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Review 3

Facilitation Cascades in Marine Ecosystems: A Synthesis and Future Directions

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FACILITATION CASCADES IN MARINE ECOSYSTEMS: A SYNTHESIS AND FUTURE DIRECTIONS

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Abstract

Facilitation cascades occur when a habitat-forming species facilitates another habitat-forming species with synergistic effects on biodiversity. This review summarizes the current state of knowledge of facilitation cascades in marine environments, describing (1) the geographic distribution of studies documenting facilitation cascades; (2) the range of habitats and organisms involved; (3) the mechanisms underpinning their establishment; and (4) the sources of their spatial and temporal patterns and variability. We synthesize this knowledge to identify ways in which facilitation cascades could be integrated with other ecological theories regarding community assembly and function, and also to explore how they may be integrated into conservation and management strategies. Finally, we identify critical knowledge gaps and future research directions for improving our understanding of the mechanisms regulating the establishment and persistence of facilitation cascades in marine environments.

Introduction

Historically, the processes structuring ecological communities have been viewed through the lens of negative species interactions such as competition and predation (Connell 1961, Paine 1966, Menge & Sutherland 1976). However, the importance of positive interactions in driving community structure has clearly emerged in the last three decades (Connell & Slatyer 1977, Bertness & Callaway 1994, Stachowicz 2001, Reise 2002, Bruno et al. 2003, Silliman et al. 2011). For example, it is now broadly recognized that spatially dominant foundation species (*sensu* Dayton 1972), such as algae, salt-marsh plants, oysters and corals, support biodiversity by defining the physical architecture of

many ecosystems. Similarly, the physical structure of autogenic ecosystem engineers (Jones et al. 1994), which may or may not be space-dominant, shapes biodiversity by creating and maintaining habitats. Together, these two groups, collectively referred to here as *habitat-forming species,* are a key focus of research on positive species interactions. The notion that a suite of organisms create or modify habitat for others has been recognized for over 150 years (Darwin 1859, Hatton 1938). In the late nineteenth century, Karl Möbius, then a professor of zoology at the University of Kiel, coined the term *biocoenosis* to describe biota living together on an oyster bed (Möbius 1877). This term explicitly acknowledged the interconnectedness among taxa from different trophic levels (Keller & Golley 2000)—in this instance, within a habitat-former. A more formal and quantitative understanding of the roles of habitat-formers has developed only recently, however (Jones et al. 1994, Bertness & Leonard 1997, Bruno & Bertness 2001, Hastings et al. 2007, van der Zee et al. 2016).

The majority of studies on positive interactions have considered the effects of habitat-formers independent of one another (Wright & Jones 2006), but habitat-forming species often co-occur in time, space or both, in spatially overlapping or adjacent configurations (Angelini et al. 2011). Multiple habitat-formers may have additive or interactive effects on biodiversity, where they vary functionally, or they cumulatively enhance the availability of a limiting resource (Thomsen et al. 2010, 2018, Angelini et al. 2011). A subset of interactions between habitat-formers, referred to as *facilitation cascades* (a term first coined by Altieri et al. 2007), are hierarchical, whereby a basal habitat-former promotes a secondary habitat-former, which in turn supports an inhabitant community. The species in such hierarchical relationships may spatially overlap (e.g. cordgrass promotes habitat-forming mussel beds between its shoots through shading and substrate stabilization; Altieri et al. 2007) or operate across landscapes (e.g. a mussel bed modifies hydrodynamic and sediment conditions to facilitate a habitat-forming cockle bed hundreds of meters away; van de Koppel et al. 2015) (Figure 1A–C). Although most examples of facilitation cascades include two levels of habitat-formers, up to five levels of co-occurring habitat-formers have been documented (Thomsen et al. 2013, 2016a, Yakovis & Artemieva 2017).

Facilitation cascades arise through three major pathways: (1) the basal habitat-former provides resources (e.g. attachment substrate) to the secondary habitat-former (Boström & Mattila 1999, Bishop et al. 2013, Thomsen et al. 2016a); (2) the basal habitat-former facilitates the secondary habitat-former by reducing environmental stress (Altieri et al. 2007, Gribben et al. 2009a); and (3) the basal habitat-former reduces consumer or competition pressure on the secondary habitat-former (Levenbach 2008, Bulleri et al. 2011, Clements & Hay 2015, Kayal & Kayal 2017, Figures 1 and 2). In many cases, the secondary habitat-former derives two or more of these benefits from the basal habitat-former. As facilitation cascades organize communities hierarchically, the presence of a basal habitat-former is a precondition for the recruitment and persistence of additional habitat-formers (Bruno & Bertness 2001, Altieri et al. 2007, Angelini et al. 2011), with subsequent positive effects on biodiversity.

Facilitation cascades have been documented in a range of terrestrial (Callaway et al. 2001, Ellwood & Foster 2004), freshwater (Blanco et al. 2008, Mormul et al. 2010, Furey et al. 2012) and marine ecosystems (Thomsen et al. 2010, Angelini et al. 2011, Gribben et al. 2017a). For example, epiphytes growing on trees and freshwater plants or drifting algae entrapped by mangrove pneumatophores enhance biodiversity relative to habitat provided by only a single or no habitat-former (Mormul et al. 2010, Bishop et al. 2012, Watson & Herring 2012). Critically, facilitation cascades can have the same or greater importance in shaping community structure than more widely recognized trophic cascades (Estes & Duggins 1995, Schmitz et al. 2000, Shurin et al. 2002), which are another form of sequential interactions (Thomsen et al. 2018). The best-documented facilitation cascades are in marine ecosystems and, more specifically, in intertidal habitats (Thomsen et al. 2018). This may partly reflect a long history of studies of habitat-formers that have focused intensively on their role in alleviating stressors, such as water flow (Fonseca et al. 1982), desiccation (Leonard 1999) and predation pressure (Heck & Orth 1980, Crowder & Cooper 1982). Moreover, interest in
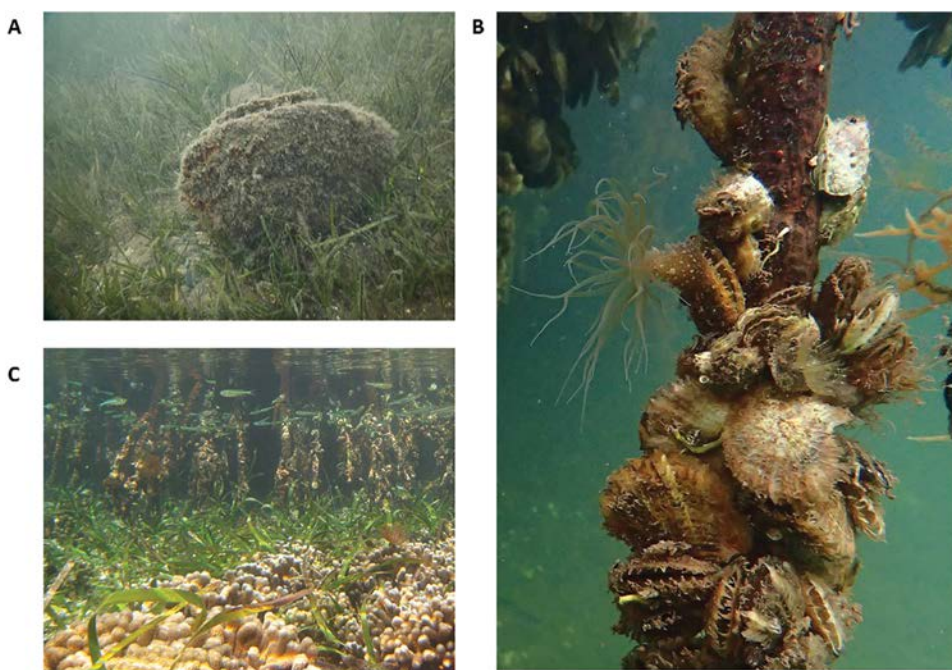
Figure 1 Examples of documented facilitation cascades. (A) Seagrass (basal habitat-former) promotes recruitment of razor clams (secondary habitat-former), possibly by reducing biotic stress (e.g. predation pressure), which in turn provide a surface for attached epibionts (inhabitants); (B) a mangrove pneumatophore (basal habitat-former) provides a surface from colonization by oysters (secondary habitat-former), which in turn provide a surface for an anemone (inhabitant) to colonize; (C) coral reefs buffer seagrass and mangroves from offshore wave energy, allowing them to establish in relative calm areas, whereas mangroves and seagrass trap terrestrial sediment and nutrients that would otherwise lead to smothering of reefs. (A) and (B) are examples of embedded facilitation cascades, whereas in (C), corals, seagrass and mangroves form zones that facilitate one another in a tropical coastal ecosystem. (Photo credits (A) Paul Gribben; (B, C) Andrew Altieri.)

the conservation and restoration of biodiversity in these environments has further motivated research on habitat-formers (Bertness & Hacker 1994, Bertness et al. 1999, Halpern et al. 2007, Wright & Gribben 2017). Among the habitat-formers that play a critical role in shaping marine biodiversity are seagrasses, salt-marsh grasses, algae and kelp, oysters, mussels, polychaete worms, mangroves and deep-sea hydrothermal vent tubeworms and bivalves (Bruno & Bertness 2001, Dubois et al. 2006, Govenar 2010, Portail et al. 2015). Each of these basal habitat-formers, except deep-sea tubeworms and bivalves, which warrant further study, have been observed in facilitation cascades (Altieri et al. 2007, Gribben et al. 2009a, 2017a, Bishop et al. 2012, 2013, Bell et al. 2014, Thomsen et al. 2016a). Nevertheless, the literature on these habitat-formers has largely focused on their aggregate effects, rather than considering interactions among the habitat-formers. One of the most obvious and common examples of this occurs in studies of coral reefs in which investigators often attribute the positive effects of multiple, structurally distinct reef-building corals on fish and invertebrate diversity to the effects of the reef as a whole (Angelini et al. 2011). The growing documentation of marine facilitation cascades suggests that the processes by which habitat-formers control biodiversity have been oversimplified and warrant further attention to inform marine ecosystem management and biodiversity conservation.

Given the burgeoning interest and increasing number of studies documenting facilitation cascades, it is appropriate at this time to review the current state of knowledge of their ecological impacts
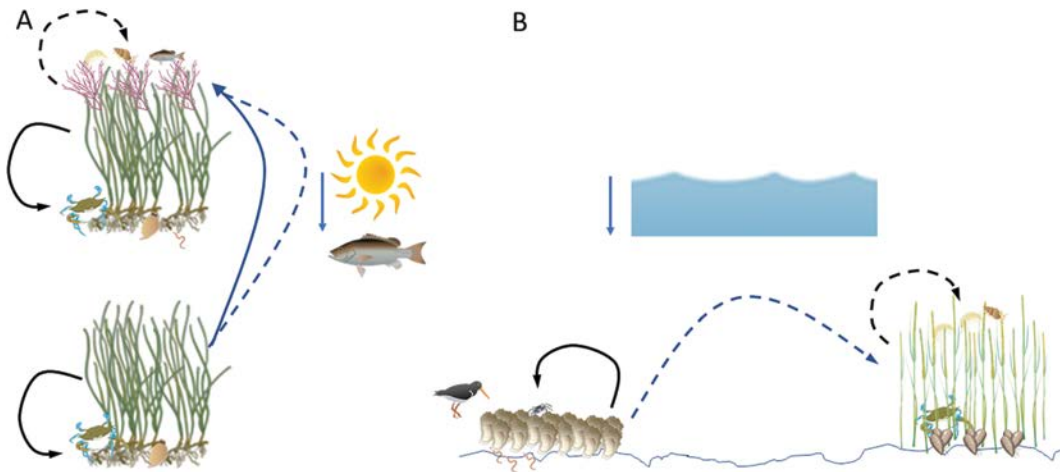
Figure 2 Examples of mechanisms underpinning (A) embedded and (B) adjacent (or landscape) facilitation cascades. For embedded facilitation cascades, basal habitat-formers directly (via substrate provisioning or propagule entrapment; solid blue line) or indirectly (via amelioration of biotic and abiotic stress; dashed blue line) facilitate secondary habitat-formers with synergistic effects on biodiversity; (A) depicts seagrass facilitation of epiphytes. These types of cascades are predicted to have strong positive effects on biodiversity at the patch or local scale. For adjacent facilitation cascades, basal habitat-formers will indirectly (via amelioration of abiotic stress) facilitate secondary habitat-formers outside the basal habitat-former. These types of cascades are predicted to have strong positive effects on biodiversity at the scale of landscapes; (B) indicates facilitation of salt marsh by oysters through buffering wave action. Inhabitants associated with basal and secondary habitat-formers are indicated with solid and dotted black lines, respectively. Pictures courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

and the mechanisms by which they influence biodiversity. In doing so, we identify how facilitation cascades can be integrated with other ecological theories such as the Stress Gradient Hypothesis (SGH; Bertness & Callaway 1994) and be applied to the management of marine ecosystems. In the following sections, we review the current understanding of facilitation cascades in marine ecosystems by (1) providing an overview of published studies on marine facilitation cascades (e.g. including a synthesis of the locations and habitat in which they have been described, and the species they involve); (2) summarizing known mechanisms by which facilitation cascades establish and promote biodiversity; (3) discussing how facilitation cascades may function across multiple spatial scales and environmental contexts; and (4) highlighting how the integration of facilitation cascades into ecological theory is essential for conserving biodiversity, restoring ecological communities and ecosystem functions and managing biodiversity. Finally, we discuss key research gaps and provide recommendations for future research.

Overview of published studies on marine facilitation cascades

Literature search

We explored trends in the geographic regions and marine ecosystem types where facilitation cascades have been documented and summarized the identity of habitat-formers involved in facilitation cascades, as well as the communities they facilitated. To do this, we searched for studies that compared the abundance or taxonomic richness of inhabitants associated with only a basal habitat-former to those associated with co-occurring basal and secondary habitat-formers. We used the methodological definition of a facilitation cascade outlined in Thomsen et al. (2018) in which they

compared and reported the abundance or taxonomic richness of inhabitants associated with only a primary foundation species to those associated with co-occurring primary and secondary foundation species based on field-data collection criteria that allow researchers to evaluate facilitation cascades quantitatively with effect sizes. Relevant studies were identified from literature searches identifying papers up to November 2017.

First, we conducted a standardized Web of Science search, with terms related to fauna, epiphytes and epibionts (because epiphytes and epibionts are typical secondary habitat-formers; Thomsen et al. 2010). Second, we searched for terms related to facilitation and habitat cascades because these processes specifically describe the effects of secondary habitat-formers on inhabitants (Thomsen et al. 2010). This was a two-tiered search, in which we next located references cited in our previous publications on facilitation and habitat cascades, or that cited those works (e.g. Altieri et al. 2007, Thomsen et al. 2010, Thomsen & Wernberg 2014). We then examined papers in which the title, abstract or keywords indicated that relevant data were collected for faunal inhabitants, such as birds, fish or invertebrates associated with a facilitation cascade.

From these searches, we identified 62 relevant papers. Based on personal research expertize and a less-structured search of the literature, we identified another 38 relevant papers that also could be classified as facilitation cascade studies but were not found in the two systematic searches (see Table 1). For each publication in the resulting database, we extracted information about the geographic study location (i.e. the geocoordinates of field data collection sites) and year of publication; latitude, which we binned into traditional climate zones (Tropical = 0–23.5°; Subtropical = 23.5–35°; Temperate = 35–66.5°; Polar = 66.5–90°); overall ecosystem type where the study was conducted (e.g. in a salt-marsh or a mangrove forest); substrate type (rock or soft-sediment substrata); and tidal elevation (subtidal versus intertidal). Additionally, we recorded the taxonomic identity of the habitat-formers (e.g. alga, bivalve, and barnacle), habitat-former type (e.g. studied as a single algal species or as a group of algal species, such as epiphytes) and structural dependencies (i.e. attached to, embedded within or entangled around habitat-formers) of the studied basal and secondary habitat-formers, as well as the type of inhabitants (e.g. invertebrates, fish) that they supported.

Results

To date, facilitation cascades have been studied in 29 countries covering all continents except Antarctica, with more than half (55%) of the cascades being in either the United States or Australia (Figures 3 and 4A). Although the term *facilitation cascade* was first coined in 2007 (Altieri et al. 2007), the first study we identified that described something that seemed to be a facilitation cascade was published in 1980. It documented the positive relationships between red drift algae entangled within seagrass beds and the abundance of banded blennies (*Paraclinus fasciatus*; Stoner & Livingston 1980). Since this publication, at least 99 more studies have documented additional facilitation cascades (Figure 4B, Table 1). Most marine facilitation cascade studies were conducted in subtropical (49%) and temperate regions (35%), with relatively few studies in tropical (10%) or polar (6%) regions (Figure 5A). Importantly, all identified studies occurred in coastal benthic habitats, with no known examples from pelagic or deep-sea benthic ecosystems (Figure 5B). Finally, we found more studies in soft- than hard-bottomed systems (Figure 5C), and in the subtidal zone than in the intertidal zone (Figure 5D).

A total of 37 species have been identified as basal habitat-formers in facilitation cascades (Table 1); most of these are seagrass species, followed by macroalgae, mangrove trees, reef-forming bivalves and salt-marsh plants (but with *Spartina alterniflora* as the only studied salt-marsh species) (Figure 6A). Interestingly, only two studies showed indirect facilitation arising from a mobile basal habitat-former: the snails, *Batillaria australis* and *Littorina littorea* (Thieltges & Buschbaum 2007, Thomsen et al. 2010). Most studies included a single basal habitat-former, although in a few instances, the basal habitat-former consisted of a mixture of species, such as when two or three co-occurring seagrass

Table 1 List of 100 reviewed studies of marine facilitation cascades

References	Basal habitat-former	Secondary habitat-former	Inhabitants	Substratum/elevation
Adams et al. 2004. *Journal of Experimental Marine Biology and Ecology* 299: 17–33	Seagrass	Alga	Fish	Soft sediments/Subtidal
Albrecht & Reise. 1994. *Helgoländer Wissenschaftliche Meeresuntersuchungen* 48: 243–256	Bivalve	Alga	Invertebrates	Soft sediments/Intertidal
Altieri et al. 2007. *American Naturalist* 169: 195–206	Salt marsh	Bivalve	Invertebrates, Alga	Rocky shores/Intertidal
Altieri et al. 2010. *Ecology* 91: 1269–1275	Salt marsh	Bivalve	Invertebrates	Rocky shores/Intertidal
Altieri & Irving 2017. *PeerJ* 5:e2848.	Salt marsh	Bivalve	Invertebrates	Rocky shores/Intertidal
Angelini et al. 2015. *Proceedings of the Royal Society B* 282: 1811	Salt marsh	Bivalve	Invertebrates	Rocky shores/Intertidal
Armitage & Sjoetun 2016. *Hydrobiologia* 776: 35–49	Alga	Alga	Invertebrates	Rocky shores/Intertidal
Armitage & Sjoetun 2016. *Hydrobiologia* 776: 35–49	Alga	Alga	Invertebrates	Rocky shores/Intertidal
Arroyo et al. 2013. *Marine Ecology* 34: 345–362	Seagrass	Alga	Invertebrates	Soft sediments/Subtidal
Barros & Rocha-Barreira. 2013. *Annals of the Brazilian Academy of Sciences* 85: 1397–1410	Seagrass	Alga	Invertebrates	Soft sediments/Intertidal
Bell & Westoby. 1987. *Australian Journal of Ecology* 12: 333–337	Seagrass	Alga	Invertebrates, Fish	Soft sediment/Subtidal
Bell et al. 2014. *Marine Ecology Progress Series* 501: 1–10	Alga	Urchin	Invertebrates	Rocky shores/Subtidal
Bishop et al. 2009. *Marine Ecology Progress Series* 392: 111–122	Mangrove pneumatophores	Alga	Invertebrates	Soft sediments/Intertidal
Bishop et al. 2012. *Ecology* 93: 1388–1401	Mangrove pneumatophores	Alga	Invertebrates	Soft sediments/Intertidal
Bishop et al. 2013. *Ecology* 94:1927–1936	Mangrove pneumatophores	Alga	Invertebrates	Soft sediments/Intertidal
Bologna & Heck 1999. *Journal of Experimental Marine Biology and Ecology* 242: 21–39	Seagrass	Alga	Invertebrates, Alga	Soft sediments/Subtidal
Bologna & Heck 1999. *Journal of Experimental Marine Biology and Ecology* 242: 21–39	Seagrass	Alga	Invertebrates, Alga	Soft sediments/Subtidal
Bologna & Heck. 2000. *Estuaries* 23: 449–457	Seagrass	Alga	Invertebrates	Soft sediments/Subtidal
Borg et al. 2010. *Marine Ecology Progress Series* 406: 91–104	Seagrass	Alga	Invertebrates	Soft sediment/Subtidal
Bostroem & Mattila. 1999. *Oecologia* 120: 162–170	Seagrass	Alga, diatoms	Invertebrates	Soft sediment/Subtidal
Bostroem & Mattila. 1999. *Oecologia* 120: 162–170	Seagrass	Alga, diatoms	Invertebrates	Soft sediment/Subtidal
Bryars & Wear. 2008. *Transaction of the Royal Society of South Australia* 132: 81–94	Seagrass	Alga	Invertebrates	Soft sediment/Subtidal
Buzá-Jacobucci & Pereira-Leite. 2014. *Latin American Journal of Aquatic Research* 42: 353–363	Alga	Alga	Invertebrates	Rocky Shores/Subtidal

(Continued)

Table 1 (Continued) List of 100 reviewed studies of marine facilitation cascades

References	Basal habitat-former	Secondary habitat-former	Inhabitants	Substratum/elevation
Buzá-Jacobucci & Pereira-Leite. 2014. *Latin American Journal of Aquatic Research* 42: 353–363	Alga	Alga	Invertebrates	Rocky Shores/Subtidal
Cardoso et al. 2004. *Journal of Experimental Marine Biology and Ecology* 308: 207–220	Seagrass	Alga	Invertebrates	Soft sediment/Intertidal
Cardoso et al. 2004. *Journal of Experimental Marine Biology and Ecology* 308: 207–220	Seagrass	Alga	Invertebrates	Soft sediment/Intertidal
Castejon-Silvo et al. 2012. *Estuarine, Coastal and Shelf Science* 112: 225–235	Seagrass	Alga	Invertebrates	Soft sediment/Subtidal
Chapman et al. 2005. *Journal of the Marine Biological Association of the United Kingdom* 85: 1481–1488	Mangrove	Alga	Invertebrates	Soft sediment/Intertidal
Christie et al. 2003. *Journal of the Marine Biological Association of the United Kingdom* 83: 687–699	Alga	Alga	Invertebrates	Rocky Shores/Subtidal
Dijkstra et al. 2012. *Oikos* 121: 646–654	Salt marsh	Alga	Invertebrates	Soft sediment/Intertidal
Dijkstra et al. 2012. *Oikos* 121: 646–654	Salt marsh	Alga	Invertebrates	Soft sediment/Intertidal
Drouin et al. 2011. *Marine Ecology Progress Series* 424: 105–117	Seagrass	Alga	Invertebrates	Soft sediment/Subtidal
Dubois et al. 2006. *Estuarine, Coastal and Shelf Science* 68: 635–646	Reef-forming tubeworm	Alga	Invertebrates	Rocky shore/Intertidal
Dubois et al. 2006. *Estuarine, Coastal and Shelf Science* 68: 635–646	Reef-forming tubeworm	Alga with bivalve	Invertebrates	Rocky shore/Intertidal
Dubois et al. 2006. *Estuarine, Coastal and Shelf Science* 68: 635–646	Reef-forming tubeworm	Bivalve	Invertebrates	Rocky shore/Intertidal
Dubois et al. 2006. *Estuarine, Coastal and Shelf Science* 68: 635–646	Reef-forming tubeworm	Bivalve with Alga	Invertebrates	Rocky shore/Intertidal
Edgar & Robertson. 1992. *Journal of Experimental Marine Biology and Ecology* 160: 13–31	Seagrass	Alga	Invertebrates, Alga	Rocky shore/Subtidal
Ekloef et al. 2006. *Marine Ecology Progress Series* 325: 73–84	Seagrass	Alga	Invertebrates	Soft sediment/Subtidal
Escapa et al. 2004. *Journal of Shellfish Research* 23: 765–772	Salt marsh	Bivalve	Invertebrates	Soft sediment/Intertidal
Gartner et al. 2013. *Journal of Experimental Marine Biology and Ecology* 143–151	Seagrass	Alga	Invertebrates	Soft sediment/Subtidal
Gartner et al. 2013. *Journal of Experimental Marine Biology and Ecology* 143–151	Seagrass	Alga	Invertebrates	Soft sediment/Subtidal
Green & Crowe. 2014. *Biological Invasions* 16: 1145–1165	Bivalve	Bivalve	Invertebrates	Soft sediment/Intertidal
Gribben et al. 2009. *Ecology Letters* 12: 1127–1136	Alga	Bivalve	Invertebrates	Soft sediment/Subtidal
Gribben et al. 2017. *Ecosphere* 8: 1–14	Seagrass	Bivalve	Invertebrates, Fish	Soft sediment/Subtidal
Grutter & Irwin. 2007. In *Marine Ecology* Oxford University Press (eds: Connell & Gillanders) p 110–137	Seagrass	Epibionts	Invertebrates	Soft sediment/Subtidal

(Continued)

Table 1 (Continued)   List of 100 reviewed studies of marine facilitation cascades

References	Basal habitat-former	Secondary habitat-former	Inhabitants	Substratum/elevation
Gutierrez & Palomo. 2016. *Journal of Sea Research* 112: 49–54	Bivalve	Barnacle	Alga	Rocky Shore/Intertidal
Hall & Bell. 1988. *Journal of Marine Research* 46: 613–630	Seagrass	Alga	Invertebrates	Soft sediment/Subtidal
Hall & Bell. 1993. *Marine Biology* 116: 137–146	Seagrass	Alga	Invertebrates	Soft sediment/Subtidal
Hamamoto & Mukai. 1999. *Marine Ecology* 20: 521–272	Seagrass	Alga	Invertebrates	Soft sediment/Subtidal
Holmquist. 1997. *Marine Ecology Progress Series* 158: 121–130	Seagrass	Alga	Invertebrates, Alga	Soft sediment/Subtidal
Hughes et al. 2014. *Marine Ecology Progress Series* 508: 129–138	Mangrove pneumatophores	Alga	Invertebrates	Soft sediment/Subtidal
Hughes et al. 2014. *Marine Ecology Progress Series* 508: 129–138	Mangrove pneumatophores	Bivalve	Invertebrates	Soft sediment/Subtidal
Inglis. 1994. *Oecologia* 99: 352–365	Seagrass	Bivalve	Alga	Soft sediment/Subtidal
Ingólfsson & Olafsson. 1997. *Journal of Plankton Research* 19: 15–24	Alga	Alga	Invertebrates	Rocky shore/Intertidal
Irving et al. 2007. *Journal of Experimental Marine Biology and Ecology* 340: 40–49	Seagrass	Epibionts	Invertebrates	Soft sediment/Subtidal
Jaxion & Speight. 2012. *Journal of Experimental Marine Biology and Ecology* 414: 19–27	Mangrove	Alga	Invertebrates	Soft sediment/Intertidal
Jones, & Thornber. 2010. *Marine Ecology Progress Series* 400: 87–100	Alga	Alga	Invertebrates	Rocky shore/Intertidal
Kelaher et al. 2001. *Journal of the Marine Biological Association of the United Kingdom* 81: 917–930	Coralline turf	Alga	Invertebrates	Rocky shore/Intertidal
Kelaher et al. 2005. *Estuarine, Coastal and Shelf Science* 63: 155–165	Coralline turf	Alga	Invertebrates	Rocky shore/Intertidal
Kelaher et al. 2007. *Journal of Molluscan Study* 73: 139–146	Coralline turf	Alga	Invertebrates	Rocky shore/Intertidal
Kochmann et al. 2008. *Journal of Experimental Marine Biology and Ecology* 364: 1–10	Bivalve	Bivalve	Invertebrates	Soft sediment/Intertidal
Koivisto & Westerbom. 2010. *Marine Biology* 157: 1463–1474	Bivalve	Alga	Invertebrates	Rocky shore/Subtidal
Koivisto & Westerbom. 2010. *Marine Biology* 157: 1463–1474	Bivalve	Alga	Invertebrates	Rocky shore/Subtidal
Koivisto et al. 2011. *Aquatic Biology* 12: 261–270	Bivalve	Alga	Invertebrates	Rocky shore/Subtidal
Kulczycki et al. 1981. *Estuarine, Coastal and Shelf Science* 12: 341–347	Seagrass	Alga	Fish	Soft sediment/Subtidal
Laegdsgaard & Johnson. 2001. *Journal of Experimental Marine Biology and Ecology* 257: 229–253	Mangrove	Alga	Fish	Soft sediment/Intertidal
Leber. 1985. *Ecology* 66: 1951–1964	Seagrass	Alga	Invertebrates	Soft sediment/Subtidal
MacDonald et al. 2008. *Estuaries & Coasts* 31: 981–993	Mangrove	Sponge	Fish	Soft sediment/Subtidal
MacDonald et al. 2008. *Estuaries & Coasts* 31: 981–993	Mangrove	Tunicate	Fish	Soft sediment/Subtidal

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Table 1 (Continued) List of 100 reviewed studies of marine facilitation cascades

References	Basal habitat-former	Secondary habitat-former	Inhabitants	Substratum/elevation
MacDonald et al. 2013. *Journal of Experimental Marine Biology and Ecology* 441: 90–98	Mangrove	Epibionts (alga, sponges, tunicates, molluscs)	Fish	Soft sediment/Subtidal
Macreadie et al. 2014. *Journal of Molluscan Study* 80: 102–106	Seagrass	Bivalve	Invertebrates, Fish	Soft sediment/Subtidal
Martin-Smith. 1993. *Journal of Experimental Marine Biology and Ecology* 174: 243–260	Alga	Alga	Invertebrates	Rocky shore/Subtidal
McAfee et al. 2016. *Ecology* 97: 929–939	Mangrove pneumatophores	Bivalve	Invertebrates	Soft sediment/Intertidal
Mendez et al. 2015. *Aquatic Ecology* 49: 441–452	Salt marsh	Barnacle	Invertebrates	Soft sediment/Intertidal
Mendez et al. 2015. *Aquatic Ecology* 49: 441–452	Bivalve	Barnacle	Invertebrates	Soft sediment/Intertidal
Mukai & Ijima. 1995. *Ecological Research* 10: 243–257	Seagrass	Cyanobacteria	Invertebrates	Soft sediment/Subtidal
Munguia & Miller. 2008. *Journal of Animal Ecology* 77: 1175–1182	Seagrass	Bivalve	Invertebrates	Soft sediment/Subtidal
Munguia. 2007. *Marine Biology* 152: 149–156	Seagrass	Bivalve	Invertebrates	Soft sediment/Subtidal
Munguia. 2014. *Oecologia* 174: 1335–1344	Seagrass	Bivalve	Invertebrates	Soft sediment/Subtidal
Newell et al. 1991. *Journal of World Aquaculture Society* 22: 134–152	Seagrass	Alga	Invertebrates	Soft sediment/Intertidal
Norling & Kautsky. 2007. *Marine Ecology Progress Series* 351: 163–175	Bivalve	Alga	Invertebrates	Soft sediment/Intertidal
Norton & Benson. 1983. *Marine Biology* 75: 169–177	Alga	Diatoms	Invertebrates	Rocky shore/Subtidal
Pavia et al. 1999. *Journal of Experimental Marine Biology and Ecology* 236: 15–32	Alga	Alga	Invertebrates	Rocky shore/Intertidal
Poore et al. 2000. *Marine Ecology Progress Series* 208: 183–196	Alga	Alga	Invertebrates	Rocky shore/Subtidal
Poore et al. 2000. *Marine Ecology Progress Series* 208: 183–196	Alga	Alga	Invertebrates	Rocky shore/Subtidal
Proches & Marshall. 2002. *Journal of the Marine Biological Association of the United Kingdom* 85: 937–942	Mangrove	Alga	Invertebrates	Soft sediment/Intertidal
Ray et al. 2014. *PLOS ONE* 9: e107751	Seagrass	Alga	Invertebrates, Fish	Soft sediment/Subtidal
Rohr et al. 2011. *Aquatic Ecology* 45: 213–219	Alga	Alga	Invertebrates	Rocky shore/Subtidal
Ross. 2006. *Wetlands Ecology & Management* 14: 167–184	Mangrove	Alga	Invertebrates	Soft sediment/Intertidal
Rutledge & Fleeger. 1993. *Estuaries* 16: 760–768	Salt marsh	Alga	Invertebrates	Soft sediment/Intertidal
Saunders & Connell. 2001. *Austral ecology* 26: 109–115	Mangrove	Seagrass	Invertebrates	Soft sediment/Intertidal

(Continued)

Table 1 (Continued) List of 100 reviewed studies of marine facilitation cascades

| References	Basal habitat-former	Secondary habitat-former	Inhabitants	Substratum/elevation
Schneider & Mann. 1991. *Journal of Experimental Marine Biology and Ecology* 145: 119–139	Seagrass	Alga	Invertebrates	Soft sediment/Subtidal
Schneider & Mann. 1991. *Journal of Experimental Marine Biology and Ecology* 145: 119–139	Alga	Alga	Invertebrates	Soft sediment/Subtidal
Schneider & Mann. 1991. *Journal of Experimental Marine Biology and Ecology* 145: 119–139	Alga	Alga	Invertebrates	Soft sediment/Subtidal
Skilleter & Warren. 2000. *Journal of Experimental Marine Biology and Ecology* 244: 107–129	Mangrove	Alga	Invertebrates	Soft sediment/Intertidal
Stoner & Lewis. 1985. *Journal of Experimental Marine Biology and Ecology* 94: 19–40	Seagrass	Alga	Invertebrates	Soft sediment/Subtidal
Stoner & Livingston. 1980. *Marine Biology* 56: 239–246	Seagrass	Alga	Fish	Soft sediment/Subtidal
Thieltges & Buschbaum. 2007. *Journal of Experimental Marine Biology and Ecology* 340: 90–95	Gastropod	Barnacle	Invertebrates	Rocky shore/Intertidal
Thieltges & Buschbaum. 2007. *Journal of Experimental Marine Biology and Ecology* 340: 90–95	Gastropod	Worm (burrowing)	Invertebrates	Rocky shore/Intertidal
Thomsen. 2010. *Aquatic Invasions* 5: 341–346	Seagrass	Alga	Invertebrates	Soft sediment/Intertidal
Thomsen et al. 2010. *Integrative and Comparative Biology* 50: 158–175	Tube worm	Alga	Invertebrates	Soft sediment/Intertidal
Thomsen et al. 2010. *Integrative and Comparative Biology* 50: 158–175	Gastropod	Alga	Invertebrates	Soft sediment/Subtidal
Thomsen et al. 2010. *Integrative and Comparative Biology* 50: 158–175	Bivalve	Alga	Invertebrates	Soft sediment/Intertidal
Thomsen et al. 2010. *Integrative and Comparative Biology* 50: 158–175	Bivalve	Alga	Invertebrates	Soft sediment/Intertidal
Thomsen et al. 2012. *Harmful Alga* 16:74–80	Seagrass	Alga	Invertebrates	Soft sediment/Subtidal
Thomsen et al. 2013. *Aquatic Invasions* 8: 133–145	Seagrass	Alga	Invertebrates	Soft sediment/Subtidal
Thomsen et al. 2013. *Aquatic Invasions* 8: 133–145	Bivalve	Alga	Invertebrates	Soft sediment/Subtidal
Thomsen et al. 2013. *Aquatic Invasions* 8: 133–145	Seagrass	Alga	Invertebrates	Soft sediment/Subtidal
Thomsen et al. 2016. *Ecology and Evolution* 6: 8291–8303	Seagrass	Alga	Invertebrates, Alga	Soft sediment/Intertidal
Thomsen et al. 2016. *Ecology and Evolution* 6: 8291–8303	Seagrass	Alga	Invertebrates, Alga	Soft sediment/Intertidal
Thomsen et al. 2016. *Ecology and Evolution* 6: 8291–8303	Bivalve	Alga	Invertebrates, Alga	Soft sediment/Intertidal

(Continued)

Table 1 (Continued)   List of 100 reviewed studies of marine facilitation cascades

| References	Basal habitat-former	Secondary habitat-former	Inhabitants	Substratum/elevation
Thomsen et al. 2016. *Marine and Freshwater Research* 67: 144–152	Alga	Alga	Invertebrates	Rocky shore/Intertidal
Trowbridge. 1993. *Marine Ecology Progress Series* 101: 263–272	Alga	Alga	Invertebrates	Rocky shore/Intertidal
Tyrrell et al. 2012. *Estuaries & Coasts* 35: 754–762	Salt marsh	Alga	Invertebrates	Soft sediment/Intertidal
Valentine & Heck. 1993. *Marine Ecology Progress Series* 96: 63–74	Seagrass	Bivalve	Invertebrates	Soft sediment/Subtidal
Verweij et al. 2006. *Marine Ecology Progress Series* 306: 257–268	Mangrove	Alga	Fish	Soft sediment/Subtidal
Viejo & Aaberg. 2003. *Marine Biology* 142: 1229–1241	Alga	Alga	Invertebrates	Rocky shore/Intertidal
Viejo & Aaberg. 2003. *Marine Biology* 142: 1229–1241	Alga	Alga	Invertebrates	Rocky shore/Intertidal
Wikstroem & Kautsky. 2004. *Biological Invasions* 6: 141–150	Alga	Alga	Invertebrates	Rocky shore/Intertidal
Williams & Hughes. 2002. *Biological Bulletin* 203: 248–249	Seagrass	Alga	Invertebrates	Soft sediment/Subtidal
Worm & Sommer. 2000. *Marine Ecology Progress Series* 202: 283–288	Alga	Alga	Invertebrates	Rocky Shore/Subtidal
Worthington et al. 1991. *Australian Journal of Ecology* 16: 289–293	Seagrass	Alga	Fish	Soft sediment/Subtidal
Yakovis & Artemieva. 2017. *Scientific Report* 7: 1–11	Bivalve	Barnacle	Invertebrates	Soft sediment/Subtidal
Yakovis & Artemieva. 2017. *Scientific Report* 7: 1–11	Bivalve	Barnacle	Invertebrates	Soft sediment/Subtidal
Yamada & Kumagai. 2012. *Hydrobiologia* 680: 125–133	Seagrass	Alga	Invertebrates	Soft sediment/Subtidal
Zakhama-Sraieb et al. 2011. *Helgoland Marine Research* 65: 203–209	Seagrass	Alga	Invertebrates	Soft sediment/Subtidal

Figure 3 Location of 100 publications documenting marine facilitation cascades. See Table 1 for details about each of these publications.
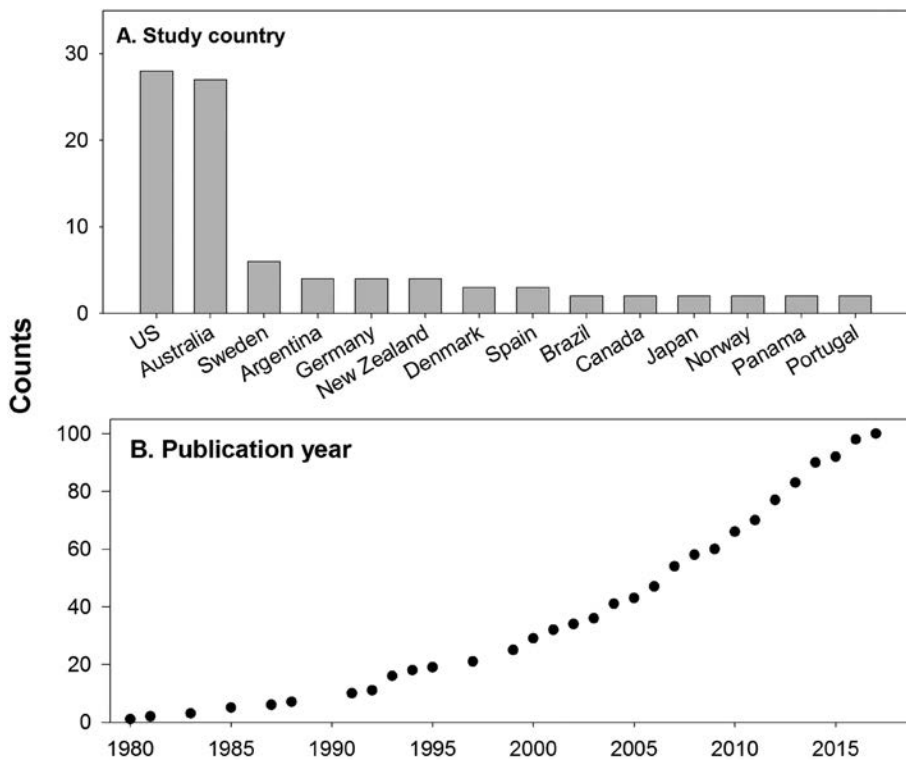
Figure 4 Study attributes of 100 marine facilitation cascade studies. (A) Countries where studies were carried out (to simplify this plot, countries with a single study were excluded—that is, Chile, Fiji, Finland, France, Honduras, Iceland, Ireland, Malta, Antilles, Russia, South Africa, Tanzania, Tunisia, the United Kingdom and Venezuela). Note that a single publication could include multiple counts, such as if it examined the incidence of facilitation cascades in several countries. (B) Cumulative list of publication from 1980 (first publication) to 2017 (100 publications).
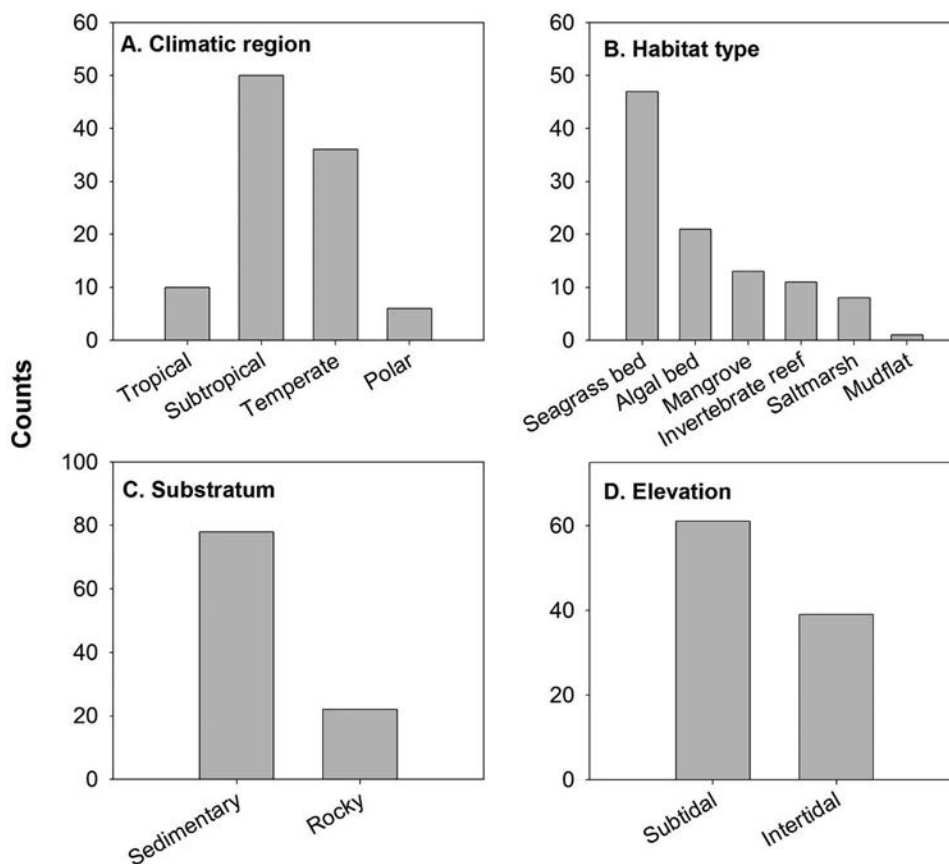
Figure 5 System attributes of the 100 marine facilitation cascade studies (summarized in Table 1). (A) Studies divided by climatic region (Tropical = 0–23.5°; Subtropical = 23.5–35°; Temperate = 35–66.5°; Polar = 66.5–90°). (B) Studies classified by the type of habitat the study was conducted in. (C) Studies divided by fundamental substratum (soft-sediments or hard) each study was conducted on (note, all studies from seagrass beds were carried out in soft-sediment systems whereas most studies from seaweed beds were carried out on rocky reefs). (D) Studies divided into subtidal or intertidal elevations. A single publication could include multiple counts, such as if a facilitation cascade study was carried out simultaneously in different habitats (e.g. adding seaweed to both a seagrass bed and a mussel reef as a secondary habitat-former).

species provide a mixed habitat for secondary habitat-forming epiphytes (e.g. Stoner & Livingston 1980, Edgar & Robertson 1992; see Figure 6B and Table 1 for details). A few studies used mimics or dead shells/tests of basal habitat-formers to elucidate the relative importance of trophic versus structural mechanisms by which they facilitate secondary habitat-formers (e.g. Bologna & Heck 1999, 2000, MacDonald et al. 2008, Yakovis & Artemieva 2017).

Algae were the most commonly recorded secondary habitat-formers, followed by bivalves (Figure 6C), which together accounted for 92% of all studies. In contrast to basal habitat-formers, a large proportion (41%) of studies on secondary habitat-formers involved multiple coexisting species (Figure 6D), typically because epiphyte assemblages are studied as an entity (Table 1). Only one study documented a facilitation cascade involving a mobile secondary habitat-former, the urchin *Holopneustes purpurascens,* which inhabits the canopy of the kelp *Ecklonia radiata* wrapping the kelp around itself, in doing so, facilitates the gastropod *Phasianotrochus eximius* (Bell et al. 2014). Similar to basal habitat-formers, however, only a few studies used mimics or shells/tests to
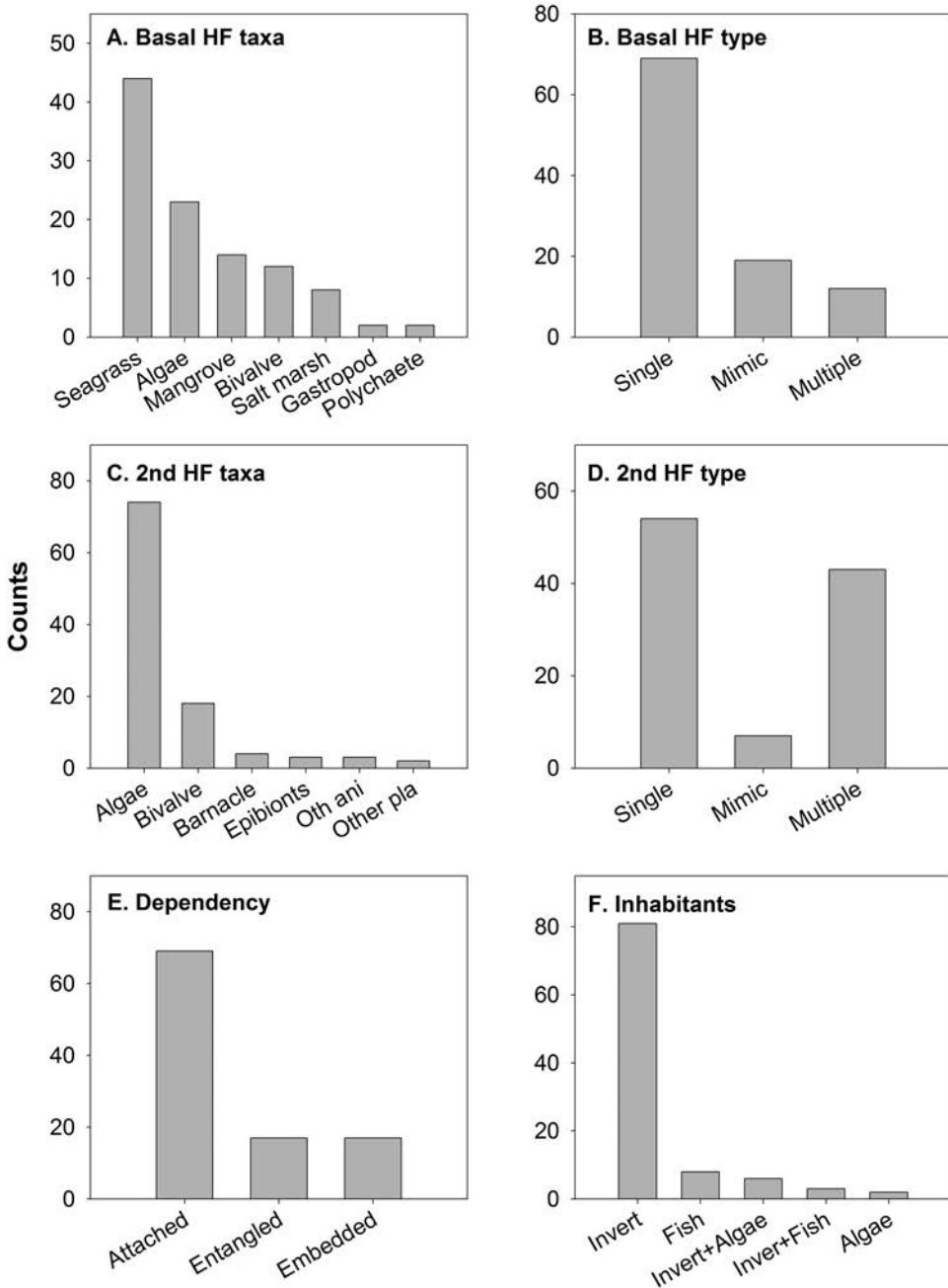
Figure 6 Organismal attributes of 100 marine facilitation cascade studies. (A) The coarse taxonomic identity habitat of basal habitat-formers. (B) Whether basal habitat-formers were Single (i.e. an individual, living species), Mimic (i.e. a single, nonliving mimic of a species) or Multiple (i.e. a group of species, such as 'seaweed' referring to multiple species). (C) and (D), same as (A) and (B), respectively, but for secondary habitat-formers. (E) The type of physical dependency between the basal and secondary habitat-formers. (F) The identity of the inhabitant species and/or assemblage that was studied. 2nd = secondary, HF = habitat-forming species. Invert = Invertebrate. A single publication could include multiple counts, for example if a facilitation cascade study was carried out simultaneously with different 2nd habitat-formers.

determine how secondary habitat-formers facilitate biodiversity (e.g. MacDonald et al. 2008, Gartner et al. 2013, Yakovis & Artemieva 2017). Most studies focused on secondary habitat-formers that are physically attached to the basal habitat-formers (Figure 6E). Macroinvertebrates were the most common inhabitants recorded, although facilitation of fish communities was demonstrated in several studies (e.g. Stoner & Livingston 1980, MacDonald et al. 2008, MacDonald & Weis 2013, Figure 6F).

The mechanisms underpinning facilitation cascades

While a growing number of studies demonstrate hierarchical positive interactions among species, the mechanisms by which facilitation cascades are established and maintained have been subject to surprisingly little investigation (Thomsen et al. 2018). The treatments that are necessary to ascertain whether facilitation occurs through resource provisioning or environmental or biotic stressor amelioration, such as structural mimics or manipulations of predators, competitors and/or stressors, are rarely included in experimental designs (Thomsen et al. 2018; but see notable exceptions discussed later in this review). Studies comparing species interactions across environmental gradients provide some insights into mechanisms, as described in the section on facilitation cascades along abiotic and biotic gradients later in this review, although such a comparative approach alone is insufficient to infer causal relationships due to their descriptive nature. Experimental tests of facilitation cascades have largely focused on how biodiversity responds to manipulations of secondary habitat-formers (e.g. Hall & Bell 1988, Koivisto & Westerbom 2010, Gartner et al. 2013). In a few instances, however, the full range of hierarchical interactions underpinning facilitation cascade control of biodiversity has been determined. For example, Gribben et al. (2009a,b) and Altieri et al. (2007) demonstrated, through the use of experimental treatments mimicking the stress-altering effects of habitat-formers, that interactions between the basal and secondary habitat-formers were largely mediated by the modification of abiotic conditions. However, secondary habitat-former effects on the associated community occurred through the provision of physical structure and further reductions in environmental stress. Thus, experiments can reveal how multiple mechanisms operate within a facilitation cascade where basal and secondary foundation species have complementary traits.

Regardless of how species benefit from positive interactions, associations between basal and secondary habitat-formers and between secondary habitat-formers and inhabitant communities may arise via active or passive processes. In some instances, the dependent species may be able to detect the facilitator and actively search for it or remain within or on it once found. In others, the dependent species may not actively choose the facilitator per se, but may suffer enhanced mortality when not associated with it, so that the two become associated. These relationships may be obligate, if survival of the dependent species is impossible in the absence of the habitat-former, or facultative, if the dependent species, although more abundant when found with the basal habitat-former, is able to survive outside the association. In obligate mutualistic associations, host recognition is vital for the survival of the participants involved (Ambrosio & Brooks 2011). In facultative relationships, however, the need for host detection is less critical, and often the proficiency of host recognition is weaker (Ambrosio & Brooks 2011). The relative importance of active and passive processes in maintaining facilitation cascades is little studied. Nevertheless, using a combination of field and laboratory experiments, Bell (2013) found that both reduced mortality and habitat selection contributed to a gastropod's greater abundance on kelp with urchins than without them. In the laboratory, the gastropod, *P. eximius*, used visual cues to locate urchins on kelp.

Resource provisioning

Facilitation commonly results from the provision of limiting resources by habitat-formers (Jones et al. 1994, 1997, Bruno & Bertness 2001, Bruno et al. 2003, Bulleri 2009). For marine organisms,

such resources commonly include settlement substrate and food. In many instances, basal habitat-formers appear to facilitate secondary habitat-formers by providing a stable or suitable substrate for colonization via larval/propagule settlement or entrapment (Figures 1A,B and 2A). For example, mollusc shells provide a hard surface for colonization by algae on rocky substrata (Dayton 1973, O'Connor & Crowe 2008, Martins et al. 2014), where consumer pressure and competition for space are great (Connell 1961, Menge 1976, Hawkins 1981, Menge & Lubchenco 1981), and in soft-sediment environments, in which suitable substrata are otherwise absent (Gutierrez et al. 2003, Thomsen et al. 2016a) and mangrove pneumatophores and seagrass shoots trap and retain floating algae (Adams et al. 2004, Bishop et al. 2012, 2013, Hughes et al. 2014). Secondary habitat-formers commonly enhance biodiversity by providing structural resources for colonization (Hall & Bell 1988, Bologna & Heck 2000, Altieri et al. 2007, Gartner et al. 2013, Figures 1A,B and 2A,B). Interestingly, via overgrowth and smothering or increasing the likelihood of dislodgment during storms, colonizing habitat-formers can also reduce the growth, health and survivorship of basal habitat-formers (Dayton 1973, Inglis 1994, O'Connor et al. 2006). Although not considered in a facilitation cascade context, such negative feedbacks have the potential to affect the facilitation of the associated community and the stability of the facilitation cascade itself.

Although not necessarily the primary mechanism by which they support inhabitant communities, basal and secondary habitat-formers may also facilitate biodiversity by enhancing the availability of food resources. First, the habitat-former may trap or retain food resources, such as detritus and other organic matter, that are drifting through a habitat. For example, intertidal ribbed mussels consume detritus that is produced and retained by the basal habitat-forming cordgrass (Kreeger et al. 1988, Altieri et al. 2007). These mussels also filter planktonic algae from the water column during high tide and through their deposition of pseudofeces, which locally alter nutrient and benthic algae composition and quantity (Bertness 1984, Derksen-Hooijberg et al. 2018). Second, inhabitants facilitated by habitat-formers may consume one another. Gribben et al. (2017a) found that predatory fish facilitated by secondary habitat-forming razor clams consumed epibionts that recruited to the surface of the clams. In a few instances, the habitat-formers in the facilitation cascade provide both physical habitat and food resources. Epiphytes on the fucoid alga *Ascophyllum nodosum* provided a physical habitat for several species of amphipod species that also fed on both the epiphytes and the alga (Pavia et al. 1999). Explicit tests that utilize mimics of habitat-formers to resolve whether facilitation occurs via food enhancement versus habitat-provisioning, however, provide mixed results. Communities on habitat mimics can be characterized by different compositions and numbers of taxa compared to a live habitat-former (Hall & Bell 1988, Verweij et al. 2006, Koivisto et al. 2011, Gartner et al. 2013). In addition to mimics, stable isotopes have been used to identify potential trophic linkages among habitat-formers and associated intertidal food webs. For example, cordgrass and mussels on New England cobble beaches and seagrass and pool-excavating crabs in West African seagrass meadows all enhanced food-web complexity, primarily through habitat modification rather than food provisioning (van der Zee et al. 2016). In both systems, the habitat-formers accounted for little to none of the diet of most species they facilitated.

When they consume habitat-forming species, dependent species may have negative effects on their biomass. For example, sea slugs facilitated by a secondary habitat-former, epiphytic algae, increased herbivory on the basal algal habitat-former (Trowbridge 1993). Clearly, for the facilitation cascade to persist, the basal and/or secondary habitat-formers cannot be consumed in quantities that result in the collapse of the facilitation cascade. Competition for space from inhabitants that do not consume the habitat-formers may be one important (but untested) mechanism reducing negative feedbacks on habitat-formers and enabling the persistence of the facilitation cascade. Regardless, consumptive effects may nevertheless result in the realized biodiversity of a facilitation cascade being lower than the potential biodiversity that would occur in the absence of consumption.

Environmental stressor amelioration

Alternatively, the role of basal habitat-formers can be that of buffering environmental stress (Figures 1C and 2A,B), a mechanism widely documented in intertidal environments (Figure 5D). For example, on cobble beaches along the Atlantic coast of the United States, cordgrass fosters the abundance of ribbed mussels, the secondary habitat-formers, by stabilizing the cobble substrates and reducing stress due to waves and desiccation (Altieri et al. 2007). On intertidal rocky shores, reduction of heat and desiccation by intertidal habitat-forming species, such as macroalgal canopies (Bertness et al. 1999, Jenkins et al. 1999), barnacles (Kawai & Tokeshi 2006) and bivalves (Silliman et al. 2011), promotes the colonization of more stress-sensitive macroalgae and invertebrates (see Bulleri 2009 for a review). In at least one instance, the exacerbation rather than the amelioration of an environmental stressor appears to be the driver of a facilitation cascade. Decreases in sediment oxygen by the invasive alga *Caulerpa taxifolia* promote a shallower burial depth of clams, enhancing the recruitment of epibionts to exposed shells (Gribben et al. 2009a, b). Although changes in habitat quality can also decrease the health and survivorship of individual clams, this is somewhat mitigated by clam behaviour (Wright et al. 2007, 2010, Wright & Gribben 2008), and there is a clear net gain in biodiversity across the landscape when this facilitation cascade is present.

Biotic stressor amelioration

The physical structure provided by habitat-formers can also facilitate associated biota by reducing negative biological interactions such as predation or competition (e.g. Orth et al. 1984, Grabowski 2004, Griffen & Byers 2006; also see Figure 2). For example, drift algae entrapped in seagrass (Adams et al. 2004) and algal cover on mangrove prop-roots (Jaxion-Harm & Speight 2012) facilitated post-settlement fish and crab survival by reducing predator foraging. On shallow rocky reefs, anemones and tube-building gastropods can constrain foraging bouts of sea urchins, thus providing a refuge for algal turf (Levenbach 2008, Bulleri et al. 2011). Although positive effects of enhanced macroalgal cover on invertebrates (the inhabitant species) have not been formally assessed in these specific cases, there is a wealth of evidence that they are very likely to occur (Sarda 1991, Kelaher et al. 2001, Teagle et al. 2017). Further, macroalgal canopies often promote understory assemblages of macroalgae and sessile invertebrates which in turn, facilitate a diversity of mobile invertebrates, likely because the canopy-forming macroalgae reduce dominance by competitively superior species, predation pressure or both (Bulleri et al. 2002, Eriksson et al. 2006, Clements & Hay 2015, Cardenas et al. 2016). This was observed where opportunistic, fast-growing macroalgal species (i.e. filamentous algal turf) readily monopolize space under full light, driving the loss of sessile invertebrate and macroalgal habitat-formers (Bulleri et al. 2002, Cardenas et al. 2016).

Variation between intertidal and subtidal environments

Research on individual habitat-formers indicates that the mechanisms underpinning positive species interactions in marine environments vary between intertidal and subtidal environments. For example, Bulleri (2009) showed that positive interactions generated through the amelioration of physical stress were more common in intertidal environments, while those arising from a reduction in consumer pressure—either predation or grazing—are more common in subtidal environments. These patterns might reflect variations in the prevalence of forces (i.e. physical versus biological) that control intertidal and subtidal communities, respectively. Are such variations in the prevalence of biological versus physical mechanisms of facilitation reflected in facilitation cascades?

There are several examples of facilitation cascades triggered by physical stress-buffering in the intertidal, including salt marshes and mangrove forests (Altieri et al. 2007, McAfee et al. 2016).

By contrast, facilitation cascades documented in subtidal environments are generally the result of resource provision (Gribben et al. 2009a, 2017a). To the best of our knowledge, no study has formally documented a subtidal facilitation cascade triggered by reduction of consumer pressure, which is at odds with convincing evidence of the relevance of this facilitation mechanism in subtidal environments (Levenbach 2008, Bulleri et al. 2011, Kayal & Kayal 2017). A likely example would be colonies of the fire coral *Millepora platyphylla* providing refuge to other coral taxa (*Acropora and Pocillopora*) against the predatory sea star, *Acanthaster planci* (Kayal & Kayal 2017). Although not investigated directly, positive effects on coral taxa susceptible to predation are very likely to propagate to a multitude of other species (fish and invertebrates) through habitat provision.

Sources of spatial and temporal variability in facilitation cascades and their impact

It is increasingly apparent that the direction and magnitude of the species interactions that underpin facilitation cascades vary both spatially and temporally (Thomsen 2010, Angelini & Silliman 2014, McAfee et al. 2016, Thomsen et al. 2016b). Identifying the factors that operate at local to landscape scales to influence these species interactions can provide insight into where facilitation cascades are more likely to be found and how they are influenced by variation in abiotic and biotic conditions.

Trait- and density-mediated effects

Both basal and secondary habitat-forming species can display considerable spatio-temporal variation in individual-level (e.g. morphology) and population-level traits (e.g. density; Bishop et al. 2013; also see Figure 7A and Table 2). Where these traits modify the availability of a limiting resource or stressor amelioration, the existence or strength of facilitation cascades may be affected (Bishop et al. 2013, Table 2). The traits and density of a basal habitat-former may influence facilitation-cascades by (1) determining whether the environment is suitable for the secondary habitat-former to colonize and form habitat, and (2) modifying traits of the secondary habitat-former.

Studies have generally examined the effects of variation in basal and secondary habitat-former traits on the enactment of the cascade independent of one another (but see Bishop et al. 2013). Surveys and experimental manipulations of habitat-formers generally demonstrate positive relationships between increasing habitat-former biomass, cover or density and the associated species' abundance or richness (Mukai & Iijima 1995, Pavia et al. 1999, Gribben et al. 2009a, Thomsen 2010, Drouin et al. 2011, Koivisto et al. 2011, Angelini et al. 2015). However, such relationships are often nonlinear as they start to plateau at higher abundances of the basal habitat-former (Bishop et al. 2013), perhaps indicating a saturation point beyond which structural habitat no longer limits colonization of the secondary habitat-former or the facilitated inhabitants, or a point beyond which increases in density no longer enhance amelioration of abiotic or biotic stress. Indeed, it is conceivable that at very high densities, the relationship between basal and secondary habitat-formers may shift from facilitative to competitive, although this has not yet been observed or tested.

In a few instances, studies have simultaneously manipulated multiple traits of basal and secondary habitat-formers, indicating independent and additive effects of them on biodiversity. For example, in a study investigating the implications of intraspecific trait variations, Bishop et al. (2013) found that both the density and height of pneumatophores of the basal habitat-former, the mangrove *Avicennia marina,* had independent and additive effects on the trapping and retention of the secondary habitat-former, the fucoid alga *Hormosira banksii*. High densities of tall pneumatophores initially served as a physical barrier to algal colonization of pneumatophore plots, but, over the longer term, they enhanced the retention of colonized algae. Increased algal biomass, in turn, facilitated epifaunal colonization. In an interspecific example, the densities of two secondary habitat-formers (*H. banksii* and the oyster *Saccostrea glomerata*), each dependent on pneumatophores, had independent and
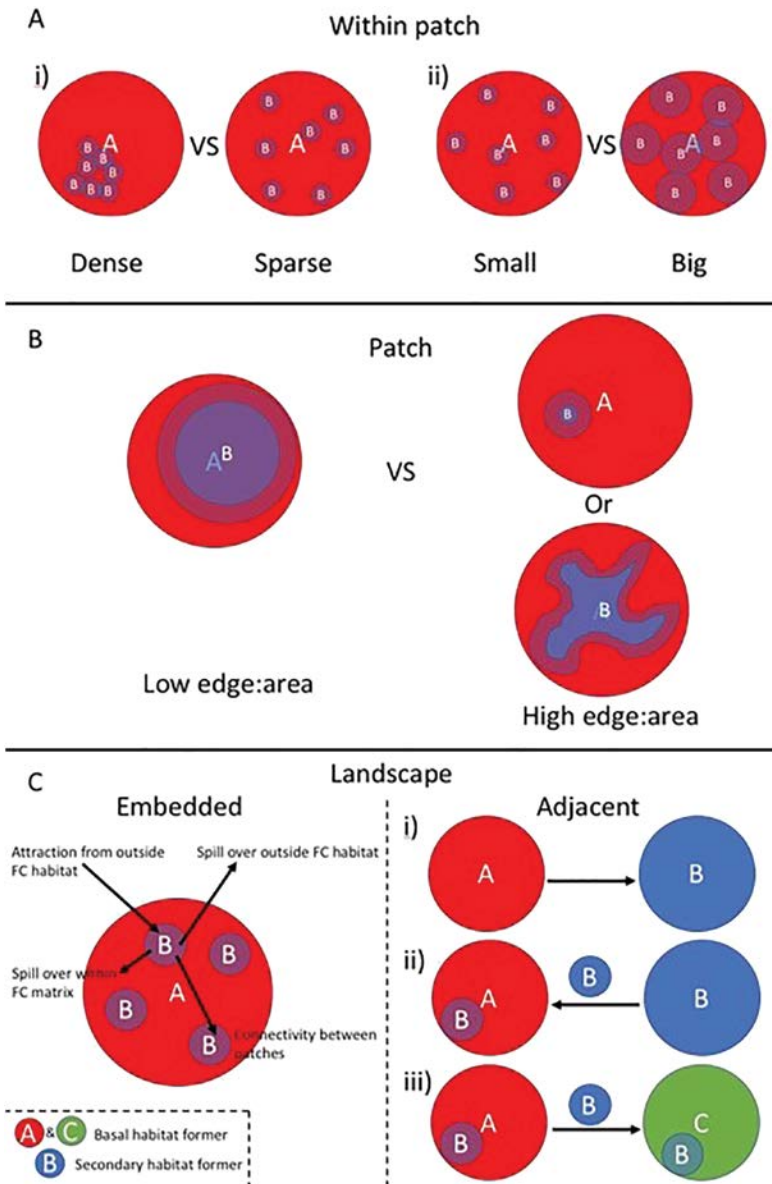
Figure 7 (A) Traits including (i) gregariousness and (ii) body size of individual habitat formers within a patch can influence facilitative interactions between the basal and secondary habitat former, or between a habitat-former and inhabitants. See Table 2 for additional traits that can influence interactions and outcomes in a facilitation cascade. (B) Characteristics of a habitat-former patch, such as edge to area ratio, can influence the outcome of facilitation cascades because habitat modification is likely to vary with distance from the edge of a patch. The proportion of a patch that is comprised of edge habitat (lighter color) can be influenced by both size and shape as seen in this diagram. See Table 2 for other patch traits that can influence the outcome of facilitation cascades. (C) Habitat-formers in a facilitation cascade interact at the landscape scale with one another, the surrounding habitat, and with inhabitants. This connectivity can take the form of habitat modification or transport of resources and propagules. The nature of the connectivity depends on whether the basal and secondary habitat-formers are in a spatially embedded or adjacent configuration. (*Continued*)

Figure 7 (Continued)   In the embedded configuration, the effects of a secondary habitat-former (B) may influence other individuals or patches of the secondary habitat-former, the matrix of the basal habitat-former (A), or spill over into the habitat outside the habitat where the basal and secondary habitat reside (including distant patches created by the facilitation cascade). When the basal and secondary habitat-former are found adjacent to one another, they can interact through (i) resource exchange, migration of inhabitants, or habitat amelioration effects that carry over distance; (ii) transport of a secondary habitat-former from a source population into a patch of a basal habitat-former, where it becomes entrained; or (iii) transport of a secondary habitat-former from the patch of one basal habitat-former to another basal habitat-former.

Table 2   Potential metrics for characterizing habitat-formers at the scale of an individual habitat-former (e.g. a single, mussel, oyster, mangrove root or tree), discrete patches of a habitat-former (e.g. a mussel bed, oyster reef, mangrove island) and arrays of habitat-former patches at the landscape scale and for assessing the effects of these habitat-former characteristics on beneficiary species- and community-level responses

	Individual traits	Patch	Landscape: embedded habitat-former assemblages	Landscape: adjacent habitat-former assemblages
Characteristics of habitat-former	Surface area, volume, fresh and dry weight, structural complexity metrics (e.g. fractal dimension, circularity, lacunarity)	Patch area, patch volume, patch edge-to-area ratio, number and size of individual habitat-formers (e.g. for mussels, oysters), patch age	Distance to nearest patch neighbor, patch cover, patch spatial configuration (e.g. random, clustered, uniform), patch persistence, patch size distribution	Distance and connectivity between habitat-former patches, size of habitat-former patches
Beneficiary species and community responses	Body size, species identity, life stage	Species abundance, species richness, food chain length, predator: prey ratios	Population size, population stability, community stability, species-area relationships	Population connectivity, trophic subsidies and feedbacks

Embedded and adjacent habitat-former patch arrays are differentiated in separate columns because of the differences in connectivity that can be manifested in these types of facilitation cascades.

additive effects on inhabitant biodiversity (Hughes et al. 2014). Finally, in an example investigating the interactive effects of traits of a basal (*A. marina* pneumatophore) and secondary (*H. banksii*) habitat-former, both the height of pneumatophores and the thallus length of *H. banksii* independently influenced the biomass of the algae retained by the mangroves (Bishop et al. 2013).

Patch size–mediated effects

Habitat-formers commonly occur in spatially discrete patches that vary in size. Patchy facilitation cascades can occur either because a basal habitat-former occurs in patches, or the secondary habitat-former occurs in patches within a large continuous habitat created by the basal habitat-former (Crotty et al. 2018). An example of each is evident in the cordgrass-ribbed mussel association in various wave exposure contexts. On wave-exposed cobble beach shorelines, where cordgrass grows in discrete beds that are each occupied by a homogenous ribbed mussel reef, patches of the facilitation cascade habitat are defined by the dimensions of the cordgrass beds (Altieri et al. 2007). On sheltered shorelines, cordgrass forms expansive salt marshes and facilitation cascades occur in the relatively small patches of ribbed mussels that dot the marsh landscape (Angelini et al. 2015).

Patch size mediates how habitat-formers influence the physical environment and other species (Figure 7A and Table 2). For example, early work with cobble beach plant communities found that the length of cordgrass beds had a nonlinear relationship with substrate stability and the diversity of forbs in areas sheltered by beds (Bruno & Kennedy 2000). Evidence is also accumulating for nonlinear relationships between the patch size of co-occurring habitat-formers and the strength of facilitation cascades. For example, in salt marshes of the southeastern United States, the functional diversity of invertebrates increased with the number of mussels in a patch following a nonlinear power function—with the greatest increases in diversity occurring with increases at the lower end of the range in patch sizes (Angelini et al. 2016). In contrast, the abundance and total biomass of invertebrates increased linearly with patch size. Nonetheless, both the diversity and biomass *per unit area* were greater in larger patches, suggesting that the function of facilitation cascades differs qualitatively between large and small patches.

There are several explanations for this nonlinear positive relationship between patch size and the strength of a facilitation cascade apparent in the diversity or abundance of inhabitants. First, large patches of co-occurring habitat-formers are likely to incorporate a greater degree of environmental heterogeneity because they are more likely than small patches to span gradients in environmental conditions, incorporate a range of size and age classes of habitat-formers and offer differentiated edge and interior habitats (Angelini et al. 2015; also see Figure 7B). Second, larger patches may support more species because they buffer against population stochasticity, as predicted by classic island biogeography theory (MacArthur & Wilson 1967). Third, larger patches can be more resilient to disturbances due to facilitation between the co-occurring habitat-formers and the increased likelihood of remnant individuals surviving a disturbance event that allows vegetative regrowth (Derksen-Hooijberg et al. 2018). This greater stability and structural continuity of large habitat-former patches may allow the development of more diverse communities, as well as the persistence of those communities once they establish.

Landscape-scale considerations

Much of the early research on facilitation cascades focused on the occurrence of facilitation within patches and on the contrasting patterns of species diversity and abundance inside versus outside these patches (Altieri et al. 2007, Gribben et al. 2009a, Bishop et al. 2013). Recently, it has been recognized that habitat-formers may interact with one another at the landscape scale, resulting in emergent properties and outcomes of facilitation cascades that extend beyond the boundary of a given patch. In particular, patches of co-occurring habitat-formers can influence the surrounding matrix through spillover of organisms (Figure 7C and Table 2). For example, patches of cordgrass and ribbed mussels observed at mid-intertidal elevations on cobble beaches form a nursery habitat for invasive crabs that enhances the number of adult invasive crabs and coexistence with native crabs in adjacent lower intertidal areas outside the patch (Altieri & Irving 2017). In other cases, the habitat-formers themselves can be mobile, with implications for the occurrence of the facilitation cascade and even the transport of associated organisms. For example, habitat-formers that initially establish in different ecosystems may form a facilitation cascade if one species is dislodged and transported over long distances, as when rocky shore algae are dislodged and then trapped among mangrove pneumatophores, facilitating an invertebrate community (Bishop et al. 2009). In another instance, entire communities of invertebrates inhabiting algae, which are facilitated by a gardening polychaete on intertidal mudflats (Byers et al. 2012), are commonly transported to adjacent salt marshes following storms and dislodgment of the algae, thereby extending mudflat cascades into salt-marsh cascades (Thomsen et al. 2009, Byers et al. 2012).

Associated biota can move in reciprocal directions as well, and patches of habitat created by a facilitation cascade also have the potential to attract mobile organisms from the surrounding matrix. An example of this is marsh organisms migrating into the alga *Gracilaria vermiculophylla*, which

is facilitated on intertidal mudflats by tubes of the worm *Diopatra* (Figure 7C). This leads to the question of the extent to which the elevated diversity and abundance of associated organisms in patches result from the higher recruitment and survivorship due to the facilitation cascade, or just the aggregation of organisms that would otherwise persist in the surrounding area. Studies demonstrating higher survivorship of juvenile blue crabs and mud crabs in *Gracilaria* algae attached to *Diopatra* worm tubes than in adjacent seagrass or bare mudflats indicate that, in at least some cases, production is increased by facilitation cascades (Johnston & Lipcius 2012, Bishop & Byers 2015). Regardless of the underlying mechanisms of how organisms come to be associated with the facilitation cascade habitat, the elevated abundance and diversity of inhabitants within patches constitute evidence that they are benefitting from conditions created by the co-occurring habitat-formers.

Modification of abiotic conditions by facilitation cascades can also extend into the surrounding areas beyond the patches where habitat-formers co-occur (Figures 2B and 7C, Table 2). Such long-distance interactions are likely to occur where patches can absorb energy such as water currents and wave movement, or intercept materials such as propagules or sediment transported passively across the landscape (Donadi et al. 2013, van de Koppel et al. 2015). For example, coral reefs, which are built through a network of facilitation cascades in which various corals, algae, and sponges facilitate one another and build the reef structure (Wulff & Buss 1979, Adey 1998), can buffer shorelines against wave energy (Gerritsen 1980, Hardy & Young 1996, Ferrario et al. 2014) and thereby allow the development of diverse shoreline communities hundreds of metres inshore of the reef crest.

Linkages of long-distance interactions can also allow habitat-forming species that are adjacent to one another, rather than embedded in the same patch, to form facilitation cascades (Figures 1C, 2B and 7C). This is evident at the edge of marshes where oysters reduce wave energy, which results in shoreline stabilization, sediment accretion and establishment of marsh grass inshore of the oysters—a powerful interaction that can be harnessed for restoration activities (Meyer et al. 1997, Piazza et al. 2005, see section on Restoration, later in this review). A diverse community of marsh occupants, including crabs, snails, fish and birds, in turn benefit from this cascade (Scyphers et al. 2011). The enactment of such long-distance facilitation cascades can be scale-dependent and influence environmental factors such as wave energy (Piazza et al. 2005). On the mudflats of the Wadden Sea, for instance, mussels have a negative competitive effect on cockles (secondary habitat-formers) in their immediate vicinity by reducing substrate stability and depleting food resources, but a positive effect on cockles that are 50–100 m away by reducing wave energy (Donadi et al. 2013). The conclusion to be drawn from these examples is that multiple habitat-formers may facilitate one another with cascading effects on the diversity and abundance of inhabitant species, but these effects may be apparent only when observations are made at appropriately large scales and when considering mechanisms of connectivity among habitat modifying species and their configuration on the landscape.

Time scale and the variability of facilitation cascades

The strength and importance of facilitation cascades are likely to vary with time for several reasons. First, the abundance of one of the habitat-formers in a facilitation cascade may change based on when it occurs, such as habitat-forming algae that are more abundant on oysters and worm tubes in summer than winter (Thomsen et al. 2007). On the time scale of days, the urchin *H. purpurascens,* which wraps itself in the blades of live *E. radiata* kelp to form shelters for the snail *P. eximius*, moves between kelp plants (Bell et al. 2014). This in turn, results in temporally dynamic associations between the snails and kelp (Bell et al. 2014). Second, inhabitants may be dependent on habitat within a facilitation cascade during only a portion of their life, such as shore crabs that associate with cordgrass and mussel habitat as recruits before moving into adjacent habitats as adults (Altieri & Irving 2017). Reciprocally, habitat-formers may have particularly strong facilitative effects during

a subset of their life stages, as occurs for pen shells (*Atrina* species, formerly called *Pinna*) that can have a greater facilitative effect on some inhabitants after they have died because their gaping shells provide habitats for nesting fish and burrowing amphipods (Munguia 2007), although a higher abundance of epibionts on live versus dead shells of pen shells has also been documented (Gribben et al. 2017a). Third, the importance of facilitation cascades may vary with time because the stress that the habitat-formers ameliorate becomes limiting for inhabitants only at certain times. For example, year to year variation in temperature resulted in algae that grow on barnacles having a positive effect on associated species by buffering against thermal stress during warmer years, but otherwise having negative effects via smothering in cooler years (Leonard 2000). Given that the strength of facilitation, as well as shifts between positive and negative interactions, are likely to vary over time scales of hours to months, the timing and interpretation of experiments and sampling require knowledge of natural history and environmental regimes.

Variation in facilitation cascades along abiotic and biotic gradients

A large body of theoretical and empirical work, stimulated by the SGH (Bertness & Callaway 1994), has provided compelling evidence that species interactions tend to shift from negative (i.e. competition) to positive (i.e. facilitation) along environmental stress or consumer pressure gradients (Brooker et al. 2008, Maestre et al. 2009, Bulleri et al. 2011, He et al. 2013). Thus, the SGH can provide a useful theoretical background for predicting how the strength and stability of facilitation cascades can change according to external biological and physical conditions. As proposed by Angelini et al. (2011) and discussed in previous sections (i.e. the section entitled "The mechanisms underpinning facilitation cascades," earlier in this review), facilitation between multiple habitat-formers is expected to be the dominant interaction at both ends of gradients of physical stress. In harsh environments, amelioration of physical stress by the basal habitat-formers can foster the persistence of less stress-tolerant habitat-formers (Altieri et al. 2007, McAfee et al. 2016). By contrast, in environmentally benign environments, basal habitat-formers can shelter secondary habitat-formers from consumers and, by enhancing the availability of or access to limiting resources, stronger competitors as well (Bulleri et al. 2002, Eriksson et al. 2006, Clements & Hay 2015, Cardenas et al. 2016). The mechanism through which basal habitat-formers facilitate secondary habitat-formers, and secondary habitat-formers facilitate inhabitants, however, may determine the sensitivity of a cascade to variations in abiotic and biotic factors.

Positive interactions at different hierarchical levels of a cascade can be elicited by either the same or different mechanisms (Figure 8; Altieri et al. 2007). Predicting how the strength of cascades will vary along abiotic and biotic gradients becomes more difficult when they involve different facilitative mechanisms. Cascades including one single mechanism of facilitation (Figures 8A–C) may respond to a restricted set of abiotic and biotic factors. Arguably, the presence of different mechanisms of facilitation broadens the set of factors influencing its strength. For example, the strength of a facilitation cascade in which the basal habitat-former facilitates a secondary habitat-former by ameliorating environmental stress and the secondary habitat-former provides shelter from predation to the focal species, or vice versa (Figures 8B,C), would respond to variations in relevant physical stressors and the density or behaviour of consumers.

Facilitation cascades in which positive effects between species depend on the provision of or enhanced access to limiting resources presumably will display less variation in persistence and strength along gradients of biotic and abiotic stresses, in comparison to facilitation cascades that occur when environmental stress, consumer pressure or both are reduced (Figure 8A). In fact, provision of resources by one habitat-former would benefit another habitat-former or inhabitants, even at increasing levels of biotic or abiotic stress. This does not imply that interactions among species in facilitation cascades based on enhanced resource provision are disconnected from background biotic and abiotic conditions.
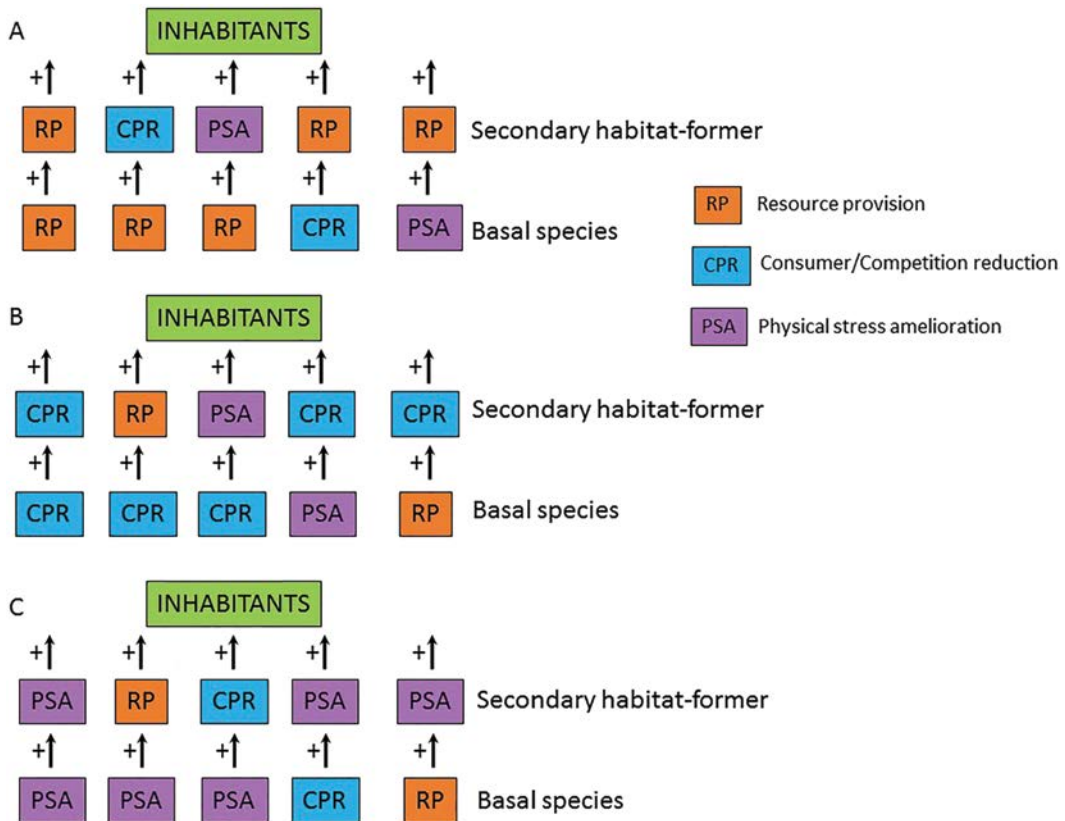
Figure 8 Diagram showing possible combinations of various facilitation mechanisms (Resource provision, Consumer/Competition reduction and Physical stress amelioration) enacting a three-level facilitation cascade. Each of the mechanisms can operate both at the first (between the basal and the secondary habitat-former) and second (between the secondary habitat-former and the inhabitant community) link. The diagram illustrates cascades in which at least one of the positive interaction is due to (A) Resource provision, (B) Consumer/Competition reduction, (C) Physical stress amelioration.

As previously discussed, there are important mediators of facilitation cascades, such as interacting species traits and density, that may respond to those background conditions. For example, enhanced nutrient loading may cause macroalgal blooms, reducing seagrass shoots' density (Holmer et al. 2011, Höffle et al. 2012) and, ultimately, their functionality as basal habitat-formers. Extreme hydrodynamic forces may dislodge or reduce the size of epiphytic or enmeshed macroalgae, impairing their ability to provide habitats to invertebrates (Bishop et al. 2009), and high herbivore pressure may reduce seagrass leaf length or macroalgal biomass to levels too low for benefits for inhabitants to accrue. In addition, failure or decline of the basal habitat-former because of unsuitable abiotic or biotic conditions may reduce its ability to deliver positive effects to the secondary habitat-former. For example, in soft sediment habitats along the Northwest Atlantic coast, the positive effects of the tube-building polychaete *Diopatra* on macroalgae decreased in strength towards lower latitudes due to the reduced density of tubes (Berke 2012). Although facilitation cascades generated by resource provisioning are known to occur both in stressful and benign environments and be characterized by relatively high stability (van der Zee et al. 2016, Derksen-Hooijberg et al. 2018, Crotty et al. 2018), their strength is still likely to vary as a function of background biotic and abiotic conditions.

When the main mechanism of facilitation between habitat-formers is physical stress amelioration, the strength of the cascade is likely to vary among patches along an environmental gradient, with greater dependence of inhabitants on the facilitation cascade with increasing stress (Angelini et al. 2011). For example, on the east coast of the United States, grasses and forbs dominate in wave-sheltered sites, but they rely upon substrate stabilization by *Spartina alterniflora* at sites moderately exposed to wave action (van Wesenbeeck et al. 2007). The facilitation cascade fails, however, at the most extreme wave-exposed sites, where abrasion by cobbles prevents the establishment of vegetation. Conversely, studies across broad latitudinal gradients have documented little variation in the strength of facilitation cascades generated by physical stress amelioration. For example, in terrestrial environments, Angelini and Silliman (2014) found that positive effects on insect assemblages generated by the oak–*Tillandsia usneoides* (Spanish moss) association did not vary across an 800-km span on the east coast of the United States. Likewise, positive effects of oysters growing on mangrove aerial roots on macroinvertebrate assemblages were consistent across 8° latitude on the east coast of Australia (McAfee et al. 2016). However, direct comparisons of how the strength of facilitation cascades vary across larger latitudinal gradients spanning tropical to temperate environments have received little attention, so it is difficult to draw any meaningful conclusions.

The analysis of pairwise interactions along one single gradient of stress may yield less predictive power of where a facilitation cascade will be found, or under which circumstances it will persist when the habitat-formers involved in a facilitation cascade are characterized by different life history-traits (e.g. size, feeding-behaviour, or trophic level) and sensitivity to different environmental stressors. For example, in the five-level habitat-former facilitation cascade documented by Thomsen et al. (2016a), an increase in suspended organic matter may benefit the basal habitat-former (a filter-feeder, the cockle *Austrovenus stutchburyi*), but be detrimental for higher-level habitat-formers (i.e. the macroalgae *Ulva* and *Sarcothalia* (formerly *Gigartina*) *atropurpurea*) through reduction in light levels. Under these circumstances, analyses of variations in the sign and strength of species interactions along multiple gradients of stress (i.e. those most likely to affect each of the species involved in the cascade) would be necessary to provide an insight into the context dependency and variability of the facilitation cascade.

To the best of our knowledge, no study has formally investigated variations in strength of facilitation cascades triggered by associational defence along gradients of consumer pressure. Facilitation cascades in which reduction of competition and consumer pressure is the predominant facilitation mechanism between pairs of habitat-formers or between a habitat-former and inhabitants will be most sensitive to spatial and temporal variations in these biological forces, which often intensify with decreasing environmental stress (Bertness & Callaway 1994). From the SGH, a decrease in the intensity of negative biotic interactions, either predation or competition, is predicted to modify the trade-off between the benefits and costs of associational defences. For example, corals can suffer lower mortality from predation by the sea star, *Acanthaster planci,* or corallivorous fish when associated with canopy-forming algae, such as *Sargassum polycystum* or *Turbinaria ornata* (Bulleri et al. 2013, Clements & Hay 2015). However, branched corals underneath macroalgal canopies exhibit lower growth rates than corals in open areas when consumer pressure is low (Bulleri et al. 2013). Similarly, the ability of a habitat-former to provide refuge from consumption for another habitat-former or for inhabitants can decrease or collapse when predation pressure exceeds a critical threshold. For example, on subtidal rocky reefs in the Santa Barbara Channel, California, USA, the intensity of positive effects of anemones on macroalgae peaked when sea urchin density was 10 per square metre and decreased thereafter, and all macroalgae were consumed when the highest density was reached (85 individuals per square metre) (Levenbach 2009).

Length and stability of facilitation cascades

To date, facilitation cascades including from two to five levels of habitat-formers have been described (Thomsen et al. 2016a, Yakovis & Artemieva 2017). Yet, to the best of our knowledge, the relationship

between facilitation cascade length and stability remains unexplored. The stability of a cascade might be predicted to decrease with increasing number of facilitation links due to its hierarchical nature (Yakovis & Artemieva 2017). The loss of one intermediate habitat-former could destabilize the whole cascade, with effects becoming greater as the perturbed level is lower in the hierarchy of interactions (i.e. close to the basal habitat-former). By contrast, redundancy of habitat-formers within levels of the hierarchy would add stability to the cascade (Yakovis & Artemieva 2017). For example, in mangrove forests, some species of echinoderms, gastropods and crustaceans are supported by both oysters and macroalgae, which act as secondary habitat-formers (Hughes et al. 2014). These facilitated species are, therefore, less susceptible to decline or local extinction following the disappearance of either of the two secondary habitat-formers compared with those invertebrates that are able to use only one of the two habitats. Similarly, the sharing of habitat-formers across levels of the hierarchy should promote cascade stability. For example, in the shallow subtidal of the White Sea, red algae are common on barnacles, ascidians and mussels, which represent the second, third and fourth levels of the hierarchy of positive interactions, respectively (Yakovis and Artemieva 2017). Similarly, mussels can grow on both cockles (the basal habitat-former) and ascidians. Thus, the decline of some of the species at intermediate levels of the hierarchy should not cause a collapse of the whole cascade.

Species in longer cascades will likely include a higher number of indirect connections with species external to the cascade (Figure 9). For example, in a New Zealand estuary, the bivalve *Austrovenus stutchburyi* starts a five-level facilitation cascade that includes green algae, trochid snails, encrusting bryozoans and, finally, the red alga *S. atropurpurea,* which supports other inhabitants (Thomsen et al. 2016a). In this case, the persistence of *S. atropurpurea* is facultatively dependent upon all the species found at lower levels of the hierarchy and, hence, is influenced by a broad range of biotic and abiotic factors that act on any one of those levels. In fact, bivalves, snails, green algae and bryozoans are likely to respond to the alteration in pressure from different consumers, the alteration of different physical conditions or both. The number of consumers or competitors directly or indirectly interacting with species involved in the facilitation cascade, and which may modify the strength of one or more links within the cascade, is thus expected to increase with cascade length (Figure 9). This suggests that facilitation cascades are framed within local food webs and are likely to be, directly or indirectly, under the control of a broader group of species than those forming the cascade itself. The relationship between food-web complexity and stability is still highly controversial (May 1971, 1972, Mougi & Kondoh 2016), and at present, there is no empirical basis for predicting how the stability of a facilitation cascade is influenced by the complexity of the food web within which it is framed.

Incorporation of facilitation cascades into natural resource management

Due to the role of habitat-forming species in ameliorating environmental stressors, and as hot spots of biodiversity, they are obvious targets for conservation and restoration initiatives (Crain & Bertness 2005, Byers et al. 2006, Marzinelli et al. 2014, Bayraktarov et al. 2016). With anthropogenic climate change, coastal development and food-web alterations further degrade coastal and marine ecosystems, thus facilitation cascades and the positive interactions upon which they are structured may play an increasingly important role in sustaining biodiversity (Silliman & He 2018). Facilitation cascades can enhance recovery from disturbance and thereby increase ecosystem resilience. For example, mussels increase salt-marsh cordgrass survival following drought and elevated snail-grazing stress because these bivalves enhance water storage, reduce soil salinity stress and promote the ability of cordgrass to compensate for grazing damage through their deposition of nutrients (Angelini et al. 2016).
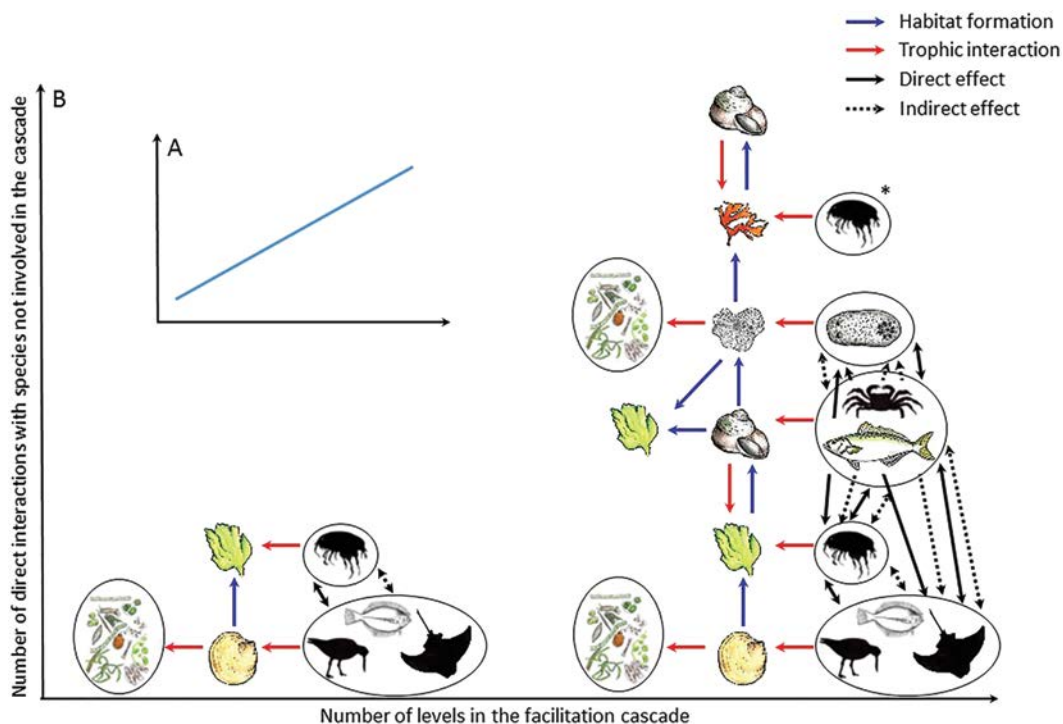
Figure 9 (A) Predicted positive relationship between the number of levels in the facilitation cascade and the number of direct interactions with species not included in the cascade; (B) in the Avon-Heathcote Estuary, New Zealand a six-level facilitation cascade includes the cockle *Austrovenus*, the green seaweed *Ulva*, the trochid snails *Micrelenchus tenebrosus* and *Diloma subrostrata*, the nonnative encrusting bryozoan *Conopeum seurati* and the red seaweed *S. atropurpurea* (Thomsen et al. 2016a). Interactions with species that are not involved in this facilitation cascade progressively accumulate with increasing cascade length. For the sake of clarity, only positive (blue) and negative (red) direct interactions are reported among species within the cascade. In a two-level cascade, the basal habitat-former (cockle) and the secondary habitat-former (*Ulva*) are connected with two external groups of species (in circles) by trophic interactions: the cockle feed on phytoplankton and can be preyed upon by eagle rays, oystercatchers and flounders, while *Ulva* is grazed upon by amphipods. In the six-level cascade, two more groups of species are potentially accumulated, the predators of Trochids (the fish *Arripis trutta* and the crab *Cyclograpsus* spp.) and the predators of encrusting (nudibranchs). Species external to the cascade can be connected by direct (black straight line) and indirect (black dotted line) interactions (either negative or positive) and are embedded in the broader food web (not reported in the diagram). *Amphipods use both *Gigartina* and *Ulva* as a food source and, hence, interact with species at different levels of the facilitation cascade. (Drawings courtesy of E. Maggi.)

Thermal stress is an important factor limiting the distribution of marine organisms at varying scales, and facilitation cascades have the potential to extend the distribution of organisms by buffering against that stress at both the local (Angelini et al. 2016) and latitudinal scales (McAfee et al. 2016). The importance of habitat-forming organisms in buffering against thermal stress should increase with climate change as temperatures become more extreme and variable (IPCC 2015); however, the geographic distribution of those effects may not be straightforward due to the geographic idiosyncrasies of thermal regimes (Helmuth et al. 2006). These predicted changes suggest the urgency of examining facilitation cascades as a tool for mitigating the anthropogenic changes to natural systems, and of understanding the range of anthropogenic stressors beyond climate change that they may ameliorate. Similarly, shifts in food-web structure due to overharvesting of targeted

species, species invasions, and changes in environmental conditions are leading to outbreaks of consumers in many systems, such as crown-of-thorn sea stars in coral reefs (Kayal et al. 2012), as well as geese (Peterson et al. 2013) and feral hogs in salt marshes (Sharp & Angelini 2016). Facilitation cascades may also play a key role in buffering against and supporting recovery after these disturbance events, although far more research is needed to untangle the mechanisms that are most important drivers of recovery.

Historically, management of marine and coastal ecosystems has focused on the protection and restoration of basal habitat-formers, using a habitat-by-habitat approach (Gillis et al. 2017). Yet, where habitat-forming species act synergistically through facilitation cascades, the full biodiversity and ecosystem service benefits of management interventions may be realized only when they protect or enhance basal, secondary and higher-order habitat-formers together (Thomsen et al. 2018). Effective management of ecosystems requires knowledge of not only the distributions of, threats to and environmental tolerances of basal habitat-formers, but also of other, dependent habitat-formers (van de Koppel et al. 2015).

Conservation

In establishing and managing marine protected areas, whether the system comprehensively, adequately and representatively protects ecosystems is typically assessed based on mapping of basal habitat-formers (e.g. seagrass meadows, kelp forests, coral or shellfish reefs) and nonbiogenic habitats (e.g. rocky reefs, sandflats, or mudflats), without consideration of the distributions or dependencies of secondary habitat-formers (e.g. IUCN 1994, Agardy 1995, Great Barrier Reef Marine Park Authority 2003). This ignores the possibility that the biogenic habitat may be composed of several interacting species with important interactions of dependency among them (Thomsen et al. 2018). For example, a coral reef may have hundreds of coral, alga, and sponge species that interact and potentially facilitate one another. In ecosystems with embedded facilitation cascades (e.g. Figure 2A), secondary habitat-formers may not be uniformly distributed within basal habitat-formers. Protection of those areas with secondary habitat-formers may lead to greater biodiversity, ecosystem functioning and ecosystem service benefits than protection of those with basal habitat-formers alone (Thomsen et al. 2018). The design of marine protected areas also needs to consider the possibility of long-distance facilitation cascades, in which dependencies between habitat-formers extend beyond habitat patch boundaries (van de Koppel et al. 2015). For example, where the persistence of cockle beds is dependent on the presence of mussel beds that dissipate wave action and modify sediment properties (Donadi et al. 2013), the conservation of cockle beds requires not only protection of the cockle beds themselves, but also of the mussel beds to which they are connected. Therefore, management systems that focus on the protection of individual habitats rather than seascapes that span areas with multiple habitat-formers may be of limited conservation value (van de Koppel et al. 2015, Gillis et al. 2017).

Restoration

Like conservation, restoration often focuses on the reestablishment and rehabilitation of individual habitat-formers (Hawkins et al. 2002), with little consideration of the ecological dependencies among them (Derksen-Hooijberg et al. 2018). Key processes that threaten ecological communities are often defined on the basis of the damage they cause to basal habitat-formers (Environment Australia 1999), and ecosystems are typically managed to keep disturbances below the level at which damage to basal habitat-formers occurs (e.g. Lindenmayer & Luck 2005). When restoring degraded ecosystems that comprise facilitation cascades, it may be important first to reduce environmental stressors to levels that allow the survival, growth and reproduction of both basal and secondary habitat-formers (Lewis 1982, 2005). It is plausible that in some instances, secondary habitat-formers may be more sensitive to stressors than basal habitat-formers. For example, whereas the grey mangrove

(*A. marina*), which is a basal habitat-former, is resilient to, and may even be used as a biological filter for, sewage (Chen et al. 2000), the fucalean alga (*H. banksii*, which is a secondary habitat-former that can be found entangled in the pneumatophores of the mangrove (e.g. Bishop et al. 2012), has early life history stages that are detrimentally affected by sewage (Doblin & Clayton 1995). Depending on the dispersal capabilities of basal and secondary habitat-formers and the availability of nearby sources of recruits, transplantation of one or both of these into the restoration site might also be required (Derksen-Hooijberg et al. 2018). Particularly where the secondary habitat-former is to be transplanted into the site, knowledge is needed about threshold densities, biomasses and/or trait values that must be attained by the basal habitat-former to support the secondary habitat-former. For example, *H. banksii* is only enmeshed in and retained by mangrove pneumatophores once they exceed a certain density (Bishop et al. 2013). This also implies that priority effects will be important for the establishment of facilitation cascades, and so the order and timing of restoration activities will be important.

In many cases, secondary habitat-formers may eventually recruit to the basal habitat-former following its restoration, but active restoration of secondary habitat-formers may be desired to accelerate assembly of the rest of the community. Therefore, when selecting source populations for transplants, knowledge about those phenotypes of basal habitat-formers that most effectively facilitate secondary habitat-formers and those phenotypes of secondary habitat-formers that best promote inhabitant communities will be beneficial. In some instances, methods of transplantation may also be adapted to encourage patterns and forms of growth that best support facilitation cascades. For example, just as the spacing between salt-marsh transplants may have large outcomes on transplant survival (Silliman et al. 2015), so may it also influence the enactment of facilitation cascades (Derksen-Hooijberg et al. 2018).

To maximize the probability of success, restoration projects also need to consider that dependencies among habitat-formers may occur across habitat boundaries that requires corestoration of multiple basal habitat-formers. For example, in seascapes where the persistence of seagrass is contingent on adjacent coral reefs dissipating wave energy, the restoration of seagrass will be successful only where coral reefs are either intact or functionally restored (Gillis et al. 2017).

In environments that no longer support native habitat-formers and where their restoration is not feasible, facilitation cascades that include nonnative foundation species may reinstate some of the ecosystem services once provided by native habitat-formers (Ramus et al. 2017). In such instances, actively incorporating established nonnative foundation species into management strategies may have stronger-than-expected benefits for the provisioning of coastal ecosystem services. Nevertheless, before nonnative species are actively facilitated by programs aimed at restoring ecosystem services, a thorough examination is needed (Gribben et al. 2013, Sotka & Byers 2019, Thomsen et al. 2019). Whereas the nonnative secondary habitat-former *Gracilaria* may superficially appear to enhance fish and invertebrate abundances (Byers et al. 2012, Wright et al. 2014, Ramus et al. 2017), it is unclear to what extent this represents an enhancement of production versus a redistribution of species otherwise supported by other habitats (Sotka & Byers 2019, Thomsen et al. 2019). Further, such benefits may come at the expense of unmeasured negative impacts (Gribben & Wright 2006, Gribben et al. 2009b, 2017b), such as the facilitation of toxic *Vibrio* species that cause shellfish poisoning (Gonzalez et al. 2014) or changes in denitrification (Gonzalez et al. 2013), microbial community structure and sulphur cycling (Gribben et al. 2017b, 2018) in sediment.

Ecological engineering

In areas where environmental conditions are no longer suitable for basal and/or secondary habitat-formers to persist, artificial mimics of these habitat-formers may be used to reinstate some of, if not all, the functions of facilitation cascades (Thomsen et al. 2018). Whether abiotic habitat mimics will be useful surrogates for live habitat-formers is contingent on the mechanisms

by which the habitat-formers support associated communities (Clark & Edwards 1999, Spieler et al. 2001; Seaman 2007). Such an approach will be most successful where the key role of the habitat-former is to provide a structural habitat, which in turn serves as a substrate for attachment, modifies resource flows (e.g. by trapping organic matter) and/or mitigates abiotic and biotic stressors (Bologna & Heck 1999, Spieler et al. 2001). Of relevance to facilitation cascades, studies comparing the communities that recruit to live habitat-formers and structural mimics (e.g. live seagrass versus artificial seagrass units) demonstrate that in many instances, the role of the habitat-formers is primarily to provide habitat structure (Cattaneo & Kalff 1979, Lee et al. 2001, Kelaher 2003).

In other cases, such as facilitation of seagrass beds and their associated communities by adjacent shellfish reefs in a long-distance cascade (van de Koppel et al. 2015), structural mimics of oyster reefs will be poor surrogates for live habitats because the mechanism by which habitat-formers are linked is a process—filtration of suspended solids from the water (Wall et al. 2008)—that depends on live habitat-formers. Whether mimics can be successfully used in place of live basal or secondary habitat-formers may also be predicted based on whether associated species are facultatively or obligately dependent on the habitat-formers. Although there are some exceptions (e.g. the epiphyte *Notheia anomala* is obligately dependent on its macroalgal host *H. banksii*; Thomsen et al. 2016b), studies utilizing artificial macrophyte mimics have shown that for many epiphytes, the biotic nature of the macrophyte involved is insignificant, with epiphytes readily growing on abiotic structures (Harlin 1973, Cattaneo & Kalff 1979). Similarly, the majority of faunal species recorded in macrophyte holdfasts are also found in surrounding habitats rather than being obligate holdfast inhabitants (Christie et al. 2003). These examples suggest that mimics are likely to be able to functionally replace components of a facilitation cascade in many ecosystems.

The concept of facilitation cascades may also be applied to the ecological engineering of artificial structures, such as seawalls, breakwaters, pontoons and pilings, to enhance their ecological value (Perkol-Finkel et al. 2012, Ng et al. 2015, Ferrario et al. 2016; for a further review of this issue, see Firth et al. 2016 and Morris et al. this issue for reviews). For example, the Elliott Bay seawall in Seattle Harbor has a textured, concrete surface aimed at promoting the growth of intertidal marine life by increasing surface area and providing crevices (Goff 2008, 2010, Haddad Drugan 2013). The design includes enlarged geometric renditions of intertidal habitat-formers of Elliott Bay, such as barnacles, mussels, anemones and rockweed, arranged vertically according to the tidal elevations at which these species would naturally be found (Haddad Drugan 2013, Figure 10). The premise of this so-called Habitat Strata concept is that these geometries will encourage the colonization and growth of secondary habitat-formers (Haddad Drugan 2013, Figure 10).

Additionally, knowledge of the mechanisms by which long-distance facilitation cascades are enacted can be applied to the design of approaches to shoreline stabilization that are a hybrid of artificial structures and living habitat-modifiers (Temmerman et al. 2013, Chee et al. 2017; also see Morris et al. this issue). For example, in environments where hydrodynamic energy is too great to allow shoreline stabilization with habitat-formers alone, artificial substrate, such as rocky rubble, is placed off shorelines to reduce wave energy to a level that allows the growth of biogenic habitat such as salt marsh (Bilkovic & Mitchell 2013) and mangrove (Hashim et al. 2010) on the landward side. The role of rocky rubble is analogous to the role of intertidal oyster reefs in promoting marsh growth by forming a barrier to wave energy in a long-distance facilitation cascade (Meyer et al. 1997).

Where habitat mimics are to be applied either in the design of coastal infrastructure or as stand-alone elements, detailed knowledge is required about how variations in the morphology of the basal and secondary habitat-formers influence the strength and enactment of facilitation cascades. For example, the structural complexity and the size (volume) of kelp holdfasts influence the diversity and abundance of associated assemblages (Norderhaug et al. 2007). As previously noted, some facilitation cascades operate only when certain threshold values of habitat-former traits are reached (Bishop et al. 2013).
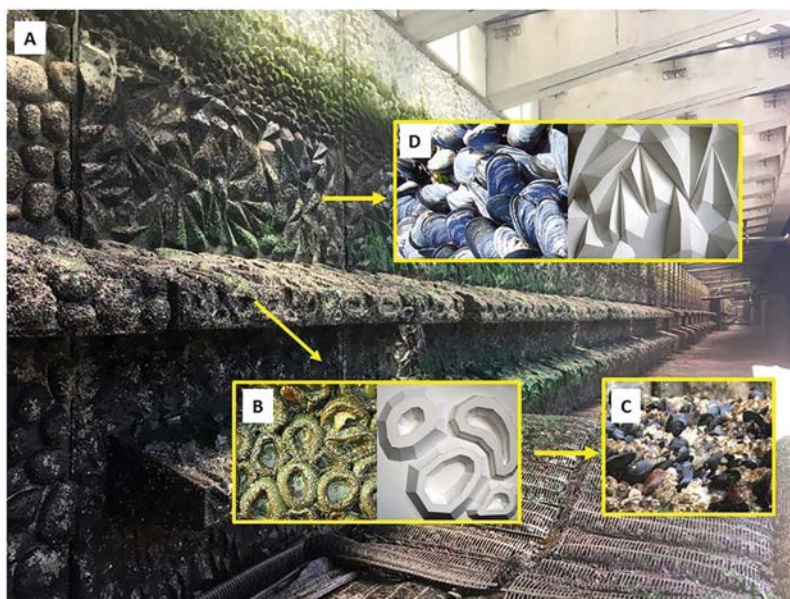
Figure 10 The concept of a facilitation cascade may be used to ecologically engineer built infrastructure to have greater ecological value. The Elliott Bay Seawall, Seattle (A) has a textured surface that has been loosely designed to mimic the textures formed by local intertidal basal habitat-formers (B, D). These mimic basal habitat formers have, in turn, been colonized by secondary habitat-formers (C). (Photo credits (A, C) City of Seattle; (B) Haddad|Drugan.)

Invasive species management

As facilitation cascades may benefit nonnative species via the same mechanisms as they benefit native species (Altieri et al. 2010, Altieri & Irving 2017), they may play a major role in the spread and proliferation of invasive species. This is particularly problematic where the nonnative species spillover from the facilitation cascade to nearby habitats. Altieri & Irving (2017) found that cobble beds adjacent to the cordgrass-mussel facilitation cascade had more than double the density of nonnative Asian shore crabs than cobble beds that were farther away. Whereas the nonnative crab was able to coexist with native crabs and prey species within the facilitation cascade due to the breadth of niche space provided (Altieri et al. 2010), outside the facilitation cascade, the nonnative species by virtue of its great abundance exerts a significant negative impact on prey species such as blue mussels (Lohrer & Whitlatch 2002). Particularly where spillover effects are apparent, effective management of nonnative species will require consideration of the role that facilitation cascades play in the proliferation of nonnatives. In such instances, whether management strategies should promote or inhibit facilitation cascades will depend on the magnitude of positive versus negative impacts, as well as the societal values placed on them.

Key knowledge gaps

While facilitation cascades have now been documented from a large range of marine habitats, it is clear from our analysis that research has been biased towards particular habitats and types of habitat-formers. This has led to gaps in our understanding of the mechanisms by which these interactions arise and are maintained, as well as how they vary in time and space. Here, we summarize the key knowledge gaps that need to be filled to fully integrate the concept of facilitation cascades into ecological theory and management.

Facilitation cascades in understudied ecosystems

From this literature review, it is evident that the study of facilitation cascades has been biased towards intertidal and shallow subtidal systems in subtropical and temperate latitudes. Thus, our knowledge of the importance of facilitation cascades to tropical, pelagic and deep-water benthic ecosystems, at very high and low latitudes, and in the Pacific and Indian Oceans is poor. Exploring facilitation cascades in these other ecosystems will allow more thorough and extensive tests of the importance of environmental stress regimes, seasonality and the size of the local species pool in shaping positive species interactions across the globe.

In addition, more information is needed on the potential role of mobile habitat-formers to start facilitation cascades. We know that drift algae can be an important secondary habitat-former in facilitation cascades once they come to settle within other habitat-formers (e.g. mangroves; Bishop et al. 2012, 2013, Hughes et al. 2014). But mobile habitat-formers have the potential to redistribute diversity through their movement within their local range (Altieri & Witman 2014), as well as transport entire communities to more distant locations (Smith 2002), and this transport process is not well understood in a cascade context.

Facilitation cascades initiated by nonstructural habitat-formers

Thus far, the focus has been on facilitation cascades involving habitat-formers that physically modify habitats through their structure. Nevertheless, there are other mechanisms by which organisms may modify habitats and contribute to facilitation cascades, which need to be explored. For example, in soft sediment, bioturbating organisms, like holothurians, clams and polychaetes, can oxygenate sediment and thereby facilitate other species (Middelburg & Levin 2009), which in turn may further alter environmental conditions and promote more organisms (Biles et al. 2002, Solan et al. 2004). For example, in seagrass beds, swimming crabs excavate subtidal pools, facilitating diverse nekton assemblages that otherwise would be excluded from intertidal seagrass beds (van der Zee et al. 2016). This suggests that facilitation cascades may consist of combinations of ecosystem engineers that do and do not provide structural habitats. An additional research gap is that no studies have documented belowground facilitation cascades in sedimentary habitats, despite their likely existence. Burrowing organisms are known to enhance the aboveground structure of salt-marsh grass (Bertness 1985) and can positively influence mangrove growth and production (Smith et al. 2009). Theoretically, belowground facilitation cascades should result from the same mechanisms that drive aboveground cascades (i.e. provisioning of resources, mediation of trophic interactions and modification of abiotic conditions).

Understanding trait and scale-dependency
across environmental gradients

The traits, densities, patch sizes and landscape configurations of habitat-formers have important consequences for interactions between them and the associated biodiversity. Evidence indicates that both linear and nonlinear relationships can occur, including threshold effects such as the presence/ absence response of oysters to pneumatophore density (Bishop et al. 2012) and mussel patch size effects of ecosystem functions in marsh (Angelini et al. 2015). To date, studies have focused on understanding how the density and traits of habitat-formers influence resource supply (e.g. physical habitat-provisioning), and more research is needed to understand the linear or nonlinear responses of environmental stressors (e.g. temperature, wave action) to the density and traits of the habitat-formers and the subsequent response of the facilitated community.

Additional research gaps that warrant attention are how biodiversity-ecosystem function relationships scale with areas in systems structured by facilitation cascades and how the body sizes

and abundances of associated communities may be related to the size structure and density of the habitat formers (e.g. Angelini et al. 2015). Moreover, a deeper understanding of the importance of facilitation cascades across latitudinal gradients and whether dominant mechanisms change with latitude is required to determine whether they play important roles in controlling biodiversity and ecosystem function at large spatial scales. Addressing these knowledge gaps will deepen mechanistic understanding of when, where and at which scales facilitation cascades are most important in sustaining biodiversity and ecosystem functioning.

Tipping points

Because the communities that depend on the structural habitat provided by habitat-formers may also be consumers of these (e.g. amphipods and other mesograzers on algae), there may be threshold densities at which interactions switch from positive to negative and facilitation cascades transition to trophic cascades. Understanding where these tipping points are is of high importance, given current rates of global and local change in marine ecosystems.

Feedbacks and cascade maintenance

Research on facilitation cascades has largely focused on how they are established, with little attention to how they are maintained. Negative feedback may have particularly important consequences for the maintenance of facilitation cascades, as the survivorship and/or density/traits of one or both habitat-formers (e.g. Trowbridge 1993, Thomsen et al. 2013) have clear effects on each other and on the community structure. Thus, for facilitation cascades to persist, negative feedbacks should be regulated such that stability is maintained. For example, negative feedbacks may be limited by competition from other space occupiers that control the abundance of internal consumers of the habitat-formers.

Moreover, the mechanisms underpinning facilitation at higher levels of the hierarchy have received less and are often vaguely described in terms of habitat provision, without a formal assessment of whether such habitat alleviates resource limitation, provides more benign environmental conditions or reduces consumer pressure. Advancing understanding of these mechanisms, as well as their relative importance, will be key to enhancing our ability to predict variations in the strength and stability of facilitation cascades.

Conclusion/Summary

Facilitation cascades are ubiquitous in most marine ecosystems (particularly benthic systems), in part because epibiosis is a common process (Wahl 1989). Here, we report on 100 studies (Table 1) documenting facilitation cascades, but we sense that this number greatly underestimates their relevance in structuring marine communities because they remain unexplored in some environments (e.g. deep seas) and overlooked in many others where co-occurring habitat-formers are often viewed as a single functional group rather than an assemblage of interacting species (e.g. coral reefs).

Until now, no review has integrated available studies to provide an overview of the functioning of facilitation cascades, synthesize their general importance, and identify factors that are likely to determine their importance in marine environments; our review, therefore, is both timely and overdue. For marine biologists, understanding trophic interactions (particularly trophic cascades) has been at the forefront of research agendas. Our review suggests that facilitation cascades require the same consideration if we are to fully understand the mechanisms shaping biodiversity and its important ecosystem functions across various scales and contexts.

Facilitation cascades may also provide a basis for an integrated framework inclusive of both negative (trophic) and positive (nontrophic) interactions for understanding the processes structuring

ecological communities. Merging recently developed concepts in the field of facilitation cascades within food chains and trophic web theories could significantly advance our understanding of community assembly and dynamics. Such integration should allow the further development of ecological theories (inclusive of interacting positive and negative interactions) and lead to the development of more robust biodiversity conservation strategies.

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