



Invited reply

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On pluralism in ecology: seeing the forest and the trees

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In response to our paper testing whether mistletoe represents a keystone resource [1], Thomsen & Wernberg (TW) [2] integrated our experiment with previous work and introduced a novel hypothesis to explain how structural complexity influences community composition. While we share their enthusiasm for unveiling generalized determinants of diversity, we caution that their approach may overlook some of the complexity our research has uncovered—complexity essential for understanding how and where these patterns arise. Here, we clarify the functional distinction between parasites and epibionts, highlighting that structural similarities belie different underlying mechanisms and pathways. Rather than purely a structural response, we posit that our findings are indicative of fundamental changes to nutrient dynamics and suggest that many cases of presumed facilitation are likely mediated by hitherto-overlooked indirect interactions. Reflecting on the search for generality in ecology, we note how the *cascading habitat-formation* hypothesis [2] exemplifies the balance between big-picture, hypothesis-generating synthesis and mechanistic, hypothesis-testing experimentation.

TW [2] were dismayed that we did not compare our findings with marine research and, whereas we concur that greater integration between research (and researchers) in terrestrial and aquatic systems is essential to inform ecological theory, this was not an oversight. Our objective was to quantify the influence of a parasitic plant on community composition and compare the magnitude of the effect and the underlying mechanisms with work on parasites more broadly and other entities deemed ecological keystones. There are no aquatic parasitic plants (freshwater or marine [3]), so all studies of plant–plant interactions are necessarily restricted to structural aspects. While it is useful to integrate research findings on both terrestrial and aquatic organisms that use other organisms for structural support (e.g. corals and strangler figs; macroalgae and vines), this framework may not be applicable to parasitic groups. Although the structural effects of mistletoe on canopy complexity were predicted to be significant [4], this prediction was not supported by our experiment, with mistletoe-nesting birds not exhibiting significantly greater declines once all mistletoe plants were removed. Indeed, the most marked response to mistletoe removal was displayed by ground-foraging insectivores, a response considered to relate to the abundant enriched litter shed by mistletoes, promoting understorey complexity, microbial activity and prey availability on the forest floor [1]. So, rather than structural complexity driving diversity, it is nutrient enrichment driving small-scale heterogeneity and thereby promoting coexistence, consistent with work on other parasitic groups [5]. These nutrients are partly reallocated from the host by the parasite but are also imported from further afield, deposited by visiting animals (the dryad hypothesis [6]).

This interplay between small-scale heterogeneity and nutrient transport at larger scales has many parallels in aquatic ecology, exemplified by the marine subsidies in freshwater systems mediated by salmon and other anadromous fishes [7]. Hence, mistletoes on eucalypts (hemiparasites) may be structurally similar to bromeliads on forest trees (epiphytes) or polychaetes on mangrove roots (epizoans), but we suggest that the network of interactions with hosts, pollinators, seed dispersers and natural enemies make mistletoe more functionally analogous to brown bears in coniferous forests surrounding salmon streams, the two organisms having disproportionate influence over productivity

and community composition by increasing heterogeneity of nutrient deposition [8]. By mapping the key interactions and conducting carefully controlled comparisons at relevant scales, the pattern can be confirmed and the mechanisms driving the process identified. As well as improving our understanding of ecosystem function, this process-based knowledge would give land-managers more precise tools to achieve specific conservation goals in degraded ecosystems.

Unfortunately, disciplinary boundaries often subdivide these networks of interactions into small subcompartments of the ecosystems being studied, exacerbated by the use of divergent terminology. While TW emphasized the terrestrial/aquatic divide, the same situation applies between plant ecology and animal ecology. Many plants share pollinators, seed vectors or natural enemies, yet the magnitude of these subsidies and trade-offs is rarely considered when investigating plant–plant competition or facilitation. We join with TW in promoting pluralism within ecology as a whole,

encouraging researchers to follow the ecological process under scrutiny rather than to stop as soon as an arbitrary discipline-defined boundary is reached.

In closing, this commentary provides rare insight into how ecologists search for general principles in nature. Rather than new ideas springing de novo, generalities emerge from an iterative process that investigates particular details previously glossed over as idiosyncrasies to reveal hitherto-overlooked congruence. Yet, in so doing, the generalist necessarily emphasizes some details over others and justifies the boundary conditions within which this new framework applies. In this instance, this search has transcended the boundaries of plants and animals, parasitology and ecology, aquatic and terrestrial biomes, stimulating a raft of novel comparisons between bromeliads and algae, seagrass beds and woodlands, salmon and guano. We are grateful to Thomsen and Wernberg for their contribution to this dialogue.

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