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REVIEW AND SYNTHESIS

Trait-based tests of coexistence mechanisms

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Abstract

Recent functional trait studies have shown that trait differences may favour certain species (environmental filtering) while simultaneously preventing competitive exclusion (niche partitioning). However, phenomenological trait-dispersion analyses do not identify the mechanisms that generate niche partitioning, preventing trait-based prediction of future changes in biodiversity. We argue that such predictions require linking functional traits with recognised coexistence mechanisms involving spatial or temporal environmental heterogeneity, resource partitioning and natural enemies. We first demonstrate the limitations of phenomenological approaches using simulations, and then (1) propose trait-based tests of coexistence, (2) generate hypotheses about which plant functional traits are likely to interact with particular mechanisms and (3) review the literature for evidence for these hypotheses. Theory and data suggest that all four classes of coexistence mechanisms could act on functional trait variation, but some mechanisms will be stronger and more widespread than others. The highest priority for future research is studies of interactions between environmental heterogeneity and trait variation that measure environmental variables at within-community scales and quantify species' responses to the environment in the absence of competition. Evidence that similar trait-based coexistence mechanisms operate in many ecosystems would simplify biodiversity forecasting and represent a rare victory for generality over contingency in community ecology.

Keywords

Biodiversity, community assembly, competition, global change, seed size, specific leaf area, wood density.

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INTRODUCTION

Plant ecologists are investing tremendous effort in understanding communities through the lens of functional traits (Grime 1977; Weiher & Keddy 1995; McGill *et al.* 2006; Westoby & Wright 2006; Shipley 2010). By capturing essential aspects of species' ecophysiology, morphology and life-history strategy, functional traits offer a mechanistic link between fundamental biological processes and community dynamics (McGill *et al.* 2006; Westoby & Wright 2006). Furthermore, because traits offer a common, taxon-independent currency for species comparisons, trait-based approaches have the potential to reveal general, synthetic and predictive relationships that studies of idiosyncratic, species-specific responses have failed to identify. One of the most ambitious goals of the trait-based programme is to understand how traits mediate community assembly and coexistence to predict the effects of global change on biodiversity (e.g. Suding *et al.* 2005). Our objective is to direct future research towards approaches with the greatest potential for achieving this goal.

Current trait-based approaches in community ecology focus on analyses of trait dispersion patterns to detect environmental filtering and niche partitioning. Evidence for environmental filtering comes from correlations between environmental gradients and community-weighted trait values (Kraft *et al.* 2008; Cornwell & Ackerly 2009; Swenson & Enquist 2009; Kraft & Ackerly 2010; Shipley 2010; Katabuchi *et al.* 2012) and from studies showing that trait differences generate competitive hierarchies (Freckleton & Watkinson 2001; Kunstler *et al.* 2012). Evidence that traits play a role in maintaining species diversity through niche partitioning comes from the great variation in trait values found within most communities (e.g. Westoby *et al.* 2002) and from studies showing that trait values of co-occurring species are over-dispersed relative to expectations from null models (Stubbs & Wilson 2004; Kraft *et al.* 2008; Paine *et al.* 2011). The rationale is that species with different traits may have different resource or habitat requirements and will compete less intensely than species with similar traits. While much of this recent work has focused on plant communities, there is a long history of exploring phenotypic trait dispersion in animal assemblages (Ricklefs & Travis 1980) and non-random dispersion patterns within communities have been documented in a wide range of phyla (e.g. Rabosky *et al.* 2007; Ingram & Shurin 2009; Gómez *et al.* 2010). These studies provide compelling evidence that trait variation influences community assembly and coexistence.

Existing trait-based approaches represent important advances, but ultimately they cannot provide the mechanistic understanding necessary to predict the effect of local and global change on species diversity. Trait-based prediction of how nitrogen (N) deposition or climate change may impact species diversity requires information

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