecies communities. An illustrative example of this comes from grassland communities where Jung *et al*. [22] found that the detection of community-wide limiting similarity was improved when intraspecific trait variation was taken into account. Nonetheless, the role and presence of intraspecific variability is usually discussed as a caveat in most community assembly studies [54,55]. Third, to understand and predict the dynamics of communities, the mean field approach is inappropriate in so far as intraspecific trait variation is the rough material for the eco-evolutionary dynamics of natural communities [56,57]. Finally, to quantify functional diversity (the kind, range and relative abundance of functional traits in a given community, [58]), there is both: (i) a theoretical understanding that intraspecific trait variation can affect the assessment of functional diversity [59] and (ii) an increasing number of field and simulation studies showing that neglecting intraspecific trait variation in the computation of functional diversity can result in a misinterpretation of the real dynamics and functioning of communities [22,26,60–63].

How do we measure intraspecific variability?

The main sources of intraspecific trait variation are well known [64]. They consist of genetic variability and phenotypic plasticity for a given sex and age class. Genetic variability and phenotypic plasticity cause similar effects in ecological communities [24,30–32,34,48]. Given this, when studying community ecology questions, we suggest measuring all phenotypic variation (i.e. intraspecific trait variation *ipso facto*) within natural populations, regardless of whether it is caused by genetic or environmental causes. Then we can estimate the variation of a given species simply by measuring the distribution of trait values in the local community. Although we focus primarily on intraspecific variation with regard to individual traits, our approach also necessitates consideration of interspecific variation (see next section). Further, our approach is readily extendable to the cases of multiple traits which often combine to determine fitness [65,66] (Box 3).

When applying a trait-based approach to community ecology, we recommend relaxing standardized protocols currently used in functional ecology [67]. Specifically, rather than aiming to minimize intraspecific variability, the goal is to accurately quantify intraspecific variation within communities. In an ideal world, all individuals of a community should be measured [61,68] but in practice this is frequently not feasible. Instead, we advocate the random selection of individuals [61], which is typically not the case today in most community ecology studies, as well as the use of individual-based trait distributions [19,20,69] to more accurately quantify the width of the niche of species and, ultimately, mechanisms of species coexistence. Furthermore, recent evidence suggests that biotic interactions and niche complementarity do appear at the neighborhood scale [29,34,52] and that individuals can modify their traits

in response to the activity of their closest neighbors [48,70,71], at least in sessile organisms. As a consequence, we strongly encourage those carrying out future studies to investigate the spatial structure of trait distribution to estimate the importance of these fine-scales processes, especially in plants.

A special case of individual variation is the polymorphism for sex or age [45,72]. In community ecology, the mean field approach is implicitly applied to 'a-gendered' adult organisms. Juveniles and adults can however use different resources thereby increasing the niche of the species [10,72]. Similarly, male and female individuals can behave differently [10]. This intraspecific polymorphism can also help a species to escape exclusion via density-dependent interactions such as interspecific competition [10]. Further, the coexistence of differently aged individuals allows for the storage effect, that is, a temporal partitioning of niches that enhances the maintenance of species diversity [73,74]. Trait-based community assembly studies can then benefit from hierarchical trait sampling to account for age- and sex- structure of populations [15]. This will also help to incorporate the storage effect in community assembly theories (Box 3). In plants, sampling traits and running assembly analyses for seedlings and adults separately can be of interest to identify the specific mechanisms controlling the establishment and success of species.

Incorporating intra- and interspecific variances into community ecology theory: introduction of T-statistics

We propose a simple approach to incorporating intraspecific variation into existing theory that starts from a

> **Box 1. Ecological filters: a plea for a more operational framework**
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> Traditionally, community assembly theories aim at predicting the arrival and persistence of species inside a community via the sorting of species across various 'ecological filters' – including dispersal, abiotic (habitat) and biotic filters – according to their trait values [87,90]. Although intuitively appealing and a useful heuristic tool to organize assembly processes [53], over the past several years the traditional paradigm of filtering has been questioned because these filters are operationally difficult, if not impossible, to separate [13,91]. For instance, facilitation and competition, both biotic filters, can actually act as 'habitat' filters by regulating microclimate and resources [70,92]. Moreover, this paradigm describes sequential filtering processes that actually occur simultaneously in natural communities.
>
> To overcome the complexity of 'traditional' ecological filters, we propose a new spatially explicit framework that invokes two operational filters: the 'external' and 'internal' filters. The advantage of this approach is that the filtering processes are relative to the spatial scale of the community being investigated. Here, the external filter includes all assembly processes outside the community, whereas the internal filter includes all of the assembly processes internal to the community. The external filter conditions the sorting of species from a regional pool. The internal filter represents all local processes, including microenvironmental heterogeneity [93] and density-dependent processes [77] that regulate species coexistence within the community. As we discuss in the main text, our revised assembly theory, based on a clearer articulation of filtering, aims at disentangling the role of both filters in the establishment and persistence of traits and taxa in the community through the comparison of intra- and interspecific trait variation at local and regional scales.

process-based perspective and translates immediately into easy-to-measure proxies for these processes. Our approach models community assembly via two different filters: external (filtering processes outside the community) and internal (filtering processes inside the community). By using this simple distinction between filtering processes,

our aim is to propose a more operational framework to community assembly (Box 1). As such, it is possible to compare the trait distribution in a local community to the total amount of trait variation within the regional pool, as a more operational way to track the assembly of communities.
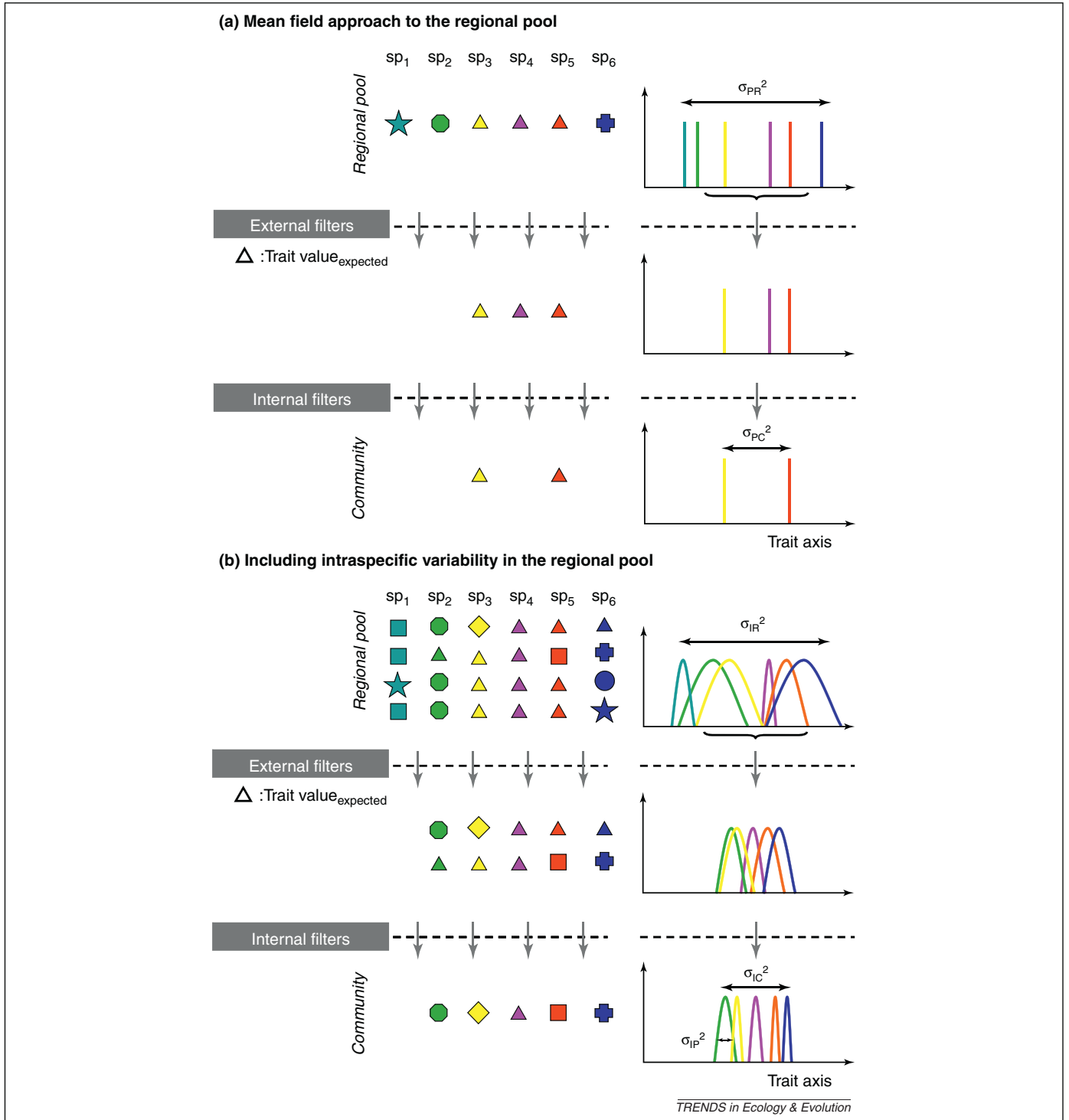

Figure 2. Community assembly theory and intraspecific variability. **(a)** Community assembly theory has been traditionally rooted in mean field theory. Only mean trait values of species present in the regional pool are considered. Dashed lines represent external and internal filters (Box 1). Each color represents a species and each symbol is a given trait value. Species enter in the community if their mean trait values match external conditions E_J. In established communities, species that possess trait values that are too similar cannot coexist (limiting similarity hypothesis) [8]. **(b)** We propose a revised community assembly theory rooted on the amount of regional intraspecific variation. Species enter in the community if their regional intraspecific variation matches, at least partially, external conditions E_J. In established communities, diversity is expected to be higher than in the mean field theory because species that display intraspecific variability can escape competitive exclusion, predation pressures or occupy more microsites. This theory is tested by partitioning variances among hierarchical levels (Box 2; Figure 3).

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Box 2. Partitioning of intraspecific and interspecific variances across hierarchical levels: the T-statistics

Four organizational levels are involved in community assembly: individual, population (i.e. community-specific species), community and regional pool (Figure I). We consider the distribution of the trait of individuals at these different hierarchical levels. Six variance components are identified: σ_{IP}^2, variation of trait values among individuals within population; σ_{PC}^2, variation of population mean trait values within community; σ_{CR}^2, variation of community mean trait values within regional pool; σ_{IC}^2, variation of trait values among individuals within community; σ_{PR}^2, variation of population mean trait values within regional pool; σ_{IR}^2, variation of trait values among individuals within regional pool.

In population and evolutionary genetics, Wright's *F*-statistics are widely used to describe the structure of genetic variation within and among populations [94]. Inspired by the machinery of quantitative genetics, we proposed T-statistics ('T' for trait) as ratios of variances to quantify the importance of internal and external filtering in the maintenance of local trait and species coexistence. We specifically highlight three ratios that can be implemented for any trait:

- $T_{IP/IC} = \frac{\sigma_{IP}^2}{\sigma_{IC}^2}$, the within-population variance conditional within the community;

- $T_{IC/IR} = \frac{\sigma_{IC}^2}{\sigma_{IR}^2}$, the community-wide variance relative to the total variance in the regional pool, assessed at the individual level;

- $T_{PC/PR} = \frac{\sigma_{PC}^2}{\sigma_{PR}^2}$, the community-wide variance relative to the total variance in the regional pool, assessed via population-level means.

$T_{IP/IC}$ represents the community-wide overlap of intraspecific trait variation, which is a measure of niche packing between the species of the community. It quantifies the strength of internal filtering. $T_{IC/IR}$ quantifies the strength of external filtering. The use of both $T_{PC/PR}$ and $T_{IC/IR}$ allows one to identify which filtering processes act on species averages or on individual values.
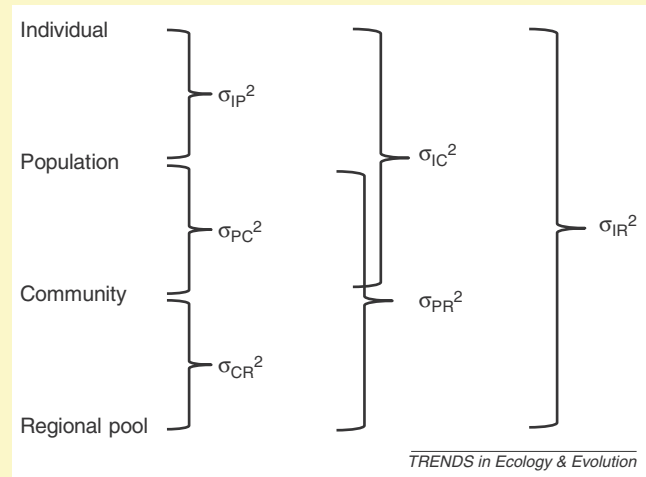

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Figure I. Hierarchical partitioning of variances among the four levels involved in community assembly. In the case of clonal plants, the 'individual' level is a clone or a ramet because ramets of a modular plant can display wide phenotypic variation in a community [95]. The 'population' level is the community-specific species. In animals, the 'community' level is preferentially a guild. The regional pool is the set of species belonging to a regional area or preferentially the set of species that are able to disperse up to the local community.

Traditional community assembly theory predicts that the filters operate on the mean values of species traits (Figure 2a). To build a more general trait-based ecology, we propose a revised assembly theory involving filtering processes that operate on individuals instead of species (Figure 2b). Our framework specifically considers the distribution of traits of individuals at different hierarchical levels. We make two explicit assumptions. First, for a given local community J, external conditions E_J select an optimal trait value T_J [75,76]. Individuals with trait values close to T_J pass through the external filter to grow and reproduce, whereas individuals with trait values far from T_J have a fitness of zero and fail to establish. This is very similar to the idea of stabilizing selection [47]. Internal filters, mostly governed by density-dependent processes such as competition [77], suggest that if most individuals in a community possess trait values close to T_J, then individuals possessing trait values away from T_J can have higher fitness [77]. This idea is also a central tenet of adaptive dynamics as applied to evolutionary theory [78]. Altogether, external and internal filtering processes create a distribution of trait values around T_J. The external and internal filters cause the trait values in a local community to have the following properties: (i) the mean trait of the community is potentially different from the mean trait of the regional pool and the modal trait value is at the optimal trait value T_J for the external conditions E_J experienced in that community; (ii) traits values in the local community will spread around T_J, with the spread (variance: σ_{IC}^2, see Box 2) being small with strong external filtering and being large with strong internal density-dependent constraints.

Box 3. Future directions

- **Develop sampling protocols to quantify intraspecific variation simultaneously for multiple traits at differing spatial scales**

  Intraspecific trait variability is expected to reflect the width of species niche [96,97]. However, the emergence of the concept of 'trait niche' [96] is still largely based on single-trait analysis. In reality the species' niche results from multiple traits and the degree of covariation between them [98]. Future elaboration of trait-based ecology will necessitate measures of intraspecific multi-trait variability.

- **Incorporate temporal variability in traits into community assembly theory**

  A community includes the complexity of age structure of its constitutive populations. Trait sampling is most often performed on mature adult individuals, which underestimates the role of age structuring within and among populations. A more complete sampling framework for community-wide intraspecific variability needs to include age as well as sex structure [72]. Trait sampling is classically done once in a community and thus represents a snapshot of realized trait distribution. However, temporal niche partitioning is also a well-known mechanism that favors species coexistence (see the storage effect) [74]. Investigating the temporal structure of interspecific and intraspecific trait variability should allow accounting for the role of temporal niche partitioning in community assembly.

- **Develop tools and methodologies to connect functional trait-based approaches to community genetics**

  Community genetics asserts that the genetic diversity of a species can influence the persistence of interacting species [35,99]. This burgeoning field classically refers to a keystone or dominant species but can also be extended to any species in the community. How do genetic differences among individuals translate into functional trait differences? What is the genetic basis of functional traits? What are the consequences of intraspecific and interspecific traits distribution in the actual community for its ecoevolutionary dynamics?

Variance partitioning gives a simple way to test these ideas and make them operational. Whereas classical assembly theory focused on differences (essentially subtractions) between means, a variance-based theory focuses on ratios of variances on differing scales. The use of ratios of variances has long-standing roots in ecology in the context of analysis of variance and the R^2 of regression. An analysis of variation is also extremely common in the study of dispersal and population structure [79] in the form of F-statistics as introduced by Sewall Wright [80,81]. It also echoes the partitioning of the niche of a population into within- and between-individual variation to assess the potential of niche variation and the level of 'individual specialization' within a population [10,40,41,43,44]. Increasingly, community ecologists are exploring variance partitioning across hierarchical levels [19,61,82]. Loosely inspired by Wright's F-statistics, we propose several 'T-statistics' ('T' for 'trait') to quantify the relative strength of internal and external filters that operate within and between species during community assembly. Specifically we considered four hierarchical levels: individual (I), population (P), community (C) and regional pool (R) (Box 2). Below, we consider three key T-statistics ($T_{IP/IC}$, $T_{IC/IR}$ and $T_{PC/PR}$) that are useful in quantifying ecological filtering processes and the level at which they act (species or individual level).

The ratio $T_{IP/IC}$ is the variance within a single species (population) belonging to the community relative to the total variance of the community over all species. The magnitude of $T_{IP/IC}$ measures the strength of internal filters; that is, how strongly local processes, such as microenvironmental heterogeneity or density-dependent processes, act on species coexistence. In essence $T_{IP/IC}$ is a measure of 'interspecific' niche packing [83]. Specifically, as more competitors are established in the community, there is a reduction of local intraspecific variation (σ^2_{IP}; i.e. σ in MacArthur and Levins' ratio). Niche packing, with nonoverlapping niches, would then lead to a $T_{IP/IC}$ close to 0 (Figures 1 and 3a). Alternative theories, including the neutral theory of biodiversity [84] and 'individual variation' theories [36,46] (Figure 3), suggest the processes that pack species are indifferent to overlap or strongly screen against niche overlap, and in these cases $T_{IP/IC}$ tends to be close to 1. A simple plot of species richness versus $T_{IP/IC}$ would then provide a strong test of these ecological theories. Negative, positive or flat slopes would reflect niche, individual variation or neutral processes (Figure 3). $T_{IP/IC}$ is close to estimators of niche overlap
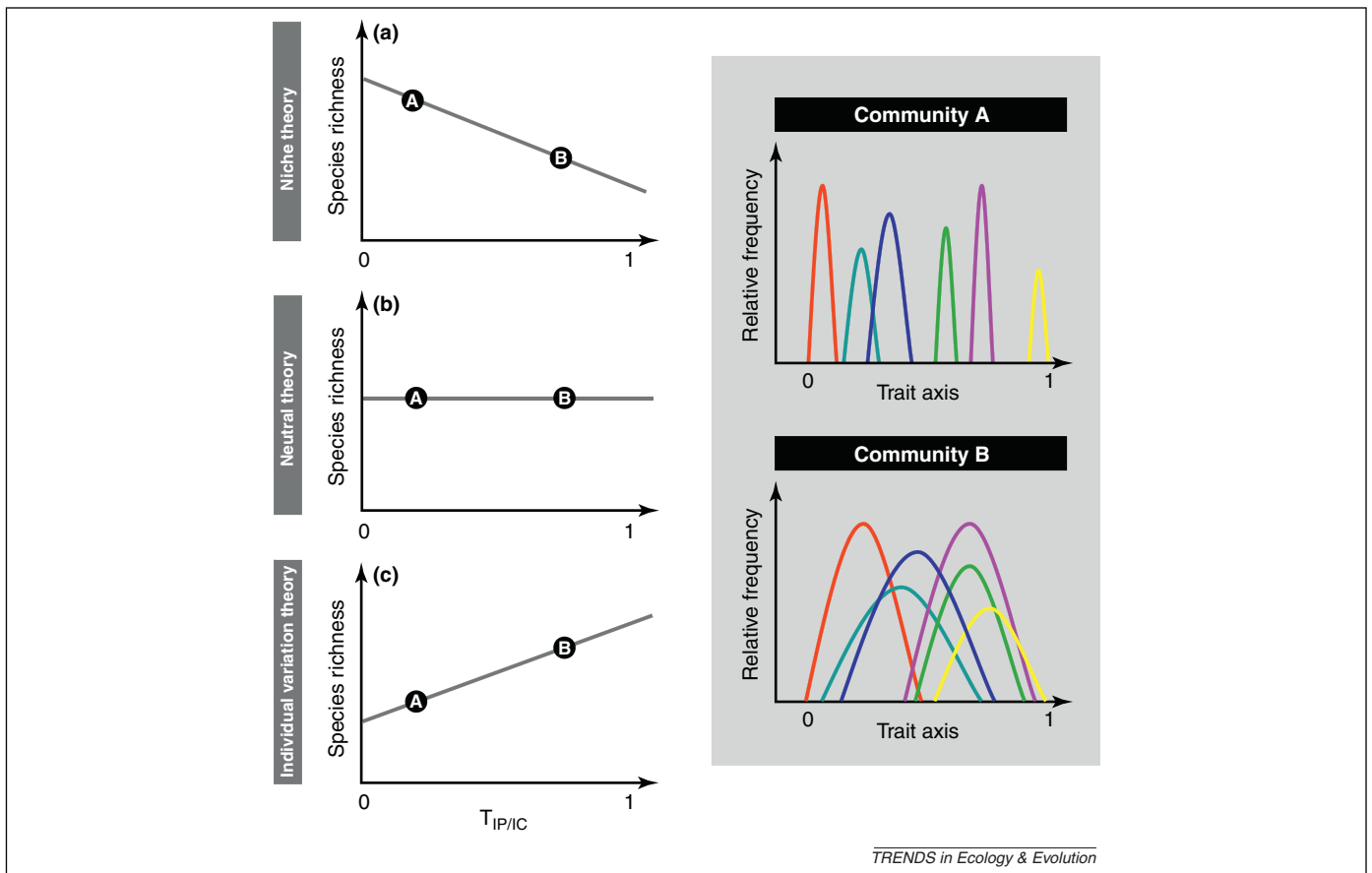

Figure 3. Community-wide intraspecific variation within a community as a signature of community assembly mechanisms: predictions from the T-statistics. Scenarios relating change in local species diversity as a function of community-wide intraspecific trait variation under different classical ecological theories. Each curve is the trait distribution of a given species within the community. The trait axis is normalized to allow comparisons between traits and communities. Community-wide intraspecific variation is higher in community B (high $T_{IP/IC}$ value) than in community A (low $T_{IP/IC}$ value). **(a)** In niche-based theory, each species uses a fraction of the resources and this fraction (niche width) decreases when the number of species increases [83,100]. We then expect that the lower community-wide variation, the greater local diversity. **(b)** In the neutral theory of biodiversity, all individuals of all species are assumed to be ecologically equivalent [84]. Community-wide intraspecific variation is not predictable and is not related to species diversity. **(c)** We recognize 'individual variation' theories that explicitly identify intraspecific variation as the main driver of local diversity [36,46]. In this case, high variation within species, generated by the existence of within-species trade-offs in life-history traits, favors the maintenance of diversity.

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developed for quantitative traits [85] and discrete traits [86]. Similarly to the tests developed in the context of niche overlapping [86], field-observed $T_{IP/IC}$ can be confronted to randomized assemblages through permutation tests.

The variance within the community relative to the total variance of the regional pool is a measure of the strength of external filters; that is, how strongly filtered the entire community is. This can be evaluated in two ways: (i) at the individual level (namely $T_{IC/IR}$; the trait values of all individuals in the community and in the regional pool are considered, regardless of species identity) or (ii) at the species level (namely $T_{PC/PR}$; only the population means are considered) (Box 2). When $T_{IC/IR}$ (respectively $T_{PC/PR}$) is close to 1, the community variance, σ_{IC}^2 (respectively σ_{PC}^2), is high in comparison to the total variance, σ_{IR}^2 (respectively σ_{PR}^2), indicative of relatively little external filtering (e.g. climatic constraints or impact of a generalist predator). Conversely, when $T_{IC/IR}$ (respectively $T_{PC/PR}$) is close to 0, then the community collectively has been strongly filtered by either abiotic stress or external interactions. Again, permutation tests can be applied to compare $T_{IC/IR}$ (respectively $T_{PC/PR}$) to a randomized filtering from the regional pool (at the individual or species level). Further, the comparison of $T_{IC/IR}$ and $T_{PC/PR}$ indicates whether filtering processes act on species averages as suggested in the mean field approach [87] ($T_{IC/IR} < T_{PC/PR}$) or on individual values [19] ($T_{IC/IR} > T_{PC/PR}$). A situation where both measures are close suggests that filtering acts on species as a consequence of filtering on individuals. An important challenge for community ecology is to then identify the 'currency' that is being filtered during community assembly.

Concluding remarks

An increasing number of studies have documented the importance of intraspecific variation to many ecological and evolutionary processes. Nonetheless, traditional ecological theory has emphasized interspecific variation. We advocate moving beyond the mean field theory in community ecology by examining the structure of intraspecific variability in actual communities as a signature of past community assembly processes. This will enhance the predictive power of the trait-based toolkit for community ecology. Altogether, theories and models incorporating intraspecific variability [25,36,38] predict higher local diversity than those based on population averages. Therefore the trait variance of species needs to be included when forecasting the fate of species and functional diversity in response to environmental changes [60] and the consequences for ecosystem functioning [88]. Ultimately, this will facilitate the shift from species-based to individual-based community ecology and lead to a more predictive ecological theory.

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