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Comments

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A new perspective on trait differences between native and invasive exotic plants: comment

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In a recent article in Ecology, Leffler et al. (2014) presented a potentially new perspective on the importance of trait differences between native and invasive exotic plants in explaining invasions in local native communities. The new perspective brought forward is that, if trait differences between invasive and native species are likely to be important in explaining exotic plant invasion, the differences must be larger than those observed between native species in the new community. A meta-analysis of previous studies searching for trait differences was presented, with the general finding that the magnitudes of trait differences between invasive and native species tend not to differ from those observed between native species only. Leffler et al. (2014) interpret this result as evidence that trait differences are highly context dependent, and that mechanisms other than trait differences are likely to be more important in most cases of invasion.

We acknowledge that there is no universal explanation of successful exotic invasion into native communities. Moreover, we do not believe that invasive plant species always have trait values that differ substantially from the traits present in the native community, or that trait differences are important for invasion in all cases. However, we cannot agree with the criterion stipulated by Leffler et al. (2014), namely that a trait difference between invasive and native species can only be important to invasion success if it is greater than the differences among natives. Leffler et al. (2014) do not explain the logic behind the criterion, but a flaw of the criterion is that it will discount cases when a successfully invading species has intermediate trait values that are not represented by native species. Leffler et al. (2014) seem to focus on trait differences as representing niche differences among species. Consider the scenarios of niche differences among native and exotic invasive species in Fig. 1. If a trait is related to the niche space occupied by native species in the community and the invader, for a trait difference to be important in invasion success under the criterion of Leffler et al. (2014), only the scenario in Fig. 1a would qualify. Here, the invader occupies a niche at the extreme of the niche space, compared to native species. The average niche-related trait difference between the invasive species and the natives will be greater than the average difference among natives. However, consider Fig. 1b. Here, the invader occupies a vacant niche that is intermediate between the native species (Stachowicz and Tilman 2005), and the invader would have an intermediate, niche-related trait value not represented by the native community. However, the average trait difference between the invader and native species in Fig. 1b will be smaller than the difference among native species, and under the criterion proposed, the native-invasive trait difference would be considered unimportant. Thus, the criterion proposed by Leffler et al. (2014) cannot distinguish between cases where trait values may lie between those of native species but are still distinct and cases where they are very similar to native species.

Exotic species may not only invade a community by having different niche-related traits compared to native species. Some of the traits considered in the meta-analysis of Leffler et al. (2014), e.g., biomass, are arguably traits related to fitness. Such fitness-related traits also do not have to be more different between invasive and native species than among natives, for them to be important for invasions. All that is required is for the trait difference to be large enough for invasive species to have greater fitness than the native species (Fig. 1c). If this occurs and there is niche overlap between the invasive species and a native species, then the invasive species should displace the native species (MacDougall et al. 2009). The trait difference between invasive and native species should always be greater than the average native-native difference only when the trait is related to niche space and the invader is occupying a vacant niche at the extremes of the niche space available to the whole community. Thus, cases that meet the Leffler et al. (2014) criterion could be viewed as representing only one of three possible scenarios where differences in traits between native and invasive species are potentially important, and the only scenario where native-native differences are relevant. The challenge is to understand which of the many traits we can measure are actually related to fitness and niches of invasive and native species, and then to identify whether fitness or niche differences (or perhaps even both) have led to invasion.

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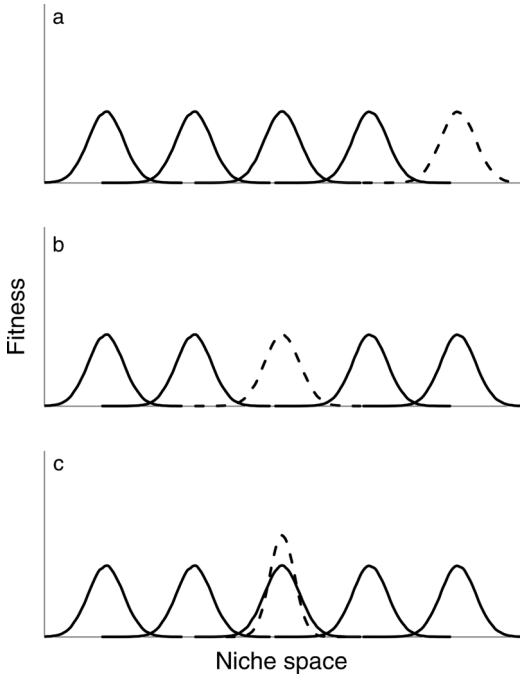

FIG. 1. Three scenarios showing what may happen when the value of a trait for an exotic invasive plant species differs from trait values of resident native species in a community. The *x*-axis represents niche space, and the *y*-axis represents fitness; the curves represent the locations of species in the niche space and their fitness. However, the location of a species curve on the *x*-axis would also represent the value of the species' niche-related trait, and the height of the curve would represent the value of a fitness-related trait. In panel (a), the invasive species (dashed line) would have a greater niche-related trait value than native species (solid line), i.e., the invasive species occupies a vacant niche at the extreme of the niche space. The average of niche-related trait differences between the invasive species and the native species would therefore be larger than the trait difference among native species, consistent with the argument of Leffler et al. (2014) that invaders may be more different from natives than natives are from one another. In panel (b), the invasive species has a distinct, intermediate niche-related trait value between native species, which would result in invasion into an open niche, even though the exotic species differs less from the native species than the native species do from one another. Thus, the Leffler et al. (2014) criterion will only be met in the scenario in panel (a), even though trait differences in panel (b) might still be important for invasion. In panel (c), even though the exotic has a similar niche to one of the native species, it is able to invade due to having greater fitness (and a greater fitness-related trait) than the native species. The differences in fitness-related traits among native species would be irrelevant.

While our major comment concerns the criterion proposed by Leffler et al. (2014), we also see a flaw in the meta-analysis that they performed. In the meta-analysis, native-native comparisons were only available in 71 of the 151 studies that contained native-invasive comparisons. Thus, for more than half of the effect sizes representing differences between native and invasive trait values, a comparison has been made with native-native differences for native species that do not co-occur or were not measured in the same studies with the invasive aliens. Taking effect sizes out of context in this manner goes against the emphasis made by the authors that context-dependency really matters when comparing invasive and native species. It would have been preferable to have seen a meta-analysis conducted on the subset of 71 studies including both types of comparison, in order to preserve study context.

Finally, in general we would advocate a move away from studies that only compare pairs of native and invasive species traits and that only consider the role of trait differences in isolation from other factors known to influence invasion of a community. Understanding whether fitness-related or niche-related trait differences explain invasion requires a whole community approach to identify the size, number and locations of gaps in niche-related trait space represented by the native community, and whether successful exotics invade by filling these gaps, or by having greater fitness than native species with similar niches. One approach to achieve this would be to artificially introduce exotic species known to be successful invaders and those that are not to native communities, and to record over time whether and how those species that successfully establish differ in their traits from the resident native species. We agree with Leffler et al. (2014) that other factors likely interact with trait differences to promote invasion. However, an experimental introduction approach with multiple exotic species would be informative in this respect. If we do this with both invasive and noninvasive exotic species and find that establishing noninvasive exotics differ as much from the native community in their traits as do invasive species, then the importance of trait differences must be contingent upon other factors such as high propagule pressure. Several studies have already experimentally staged invasions of native communities (Kempel et al. 2013, Maron et al. 2014), and we believe that more studies such as these will further our understanding of if and when trait differences between invasive and native species are important for invasion.

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A new perspective on trait differences between native and invasive exotic plants: reply

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Dawson et al. (2015) critique three aspects of our study, *A new perspective on trait differences between native and invasive exotic plants*. First, they suggest our assertion that differences between trait values of native and invasive species need to be larger than differences among native species is not an appropriate criterion for considering trait differences as a mechanism of invasion. They present a graphical description of the shortcomings of our assertion and suggest it cannot apply when an invader occupies an empty niche with a trait value intermediate to native species in the community. Here, we might instead assert that the vacant niche Dawson et al. (2015) show in Fig. 1b, a characteristic of the community, is as important as the trait value of the invading species (Heger and Trepl 2003). We might ask the question, "Would this species invade if a different niche were vacant?" The answer would be "no" and consequently invasion is conditioned on the trait of the invader and the community potentially being invaded—what we refer to as context dependence. We concede that in the case of an "over-dispersed" community our criterion might not hold because of large differences among native species, however, leaf-trait convergence appears more common than over-dispersion (Freschet et al. 2011).

The second assertion is that trait differences only need to be large enough for the invader to be more fit than the native. We fully agree, but fitness differences arise from an interaction of traits and the environment that result in basic trade-offs (Wright et al. 2004, Westoby and Wright 2006). Traits considered advantageous to invaders do not always result in invasion (Thomsen et al. 2006) because species with those traits are not always the most fit. For example, a high maximum photosynthetic rate could only promote invasion under high soil moisture and nitrogen availability, which are characteristics of the system being invaded (Leishman et al. 2010). Furthermore, since traits are correlated (i.e., the leaf economics spectrum; Wright et al. 2004) and species are embedded in communities, we agree that comparing traits in isolation or comparing pairs of native and invasive species is of limited use; however, the literature is full of such comparisons and the motivation for this meta-analysis was drawing broader conclusions from these studies.

Finally, Dawson et al. (2015) suggest that our meta-analysis was not conducted properly because we included approximately twice as many studies with native-invasive comparisons as we did for native-native comparisons. We made this decision to increase our sample size and we chose to include only native-native comparisons that came from the same studies as our native-invasive comparisons to avoid introducing extraneous variation. We have reanalyzed our data with only the 71 studies that include both types of comparison. Our results (Table 1) lead to the same conclusion as the original study: exotic invasive plants only differ minimally more from native plants than native plants differ from each other.

Our goal was to place a baseline on trait value differences between native and invasive species for these differences to potentially be considered important in the invasion process (Leffler et al. 2014). Despite recent successes in explaining higher-level processes such as ecosystem function using measures of plant form (Lavorel et al. 2011, Grigulis et al. 2013), native and invasive plants share similar traits and function by the

Table 1. Reanalyzed tests of residual heterogeneity (Q_E) and moderators (Q_M) using 71 studies that contained native-invasive and native-native comparisons.

Test	Q_E	Q_E df	Q_E P	Q_M	Q_M P†
All	314.4	142	<0.001	142.1	0.704
Type	511.5	171	<0.001	215.0	0.017
Biome	285.1	134	<0.001	154.6	0.269
Functional group	268.6	144	<0.001	187.1	0.285
Trait	645.4	328	<0.001	658.3	0.189

† Q_M P values are derived from the resampling procedure detailed in Adams et al. (1997).

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