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Ecology, 96(4), 2015, pp. 1152–1153
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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

Manuscript received 13 October 2014; revised 21 October 2014; accepted 24 October 2014. Corresponding Editor: D. C. Laughlin.

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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).

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

same ecological rules (Thompson et al. 1995, Meiners 2007, Leishman et al. 2010). The expected expansion of nonnative species worldwide is likely a result of disturbance and land-use change rather than difference in key traits (Leishman et al. 2010, Thompson and Davis 2011).

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