

Indirect facilitation can unify common interaction chains in Ecology

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Abstract

Many studies have shown that indirect facilitation is of fundamental ecological importance. However, different indirect facilitation processes have been studied in isolation (e.g., trophic cascades), or largely overlooked (e.g., competition cascades), resulting in insular and inconsistent experiments, terminologies, theories, and models. Here I reconcile Robert Paine's seminal cascade and keystone concepts into a process-based framework that unite eight forms of indirect facilitation arising from 3-tiered interaction chains of common inhibitory (competition and consumption) and facilitative (mutualism and habitat-formation/modification) species interactions. The framework is simple to explain, reduce terminological ambiguity, encourages comparisons between different types of ecological interactions, is hierarchical and flexible so that it can be expanded or collapsed depending on research questions, and highlights the existence of understudied interaction chains, like competition cascades. I also propose future research to compare, rank and contrast indirect facilitation chains and suggest, more generally, that uniting apparently disparate ecological

concepts into hierarchical frameworks can help students, managers, and scientists to grasp the complexities and bewildering number of species interactions and stimulate research into more complete theories of ecology.

Keywords: Indirect effects, hierarchical framework, facilitation, concept cluster

The emergence of indirect facilitation

For more than a century, ecologists have understood and documented that **direct facilitation** can control communities, biodiversity and ecosystem functioning through mutualism and habitat formation and modification. For example, early studies showed mutualism between pollinators and plants (Riley 1892), ants and plants (Ridley 1910), fungi and algae (Fink 1913; Pound 1893), gardeners and their crops (Verwey 1930), cleaner fish and their parasite-infested hosts (Brusca 1857), and dinoflagellates and corals (Boschma 1925). Similarly, the roles of biogenic habitat-formation (Möbius 1877) and successional habitat-modifications (Clements 1936; Cowles 1899) have been well described. Today, our understanding of direct facilitation is general and predictive (e.g., Bertness and Callaway 1994; Bronstein 1994; Bruno et al. 2003; Bulleri et al. 2016; Stachowicz 2001), and is covered in great detail in ecological textbooks (e.g., Begon et al. 1986; Begon and Townsend 2021; Krebs 2014; Molles and Sher 2019; Smith et al. 1998; Townsend et al. 2003).

However, species can also facilitate other species through **indirect facilitation** (hereafter **IF**), where basal species have positive effects on focal species in the presence of at least one intermediate species (Wootton 1994). Indirect facilitation was first coined by Davidson (1980) to describe how competitive interactions chains resulted in indirect positive

effects between ant species. Regardless of Davidsons early study, many other forms of IF have been described in case-studies, using unrelated, different, inconsistent, and changing terminologies. For example, Waser and Real (1979) described IF arising through time-staggered pollinators visiting different flowering plants as ‘sequential mutualism’, whereas Mouritsen (2004) coined IF arising from burrowing shrimps on seabirds by increasing prey availability of cockles for a ‘facilitation cascade’. However, a few years later Altieri et al. (2007) described facilitation cascades as a ‘suite of positive interactions, in which the positive effects of a secondary facilitator was contingent on habitat amelioration by a primary foundation species’.

Recent network studies have shown that indirect species interactions – sometimes visualised and analysed as small unnamed ‘community modules’ – or ‘motifs’ - are of fundamental ecological importance (e.g., Cirtwill et al. 2018; Grilli et al. 2017; Guimarães et al. 2017; Holt and Hochberg 2001; Levine et al. 2017; Losapio et al. 2021; Mayfield and Stouffer 2017b; Rasher et al. 2020). However, to advance ecology, unnamed motifs that are common and important should be recognized, objectively and unambiguously classified, and studied in detail. The two most famous motifs that can cause IF are ‘keystone predation’ and ‘trophic cascades’ (Fig. 1) (Paine 1966; Paine 1969; Paine 1980). In 1969, Robert Paine coined the term keystone predation after experimentally showing that sea stars indirectly facilitate some animals, like barnacles, by consuming mussels that are dominant space holders and the main competitor for barnacles (Paine 1966; Paine 1969). Keystone predation has since been redefined many times creating some confusion amongst ecologists (Cottee-Jones and Whittaker 2012; Davic 2000; Higdonin 2002; Hurlbert 1997; Mills et al. 1993; Power et al. 1996; Valls et al. 2015). Paine later coined the term trophic cascades (1980) to describe Estes and Palmisano’s (1974) influential study that showed that otters indirectly facilitate kelp by consuming herbivorous urchins (Fig. 1, 2). Today, trophic cascades represent the go-to

example of indirect species interactions in ecological textbooks (e.g., Begon et al. 1986; Begon and Townsend 2021; Krebs 2014; Molles and Sher 2019; Smith et al. 1998; Townsend et al. 2003) and have been documented in thousands of case-studies (Fig. 1). Trophic cascades have also been important for theoretical development (Holt et al. 2010; Pace et al. 1999; Polis et al. 2000; Ripple et al. 2016), in applied sciences, such as for restoration (Jeppesen et al. 1990), to understand efficacy of protected areas (Pinnegar et al. 2000), and, have been analysed repeatedly with comprehensive meta-analyses (e.g., Borer et al. 2005; Brett and Goldman 1996; Eger and Baum 2020; Mäntylä et al. 2011; Marczak et al. 2007; Rodríguez-Castañeda 2013; Shurin et al. 2002). The concept of trophic cascades has been redefined countless times in a similar manner to the terminology and ideas around keystone predation. Such inconsistent use of different definitions may impede research progress and lead to confusion among students, managers, and scientists (e.g., Holt et al. 2010; Lane 2017; Pace et al. 1999; Polis et al. 2000; Ripple et al. 2016). For example, inconsistent and changing definitions makes it difficult to track, identify and compile exponentially increasing publication outputs, resulting in weaker meta-analyses and less ecological insights (Bornmann and Mutz 2015; Larsen and Von Ins 2010; Thomsen et al. 2018b). The long-standing debates about how to define and study keystone predation, trophic cascades and other types of IF reflects the wider issue of ‘concept clusters’ (Peters and Peters 1991), with similar critiques about ecological concepts such as habitat (Hall et al. 1997; Mitchell 2005), resilience and resistance (Brand and Jax 2007; Connell and Ghedini 2015; Connell et al. 2016; Sundstrom et al. 2016), and ecosystem engineering (Wilby 2002; Wright and Jones 2006).

Here, the objective is to address calls for conceptual unification by outlining a framework that encompasses eight types of three-tiered IF interaction chains that reconcile Paine’s original keystone and cascade terminologies (Fig. 2). The eight IF interaction chains follow logically because (i) three-tiered IF can arise from either sequences of two negative or

two positive direct species interactions (corresponding to ‘an enemy of my enemy is my friend’ and ‘a friend of my friend is my friend’, respectively), and (ii) most direct species interactions happen through negative competition and consumption (inhibition processes) or positive habitat-formation/modification (hereunder also commensalism) and mutualism (facilitation processes) (e.g., Begon et al. 1986; Begon and Townsend 2021; Krebs 2014; Molles and Sher 2019; Smith et al. 1998; Townsend et al. 2003). This framework thereby defines different IF in unity and promote a broader approach to designing experiments, testing hypotheses, and analysing and interpreting data. Note, however, that the framework is not attempting to unify and classify all positive and negative indirect species interactions, a daunting task that may not be possible (see the discussion and Wootton 1994 for an introduction to the wider topic of indirect interactions).

Keystones; indirect facilitation arising through *different* 3-tiered species interactions

IF arising through different species-interactions can be described with Paine’s keystone terminology. A **keystone** is a ‘a wedge-shaped stone at the top of an arch’ or more generally, ‘the central supporting element of a whole’ (<http://www.thefreedictionary.com>). Paine used the keystone concept to highlight how two different sequential inhibitory interactions, consumption, and competition, resulted in IF. More specifically, Paine used experimental removals to demonstrate, that the sea star *Pisaster ochraceus* (the ‘central supporting element – the keystone’) indirectly facilitated a community of inferior competitors for space (the ‘whole’, here sessile organisms like barnacles), because *Pisaster* preferentially consumed competitively superior mussels (Fig. 2.3) (Paine 1966; Paine 1969). To adhere to Robert Paine’s famous empirical example, reduce conceptual ambiguities, and align with cascade terminology (see next section), I suggest to broaden Paine’s keystone predation example to

keystone consumption because herbivores, pathogens, and parasites, like true predators, can fully or partly consume strong competitors and thereby indirectly facilitate weak competitors (Hajishengallis et al. 2012; Poulin 1999; Rakhshani et al. 2013; Waller and Alverson 1997). In other words, keystone predation, keystone grazing, and keystone parasitism are interactions nested within the concept of keystone consumption. In this description of keystone consumption, IF arises through ‘consumption-followed-by-competition’. Using consistent terminology, I therefore suggest that chains where the order of these two interactions is reversed (‘competition-followed-by-consumption’) are called **keystone competition**, because competition (not consumption) is now ‘the central supporting element of the whole’ – in other words, competition drives IF in this three-tiered interaction chain. As an example of keystone competition, Perry et al. (2004) demonstrated that wood ants indirectly facilitate yucca plants by outcompeting caterpillars that would otherwise consume yucca seeds (Fig. 2.4).

IF arising through keystone interaction chains can also occur through sequences of habitat-formation and mutualism (Gribben et al. 2019). Following the same consistent terminology, **keystone habitat-formation** describes a sequence where a basal habitat forming species provides living space for an intermediate species that subsequently is involved in mutualism with focal organisms. For example, trees provide habitat for pollinators that subsequently facilitate flowering plants (Fig. 2.7) (Tylianakis 2013). Analogous cases are likely common where the basal species, instead of being a biogenic habitat-former, is a habitat-modifier or in commensalism with an intermediate species (for simplicity I focus here on the former examples). Finally, **keystone mutualism** describes the sequence where basal and intermediate species have reciprocal positive effects on each other and where the intermediate species subsequently facilitate focal organisms through habitat formation (but without strong positive reciprocal effects on the intermediate species, because that interaction chain would be described more precisely as ‘cascading mutualism’, see next section). For example, non-

habitat-forming pollinators (e.g., bees that pollenate trees), cleaners (e.g., fish that graze epiphytic microalgae), protectors (e.g., bees that protect trees from herbivores) or C/N-fixers (such as symbiotic dinoflagellates or mycorrhiza) facilitate trees and corals (Berkelmans and Van Oppen 2006; Boschma 1925; Marschner and Dell 1994) and thereby indirectly facilitate the many species that inhabit trees and corals (Fig. 2.8) (Bellwood and Hughes 2001; MacArthur 1960). Note finally that the broader term ‘keystone species’ typically refer to any species that has a disproportional large effect on a local community compared to its biomass (Begon et al. 1986; Begon and Townsend 2021; Power et al. 1996; Smith et al. 1998). In this context the basal species that initiate keystone consumption, keystone competition, keystone habitat formation, and keystone mutualism (see Fig. 2), are typically also keystone species because they, through indirect facilitation, can have large effects on local communities. Unfortunately, true ‘keystone species’ are difficult to document in complex species-rich natural systems because it requires measurements (and ordering) of interaction strengths between all species pairs in the community – and the terminology is therefor often considered heuristic rather than operational (Cottee-Jones and Whittaker 2012; Davic 2000; Higdonin 2002; Mills et al. 1993; Peters and Peters 1991; Power et al. 1996). By contrast, keystone interaction chains can, like cascades (see next section), be quantified simply by manipulating the abundances and/or activities of a basal and intermediate species and reporting effects on focal species (Hajishengallis et al. 2012; Paine 1966; Paine 1969; Poulin 1999; Rakhshani et al. 2013; Waller and Alverson 1997).

Cascades; indirect facilitation arising through *similar* 3-tiered species interactions

A **cascade** is generally defined as “*a sequence or succession of stages, operations or processes*” (<http://www.thefreedictionary.com>). I therefore suggest that ecologists use

‘cascade’ to refer to *any specific ecological process that occurs sequentially over two or more successive interactions*, aligning the terminology with cascades in microbiology, physiology, physics and network analysis (Buldyrev et al. 2010; Fahlman and Lebiere 1990; Hardy and Higgins 1992; Macfarlane 1964; Viola and Jones 2001). Cascades therefore differ from keystone interactions as the former describe sequences of the *same* interaction (e.g., consumption followed by consumption; Fig. 2.1), whereas the latter describe sequences of *different* interactions (e.g., consumption followed by competition; Fig. 2.3).

The most studied IF interaction chains are trophic cascades (Fig. 1) where consumption of prey is the repeated interaction (Paine 1980; Ripple et al. 2016). For example, sea otters consume herbivorous urchins and thereby indirectly facilitate kelp (Fig. 2.1) (Estes and Palmisano 1974). More specifically, cascading consumption occurs where predators, grazers, parasitoids or parasites consume prey in sequences. Following the formal definition of what a cascade is, I describe trophic cascades as **cascading consumption** where (as for keystone consumption) cascading predation (Heithaus et al. 2008) and cascading parasitism (Lafferty et al. 2006) are nested types of interaction chains.

IF can also arise through **cascading competition** (competition cascades in Thomsen et al., 2010) where pairs of competitors compete for different resources in sequences (Davidson 1980; Levine 1999; Sotomayor and Lortie 2015). For example, the basal ant species *Pogonomyrmex rugosus* facilitates the focal ant species (*Pheidole xerophila*) by inhibiting a different intermediate ant species (*P. desertorum*) (Fig. 2.2) (Davidson 1980) and light-limited plants can indirectly facilitate water-limited competitors by inhibiting intermediate plant competitors (Levine 1999; Levine 1976; Mayfield and Stouffer 2017a; Sotomayor and Lortie 2015). Finally, **cascading habitat-formation** (and habitat-modification, commensalism, Fig. 1.7) (habitat cascades in Thomsen et al., 2010) and **cascading mutualism** (Fig. 2) (sequential mutualism in Waser and Real 1979) are IF that arise through sequential positive species

interactions. In cascading habitat-formation, basal habitat forming species build and modify biogenic habitats to intermediate habitat forming species that then provide habitat to focal organisms (Thomsen et al. 2018b). For example, the polychaete *Diopatra cuprea* provides habitat to the invasive seaweed *Gracilaria vermiculophylla* that is a habitat itself for invertebrates and fish (Fig. 2.5), an interaction chain that has altered ecosystem functions along the US east coast (Ramus et al. 2017; Thomsen and McGlathery 2005; Thomsen 2004; Thomsen et al. 2010). Similarly, trees are habitat for epiphytes whose different morphologies increase the diversity and abundance of invertebrates and birds (Angelini and Silliman 2014; Cruz-Angon and Greenberg 2005; Watson and Herring 2012). In tropical rainforests, for example, such interaction chains with basal trees and intermediate epiphytes can double biodiversity (Ellwood and Foster 2004). By comparison, cascading mutualism occurs where basal and intermediate and intermediate and focal species have clear reciprocal positive effects, like when early-flowering basal plants indirectly facilitate late-flowering focal plants through shared pollinators (Fig. 2.6) (Waser and Real 1979). Other examples of cascading mutualism include sulphur-detoxifying bacteria that indirectly facilitate seagrasses through mutualisms with filter-feeding bivalves (van der Heide et al. 2012), pollinating humming birds that indirectly facilitate seed-dispersing focal marsupials through mutualism with mistletoes (Fonturbel et al. 2015), saltmarsh plants that indirectly facilitate other marsh plants through mutualism with ribbed mussels (Angelini et al. 2016), or communities of plant and pollinators that interact in complex mutualistic networks (Bascompte and Jordano 2013; Bastolla et al. 2009).

Discussion and research opportunities

Thousands of studies have documented specific forms of IF (Fig. 1) and ecological network analyses are increasingly recognizing their importance (e.g., Cirtwill et al. 2018; Grilli et al. 2017; Guimarães et al. 2017; Levine et al. 2017; Losapio et al. 2021; Mayfield and Stouffer 2017b; Rasher et al. 2020), but data, models, theories and concepts have rarely been linked across different forms of IF. I suggest that novel research can emerge by adopting a more unified approach to IF.

The proposed framework is hierarchical and therefore, depending on specific study or learning objectives, can be collapsed, or expanded to include either fewer or more species interactions. For example, cascading inhibition and cascading facilitation are higher-level groupings, that highlight the basal species either inhibits or facilitates intermediate species that then inhibit or facilitate focal species (Fig. 2). The framework also highlight that indirect effects on focal organisms result in indirect facilitation irrespective of the length of a facilitation cascade (Fig. 2.5-2.8, Thomsen et al. 2016a) but alternates between indirect facilitation and indirect inhibition for even and odd numbered sequences of inhibition cascades (Fig. 2.1-2.4, Tronstad et al. 2010). The framework can also be expanded to differentiate between density vs. trait-mediated effects, as done for trophic cascades (Gribben et al. 2009; Peckarsky et al. 2008; Thomsen et al. 2010; Trussell et al. 2002), or by including detailed descriptions of the processes involved, such as predation, grazing, and parasitism (nested within consumption) or asymmetrical vs. symmetrical interactions (e.g., for competition). Furthermore, more interactions can be added to describe longer chains, as in long consumption or habitat-formation cascades (Thomsen et al. 2016a; Tronstad et al. 2010), and new terms can be added to incorporate important ecological traits such as organismal sizes, niche-width, and interaction-specificity (like omnivory) (Brouat et al. 2004; Thomsen et al. 2016a; Wagner et al. 2015). For example, cascading effects and stability of interaction chains may vary between chains dominated by specialists or generalists or if interactions occur within or across trophic

levels (Ali and Agrawal 2012; Thompson et al. 2007). Facilitation and inhibitory interactions could also be combined to form an even broader indirect species interaction framework, for example by including longer more complex indirect effects, interaction modifications, like associational and shared defences (Callaway 2007; Hay 1986; Levine et al. 2017; Wootton 1994), and indirect negative effects such as apparent competition (Holt 1977). Finally, new ecological processes could be added to the framework, for example by including biological disturbances, amensalism, or ecosystem engineering (Jones et al. 1994; Thomsen et al. 2010; White 1985).

Most studies of IF have focused on population-level responses such as species-abundances (Polis et al. 2000; Shurin et al. 2002; Thomsen et al. 2018b) or impacts on community structures, biodiversity and ecosystem functions (Angelini et al. 2015; Rasher et al. 2020; Thomsen et al. 2018b). However, new studies should also test how IF affect smaller genetic, cellular, physiological and microbial scales (Flemming et al. 2016), as well as larger biogeographical and evolutionary scales (Bronstein 2009; Guimarães et al. 2017), or if certain underpinning mechanisms are important across different types of IF. Examples to explore include the importance of spatial heterogeneity, complexity of interaction webs, resource availability and energy conversion efficiency (borrowed from trophic cascades hypotheses) (Borer et al. 2005) or form-functional differences between basal and intermediate species, and affinity of focal species for intermediate species (borrowed from facilitation cascade hypotheses) (Angelini and Silliman 2014; Gribben et al. 2019; Thomsen et al. 2016a; Thomsen et al. 2010). For example, IF portrayed as linear interaction chains (Fig. 2) can alternatively be visualised as triangular network motif (Fig. 3) like apparent competition and exploitation competition and perhaps better align with complex network community analysis.

Many other ecological topics may also benefit from research on IF, such as studies focusing on ecosystem stability, the relationship between biodiversity and ecosystem function,

ecological multi-functionality, spill-over effects, or the spatial configurations of basal, intermediate and focal organisms in landscapes (Angelini et al. 2016; Angelini et al. 2015; Thomsen et al. 2016a; Tylianakis et al. 2010). In addition, IF theories could be applied to environmental impact studies, conservation, restoration and production ecology (Jeppesen et al. 1990; Mills et al. 1993; Pinnegar et al. 2000; Tylianakis et al. 2010), as has been done for direct facilitation (Halpern et al. 2007; Padilla and Pugnaire 2006). For example, in integrated multi-trophic aquaculture the production of species with supplementary functions depends on both direct and indirect facilitation to produce neutral nitrogen-budgets and enhance biodiversity, while growing financially viable products (Neori et al. 2004). Similarly, IF models are important in the study of species invasions, climate changes, pollution and habitat destruction, to predict and mitigate future anthropogenic stressors and preserve biodiversity (Altieri et al. 2010; Brondizio et al. 2019; Rasher et al. 2020; Siciliano et al. 2019; Thomsen et al. 2018a; Thomsen et al. 2021; Thyrring et al. 2015). For example, indirect facilitation of invertebrates and epiphytes can collapse under high sediment stress in seagrass-seaweed dominated estuaries (Siciliano et al. 2019), and after heatwaves and earthquakes decimated kelp and rockweed beds on the South Island of New Zealand (Thomsen et al. 2020; Thomsen et al. 2019; Thomsen et al. 2021; Thomsen and South 2019).

New studies could also compare the relative strength of different IF interaction chains within and across habitats and ecotones and along environmental gradients and transition zones to identify fundamental ecological principles (Angelini et al. 2015; Shurin et al. 2002; Thomsen et al. 2022), just like studies have compared direct ecological interactions like mutualism vs. competition (Morris et al. 2007) or competition vs. predation (Gurevitch et al. 2000). This research could include field surveys and factorial experiments, analysing data with structural equation models, meta-analysis, and network analysis of indirect species effects (Bascompte and Jordano 2013; Grilli et al. 2017; Levine et al. 2017; Mayfield and Stouffer 2017a; Rasher

et al. 2020; Simba et al. 2018; Thomsen and South 2019). For example, factorial experiments that manipulate the abundance of both basal and intermediate organisms would be especially useful to identify synergistic effects arising from intermediate species (Altieri et al. 2007; Bishop et al. 2012; Thomsen et al. 2022; Thomsen et al. 2016a). As a simple proof-of-concept analyses, I compared the magnitude of indirect facilitation between four IF interaction chains by calculating standardized effects sizes (Ln RR) extracted from research papers on benthic marine study systems. The mean Ln RR values for cascading habitat formation and cascading consumption were calculated from online supplements of existing meta-analyses (Shurin et al. 2002; Thomsen et al. 2018b), but only from a very preliminary dataset for keystone consumption and cascading competition (Fig. 4, Supplement 1). This preliminary analysis highlights that different IF processes can be compared quantitatively, and that they may have relatively similar strengths (Fig. 4). Clearly, this proof-of-concept analysis should be expanded with more types of IF, by including more underpinning case-studies, by using standardized and robust meta-analytical methods (Koricheva et al. 2013) and aim to identify the underpinning important mechanisms within and between different IF processes (Borer et al. 2005; Shurin et al. 2002; Thomsen et al. 2018b).

Finally, to demonstrate conceptually how the eight IF interaction chains (motifs, Fig. 2-3) outlined in the framework can be compared, I constructed a simplified interaction network from expert knowledge of an intertidal rocky shore in New Zealand (adapted from Kéfi et al. 2012). Intertidal rocky systems are often dominated by a few canopy-forming seaweed species (here *Cystophora torulosa* and *Hormosira banksii*), epiphytes (here *Notheia anomala* and *Jania sphaeroramosa*), periphytic diatoms, meso-grazers (like trochid snails), and small predatory fish (like triplefins and blennies) (Lilley and Schiel 2006; Schiel 2004; Thomsen et al. 2016b; Thomsen and South 2019; Wood et al. 2010). This simplified intertidal system composed of only 10 key taxa had 24 direct interactions and 30 three-tiered IF interaction

chains, including all the eight forms described in the framework (Fig. 4). A more realistic rocky shore community, composed of many more canopy-forming species, epiphytes, microalgae, herbivores, and predators, would therefore likely include 100s of IF interactions, highlighting their ubiquity. This simple example suggests that three-tiered IF chains can be analysed in a unified framework and compared to other types of direct and indirect species interactions.

Concluding remarks

Today, it is well-established that indirect facilitation (IF) is of fundamental ecological importance, but no overview or framework has described these interactions in unity. Robert Paine coined the seminal ‘trophic cascade’ and ‘keystone predation’ terminologies to describe two specific types of IF and these interaction chains have since been studied, albeit separately, in great detail. However, rather than studying trophic cascades, keystone predation, or other IF interaction chains, as isolated case-studies, I suggest there are advantages of examining them within a hierarchical framework that links ubiquitous direct ecological interactions, to three-tiered IF. The framework is relatively simple to explain to students, managers, and scientists, and is flexible so that different processes can be linked, and hierarchical levels added or removed. Following this framework, trophic cascades and keystone predation are synonyms with cascading consumption and keystone consumption, respectively, a new terminology that explicitly highlight their similarities (the primary controlling interaction is consumption) and differences (the secondary controlling interaction are different enemy effects). The framework also demonstrates how these two intensively studied interaction chains relate to less studied IF, such as cascading competition, keystone competition, and cascading habitat formation. In short, I suggest that the outlined indirect facilitation framework will simplify, unite, and merge

key ecological concepts and processes, help to unravel the complexity of ecological systems, and motivate ecologists to study less well-known IF processes.

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Figure 1. Different indirect facilitation processes, based on either inhibition (blue), facilitation (red), or unspecified (black) interaction sequences, have received different research scrutiny. The processes are listed in order of number of ‘hits’, identified from a Google Scholar search on December 18 2022 using the following search terms: “trophic cascade” (TC), “indirect facilitation” (IF), “keystone predation” (KP), “indirect mutualism” (IM), “facilitation cascade” (FC), “keystone mutualism” (KM), “habitat cascade” (HC), “competition cascade” (CC), “sequential mutualism” (SM), “keystone consumption” (KCons), “keystone competition” (KComp), “mutualism cascade” (MC) and “keystone habitat-formation” (KH). Note the logarithmic scale, i.e., trophic cascades are studied more than ten times any other indirect facilitation process.

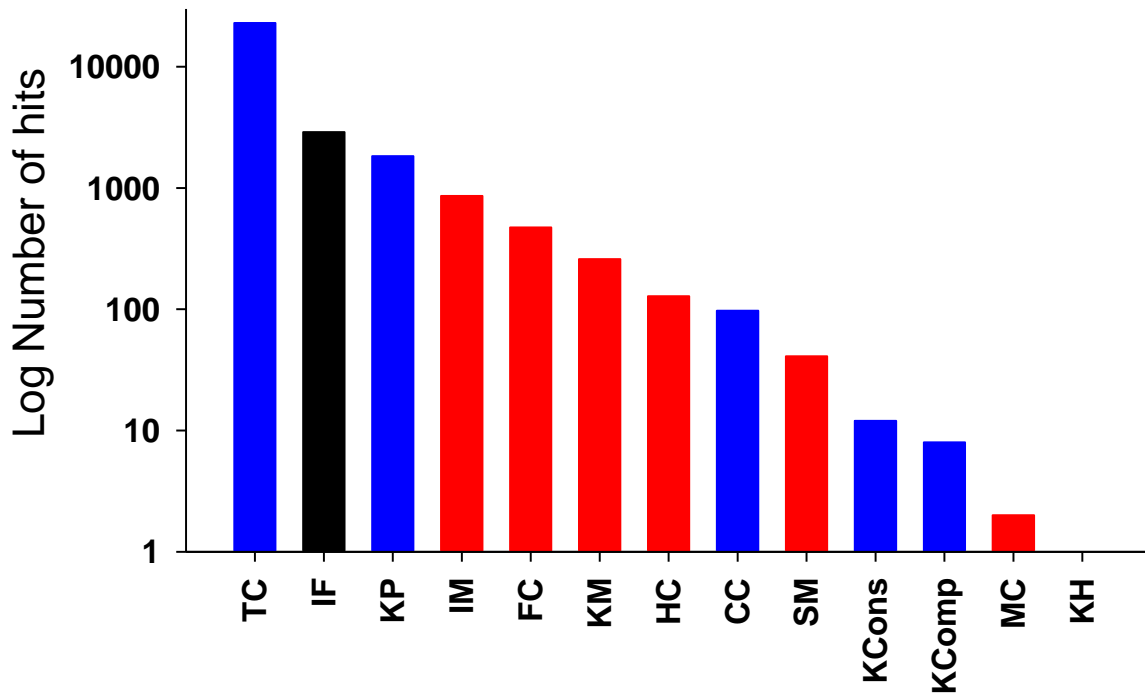


Figure 2. Framework merging direct negative (blue: consumption, competition) and positive (red: mutualism, habitat-formation/modification – hereunder commensalism) species interactions with ‘cascade’ and ‘keystone’ concepts to unite eight three-tiered indirect facilitation processes (arched red line). Chain 1-4 are inhibition (or enemy) cascades caused by sequential negative effects between organisms (*‘an enemy of my enemy is my friend’*) whereas 5-8 are facilitation cascades caused by sequential positive effects between organisms (*‘a friend of my friend is my friend’*). Intermediate organisms have dual functions, for example being both prey and consumers in chain 1. Chain 1, 2, and 6 result in reciprocal indirect positive feedbacks from focal to basal species, and are therefore examples of ‘indirect mutualisms’ (Connor 1995). Basal, intermediate, and focal organisms are also referred to as primary (1°), secondary (2°) and tertiary (3°) organisms, to highlight that longer interaction chains can occur. Indirect effects on focal organisms result in facilitation irrespective of the length of a facilitation cascade but alternate between facilitation and inhibition for even and odd numbered sequences of inhibition cascades. The eight schematized case studies are described in the manuscript text. Symbols are from The Integration and Application Network (ian.umces.edu/media-library), licenced free under CC BY-SA 4.0.

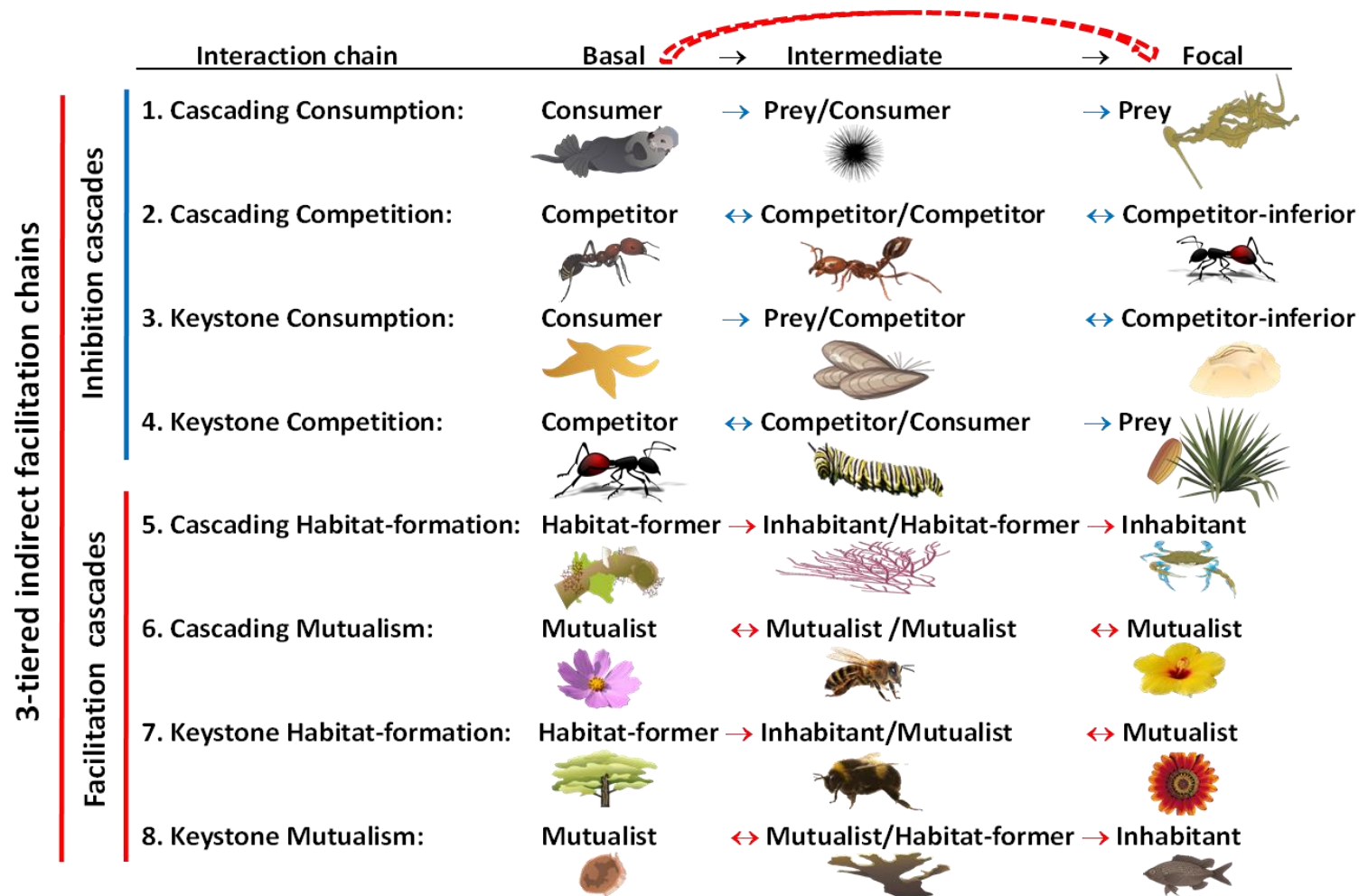


Figure 3. Common ecological modules/motifs over indirect species effects. A. Common indirect effects as typically schematized in ecological reviews, here adapted from Fig. 2 in Wootton (1994) - see also (Menge 1995). These indirect effects emphasize trophic linkages and have no unified terminology being referred to as trophic cascades (1), exploitative competition (9), apparent competition (10), indirect mutualism with interference competition (11), and indirect mutualism with exploitative competition (12). Horizontal arrows = interference competition where arrows show impacted species, and vertical arrows = consumer-resource interactions where arrows determine direction of energy flow. a-e=different species. B. Framework over 8 forms of indirect facilitation derived from 4 common direct interactions: consumption (hereunder predation, parasitism, herbivory), competition (weak or strong), mutualism, and habitat-formation (hereunder habitat-modification and commensalism). These processes are shown as linear chains in Fig. 2 but here as triangular motifs to better represent network-properties and indirect effect (process numbers and case-study examples are described in Fig. 2 and the text). Red = positive effects, blue = negative effects, full arrow = direct effects, dashed line = indirect effects, thick lines = strong effects, thin lines = weak effects, black arrows = minor unknown effects from inhabitants on their habitat (in some cases these minor effects may change to strong negative or positive effects resulting in breakdown or acceleration of indirect facilitation, respectively). C = Consumer, P = Prey, SC = Strong Competitor, WC = Weak Competitor, HF = Habitat Former, I = Inhabitant (= habitat-user), M = Mutualist.

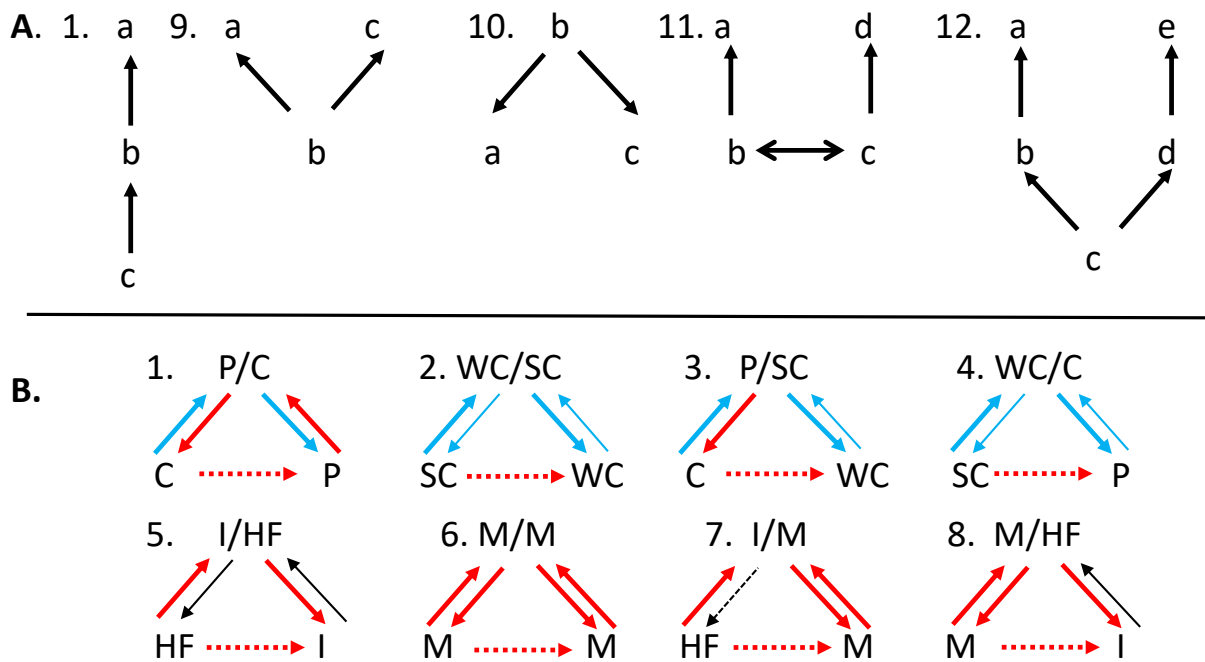
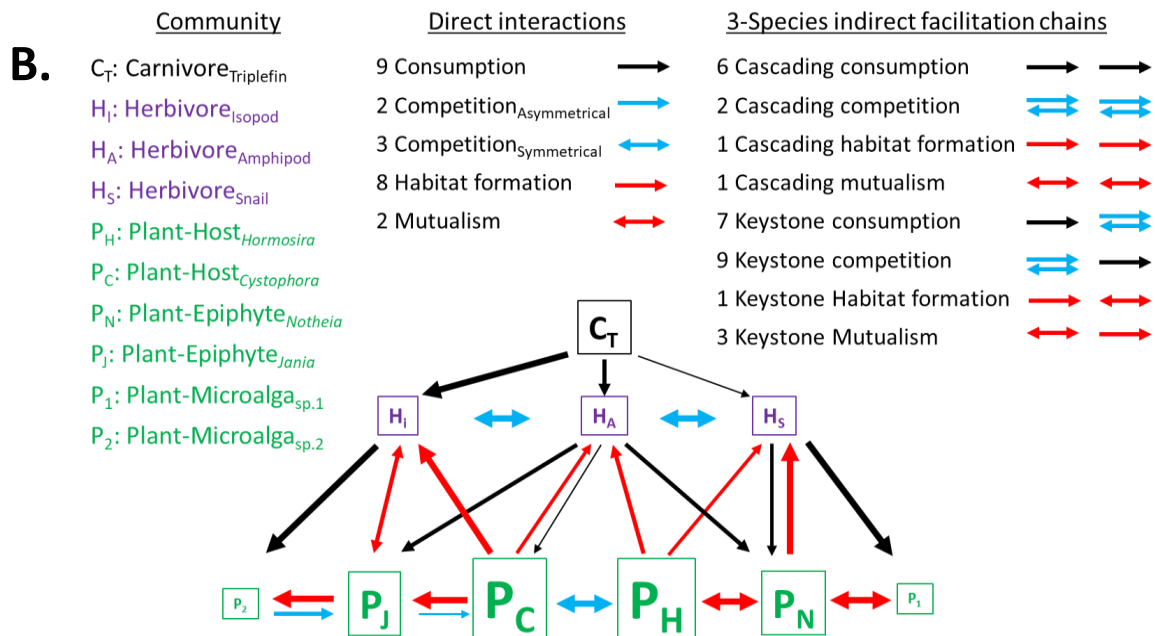
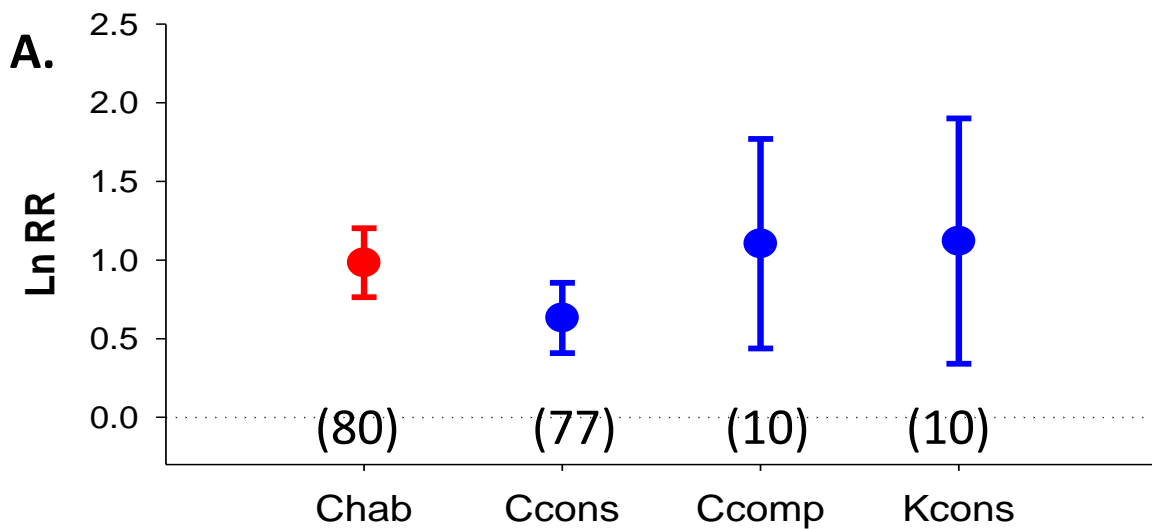


Figure 4. Examples of new research embedded within a framework over indirect facilitation: Comparing magnitudes (A) and commonality (B) of different types of indirect facilitation. A: Strength of indirect facilitation in systems divided into inhibition (blue) and facilitation (red) cascades: Log response ratios ($\ln RR \pm 95\% CI$) were extracted for cascading habitat-formation (C_{Hab}) and cascading consumption (C_{Cons}) using data listed in S1 in Thomsen et al. (2018) and from the primary literature for cascading competition (C_{Comp}) and keystone competition (C_{Comp}) (see S1 for details, the numbers of replicated studies are shown in brackets). The positive values reflects that the measured interaction chains resulted in indirect facilitation across studies (whereas negative values would correspond to indirect inhibition). B: Indirect facilitation in an interaction network constructed from expert knowledge: Simplified intertidal rocky habitat in New Zealand, composed of two habitat-forming seaweed ‘hosts’, two epiphytic seaweed, two periphytic microalgae, three meso-grazers, and one predatory fish. The network is characterized by 25 direct interactions and 30 three-tiered indirect facilitation cascades (a more diverse community will include 100s of indirect facilitation processes). The size of the letters and thickness of arrows correlate with organismal sizes and interaction strengths.



Supplement 1

Effect sizes for different interaction chains used in proof-of-concept ‘meta-analysis’ comparing strength and direction between four types of indirect facilitation. Mean Ln RR values are summarized in Fig. 4A; for underpinning data related to cascading habitat formation and cascading consumption, see Thomsen et al 2018. Ln RR were calculated like for trophic cascades and facilitation cascades (Thomsen et al. 2018), i.e., positive, and negative values reflect measured indirect facilitation and inhibition, respectively.

| Cascading competition studies | Fig/Text | Interaction chain | Focal organism | Ln RR |
|---|-----------------|--|-------------------------------|--------------|
| Arkema et al. 2009. Ecology 90: 3126-3137 | 2b | kelp-fast alga-slow alga/inverts | Sessile invertebrate | 0.7126 |
| Benes & Carpenter. 2015. Ecology 96: 241-251 | 2b | kelp-fast alga-slow alga/inverts | Red foliose alga | 1.3152 |
| Benes & Carpenter. 2015. Ecology 96: 241-251 | 2d | kelp-fast alga-slow alga/inverts | Articulated coralline alga | 0.1896 |
| Cuesta et al. 2010. J Ecology 98: 687-696 | 2a | nurseplant-herb+treeseedling | Quercus ilex | 0.3778 |
| Cuesta et al. 2010. J Ecology 98: 687-696 | 2b | nurseplant-herb+treeseedling | Quercus ilex | 1.6704 |
| Flukes et al. 2014. MEPS 514: 57-70 | 1e | kelp-fast alga-slow alga/inverts | Encrusting red alga | 0.1212 |
| Flukes et al. 2014. MEPS 514: 57-70 | 1h | kelp-fast alga-slow alga/inverts | Encrusting sponge | 0.4417 |
| Flukes et al. 2014. MEPS 514: 57-70 | 1i | kelp-fast alga-slow alga/inverts | Bryozoan | -0.435 |
| Flukes et al. 2014. MEPS 514: 57-70 | 1j | kelp-fast alga-slow alga/inverts | Non-geniculate coralline alga | -0.307 |
| Jensen et al. 2012. Plant Ecology 213: 535-543 | 2a | shrub-grass/herb-treeseedling | Quercus robur | 0.0452 |
| Jensen et al. 2012. Plant Ecology 213: 535-543 | 2b | shrub-grass/herb-treeseedling | Quercus robur | 0.0558 |
| Jensen et al. 2012. Plant Ecology 213: 535-543 | 2c | shrub-grass/herb-treeseedling | Quercus robur | 0.2229 |
| Jensen et al. 2012. Plant Ecology 213: 535-543 | 2d | shrub-grass/herb-treeseedling | Quercus robur | 0.0936 |
| Kunstler et al. 2006. J of Vegetation Science 17: 379-388 | 1a | shrub-grass/herb-treeseedling | Quercus pubescens | -0.130 |
| Kunstler et al. 2006. J of Vegetation Science 17: 379-388 | 1b | shrub-grass/herb-treeseedling | Fagus sylvatica | 2.0439 |
| Levine. 1999. Ecology 80: 1762-1769 | 3B | Sedge/carunx-mimulus guttatus-other plants | Conocephalum conicum | 0.9737 |
| Levine. 1999. Ecology 80: 1762-1769 | 3c | Sedge/carunx-mimulus guttatus-other plants | Mimulus cardinalis | -0.419 |
| Levine. 1999. Ecology 80: 1762-1769 | 3d | Sedge/carunx-mimulus guttatus-other plants | Brachythecium frigidum | 0.0905 |
| Rousset & Lepart. 2000. Journal of Ecology 88: 401-412 | 1 | shrub-grass/herb-treeseedling | Quercus humilis | 1.5477 |
| Wernberg & Connell. 2008. Journal of Sea Research 59: 237-248 | 4d | kelp-fast alga-slow alga/inverts | Encrusting alga | 3.6730 |
| Wernberg & Connell. 2008. Journal of Sea Research 59: 237-248 | 4f | kelp-fast alga-slow alga/inverts | Sessile animals | 3.0326 |
| Young et al. 2005. Biological Conservation 122: 351-359 | 1 | Elephant-Cattle-Zebra | Zebra | 2.4228 |

| Keystone consumption studies | Fig/Text | Interaction chain | Focal organism | Ln RR |
|--|-----------------|--------------------------|-----------------------|--------------|
| Burkepile & Hay. 2010. PlosOne 5: e8963 | 5 | grazer-weed-coral | Porites porites | 0.4912 |
| Dudley. 1992. Oikos 65: 121-127 | 1 | grazer-epiphyte-host | Cladophora glomerata | 0.5431 |
| Hughes et al. 2007. Current Biology 17: 360-365 | 2b | grazer-weed-coral | Corals | 0.8527 |
| Hughes et al. 2007. Current Biology 17: 360-365 | 3B | grazer-weed-coral | Corals | 1.0656 |
| Jompa & McCook. 2002. Limnology & Oceanography 47: 527-534 | 2 | grazer-weed-coral | Porites cylindrica | 1.0685 |
| Jompa & McCook. 2002. Limnology & Oceanography 47: 527-534 | 3 | grazer-weed-coral | Porites cylindrica | 0.1286 |
| Kupferberg. 1997. Freshwater Biology 37: 427-439 | 1a | grazer-epiphyte-host | Cladophora glomerata | 0.7227 |
| Kupferberg. 1997. Freshwater Biology 37: 427-439 | 1b | grazer-epiphyte-host | Cladophora glomerata | 0.5151 |
| Lirman. 2001. Coral Reefs 19: 392-399 | 5 | grazer-weed-coral | Porites astreoides | 0.6982 |
| Lirman. 2001. Coral Reefs 19: 392-399 | 6 | grazer-weed-coral | Porites astreoides | 2.3355 |
| Lirman. 2001. Coral Reefs 19: 392-399 | 7a | grazer-weed-coral | Montastrea faveolata | -0.684 |
| Lirman. 2001. Coral Reefs 19: 392-399 | 7b | grazer-weed-coral | Montastrea faveolata | -0.547 |
| McCall & Rakocinski. 2007. Ecology 88: 618-624 | 1a | grazer-epiphyte-host | Ruppia | 1.0726 |
| McCall & Rakocinski. 2007. Ecology 88: 618-624 | 1b | grazer-epiphyte-host | Ruppia | 2.1920 |
| McCall & Rakocinski. 2007. Ecology 88: 618-624 | 1c | grazer-epiphyte-host | Ruppia | 0.6128 |
| McCall & Rakocinski. 2007. Ecology 88: 618-624 | 2a | grazer-epiphyte-host | Ruppia | 0.6462 |
| McCall & Rakocinski. 2007. Ecology 88: 618-624 | 2b | grazer-epiphyte-host | Ruppia | 2.0492 |
| McCall & Rakocinski. 2007. Ecology 88: 618-624 | 2c | grazer-epiphyte-host | Ruppia | 0.3605 |
| Myers & Heck. 2013. MEPS 483: 133-142 | 3B | grazer-epiphyte-host | Halodule wrightii | 0.4086 |
| Myers & Heck. 2013. MEPS 483: 133-142 | txt p138 | grazer-epiphyte-host | Halodule wrightii | 0.4376 |
| Reynolds et al. 2014. Limnology & Oceanography 59: 1053-1064 | 1c | grazer-epiphyte-host | Zostera marina | 1.0615 |
| Reynolds et al. 2014. Limnology & Oceanography 59: 1053-1064 | 3a | grazer-epiphyte-host | Zostera marina | 0.9552 |
| Reynolds et al. 2014. Limnology & Oceanography 59: 1053-1064 | 3B | grazer-epiphyte-host | Ruppia | 1.3723 |
| Reynolds et al. 2014. Limnology & Oceanography 59: 1053-1064 | 3c | grazer-epiphyte-host | Zostera marina | 1.0801 |
| Reynolds et al. 2014. Limnology & Oceanography 59: 1053-1064 | 3d | grazer-epiphyte-host | Ruppia | 1.6834 |
| Smith et al. 2010. Oecologia 163: 495-507 | 2f | grazer-weed-coral | Scleractian corals | 4.6052 |