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On the generality of cascading habitat-formation

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Ecology is the study of interactions that determine the distribution and abundance of organisms and its main goal is to discover widely applicable, general principles in nature [1]. Ecology therefore integrates traditional disciplines like zoology and botany, and terrestrial, marine and freshwater ecosystems. To this end, it is the objective of the *Proceedings of the Royal Society B* to show the best results of 'general ecology' and publish articles that are of 'interest to a wide spectrum of biologists'. In a recent paper, Watson & Herring (WH) [2, p. 3853] *found support for their hypothesis, that mistletoes function as a 'keystone resource'*, as birds occurred in lower abundances and with fewer species in woodlands where mistletoes were removed from eucalypt trees, compared to control plots where mistletoes were left intact (mistletoes are obligate hemiparasitic plants that attach to and penetrate a host tree by a haustorium, through which they absorb water and nutrients). The study generated discussions among scientists and websites [3,4], perhaps because the positive effects of mistletoes on bird life appeared paradoxical as mistletoes can have negative effects on some host trees, which are the primary habitat for many birds [5]. WH suggested that their mistletoe removals were the first experimental test of a purported keystone resource. While we appreciate WH's elaborate large-scale field experiment, we do not agree with this statement of priority as many analogous experiments from other systems have been published. More specifically, WH make no references to experimental removals (or additions) of *other sessile species that are structurally dependent on a biogenic host* (e.g. structural parasites in [6], intermediate or secondary biogenic habitat-formers in [7] and epiphytes or epizoans i.e. plant or animal epibionts, respectively, in [8]). These experiments have also tested for effects of 'purported keystone resources' in aquatic ecosystems [8,9–16] or different types of forests [17–19]. For example, Cruz-Angon & Greenberg [18, p. 150] previously stated that they conducted 'the first experimental assessment of the importance of epiphytes for birds'.

Here, we highlight the understated ecological generality in WH's study, emphasizing that WH, in essence, quantified how *primary habitat-formers* (here eucalyptus trees) *have indirect positive effects on end-users* (i.e. client-, focal- or dependent-organisms; here birds) *by structurally controlling secondary habitat-formers* (here mistletoes). Thus, WH's ecological context represents a prime example of a habitat cascade, which has been demonstrated in many terrestrial and aquatic studies (a special type of facilitation cascade [7,15]). For example, analogous experiments have documented that secondary habitat-formers increase abundances of end-users for bromeliad epiphytes attached to small coffee trees [17,18] or to large emergent trees in temperate rainforests [19,20], filamentous epiphytes attached to marine seagrasses [9,10], drift seaweeds incorporated into estuarine polychaete and mussels reefs [7,21] or entangled around seagrass leaves and mangrove pneumatophores [12,22], and mussels protected by semiterrestrial salt marshes [14,15]. These and many other studies show similar, and sometimes greater, reduction in abundances of habitat-associated end-users when secondary habitat-formers are removed, irrespective of whether the end-users are terrestrial birds and invertebrates or marine invertebrates and plants (cf. electronic supplementary material, figure S1 and table S1). Although WH's experimental design and results were similar to other studies on cascading habitat-formation, their experiment did differ from previous studies by its very large sample grain and spatial extent, and by manipulating secondary habitat-formers that are obligate hemiparasites [23,24]. It is therefore possible that mistletoes have different effects on end-users compared with other secondary habitat-formers that are not hemiparasitic (e.g. lianas, vines, nest epiphytes, seaweeds and sessile invertebrates). However, many aquatic and terrestrial secondary habitat-formers that are not hemiparasitic have similar ecological traits, including negative effects on their hosts, strong host specificity, high litter production and strong influence on nutrient cycling [6,25,26–32]. Furthermore, cursory comparisons of magnitudes of indirect facilitation by different types of secondary habitat-formers show that WH's results are not unusual (e.g. electronic supplementary material, table S1). We therefore suggest that until it has been demonstrated, overall, hemiparasitic and other secondary habitat-formers are ecologically equivalent, being structurally dependent on primary habitat-formers and typically facilitating end-user communities.

The lack of cross-references to aquatic examples in WH's paper is unfortunate because aquatic systems often have been instrumental to conceptual development and testing in ecology [1,33]. It is, however, symptomatic as others have shown how terrestrial ecologists often under-cite aquatic research [1,33]. For example, there are virtually no references to aquatic case studies in past forest studies on cascading habitat-formation [17,18,20,34,35–40]. To increase the generality of ecology, Menge *et al.* [1] recently pleaded for aquatic scientists to increase pressure on terrestrial-oriented authors and editors to cite aquatic literature. By highlighting the overlooked generalities between cascading habitat-formation in woodlands infected with mistletoe and cascading habitat-formation in aquatic and other terrestrial systems, we hope our comment will provide additional impetus to act on Menge *et al.*'s plea. Until recently, cascading habitat-formation was mainly studied without much consideration of broader ecological theory across ecosystems. However, identifying general principles underpinning cascading habitat-formation (or cascading facilitation/habitat-modification) is important from both a theoretical and an applied perspective. For example, indirect positive effects of cascading habitat-formation are similar to effects of trophic cascades, keystone predation and keystone competition, manifesting through repeated competition and consumption [7]. For decades, these 'enemy-driven' processes have been compared across ecosystems to identify ecological generalities [41,42], and today they are acknowledged to be of fundamental importance in many ecosystems. Interestingly, these enemy-driven interactions and cascading habitat-formation both cause indirect facilitation of end-users by primary organisms mediated by secondary habitat-formers [7]. As such, their theoretical foundations could be compared and contrasted, and potentially unified. Furthermore, it is important to understand cascading habitat-formation because habitat-formers are threatened worldwide by ever-expanding human activities. For example, primary habitat-formers like rainforests, salt marshes and mangroves are being converted to agricultural and urban landscapes, while coral reefs, seagrass beds and kelp forests are increasingly affected by climate change, invasions and pollution. Most conservation research has focused on more obvious effects associated with the direct loss of these primary habitat-formers [43,44]. However, neglecting how structurally dependent secondary habitat-formers might change productivity, biodiversity and ecosystem functioning could underestimate the loss of ecosystem services associated with the continued degradation of natural ecosystems, and make it more difficult to predict, prevent or ameliorate the loss of primary habitat-formers [7,45].

In summary, cascading habitat-formation has been documented for more than 25 years in terrestrial, freshwater and marine systems, and across biogeographic and taxonomic realms. Studies that do not consider similar research from other fields miss an opportunity to discover and develop important unifying principles in ecology. This commentary is an open invitation to new collaborations on cascading habitat-formation across habitats and ecosystems, aimed at better understanding the generality of these processes and the ecosystem services derived from co-occurring habitat-formers.

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