SYMPOSIUM

Habitat Cascades: The Conceptual Context and Global Relevance of Facilitation Cascades via Habitat Formation and Modification

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Synopsis The importance of positive interactions is increasingly acknowledged in contemporary ecology. Most research has focused on direct positive effects of one species on another. However, there is recent evidence that indirect positive effects in the form of facilitation cascades can also structure species abundances and biodiversity. Here we conceptualize a specific type of facilitation cascade—the habitat cascade. The habitat cascade is defined as indirect positive effects on focal organisms mediated by successive facilitation in the form of biogenic formation or modification of habitat. Based on a literature review, we demonstrate that habitat cascades are a general phenomenon that enhances species abundance and diversity in forests, salt marshes, seagrass meadows, and seaweed beds. Habitat cascades are characterized by a hierarchy of facilitative interactions in which a basal habitat former (typically a large primary producer, e.g., a tree) creates living space for an intermediate habitat former (e.g., an epiphyte) that in turn creates living space for the focal organisms (e.g., spiders, beetles, and mites). We then present new data on a habitat cascade common to soft-bottom estuaries in which a relatively small invertebrate provides basal habitat for larger intermediate seaweeds that, in turn, generate habitat for focal invertebrates and epiphytes. We propose that indirect positive effects on focal organisms will be strongest when the intermediate habitat former is larger and different in form and function from the basal habitat former. We also discuss how humans create, modify, and destroy habitat cascades via global habitat destruction, climatic change, over-harvesting, pollution, or transfer of invasive species. Finally, we outline future directions for research that will lead to a better understanding of habitat cascades.

Introduction

The fundamental importance of positive interactions is increasingly acknowledged in contemporary ecology (e.g., Bertness and Callaway 1994; Bronstein 2001; Bruno and Bertness 2001; Stachowicz 2001; Bruno et al. 2003; Brooker and Callaway 2009). Early observations of positive interactions include mutualisms between pairs of species, guilds, or functional groups such as fungi, algae and lichens (Scott 1960), mycorrhizae and plants (Chiariello et al. 1982), ants and plants (Ridley 1910), pollinators and plants (Riley 1892), cleaners and parasite-infested hosts (Gorlick et al. 1978), and dinoflagellates and corals (Muscatine and Porter 1977). Positive interactions were also recognized in early studies of succession in which it was noted how primary colonizers had positive effects on secondary colonizers via amelioration of the habitat (the place where an organism normally occurs) and by providing limiting resources (Cowles 1899; Shreve 1931; Clements 1936). These

studies inspired researchers to apply experimental methods to quantify direct positive effects as a general mechanism influencing community structure. Some researchers have used experimental manipulations of species-pairs to emphasize causal mechanisms and feedbacks between interactors, thereby documenting mutualism and commensalism (e.g., Bertness 1984; Stachowicz and Hay 1999; Stachowicz and Whitlatch 2005). Other researchers have investigated how certain organisms benefit multiple focal organisms (focal = point of interest, dependent variable) via amelioration of environmental stress and by providing living space and resources such as foraging, mating and nesting grounds, and a refuge from predation. These studies typically emphasize community-wide facilitation, and often have less emphasis on feedback mechanisms. These key facilitating organisms have been designated as foundation species (Dayton 1972; Bruno and Bertness 2001), dominants (Grime 1987; Power et al. 1996), structural species (Huston 1994) or ecosystem engineers (Jones et al. 1997), depending on the specific ecological context. Semantics aside, these organisms are all considered to be ecologically important "because they form and modify habitats."

Our mechanistic understanding of how the species that form and modify habitats have "direct positive effects" on focal organism has become increasingly predictive and general (e.g., Bruno et al. 2003; Byers et al. 2006; Crain and Bertness 2006; Padilla and Pugnaire 2006; Halpern et al. 2007). However, fewer studies have considered how habitat formers can also have "indirect positive effects" on focal organisms via cascading interactions between organisms (cascade = a succession of stages, processes, operations, or units).

In a recent paper, Altieri and colleagues (2007) provided evidence that communities can be fundamentally dependent on indirect positive interactions, involving successions of positive interactions among species. Through manipulative experiments and large-scale observations, they found that cordgrass on cobble-beaches had direct positive effects on mussels that in turn had direct positive effects on seaweeds, crustaceans, and other molluscs. This sequence of interactions was coined a "facilitation cascade." The facilitation cascade represented a hierarchically organized community (Bruno and Bertness 2001) because facilitation by mussels was nested within a community that itself was dependent on the primary facilitation by cordgrass. Altieri et al. (2007) thereby tied together two emerging areas of ecological interest: facilitation (positive interactions) and cascades (successive interactions). The study has

subsequently stimulated the development of conceptual models of community organization and conservation (Halpern et al. 2007; Jones and Callaway 2007; van Wesenbeeck et al. 2007; Gribben et al. 2009; Kikvidze and Callaway 2009; Altieri et al. 2010).

Altieri et al. (2007) provided an introduction to the concept of facilitation cascades based on an empirical example. However, the article did not discuss whether similar processes occur in other ecosystems, and only touched briefly upon how facilitation cascades relate to other forms of indirect positive effects. Here, we expand the conceptual context of facilitation cascades and describe in detail a common type of facilitation cascade: the "'habitat cascade' where indirect positive effects on focal organisms are mediated by successive formation or modification of biogenic habitat" (Fig. 1). This definition explicitly excludes processes associated with abiotic formation or modification of habitats (e.g., rocks that provide substratum for seaweeds).

First, we frame the habitat cascade within the context of facilitation cascades and other forms of indirect positive effects caused by successive interactions between three interacting organisms. To document that habitat cascades are general ecological phenomena, we review published examples from terrestrial and marine ecosystems and present new data from soft-bottom estuaries. We summarize generalities of habitat cascades and propose standardized measures to compare across ecosystems how habitat cascades impact abundances and diversity of focal organisms. Finally, we discuss human impacts on habitat cascades, and outline research topics that will allow a better understanding of ecosystems by incorporating concepts about facilitation and habitat cascades.

The concept of habitat cascade was, on purpose, framed without references to ecosystem engineers, foundation species, structural species, or dominants. This was done for reasons of history (habitat is the oldest term) (Warming 1895), simplicity (habitats is defined in primary to tertiary educational biology text books), and precision (most reviewed studies only quantified where species were found, not what they did). These terms were also excluded to minimize ambiguity (e.g., the phrase "biogenic habitat formation by ecosystem engineers" is almost tautological) and overlap in definitions (definitions of ecosystem engineers or foundation species differ and they overlap depending on the particular research area and have changed within a short time) (Bruno and Bertness 2001; Wright and Jones 2006). Still, we do see the benefit of relating these terms to habitat cascades and other indirect positive effects
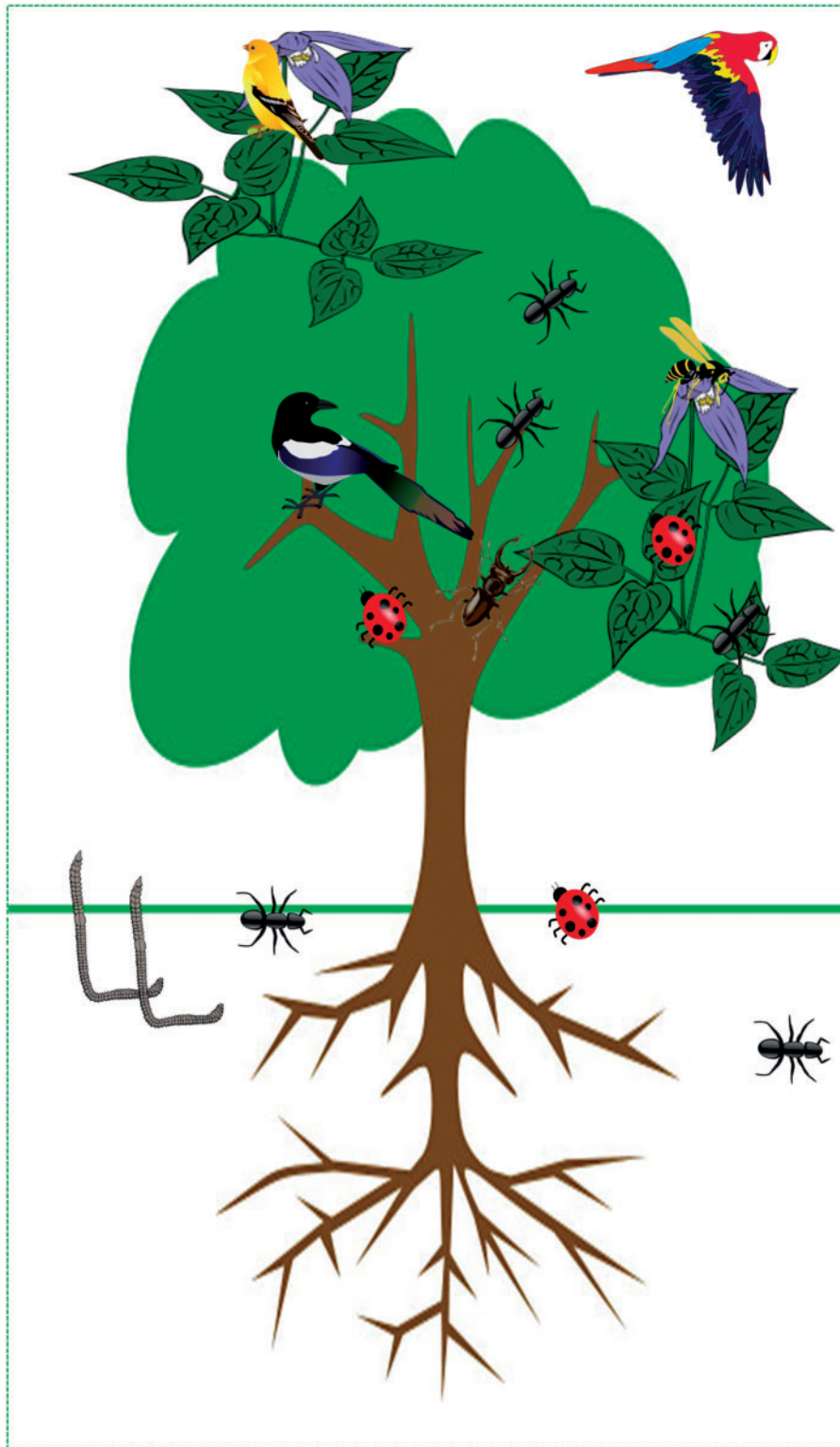
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Fig. 1 A hypothetical biogenic habitat cascade. Biogenic = produced by living organisms. Habitat = place where an organism normally occurs. Cascade = succession of stages, processes, or units. A biogenic habitat cascade is composed of a matrix, basal habitat, intermediate habitat and focal organisms. Matrix = ground substance in which things are embedded; here soil and air. Basal habitat former = primary habitat; here tree. Intermediate habitat former = secondary habitat; here climbing vine. Focal organisms = dependent variables; here birds and insects. Focal organisms will, at any given time, be sampled or observed within the matrix, or the basal or intermediate habitats. Focal species only found in a single habitat = obligate; here earthworm and parrot in soil and air matrix, longhorn beetle and magpie in tree, and finch and bee in vine. Focal species found in multiple habitats = facultative; here ladybirds and ants. Most organisms in real habitat cascades are facultative with different affinities for different habitats. Units of habitat cascades are repeated in space (trees to forest, forest to shrubs or grassland) with widely different proportions of habitat formers and focals. Habitat cascades typically have a hierarchical size structure (but see examples from estuaries, Table 1).

Table 1 Overview of existing studies of habitat cascades

Study	Habitat (Region)	Habitat cascades; B → I → Focals	M–C	S	B	B(S)	I	I(S)	B + I	B(S) + I
Altieri et al. 2007	Temperate salt marsh (New England)	Marsh → Mussel → Epibiota	M	X		X		X		X
Altieri et al. 2010	Temperate salt marsh (New England)	Marsh → Mussel → Epibiota	M	X		X		X		X
Bologna and Heck 1999	Tropical Seagrass bed (Florida)	Seagrass → Epiphyte → Mobile Epifauna	M			X				X
Cruz-Angon and Greenberg 2005	Tropical forest (Mexico)	Tree → Epiphyte → Bird	M			X				X
Cruz-Angon et al. 2008	Tropical forest (Mexico)	Tree → Epiphyte → Bird	M			X				X
Cruz-Angon et al. 2009	Tropical forest (Mexico)	Tree → Epiphyte → Mobile Epifauna	M			X				X
Edgar and Robertson 1992	Temperate seagrass bed (Western Australia)	Seagrass → Epiphyte → Mobile Epifauna	M			X				X
Ellwood and Foster 2004	Tropical forest (Malaysia)	Tree → Epiphyte → Mobile Epifauna	C		X		X			
Ellwood et al. 2002	Tropical forest (Malaysia)	Tree → Epiphyte → Mobile Epifauna	C		X		X			
Gribben et al. 2009	Subtropical seaweed meadow (New South Wales)	Seaweed → Clam → Epibiota	CM	X		X		X		X
Hall and Bell 1988	Tropical seagrass bed (Florida)	Seagrass → Epiphyte → Mobile Meiofauna	CM		X				X	
Karasawa and Hijii 2006	Subtropical forest (Japan)	Tree → Epiphyte → Mites	C		X		X			
Martin-Smith 1993	Tropical coral-algal bed (Queensland)	Seaweed → Epiphyte → Mobile Epifauna	M		X				x	
Ødegaard 2000	Tropical forest (Panama)	Tree → Liana → Beetles	C		X		X			
Stuntz 2001	Tropical forest (Panama)	Tree → Epiphyte → Mobile Epifauna	C		X				X	
This study	Temperate estuary (New Zealand)	Cockle → Seaweed → Epibiota	C		X				X	
This study	Temperate estuary (Denmark)	Mussel → Seaweed → Epibiota	C		X				X	
This study	Temperate estuary (Western Australia)	Gastropod → Seaweed → Epibiota	C		X				X	
This study	Temperate estuary (Virginia)	Polychaete → Seaweed → Epibiota	CM	X	X	X			X	X

Soil/sediments samples without habitat formers and samples of the Basal and the Intermediate habitats with both habitat formers as "B+I." Typically, data on "B," "I," and "B+I" (i.e., without "S") are obtained when focal organisms are quantified from traps in the crowns of trees or by collection of grass leaves, seaweeds, or nest epiphytes. Focal organisms collected from ground-based areal sampling (e.g., sediment cores and quadrats) include organisms also associated with the sediment matrix, and are here referred to as "B(S)," "I(S)," and "B(S) + I." An "X" refers to the habitats from which focal organisms were quantified. Most studies that included habitat "S," quantified surface dwellers only, although below-ground focals were also quantified from cores in the estuarine habitat cascades. Most cascades are hierarchical, both in regard to size and dependency (founded on a large independent primary producer). Note that the estuarine cascades differ; in those, the basal habitat former is a consumer (invertebrate) that typically is smaller than the intermediate habitat former (a seaweed).

under some circumstances. For example, ecosystem engineering and foundation species may emphasize specific functions and processes more than habitat formation does, e.g., as the cause of state changes in abiotic materials or by providing specific resources for other organisms (Dayton 1972; Jones et al. 1997; Bruno and Bertness 2001).

Facilitation cascades, habitat cascades, and other indirect positive effects: conceptual overview

Altieri et al. (2007) defined a facilitation cascade as successive interactions "in which the positive effects of a secondary facilitator are contingent on amelioration of the habitat by a primary foundation species" (p. 204). Here, facilitation refers broadly to any positive effect of one species on another species, regardless of possible negative feedbacks (Rodriguez 2006; Altieri et al. 2007; Brooker and Callaway 2009). Based on this broad definition we can describe several forms of facilitation cascades that differ in the processes that are emphasized and how they can be quantified.

Studies of positive interactions have traditionally emphasized habitat formation or mutualism (see Introduction section). Although these terms are not mutually exclusive they typically focus on different biological processes whereby positive effects can structure communities. For example, mutualism between cleaners and fish infected by parasites do not involve habitat formation. Similarly, provision of habitat by trees or kelps for understory or epiphytic species are typically not mutualistic interactions (Dayton 1972; Huston 1994; Jones et al. 1997; Bronstein 2001; Brooker and Callaway 2009). Based on these two types of processes, four forms of facilitation cascades can be distinguished when three organisms interact in succession (Fig. 2A–D).

First, some studies of facilitation cascades emphasize "successive habitat formation" (or modification) between a primary (hereafter basal) and a secondary (hereafter intermediate) interacting organism, with direct and indirect benefits for focal organisms (Figs 1 and 2A). In this "habitat cascade" it does not matter whether positive or negative feedbacks occur on the basal or the intermediate organisms. Note that the facilitation cascade documented by Altieri et al. (2007) also took the form of a habitat cascade since cordgrass provided habitat for mussels, and mussels in turn modified that habitat for focal species. In studies of habitat cascades, the emphasis is first on where species live, and then on why they

live where they do (e.g., because of amelioration of stress) or what they do (e.g., utilize resources). Habitat cascades can therefore be quantified directly from observations and collections of samples of the basal and intermediate habitat formers.

Secondly, research focus can be on "mutualism" (and/or commensalism) "between successive interactors." For example, focal organisms can be individual barnacles that recruit onto mussels [already in mutualism with cordgrass; Altieri et. al (2007)] that in a positive feedback again have positive effects on mussel recruitment (Lively and Raimondi 1987). In this case the chain of interaction represents successive sequences of mutualism. This cascade represents a more stringent ecological definition of facilitation as a process that benefits at least one of the participants and causes harm to neither (Bertness and Callaway 1994; Stachowicz 2001; Brooker and Callaway 2009). This chain of interaction is a "mutualism cascade" because mutualism (or commensalism) is repeated between the basal and intermediate organism, and the intermediate and focal organism (Fig. 2B). Essentially, to quantify mutualism cascades, three-factorial experiments are needed, with manipulations of the abundances of the basal, the intermediate, and the focal organisms.

Facilitation cascades can also include combinations of the processes of mutualism and habitat-formation. In the third form of facilitation cascade (Fig. 2C), basal non-habitat forming pollinators, seed dispersers, animal cleaners and guards, or microscopic C/N-fixers such as symbiotic dinoflagellates or mycorrhiza, can be involved in mutualisms with intermediate habitat-forming trees or corals (Stachowitch 2001). The basal organisms thereby have indirect positive effects on the focal organisms that utilize the intermediate habitat former. This chain of interactions is referred to as keystone mutualism (Mills et al. 1993) because a keystone species causes disproportionately large effects compared to its abundance or biomass (Power et al. 1996). Finally, basal habitat-forming organisms can provide living space for intermediate organisms that, in turn, are involved in mutualism with focal organisms (Fig. 2D). For example, a tree may provide habitat for a bee's nest and the bees may pollinate nearby flowering plants.

The above facilitation cascades represent the truism that "a friend of my friend is my friend." However, indirect positive effects can also occur when direct negative interactions, i.e., competition and consumption (the later here encompasses predation, grazing, and parasitism) occur in succession.
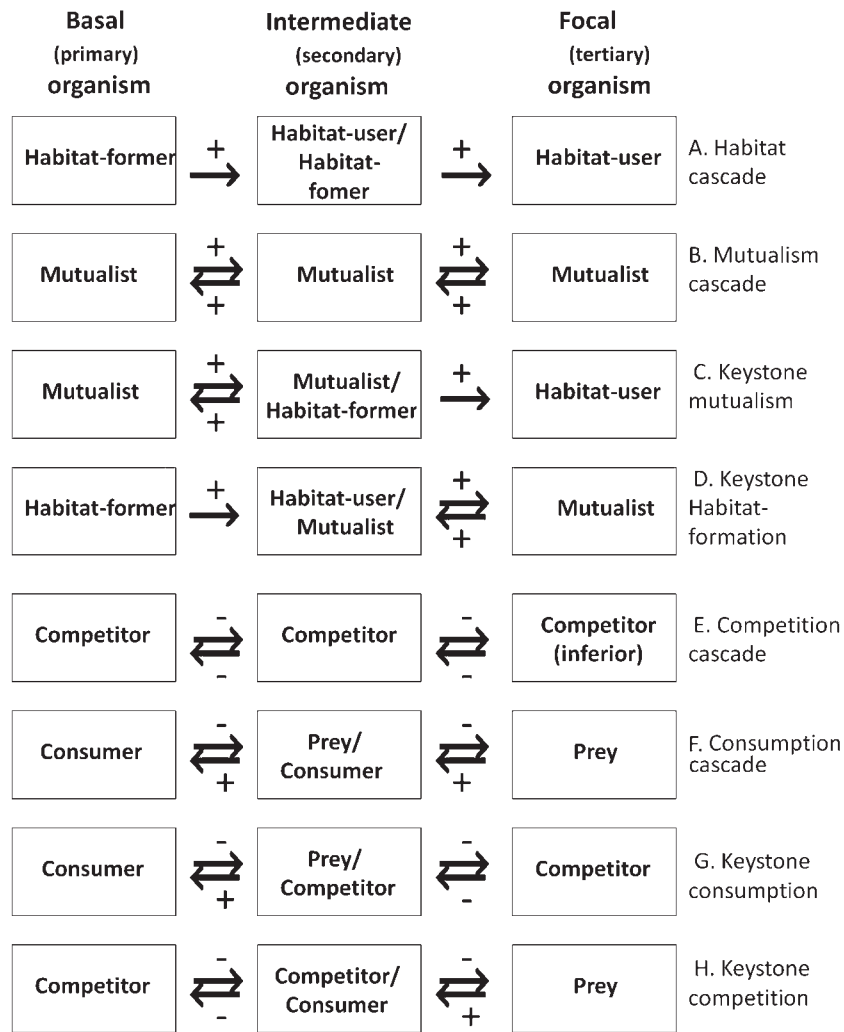
Basal (primary) organism		Intermediate (secondary) organism		Focal (tertiary) organism	
Habitat-former	+ →	Habitat-user/ Habitat-fomer	+ →	Habitat-user	A. Habitat cascade
Mutualist	+ ⇄ +	Mutualist	+ ⇄ +	Mutualist	B. Mutualism cascade
Mutualist	+ ⇄ +	Mutualist/ Habitat-former	+ →	Habitat-user	C. Keystone mutualism
Habitat-former	+ →	Habitat-user/ Mutualist	+ ⇄ +	Mutualist	D. Keystone Habitat-formation
Competitor	− ⇄ −	Competitor	− ⇄ −	Competitor (inferior)	E. Competition cascade
Consumer	− ⇄ +	Prey/ Consumer	− ⇄ +	Prey	F. Consumption cascade
Consumer	− ⇄ +	Prey/ Competitor	− ⇄ −	Competitor	G. Keystone consumption
Competitor	− ⇄ −	Competitor/ Consumer	− ⇄ +	Prey	H. Keystone competition

Fig. 2 Habitat cascades compared to other indirect positive effects arising from three organisms interacting in succession. The terminology of well-known chains of interaction was changed to highlight that two positive (habitat formation and mutualism) and two negative (competition and consumption) processes cause eight forms of indirect positive effects. Habitat formation and mutualism are not mutually exclusive, but emphasize different processes and different requirements regarding feedback mechanisms (compare examples A and B). Indirect positive effects are caused by direct positive effects between organisms in example A–D (a friend of my friend is my friend) and direct negative effects in example E–H (an enemy of my enemy is my friend). The first four examples represent facilitation cascades in its broadest meaning (facilitation = positive effect of species 1 on species 2 regardless of species 2's effect on species 1). Example A shows the habitat cascade that is characterized by "successive biogenic habitat formation" or modification between organisms (Ellwood and Foster 2004). Example B is a mutualism cascade in which focus is on "successive mutualism" (or commensalism, i.e., corresponding to facilitation in its strict ecological definition) (Bertness and Callaway 1994). Examples C and D combine processes of mutualism and habitat formation. Example C can occur when non-habitat-forming pollinators, seed-dispersers, cleaners, protectors, or C/N-fixers such as symbiotic dinoflagellates or mychorrhiza, facilitate habitat formers, like trees or corals. This chain of interactions is called keystone mutualism (Mills et al. 1993), because a keystone species causes disproportionately large effects compared to its abundance or biomass (Power et al. 1996). In example D, a habitat former provides living space for an organism that is involved in mutualism with a focal organism. Thus, a tree can provide habitat for a bee nest, and the bees can pollinate nearby flowering plants. This process is referred to as keystone habitat formation, because the importance of habitat formation extends beyond the direct effects on the intermediate organisms (Mills et al. 1993; Power et al. 1996). The last four examples represent enemy cascades (successive enemy interactions). Example E is a competition cascade, i.e., with "successive competition" between organisms. Competition cascades occur in assemblages in which pairs of competitors compete for different resources (also coined indirect facilitation) (Levine 1999). Example F is a consumption cascade, i.e., with "successive consumption" between organisms (=trophic cascades, emphasizing that interacting organisms occupy successive trophic layers) (Paine 1980). Example G shows keystone consumption, a chain that combines consumption and competition processes. In keystone consumption a predator or grazer consumes a dominant competitor, thereby indirectly facilitating an inferior competitor (referred to as keystone predation by Paine [1969]). Finally, example H shows keystone competition. Here a competitor reduces the performance of a consumer with indirect positive effects on the prey (Perry et al. 2004). Example B, E, and F result in indirect positive feedbacks from the focal to the basal organism. These three examples also represent indirect mutualisms, as both the focal and the basal organisms benefit from indirect effects (Connor 1995).

With two direct negative processes operating, four "enemy cascades" (an enemy of my enemy is my friend) can be distinguished. First, "successive competition" can lead to indirect positive effects (Fig. 2E). Here one competitor reduces the performance of another competitor that otherwise is superior to a third competitor. Such competition cascades typically arise in assemblages in which competitors compete for different resources (Levine 1999). Secondly, "successive consumption" can result in indirect positive effects (Fig. 2F). This sequence of interactions is better known as a trophic cascade, a term that highlights that interactors occupy successive trophic levels in a food chain (Estes and Palmisano 1974; Paine 1980; Carpenter et al. 1985; Silliman and Bertness 2002). Consumption and competition processes can also be combined in chains of interactions. Thus, if predators, grazers, or parasites consume strong competitors, inferior competitors may benefit indirectly (Fig. 2G). For example, Paine (1966, 1969) demonstrated that starfish control mussels, thereby freeing up space for inferior sessile competitors. Finally, strong competitors can reduce the performance of other competitors that also are consumers, thereby indirectly facilitating prey organisms (Fig. 2H). Thus, ants may deter moths that graze on plant seeds, with indirect positive effects on plants (Perry et al. 2004). These two chains of interactions are referred to as "keystone consumption" and "keystone competition," to emphasize the disproportionately large effect of consumption and competition, respectively (Power 1996).

Review of terrestrial and marine facilitation and habitat cascades

The general importance of facilitation cascades is apparent through their widespread occurrence in a variety of ecosystems and biogeographical regions. We document this importance through a literature review and presentation of new data from soft-bottom estuaries. The review focuses specifically on habitat cascades because this form of facilitation cascade is best documented (Table 1).

Terrestrial host-epiphyte habitat cascades

Tropical and subtropical trees (basal habitat) often provide habitat for nest epiphytes, lianas, and vines (intermediate habitat) that in turn provide habitat for various focal organisms (Fig. 1). For example, it has been shown that species richness of beetles in climbing lianas equals beetle richness of the host trees (without the lianas), and that the beetles from

the lianas are more specialized than are the beetles from the tree habitat (Ødegaard 2000). High abundances of invertebrates have also been quantified from *Asplenium nidus* nest epiphytes in rainforests (Ellwood et al. 2002; Ellwood and Foster 2004). Based on surveys of focal invertebrates in tree crowns and in nest epiphytes, Ellwood and colleagues calculated that about half of the invertebrate biomass in a tropical rainforest was dependent on the intermediate epiphyte habitat. Insects associated with the intermediate habitat were also larger and of different taxonomic compositions compared to insects from the basal habitat. In a subtropical *Castanopsis* forest in Japan, *A. nidus* has also been shown to support high densities of mites, particularly among its roots (Karasawa and Hijii 2006). This study again documented that epiphytes contribute significantly to the total abundance and diversity of invertebrates. Stuntz and colleagues compared the invertebrate assemblages in the small tropical tree, *Annona glabra*, free of epiphytes, to trees of the same speces occupied by *Dimerandra*, *Tillandsi* and *Vriesea* epiphyte nests. They found the invertebrate assemblages to be distinct among the three epiphytes, with more spiders in trees with epiphytes than in trees without them (although results were less clear for ants and beetles) (Stuntz et al. 1999; Stuntz 2001; Stuntz et al. 2002; Stuntz et al. 2003). Finally, Cruz-Angon and Greenberg (2005) and Cruz-Angon et al. (2008, 2009) have provided experimental evidence that *Inga jinicuil* (in coffee plantations) with epiphytes support higher abundances of many species of birds compared to trees without epiphytes. These birds may utilize the epiphytes for feeding, resting, nesting, and to hide from predators. The trees with epiphytes also contained more, larger, and more diverse, focal invertebrates than did the trees from which epiphytes were manually removed.

Marine host-epiphyte habitat cascades

Focal invertebrates have also been quantified on hosts and epiphytes from marine systems. Hall and Bell (1988) combined surveys and experiments that documented effects on focal meiofauna associated with the seagrass *Thalassia testudinum* and its epiphytes. They found positive correlations between the abundance of copepods, nematodes and amphipods and the abundance of the epiphytic algae, *Giffordia michelliae*, and artificial epiphytes on the seagrass blades. This study concluded that the physical structure of the intermediate habitat was an important driver of this habitat cascade. Edgar and Robertson

(1992) carried out an experiment involving the removal of epiphytes in an *Amphibolis* seagrass bed. Again, fewer species and lower abundances of focal organisms were found when epiphytes were removed. Finally, Bologna and Heck (1999) compared focal invertebrates associated with habitat mimics with, and without, natural or artificial epiphytes in a mixed seagrass bed (i.e., utilizing mimics to represent both the basal and the intermediate habitat former). Abundances of many focal organisms were found to be higher on mimics with natural epiphytes compared to mimics with artificial epiphytes. This suggests that food subsidy between focal organisms and the intermediate habitat was of some importance as a driver of this habitat cascade.

In addition to experiments conducted in sandy seagrass beds, at least one study has demonstrated the existence of habitat cascades from seaweed-dominated rocky reefs. Martin-Smith (1993) experimentally removed epiphytes from two types of *Sargassum* seaweed mimics in Queensland, Australia. Again, community composition differed between the epiphyte-covered and the clean mimics, and again there were higher abundances of focal crustaceans, polychaetes and gastropods in the presence of the epiphytes.

A habitat-modification cascade

The studies reviewed so far have mainly focused on how basal and intermediate habitat formers generate structure suitable for subsequent colonization. However, habitat cascades include habitat-modifying processes (in addition to creation of habitat). Recently, Gribben et al. (2009) showed that a basal habitat former, the invasive seaweed *Caulerpa taxifolia*, reduced the burial-depth of an intermediate habitat former, the clam *Anadara trapezia*. The clam thereby became exposed to focal organisms that recruited onto the clam shells from the water column. The abundance and diversity of focal organisms on clam shells was then enhanced via a changed behavior of the intermediate habitat in the presence of the basal habitat. *Caulerpa* probably caused this reduced depth of clam burial via increasing anoxia and toxins in the sediments (i.e., an adverse modification of the habitat) (Gribben et al. 2009).

Habitat cascades as hierarchically structured processes

The above examples suggest that habitat cascades can be an important class of indirect positive effects, particularly in epiphyte-rich terrestrial and marine ecosystems. All of the examples above are hierarchically structured in two ways. First, they are hierarchically organized in their dependence of organisms on one another (Bruno and Bertness 2001). The basal habitat former is a large primary producer that can exist independently of the intermediate habitat former (and may perform better). In contrast, the intermediate organism is typically dependent, physically or physiologically, on the basal habitat, as substratum or as ameliorators of environmental stress. Second, they are hierarchical in size since the large basal plant creates habitat for smaller intermediate organisms that, in turn, create or modify habitat for focal organism (Fig. 1). In the next section we present new data to describe different habitat cascades from soft-bottom estuaries. Here the basal habitat formers are relatively small invertebrate consumers and these habitat cascades do not exhibit hierarchical size structures.

An estuarine case study of a different habitat cascade

Most estuaries are soft-bottom topographically simple systems. In estuaries, escape from predators typically depends on burial or swimming skills or simply being unpalatable. Any organism that provides living space and shelter for other species should therefore be a candidate as a habitat former. For example, estuarine molluscs, polychaetes, vascular plants, and seaweeds can provide habitat for numerous sessile and mobile focal organisms (Bell 1985; Gutierrez et al. 2003; Thomsen et al. 2005; Nyberg et al. 2009). Most of these studies have focused on the direct positive effects associated with habitat formation, although Thomsen et al. (2005) suggested that indirect positive interactions, based on successive habitat formation, could also be important.

It has been shown that estuarine seaweeds within the genus *Gracilaria* often live attached to benthic invertebrates (Thomsen et al. 2007a, 2007b). On the Eastern Shore of Virginia and in Danish estuaries *Gracilaria* is incorporated into the tubes of the gardening polychaete *Diopatra cuprea* (Thomsen and McGlathery 2005; Thomsen et al. 2009a) and the byssal threads of the bivalve *Mytilus edulis* (Thomsen et al. 2007b; Nyberg et al. 2009). Similarly, in Pauatahanui Inlet (New Zealand) and the Swan River (Western Australia) *Gracilaria* is found attached to the live shells of the cockle *Austrovenus stutchburyi* and the mudsnail *Batillaria australis*, respectively (Thomsen et al. 2007b, 2010). In each case the invertebrate provides hard substratum, i.e., a limiting resource, for the seaweed. It has also been shown that *Gracilaria* itself provides

habitat for flora and fauna (Thomsen and McGlathery 2005; Nyberg et al. 2009; Thomsen et al. 2009a). However, no previous study has partitioned the relative dependence of these estuarine focal organisms on the basal (e.g., *Diopatra*) and intermediate (e.g., *Gracilaria*) habitats.

Experimental study: removal of the intermediate habitat-forming seaweeds

A manipulative experiment was conducted on the Eastern Shore of Virginia in July 2006 to test whether removal of the intermediate habitat reduces richness and abundance of focal organisms (as in Edgar and Robertson 1992). We removed the intermediate habitat (*Gracilaria vermiculophylla*) from 12 plots, each of 0.3 m^2. These "removal" plots were compare with 12 untouched control plots in which both the basal (*D. cuprea* and its tube structure) and intermediate habitats were present. Seaweeds were removed by pulling algae off polychaete tubes with minimal disturbance to the structure of the tube. We also marked 12 untouched control plots of bare sediment, to quantify focal organisms in samples in which both biogenic habitat formers were absent (=the matrix; Fig. 1). The experiment was repeated at three intertidal sites (see Supplementary Tables 1 and 2). After 2 weeks the removal treatments were repeated, and after two more weeks, sediment cores (10 cm inner diameter; 10 cm into the sediment) were collected from the center of each plot on a falling tide. All samples were submerged by at least 10 cm of water at the time of collection. Cores were sieved through a 2-mm mesh. *Gracilaria* thalli and sessile epiphytic algae and modular animals were separated, blotted with paper towels and weighed, whereas single animals were counted.

We classified the three treatment habitats as Sediment infauna (=S, corresponding to the matrix; Fig. 1), Sediment infauna nested within the Basal habitat (=B(S), corresponding to removal plots) and Sediment infauna nested within the Basal habitat plus Intermediate habitat (=B(S) + I; corresponding to the control plots). Data were analyzed by factorial ANOVA where "habitat" was treated as a fixed factor and "site" as an orthogonal random factor. Significant habitat effects were followed by SNK tests.

We found more sessile taxa (Fig. 3A) and higher abundances of both sessile (Fig. 3C) and mobile (Fig. 3D) organisms when both habitat formers were present, compared to plots in which the intermediate habitat-former was removed or to sediment plots lacking habitat formers. However, differences in individual treatments were not significant for abundance of sessile species (because of large variability among samples) and only nearly-significant for abundance of mobile organisms (because of the small effect of size) (Supplementary Tables 1 and S2). In contrast, no differences were observed for richness of mobile taxa among any of the treatments (Fig. 3B). In short, this experiment also indicates that removals of the intermediate habitat former decrease the abundance and diversity of estuarine focal organisms, as previously shown for seagrass meadows, seaweed beds, forests, and salt marshes.

Correlative study: comparing basal invertebrates with low versus high abundance of intermediate seaweed

A broad-scale survey was conducted to identify whether focal organisms are more abundant and species rich when the intermediate habitat is large compared to small in the presence of the basal habitat (Hall and Bell 1988; Ellwood and Foster 2004). We haphazardly collected basal habitat formers with different levels of attached *Gracilaria* from each biogeographical region (4–10 nested sites per region; all individuals were collected in summer months from 2005 to 2007; see Supplementary Tables 3 and 4 for details). Each basal host and its associated algal specimen were swiftly collected, placed in a plastic bag and kept cold until arrival at the laboratory. All samples were submerged in at least 10 cm of water at the time of collection. This is a common method of sampling seaweed-associated epibiota (Wernberg et al. 2004; Nyberg et al. 2009). *Gracilaria* thalli, and sessile epiphytic algae and modular animals were quantified as described for the experiment. Individual samples were grouped as basal organism with low biomass of intermediate habitat [=B(I)] or large biomass of intermediate habitat (=B + I; see Supplementary Tables 3 and 4 for details). Samples were grouped into the two treatments to ensure relatively equal sample sizes within a sample location. The biomass of the intermediate habitat varied widely between locations and regions, and a "B + I" treatment in one location could therefore equal a "B(I)" treatment from another location. However, our test focused on the effects of intermediate habitat formers within a location, so differences in biomass between locations were of secondary importance. We used nested ANOVA to test whether "B+I" had higher taxonomic richness and higher total abundances than "B(I)" for both sessile and mobile organisms (habitat = fixed factor; region and sites = nested random factors; all data were log
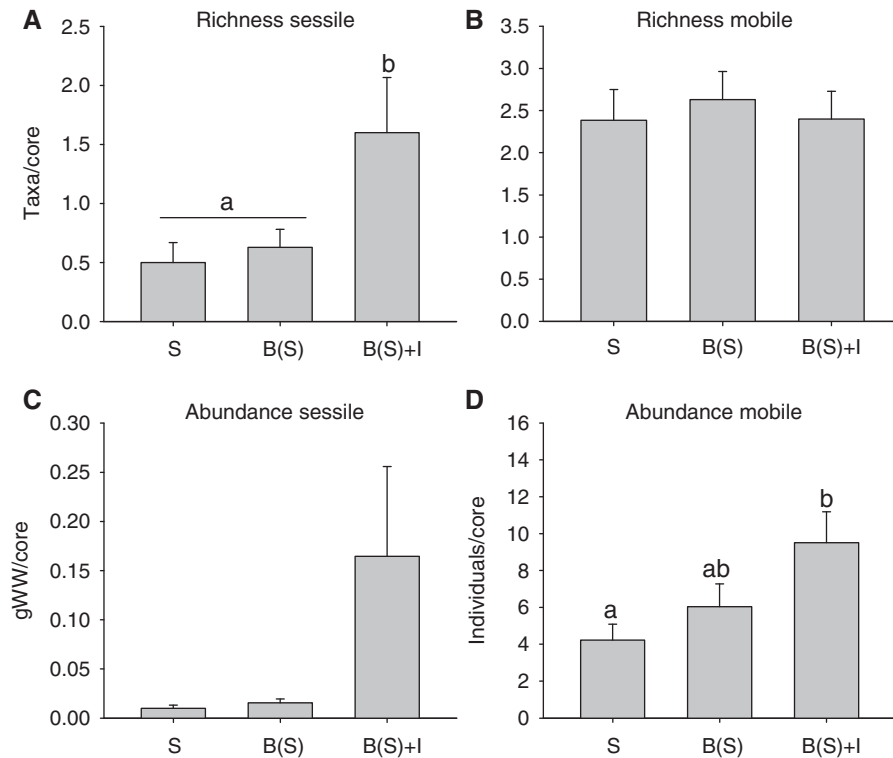
Fig. 3 Effects of removal of intermediate habitat on estuarine focal organisms. Taxonomic richness and total abundances (±SE) of sessile and mobile organisms, with and without removal of the intermediate habitat former. S = untouched sediment plots with absence of biogenic habitat formers; B(S) = Basal habitat former (*D. cuprea* in sediment core) and removal of the intermediate habitat former *G. vermiculophylla*; B(S)+I = untouched control plots with co-occurring basal and intermediate habitat formers. Mean values are pooled from similar experiments conducted at three sites (there were no site sites × habitat effects). See Supplementary Tables 1 and 2 for details of samples sizes, mean values from individual sites, and ANOVA tables. Letters designate different treatments based on SNK-tests.

x + 1 transformed; see Supplementary Table 4 for detailed test results).

We found significantly higher taxonomic richness and abundances both of sessile and mobile focal organisms associated with the basal habitat with high levels of intermediate habitat formers (Fig. 4A–D). These effects were statistically consistent between biogeographical regions for taxonomic richness of sessile and mobile organisms, and for abundance of sessile taxa [i.e., no site (region) × habitat interactive effects; Supplementary Table 4]. However, a significant site (region) × habitat interaction for abundance of sessile organisms suggested that effects varied between biogeographical regions. Thus, the effects of the intermediate habitat were particularly large in samples from Virginia and Denmark [note the large difference between B(I) and B+I in Fig. 4D from these two regions]. In short, this survey demonstrated that the intermediate habitat former (sampled together with the basal habitat former) controls abundances and diversity of estuarine focal organisms in several biogeographical regions.

Based on the experiment and broad-scale survey, we conclude that habitat cascades are also common in soft-bottom estuaries, where they contribute to maintaining high abundances and diversity of focal organisms. We emphasize that these data are exploratory and only aimed to introduce estuarine habitat cascades. Future studies should investigate multivariate impacts on the community, why focal organisms vary widely between sites and bioregions, and the importance of temporal variability, and should test for specific mechanisms whereby facilitation may occur (see also Discussion section).

Discussion

For decades, research has focused on how organisms that interact in succession via enemy cascades can cause indirect positive effects (Paine 1966, 1969, 1980; Estes and Palmisano 1974; Carpenter et al. 1985; Silliman and Bertness 2002; Fig. 2E–H). However, we suggest that indirect positive effects that occur via facilitation cascades are also widespread and important. From processes associated
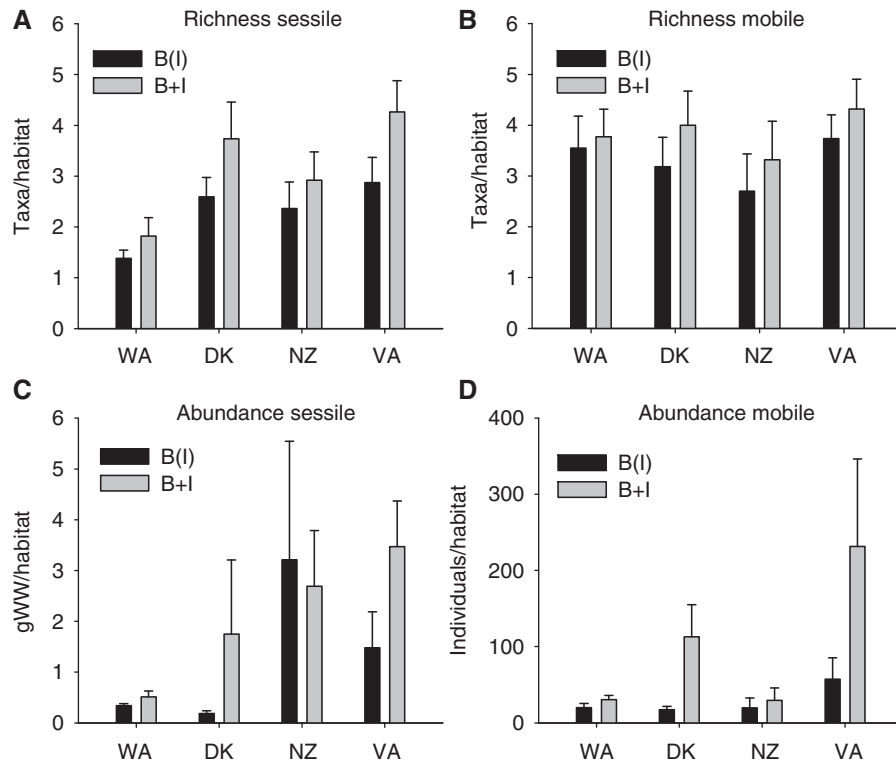
Fig. 4 Broad-scale survey of focal organisms associated with estuarine intermediate habitats. Taxonomic richness and total abundances (±SE) of sessile and mobile taxa associated with basal invertebrate habitat formers with either low (= "B(I)") or high (= "B + I") attached biomass of the intermediate seaweed *Gracilaria* spp. There were significantly more focal organisms when the intermediate habitat former occurred with high biomass (significant for all four responses; log $x + 1$ transformed data). See Supplementary Tables 3 and 4 for details of samples sizes, mean values from nested sites within regions, and ANOVA tables. WA = Swan river estuary, Western Australia; NZ = Pauatahanui Inlet, New Zealand; DK = Danish estuaries; and VA = lagoons at the Eastern Shore of Virginia.

with habitat formation and mutualism, we conceptualized four basic forms of facilitation cascades (Fig. 2A–D). We also reviewed the empirical evidence for the simplest of the facilitation cascades; the habitat cascade (Figs 1 and 2A). We documented that habitat cascades have broad ecological relevance, sometimes controlling species abundances and biodiversity in salt marshes, subtropical and tropical forests, seagrass beds, hard-bottom reefs, and soft-bottom estuaries. However, we found no published examples of habitat cascades from open pelagic waters, polar tundra, freshwater stream or lakes, grasslands, or temperate forests. It is likely that habitat cascades are less prevalent in these ecosystems. Still, they may just be less obvious in these ecosystems in which large structural organisms do not dominate. For example, in pelagic systems, whales and jellyfish can provide habitats for barnacles or fish, respectively. In addition, focal ecto-parasites or endo-parasites can be associated with the intermediate barnacles and fish and thereby would represent (undocumented) pelagic habitat cascades. Below, we compare habitat cascades in a quantitative

framework, discuss their driving mechanisms and human impacts, and suggest future avenues for research.

Comparisons of habitat cascades

Habitat cascades can affect the abundances of a few species or form-functional groups or have community-wide impacts (a distinction also emphasized for trophic cascades) (Polis et al. 2000). Here we calculate exactly how much the addition of the intermediate habitat enhances (i.e., "magnifies") the abundance of specific focal organisms as well as community-wide metrics, such as the total abundance of organisms and taxonomic richness. Focal organisms associated with the basal habitat were used as a unit reference. A "magnification ratio" (MR) was then calculated for focal organisms associated with the intermediate habitat [MR = (Intermediate + Basal)/Basal, e.g., MR = 2 corresponds to a doubling in abundance by including an intermediate habitat former]. Data on the abundance and richness of focal organisms were extracted from figures, tables and text from representative

examples of habitat cascades (Supplementary Table 5). These data were used to calculate average MR values (Table 2). Most studies have compared focal organisms associated with the basal habitat to the combined basal-intermediate habitat. These MR values ranged from 2.4 to 8.4 for group abundances, 1.3 to 10.5 for total abundances, and 1.0 to 2.5 for taxonomic richness (Table 2). Note that the single largest MR values for both total abundances and taxonomic richness were found in our seaweed-removal experiments. This is not surprising given that this study is the only one in which the intermediate habitat former was both larger and functionally different from the basal habitat. Note also that these estuarine MR values are conservative, in part because small numbers of basal habitat formers were found in the removal treatments (Supplementary Table 1), and in part because the sediment matrix was included in the samples (adding taxonomic noise).

Combined, the MR values presented in Table 2 demonstrate the importance of including intermediate habitats when estimating population abundances across several ecosystems and biogeographical regions [emphasized for rain forests by Ellwood and Foster (2004)]. The low MR values observed for richness were not surprising given that richness is a simple community measure (it only takes one new individual in a single sample to increase richness by one). These values do not imply that more complex community structures or species' identities are unaffected by habitat cascades. Indeed, multivariate tests typically find different community structures between basal and intermediate habitats (Edgar and Robertson 1992; Bologna and Heck 1999; Stuntz 2001). To document whether synergy exists between the basal and intermediate habitat, it is necessary to quantify focal organisms from both habitats alone "and" in combination [i.e., "B," "I," and "B + I," (Table 2)]. Synergy exists if focal organisms are more abundant in samples combining both habitats, compared to the sum of focal species collected from each habitat individually (i.e., if "B + I" > "B" + "I"). Three studies quantified focal organisms for all relevant combinations of basal and intermediate habitats (Altieri et al. 2007; Gribben et al. 2009; Altieri et al. 2010). Of these, both Altieri et al. 2007 and Altieri et al. 2010 suggest synergistic effects on the abundances and richness of focal organisms.

Habitat cascades have been quantified based on two sampling methods: sampling of the habitat

Table 2 Habitat cascade magnification ratios for selected studies

Response of focal organisms	Study	Habitat			
		S	B	I	B + I
Abundance	Altieri et al. 2007[a]	0.2	1.0	0.4	2.8
Group	Altieri et al. 2010[a]		1.0	0.3	3.0
	Hall and Bell 1988		1.0		8.4
	Martin-Smith 1993		1.0		2.4
Abundance	Bologna and Heck 1999[a]		1.0		1.7
Total	Cruz-Angon and Greenberg 2005[a]		1.0		1.5
	Edgar and Robertson 1992[a]		1.0		2.0
	Ellwood and Foster 2004 (g/ha)		1.0	1.0	
	Gribben et al. 2009	0.5	1.0	1.1	1.3
	Thomsen et al. (Sessiles, Fig. 3C[a])	0.6	1.0		10.5
	Thomsen et al. (Mobiles, Fig. 3D[a])	0.7	1.0		1.6
Taxonomic	Altieri et al. 2010[a]	0.5	1.0	0.8	1.1
Richness	Bologna and Heck 1999[a]		1.0		1.2
	Cruz-Angon and Greenberg 2005[a]		1.0		1.0
	Edgar and Robertson 1992[a]		1.0		1.4
	Gribben et al. 2009	0.8	1.0	1.3	1.4
	This study (Sessiles, Fig. 3A[a])	0.8	1.0		2.5
	This study (Mobiles, Fig. 3B[a])	0.9	1.0		1.0

Average magnification ratios (MR values) calculated from data presented in Supplementary Table 5 and in Fig. 3. "Abundance Group" = averaged MR values that include a few distinct taxonomic or form-functional groups; "Abundance Total" = average MR values that include all focal individuals collected in a sample. See Table 1 and Supplementary Table 5 for details of the responses of focal organisms.
[a]Ground-based studies that include "Habitat S" (the soil or sediment matrix) in their sampling methodology.

formers either with, or without, inclusion of the abiotic matrix (soil, sand, and mud; Fig. 1). When the sampled variable is area and ground-based (cores, quadrats, and benthic suction), focal organisms associated with the matrix will appear in samples otherwise targeting basal and intermediate habitats. However, when focal taxa are collected from traps from tree crowns or stems, or by collection of seagrass leaves, seaweeds or nest epiphytes, focal organisms from the matrix are not included. We argue that inclusion of the matrix is important to understand the relative importance of habitat-cascade effects on the ecosystem level and is particularly useful when scaling data. However, inclusion of the matrix could weaken the ability to detect true cascading effects between successive habitats because re-occurring fauna from the soil and sediment dilute contrasts. Thus, sampling that focuses only on the basal and intermediate habitats may be easier to collect, should provide better estimates of the effect of true biogenic habitat cascading and may lead to better insights into the driving factors.

Human impacts on habitat cascades

Habitat cascades can be enhanced, created or destroyed by human activity. For example, the five main threats to conservation of biodiversity—habitat destruction, climatic change, over-harvesting, pollution, and invasions by non-native species (Anon 2006)—can all impact habitat cascades.

Habitat destruction is considered the single most important threat caused by humans to biodiversity. For example, rainforests and salt marshes are converted into urban areas or agricultural fields (Bertness et al. 2004; Anon. 2006). Habitat destruction can also be important on smaller scales. Thus, in marine seagrass beds and estuarine mud-flats, habitat destruction typically follows local land-reclamation projects or the construction of ports and causeways (Kennish 2002; Orth et al. 2006). When habitat cascades are hierarchically organized, the destruction of basal habitat formers (as described above) will cascade to impact on intermediate habitats and focal organisms. This highlights that the impacts of humans will be significantly underestimated when the effects of indirect cascading are ignored.

Climatic change, over harvesting, and pollution also affect habitat cascades. Negative effects of climatic change will probably dominate several basal habitats, including rainforest, seagrass beds, and salt marshes (Williams et al. 2003; Silliman et al. 2005; Orth et al. 2006). Climatic change will therefore have negative effects on intermediate habitats and focal organisms. However, for estuarine habitat cascades, effects are likely to be idiosyncratic, and potentially facilitate many focal organisms because basal invertebrates and intermediate seaweeds can have broad temperature requirements (Thomsen et al. 2007b, 2010). Harvesting of basal or intermediate habitat formers has obvious negative consequences for focal organisms. For example, it is common practice to remove epiphytes from coffee plantations because they are perceived to have a negative effect on coffee yields (Cruz-Angon and Greenberg 2005; Cruz-Angon et al. 2009). Similarly, many of the estuarine basal habitat formers, such *Diopatra* or *Mytilus* are locally overexploited for human consumption or for bait (Dankers and Zuideema 1995; Cunha et al. 2005). In contrast, aquaculture and transplantation of cockles, mussels, and other shellfish may enhance cascades, if the intermediate habitat former is present in the ecosystem. Pollution by nutrients in marine ecosystems may at first stimulate the growth of intermediate epiphytes and seaweeds (McGlathery 2001), possibly with a net benefit for focal organisms (i.e., more habitat becomes available). However, excessive growth of the intermediate habitat formers may ultimately destroy the habitat cascade. This can occur if the seagrasses and invertebrates are killed by epiphytic shading, physical smothering of the filtering apparatus, or anoxia (McGlathery 2001; Holmer and Nielsen 2007).

Non-native species can also modify, or even create, new habitat cascades. In many cases focal organisms are non-native species (Altieri et al. 2010). This demonstrates how habitat cascades can cause positive relationships between the abundances of native and non-native species on local scales. Basal and intermediate habitat formers can also be non-native species. For example, the marsh plants *Spartina* and *Phragmites* have invaded large coastlines worldwide (Silliman and Bertness 2004, Williams and Grosholz 2008). These invasions potentially alter existing habitat cascades (displacing native marsh plants) or may create new ones (invading mudflats). Non-native species can also be important in terrestrial host-epiphyte habitat cascades. Thus, invasive ants can utilize nest epiphytes; invasive vines and epiphytes are known to climb on and infest native trees; and invasive trees can host native epiphytes (Greenberg et al. 2001; Ward 2008). In marine systems, translocation of shellfish has, in particular, stimulated habitat cascades. This has occurred by increasing the range and abundances of deliberately introduced non-native habitat-forming shellfish and by facilitating transport of hitchhiking, non-native habitat formers (Ruesink et al. 2005; Thomsen

et al. 2006b). For example, the basal habitat former *B. australis* has likely been introduced into the Swan River via oyster transplants. This invasive snail has created an entire new habitat cascade, because no similarly abundant and large shell-forming snails exist in this estuary (Thomsen et al. 2010). Finally, intermediate habitat formers can also be non-native. Many epiphytes have invaded seagrass beds (Williams 2007) and the intermediate habitat former in Danish fjords and Virginia is the non-native seaweed *G. vermiculophylla* (Thomsen et al. 2006a, 2007b). The range expansion of this single species in the eastern Pacific and in the eastern and western Atlantic oceans (Nyberg et al. 2009; Saunders 2009; Thomsen et al. 2009a) suggest that estuarine habitat cascades are being altered over large geographic scales. Thus, widely distributed and abundant basal and intermediate habitat formers are often non-native species, demonstrating that invaders can facilitate the abundance and diversity of native species (Simberloff 2006).

Future research on habitat cascades

Few studies have documented habitat cascades and an exhaustive discussion of future studies are therefore beyond the scope of this article. Here we list a few key gaps in research.

First, it is important to test hypotheses that increase our understanding of causal mechanisms that underpin habitat cascades. It is well-known that the abundance of focal organisms associated with an individual habitat depends on the habitat size, density, structural complexity, biogeochemical make-up, and how "different" this habitat is compared to a reference (Bell et al. 1991). This knowledge can be extended to the following working hypothesis for habitat cascades: "magnification ratios of habitat cascades depend on how different interacting habitat formers are" (or how differently they modify the habitat). For example, we expect high magnification ratios when the intermediate habitat is larger and functionally different from the basal habitat. We found preliminary support for this hypothesis by comparing our experimental study (no hierarchical size structure; interactors occupy different trophic levels) to other studies reviewed in Table 2. We also hypothesize that on larger scales, spatial heterogeneity, increasing complexity of the food-web, and presence of interspersed alternative habitats will reduce magnification ratios due to diffusion and substitution of focal organisms to alternative pathways and habitats (see Borer et al. 2005 for a similar hypothesis for trophic cascades). To test the above

hypotheses, similar experiments should be conducted in multiple habitats, using standardized methods. For example, by using identical mimics (e.g., artificial plastic seaweeds) and real species that live in multiple habitats (e.g., *Gracilaria* seaweeds) it is possible to test simultaneously for the relative importance of basal and intermediate habitats, and of habitat size, structural complexity, and trophic subsidy, in sandy seagrass beds, rocky seaweed meadows, and estuarine mudflats.

It will also be important to refine the concept of the habitat cascade. We have focused on where the focal organisms most likely occur (its habitat) with little discussion of what the focal organisms do (see Hall and Bell 1988; Bologna and Heck 1999 for introductions to this subject). A niche-based resource-utilization approach (Chase and Leibold 2003) would be useful in promoting better understanding of what organisms do within habitats, if habitat cascades are stable or instable, and how they affect food-web complexity and biogeochemical cycling. We suggest future work should test for density-dependent feed-back impacts of focal organisms on habitat formers, for impacts of intermediate habitats on basal habitats, and how focal organisms utilize different habitat formers (for feeding, predation escape, breeding, nesting, or resting). Mimics simulating the habitats themselves (Hall and Bell 1988; Bologna and Heck 1999) will also be a useful tool, as they do not provide trophic subsidy and the chemical and physical structure can be controlled. Similarly, it is important to mimic the processes that lead to facilitation. For example, Altieri (2007) manipulated substrate stability, moisture, light, and temperature to show that the basal habitat (cordgrass) facilitates the intermediate habitat (mussels) via amelioration of stress. It is also important to test whether external agents control the distribution and abundances of basal and intermediate habitat formers. Such external agents could be parasites or predators that alter the behavior of basal habitat formers like the depth of burial of cockles (and thereby the time the cockle is exposed to fouling organisms) (Mouritsen 2004; Gribben et al. 2009), or bottom-up forces that stimulate growth of intermediate habitat formers (McGlathery 2001).

We also advocate that habitat cascades should be documented from new ecosystems, new regions, along environmental gradients, for new basal and intermediate habitat formers and on different spatio-temporal scales to quantify where and when habitat cascades create large magnification ratios. For example, mosses and ferns from temperate forests provide habitats for many insects (Gerson 1969;

Cooper-Driver 1978). If mosses and ferns are epiphytic, this tree-moss/fern-insect sequence may represent the first demonstrated habitat cascade from temperate forests. Similarly, estuarine oysters can provide alternative basal habitat (instead of snails, mussels, or polychaetes), and seaweeds like *Codium*, *Ulva*, and *Fucus*, can provide alternative intermediate habitats (instead of *Gracilaria*) (Thomsen and McGlathery 2006; Thomsen et al. 2007a). However, little is known about how qualitative differences in the texture, structure, or chemicals between such different combinations of alternative basal and intermediate estuarine habitat formers affect focal organisms. Finally, given that the majority of the world's undiscovered biodiversity is located in rainforests it is particular important to quantify habitat cascades in these critical systems in great detail (Ellwood and Foster 2004).

Conclusions

Habitat cascades represent an important type of facilitation cascade. Habitat cascades are best documented from host-epiphyte-dominated ecosystems such as tropical forests, rocky seaweed forests, or sandy seagrass beds, but can also be important in salt marshes and on estuarine mudflats. In each of these systems, habitat cascades can increase the abundances and richness of focal organisms. The estuarine case studies presented here differ from previously documented habitat cascades because the basal habitat former is an invertebrate consumer (instead of a large primary producer) that often is smaller than the intermediate habitat former (i.e., the cascade does not have a hierarchical size structure). This can have important ecological consequences; we proposed a simple working hypothesis stating that the importance of habitat cascades depends on differences in size and form-function between habitat formers (or how differently they modify the environment). For example, if focal organisms respond only to the quantity of the habitat (size of living space), and not its quality (e.g., trophic subsidy, structural complexity, chemicals), habitat cascades from estuaries should cause higher magnification ratios than found in many other habitat cascades. We also discussed how habitat cascades are impacted by habitat destruction, climatic change, over-exploitation, nutrient pollution, and invasive species. Thus, there are several examples of invaders being basal or intermediate habitat formers. This highlights how local-scale invasion can have direct or indirect positive effects on the diversity and abundances of native species.

We finally conclude that if habitat cascades are ignored in surveys and experiments in ecosystems where they are common, effects of anthropogenic stress may be significantly underestimated.

Supplementary Data

Supplementary Data available at *ICB* online.

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