

A host-specific habitat former controls biodiversity across ecological transitions in a rocky intertidal facilitation cascade

Mads S. Thomsen^{A,B,C}, Isis Metcalfe^A, Paul South^A and David R. Schiel^A

^AMarine Ecology Research Group, School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch, New Zealand.

^BUWA Oceans Institute and School of Plant Biology, University of Western Australia, Hackett Drive, Crawley, WA 6009, Australia.

^CCorresponding author. Email: mads.solgaard.thomsen@gmail.com

Abstract. Few studies have quantified facilitation cascades from rocky intertidal systems, across ecological transition zones, or where the secondary facilitator is an obligate epiphyte. Here, we address these research gaps. We first quantified distributions of the seaweed host *Hormosira banksii* and its obligate epiphyte *Notheia anomala* at different tidal elevations in summer and winter at Kaikoura, New Zealand. This analysis showed that the host and the epiphyte were, in both seasons, most abundant at ‘high’ and ‘low’ tidal elevations respectively, probably driven by contrasting responses to competitors and desiccation. We subsequently quantified richness and abundances of mobile invertebrates associated with *Hormosira* and various levels of epiphytic *Notheia*. *Hormosira* fronds were collected from different elevations, seasons, diurnal cycles, with different neighbouring algae and following an epiphyte-removal experiment. All tests showed positive density-dependent effects of *Notheia*-epiphytism on richness and abundances of invertebrates, with strongest facilitation occurring at the transition from intertidal to subtidal habitats. Our results support a growing number of facilitation cascade studies from different ecosystems and habitats, and suggest that habitat formation-driven facilitation cascades may be particularly common in marine benthic systems where epibiosis can be a dominant life form.

Additional key words: algae, biodiversity, biofouling, coexisting ecosystem engineers, epiphyte, epibiosis, foundation species, habitat cascade, invertebrates

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Introduction

Facilitation cascades, mediated through sequences of positive species effects such as habitat formation, habitat modification, mutualism, or commensalism, are poorly studied compared with other types of indirect facilitation (Altieri *et al.* 2007; Thomsen *et al.* 2010; Bell *et al.* 2014). For example, a Google Scholar search showed 130 and 32 hits on ‘facilitation cascade*’ and ‘habitat cascade*’, compared with 9940 and 967 hits for ‘trophic cascade*’ and ‘keystone predation’ (accessed on 22 May 2014). Of the many different types of facilitation cascades, habitat cascades, where ‘clients’ (an organism associated with a specific habitat) are facilitated through sequential habitat formation or modification, have been studied most, in part because it is easier to document habitat formation or modification than commensalism or mutualism (Thomsen *et al.* 2010). Habitat cascades are likely to be a common ecological process, particularly in ecosystems where epibiosis (i.e. organisms living on other organisms) is common, such as in forests (Zotz and Bader 2011) and in marine benthic systems (Wahl 2009; Wernberg *et al.* 2010). It is therefore no surprise that habitat cascades have mainly been documented from a few habitats dominated by large primary

habitat formers such as tree stands (Cruz-Angon and Greenberg 2005), salt marshes (Altieri *et al.* 2007), seagrasses (Edgar and Robertson 1992; Thomsen 2010) and mangroves (Bishop *et al.* 2012). Still, it remains a significant challenge to document habitat cascades from different habitats and ecosystems. For example, we are aware of only a single experiment where a secondary habitat former has been removed from rocky intertidal systems to document impacts on clients (Pavia *et al.* 1999 – this study was evaluated in a different predation escape context), even though habitat cascades theoretically should be common (because epibiosis is common). Second, few studies have documented whether habitat cascades vary systematically across transition zones (for example, along environmental gradients and temporal cycles). However, it is important to research habitat cascades across ecological transition zones to build better predictive ecological models, as previously done for direct positive species effects (Bertness and Callaway 1994) or for interspecific neighbour effects (Dalby 1995). Third, most habitat cascade studies have quantified facilitation through facultative interactions between habitat formers. Secondary habitat formers can typically use many hosts. For example, vines

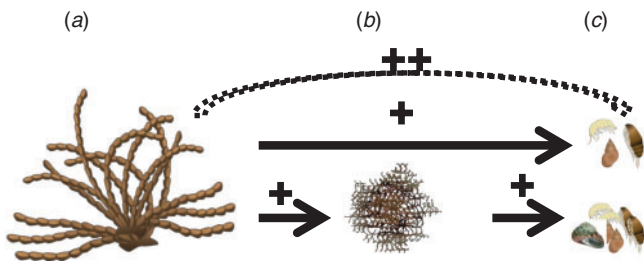


Fig. 1. Diagram outlining the rocky intertidal *Hormosira*–*Notheia*–invertebrate facilitation cascade. The primary habitat former, *Hormosira*, (a) has indirect positive effects (bend arrow) on small invertebrate clients like snails, amphipods and copepods (c) by providing structural support to the secondary habitat former, *Notheia* (b). More client taxa and individuals were inhabiting *Notheia* than *Hormosira* per gram dry weight biomass, suggesting that *Notheia* increases the likelihood of clients to find facilitators and resources and avoid enemies and stress.

can grow on most substrates (Nesheim and Økland 2007; Vaughn and Bowling 2011), marine drift seaweed can accumulate around almost any protruding structure (Thomsen and McGlathery 2006; Bishop *et al.* 2012) and even host-specific habitat formers, like parasitic mistletoes, can inhabit many different tree species (Norton and Carpenter 1998). Host-specificity of habitat formers may have significant ecological implications. For example, if a primary habitat former becomes locally extinct, generalist (facultative) secondary habitat formers, like vines, can use substitution substrates, whereas host-specific (obligate) secondary habitat formers will be lost with their host, thereby breaking down the habitat cascade. We are not aware of any studies that have quantified habitat cascades associated with obligate secondary habitat formers, making it difficult to predict impacts from human stressors in systems where host-specific, secondary habitat formers are common.

We address these research gaps by (1) providing an explicit test of the habitat cascade concept from intertidal rocky reefs, (2) testing whether habitat cascades change along ecological transition zones, and (3) testing (1) and (2) on a habitat cascade mediated by an obligate secondary habitat former (*Notheia anomala* Harvey & Bailey, 1851, hereafter *Notheia*) that exists on only a single host habitat former (*Hormosira banksii* Turner 1808, hereafter *Hormosira*). We hypothesise that biodiversity of clients (here taxonomic richness and total abundances of small mobile invertebrates) peak at places and times where the secondary habitat former is most abundant (Fig. 1; Thomsen 2010; Bishop *et al.* 2012).

Materials and methods

Model habitat formers

The primary habitat former, *Hormosira*, is a dominant fucoid canopy species in the intertidal zone in temperate Australasia, and its ecology has been extensively studied (e.g. Lilley and Schiel 2006; Schiel 2006; Bellgrove *et al.* 2010). By contrast, almost nothing is known about the ecology of the secondary habitat former – the obligate epiphyte *Notheia* – although its cell chemicals have been researched in detail (e.g. Warren *et al.* 1980; Raven *et al.* 2001). Although *Notheia* has been observed

on *Xiphophora chondrophylla* (another fucoid that can produce the rare hexitol D-altrito) (Wright *et al.* 1987), it exists virtually only on *Hormosira*, typically infecting sexually mature host fronds (male and female fronds being equally affected), attaching to, but not penetrating, the ostiole (Hallam *et al.* 1980). Interestingly, *Notheia* is also a fucoid species but it diverged from the other non-epiphytic canopy-forming fucoids *c.* 70 million years ago (Silberfeld *et al.* 2010).

Distribution of habitat formers

The distribution of *Hormosira* and *Notheia* was quantified from three elevation zones on an intertidal platform at Kaikoura peninsula (42°25'12"S, 173°42'37"E) in summer (7 January 2014) and early winter (18 May 2014). The three elevations represent a 'high' zone within dense *Hormosira* beds (~1 m above mean sea level), a 'low' zone within *Hormosira* beds (~0.5 m above mean sea level before being gradually replaced by *Cystophora* species) and interspersed submerged rock pools in which algae are constantly submerged. For each elevation and season, percentage cover of *Hormosira* and *Notheia* was quantified from 10 haphazardly collected 0.25-m² quadrats by visually estimating the perpendicular cover within the quadrat (which was subdivided by strings into 100 smaller units).

Distribution of clients

The distributions of mobile invertebrate species (here termed 'clients') were quantified by collecting *Hormosira* fronds characterised by various levels of *Notheia* epiphytism under different environmental conditions. Each frond was collected by pulling the frond with a steady motion just above the minuscule holdfast (preliminary sampling suggested that virtually no clients were associated with this small structure) during low tide, i.e. only rock pool fronds were submerged. The frond was carefully added to a plastic bag to ensure that the mobile invertebrates remained on the frond (as in Thomsen *et al.* 2010). Fronds were kept on ice or refrigerated until invertebrates could be rinsed onto a 250-µm mesh, before being conserved in 70% alcohol. Invertebrates were sorted and counted, under a dissecting microscope, into readily identifiable operational taxonomic units dominated by amphipods, harpacticoid copepods, gastropods, bivalves, ostracods, and tanaids. For each sample we also recorded the dry weight of *Hormosira* and *Notheia* separately.

We first collected 'random' *Hormosira* fronds to quantify the distribution of clients at the three elevation levels and in two seasons ($n = 40$ and 15 per elevation level for summer and winter seasons respectively – see the previous section for collection dates). We subsequently collected 'targeted' *Hormosira* individuals to test specific hypotheses, comparing clients on 'clean' v. 'epiphytised' fronds (i.e. with <0.01 and >0.02 g dry weight of *Notheia* respectively) (collected 27 May 2014). We tested whether clients varied over a diurnal cycle by collecting fronds during the night and 12 h later during the day ($n = 3$ per test combination) and by presence of interspecific neighbours by collecting fronds touching either adjacent *Hormosira* or *Cystophora* ($n = 3$ per test combination). Note that, in contrast to the test for *Notheia* and elevation effects, the mensurative tests for seasonal, diurnal and neighbourhood effects are 'unreplicated'

Table 1. Permutation based ANOVA: distribution of *Hormosira* and *Notheia* at two seasons (SEA: summer and winter) and three elevation levels (ELE: high, low tide pool)

Significant factors ($P < 0.05$) are shown in bold. P -values from Levine's F -test for variance homogeneity are shown in brackets following each test factor

Test	Treatment	s.s.	d.f.	Pseudo- F	P
<i>Hormosira</i>	ELE [0.809]	18 073	2	13.385	<0.001
	SEA [0.238]	84	1	0.124	0.726
	ELE \times SEA	46	2	0.034	0.966
	Error	36 457	54		
<i>Notheia</i>	ELE [0.009]	24.6	2	6.953	0.002
	SEA [0.369]	1.4	1	0.780	0.381
	ELE \times SEA	1.4	2	0.409	0.666
	Error	95.5	54		

(i.e. based on a single collection event per *Notheia* and elevation levels) and interpretations about these factors should therefore be cautious. To increase our ability to infer causality we supplemented the mensurative tests with a removal experiment. On 28 February 2014 we marked 8 plots (20 \times 20 cm) in each of the high and low tidal levels. All plots bordered \sim 20 cm-deep tidal channels dominated by *Cystophora* (at high tide these larger plants may shade and whiplash *Hormosira* and *Notheia*). We applied randomly allocated removal treatments in the following experimental design: \pm *Notheia* removal \times \pm *Cystophora* removal \times 2 elevation zones \times 2 replicates. Epiphytes were removed on 28 February and 5 May 2014 by holding the *Hormosira* fronds and nipping *Notheia* off. All *Notheia* 'clumps', representing $>95\%$ of the epiphytic biomass (M. S. Thomsen, unpubl. data) were removed and control plots were hand-disturbed in a similar fashion but without removing *Notheia*. Similarly, *Cystophora* was removed from the bordering channels in half the plots by pulling plants off the reef. Again, control plots were disturbed in a similar way but without removing any plants. On 27 May 2014 we collected a frond from each of the 16 plots.

Taxonomic richness and abundances of clients were analysed with factorial analysis of variance (ANOVA) to test for interaction effects between *elevation* and presence of *Notheia* and *season*, *diurnal cycle*, and *interspecific neighbours* from mensurative and manipulative experiments. All factors were treated as fixed and analysed with permutation-based ANOVA in the PERMANOVA software package, by using Euclidian distance metrics (Anderson *et al.* 2008). Most test factors had homogeneous variances or low variance heterogeneity (typically $P > 0.01$ in Levene's test, cf. Tables 1–5) and we therefore performed the analysis on untransformed data (ANOVA is robust to minor heteroscedasticity for balanced designs) thereby simplifying our interpretations of significant interaction effects (Quinn and Keough 2002). Significant ANOVA results were followed by SNK tests to identify differences between treatments. We finally pooled all random and targeted *Hormosira*–client samples ($n = 153$) to conduct rank correlation tests between the biomass of *Hormosira* or *Notheia* against client richness and abundances.

Table 2. Permutation based ANOVA: Distribution of invertebrates associated with randomly collected *Hormosira* fronds at two seasons (SEA: summer and winter) and three elevation levels (ELE: high, low tide pool)

Significant factors ($P < 0.05$) are shown in bold and near-significant effects ($P < 0.10$) in parentheses. P -values from Levine's F -test for variance homogeneity are shown in brackets following each test factor

Test	Treatment	s.s.	d.f.	Pseudo- F	P
Richness	ELE [0.021]	42.022	2	14.912	<0.001
	SEA [0.387]	38.218	1	27.124	<0.001
	ELE \times SEA	6.808	2	2.416	(0.096)
	Error	116.948	83		
Abundance	ELE [0.002]	1 268 231	2	16.094	<0.001
	SEA [0.010]	296 272	1	7.519	0.007
	ELE \times SEA	194 166	2	2.464	(0.091)
	Error	3 270 238	83		

Table 3. Permutation based ANOVA: effect of diurnal sampling (DIU) and presence of epiphytic *Notheia* (NOT) on invertebrates associated with *Hormosira* fronds at two elevation levels (ELE)

Significant factors ($P < 0.05$) are shown in bold and near-significant effects ($P < 0.10$) in parentheses. P -values from Levine's F -test for variance homogeneity are shown in brackets following each test factor

Test	Treatment	s.s.	d.f.	Pseudo- F	P
Richness	ELE [0.239]	5.958	1	4.539	0.0490
	NOT [0.039]	5.875	1	4.476	(0.0504)
	DIU [0.770]	0.165	1	0.126	0.7272
	ELE \times NOT	8.414	1	6.411	0.0222
	ELE \times DIU	0.066	1	0.050	0.8254
	NOT \times DIU	0.007	1	0.006	0.9416
	ELE \times NOT \times DIU	0.253	1	0.192	0.6668
	Error	21.000	16		
Abundance	ELE [0.018]	126 927	1	14.072	0.0017
	NOT [0.013]	138 371	1	15.341	0.0012
	DIU [0.361]	200	1	0.022	0.8835
	ELE \times NOT	57 106	1	6.331	0.0229
	ELE \times DIU	79	1	0.009	0.9265
	NOT \times DIU	21 770	1	2.414	0.1398
	ELE \times NOT \times DIU	7 663	1	0.850	0.3704
	Error	144 318	16		

Results

Distribution of habitat formers

The abundances of *Hormosira* and *Notheia* were not affected by season (or season \times elevation interactions; F -tests were non-significant: Table 1). However, both species were significantly affected by elevation, but with contrasting patterns: *Hormosira* was least and *Notheia* was most abundant in rock pools (Fig. 2a). Graphical analysis indicated that *Notheia* was also more abundant at low than high tidal elevation but this pattern was not significant (Fig. 2b, SNK test). The contrasting distribution pattern between the host and its epiphyte was reflected in a significant negative rank correlation between the percentage covers of *Hormosira* and *Notheia* ($P = 0.0009$, $r_s = -0.39$).

Table 4. Permutation based ANOVA: effects of presence of neighbouring *Cystophora* (CYS) and presence of epiphytic *Notheia* (NOT) on invertebrates associated with *Hormosira* fronds at two elevation levels (ELE)

Significant factors ($P < 0.05$) are shown in bold and near-significant effects ($P < 0.10$) in parentheses. P -values from Levine's F -test for variance homogeneity are shown in brackets following each test factor

Test	Treatment	s.s.	d.f.	Pseudo- F	P
Richness	ELE [0.042]	7.736	1	8.635	0.010
	NOT [0.039]	10.334	1	11.535	0.004
	CYS [0.841]	0.004	1	0.005	0.945
	ELE \times NOT	4.293	1	4.792	0.044
	ELE \times CYS	0.048	1	0.054	0.819
	NOT \times CYS	0.749	1	0.836	0.374
	ELE \times NOT \times CYS	1.707	1	1.906	0.186
Error		14.333	16		
Abundance	ELE [0.180]	167 773	1	28.865	<0.001
	NOT [0.408]	122 280	1	21.038	<0.001
	CYS [0.535]	11 698	1	2.013	0.175
	ELE \times NOT	11 007	1	1.894	0.188
	ELE \times CYS	5 161	1	0.888	0.360
	NOT \times CYS	28 556	1	4.913	0.041
	ELE \times NOT \times CYS	47 346	1	8.146	0.011
Error		92 997	16		

Table 5. Permutation based ANOVA: effects of removing neighbouring *Cystophora* (CYS) and removing epiphytic *Notheia* (NOT) on invertebrates associated with *Hormosira* fronds at two elevation levels

Significant factors ($P < 0.05$) are shown in bold and near-significant effects ($P < 0.10$) in parentheses. P -values from Levine's F -test for variance homogeneity are shown in brackets following each test factor

Test	Treatment	s.s.	d.f.	Pseudo- F	P
Richness	ELE [0.236]	5.063	1	4.765	(0.061)
	NOT [0.137]	5.063	1	4.765	(0.061)
	CYS [0.208]	7.563	1	7.118	0.028
	ELE \times NOT	0.563	1	0.529	0.488
	ELE \times CYS	1.563	1	1.471	0.260
	NOT \times CYS	5.063	1	4.765	(0.061)
	ELE \times NOT \times CYS	0.563	1	0.529	0.488
Error		8.500	8		
Abundance	ELE [0.291]	148 418	1	9.474	0.015
	NOT [0.052]	132 314	1	8.446	0.020
	CYS [0.531]	8 145	1	0.520	0.491
	ELE \times NOT	5 439	1	0.347	0.572
	ELE \times CYS	2	1	0.000	0.992
	NOT \times CYS	14 340	1	0.915	0.367
	ELE \times NOT \times CYS	4 323	1	0.276	0.614
Error		125 329	8		

Distribution of clients

Invertebrate richness and abundances associated with the randomly collected *Hormosira* fronds varied significantly between seasons and elevation levels (Table 2). Thus, richness and abundances were greatest in the summer season and in rock pools and at low elevations (Fig. 3a, b). Richness and

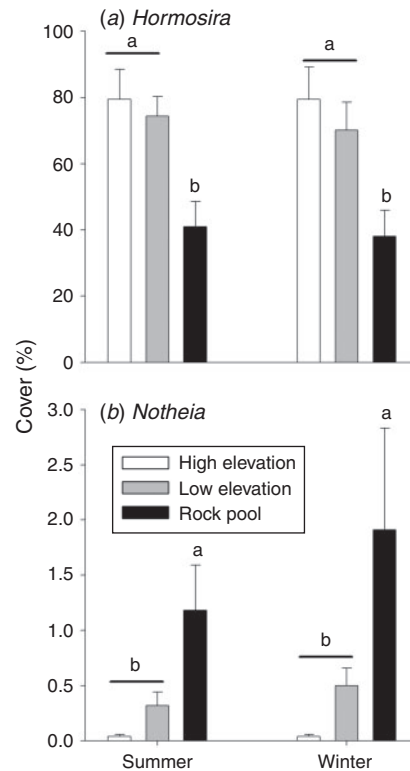


Fig. 2. Distribution of primary (*Hormosira*) and secondary (*Notheia*) habitat formers in two seasons and at three elevation levels. $n = 10$; error bars are standard errors. The same letters above bars denote values that were statistically similar (SNK-test on factors where $P < 0.05$, see Table 1 for P -values).

abundances associated with the targeted collected *Hormosira* fronds were not affected by diurnal sampling; client distributions were similar from day and night samples (Table 3). However, we detected a significant elevation \times *Notheia* interaction, showing most taxa and individuals at low elevations in the presence of *Notheia* (Fig. 4a, b). Similarly, we found no effect of *Cystophora* neighbours on client richness (Table 4), but detected a significant elevation \times *Notheia* interaction, again counting more taxa at low elevations in the presence of *Notheia* (Fig. 5a). Client abundances were, however, significantly affected by the 3-factorial elevation \times *Notheia* \times *Cystophora* interaction term. In this analysis, abundances were again highest at the low-elevation level in the presence of *Notheia*, although abundances were also relatively high at low elevations without *Notheia* but with *Cystophora* as a neighbour (Fig. 5b). In the manipulative experiment, we found a significant effect of removing *Cystophora* neighbours and near-significant effects ($P < 0.1$) of elevation, epiphyte removal and *Notheia* \times *Cystophora* interaction on client richness. Here, taxonomic richness was greatest when *Cystophora* was left intact. The near-significant effects suggested that more taxa could be found at the low-elevation level in the presence of *Notheia* (Fig. 6a). In this experiment, we found significant single-factor effects of elevation and epiphyte removal on client abundances, with highest abundances at low elevation and in the presence of *Notheia* (Fig. 6b). Finally, our correlation analysis showed significant ($P < 0.001$) in

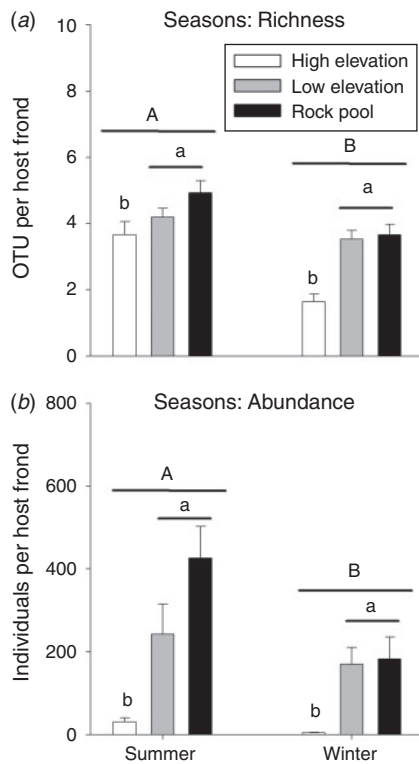


Fig. 3. Distribution of invertebrates associated with randomly collected *Hormosira* fronds in two seasons and from three elevations levels. $n = 15$; error bars are standard errors. OTU, operational taxonomic units. The same letters above bars denote values that were statistically similar (SNK-test on factors where $P < 0.05$, see Table 2 for P -values).

all tests) positive associations between *Hormosira* and richness (Fig. 7a, $r_s = 0.26$), *Notheia* and richness (Fig. 7b, $r_s = 0.53$), *Hormosira* and abundances (Fig. 7c, $r_s = 0.41$) and *Notheia* and abundances (Fig. 7d, $r_s = 0.75$). Thus, these analyses showed that clients were more strongly associated (larger r_s values) with *Notheia* than *Hormosira*, despite it having orders of magnitude less biomass (compare x -axes on Fig. 7a, b v. 7c, d).

Discussion

We documented positive effects from the secondary habitat former *Notheia* on biodiversity of small mobile invertebrate clients on intertidal rocky reefs and found support for our hypothesis that facilitation was strongest when and where the secondary habitat former was most abundant. Our data thereby aligns with a growing number of studies documenting habitat cascades from forests (Cruz-Angon and Greenberg 2005), salt marshes (Altieri *et al.* 2007), seagrass beds (Edgar and Robertson 1992; Thomsen 2010), mangroves (Bishop *et al.* 2012) and mudflats (Thomsen *et al.* 2010). More specifically, we found that *Notheia* and elevation in concert and across our tests explained most of the variability in the data, that biodiversity of clients generally increased if *Notheia* increased in abundance, and that facilitation therefore was strongest at low elevations and in rock pools, where *Notheia* is most abundant.

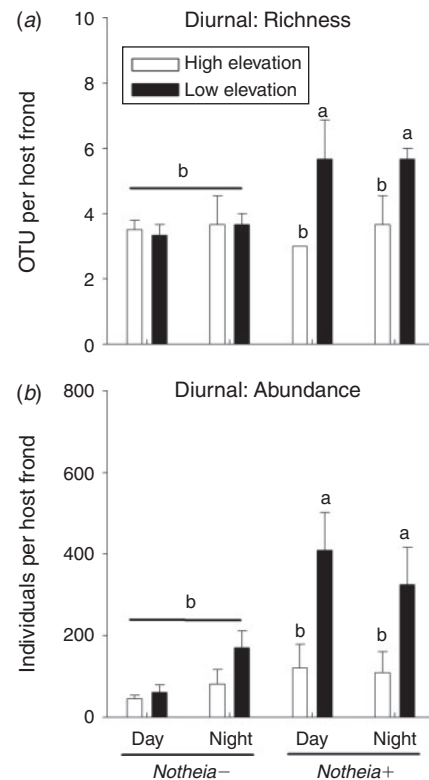


Fig. 4. Effects of diurnal sampling and presence of epiphytic *Notheia* on invertebrates associated with *Hormosira* fronds from two elevation levels. $n = 3$; error bars are standard errors. OTU, operational taxonomic units. The same letters above bars denote values that were statistically similar (SNK-test on factors where $P < 0.05$, see Table 3 for P -values).

Distribution of habitat formers

Notheia is an obligate epiphyte on *Hormosira* and its distribution is therefore intricately linked to its host. This host-dependency results in a strong range-overlap; for example, a cursory inspection of maps over geopositioned herbarium collections reveal almost identical distribution patterns, except that *Notheia* has not (yet?) been collected at *Hormosira*'s northern distribution or on the west coast of southern New Zealand (maps extracted from online New Zealand and Australian Virtual Herbariums on 5 June 2014). However, within this host-dependent range we found contrasting distributions on a much smaller local scale; *Notheia* dominated in the constantly submerged rock pools where its host *Hormosira* was least abundant. It has been suggested that *Hormosira* is the most desiccation-resistant canopy former in temperate Australasia, making it the dominant marine plant in the mid intertidal zone, particular where wave action and grazing pressure is limited (Schiel 1988, 2004, 2006). However, at lower tidal elevations, larger and faster-growing canopy formers (e.g. *Cystophora* spp.) typically outcompete *Hormosira* (Schiel 2006). Thus, competitive effects through shading, whiplash, nutrient depletion and drag increase close to the subtidal zone where canopy formers and epiphytes become increasingly abundant. In comparison to *Hormosira*, we hypothesise that *Notheia* is more susceptible to desiccation stress, but more tolerant to whiplash and shading, probably

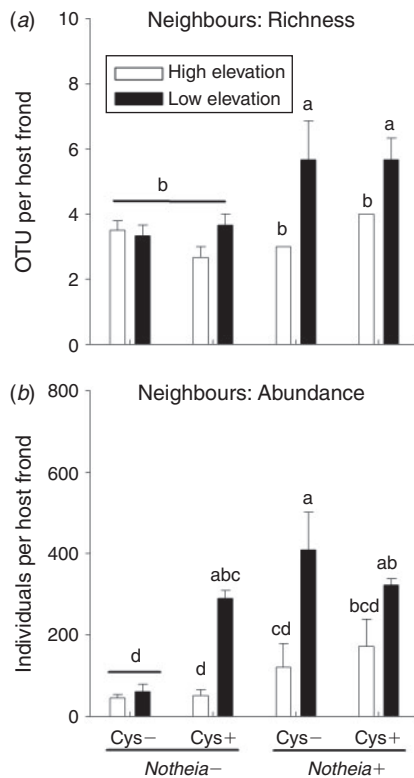


Fig. 5. Effects of presence of neighbouring *Cystophora* competitor and presence of epiphytic *Notheia* on invertebrates associated with *Hormosira* fronds from two elevation levels. $n = 3$; error bars are standard errors. OTU, operational taxonomic units. The same letters above bars denote values that were statistically similar (SNK-test on factors where $P < 0.05$, see Table 4 for P -values).

because of its evolutionary adaptations as an obligate epiphyte (i.e. it has evolved to succeed on canopy-formers). Thus, *Notheia* appears to differ in desiccation tolerance from another obligate seaweed epiphyte, *Vertebrata lanosa*, that is most abundant at mid-to-high elevation levels on its fucoid canopy-forming host, *Ascophyllum nodosum* (Longtin *et al.* 2009). Future experiments should test ecological hypotheses about *Notheia*'s fundamental and realised niche and its competitive effect on its host.

Distribution of clients

We found strong positive effects of *Notheia* on the biodiversity of small mobile invertebrate clients (Figs 4–7). This facilitation was consistent for both mensurative and manipulative experiments supporting realistic and causal linkages between *Notheia* and its clients. We here focussed on whole-community indirect facilitation associated with two simple community metrics (total abundance and richness) but found similar results for the dominant lower-resolution taxonomic units, including gastropods, copepods, amphipods and isopods (Thomsen, unpubl. data). Similar positive effects of epiphytes on clients have been documented experimentally in a Northern Hemisphere rocky intertidal study (Pavia *et al.* 1999) and from many other ecosystems, including rocky subtidal zones (Martin-Smith 1993),

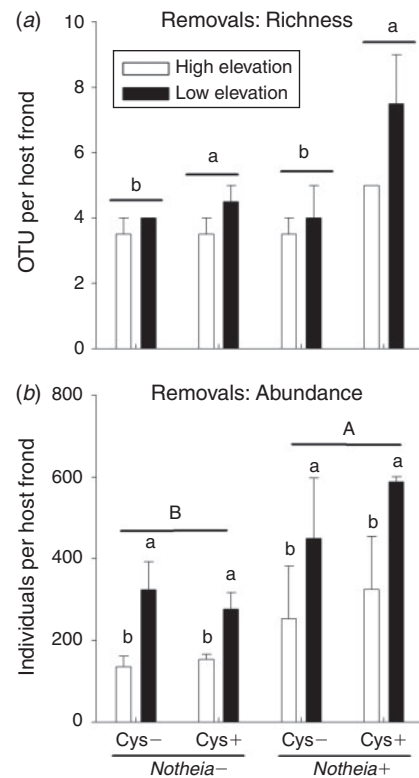


Fig. 6. Effects of removing neighbouring *Cystophora* and removing epiphytic *Notheia* on invertebrates associated with *Hormosira* fronds from two elevation levels. $n = 2$; error bars are standard errors. OTU = operational taxonomic units. The same letters above bars denote values that were statistically similar (SNK-test on factors where $P < 0.05$, see Table 5 for P -values).

forests (Cruz-Angon and Greenberg 2005; Díaz *et al.* 2012; Watson and Herring 2012) and seagrass beds (Hall and Bell 1988; Edgar and Robertson 1992; Gartner *et al.* 2013). Most of these studies, however, were not evaluated in an explicit habitat-cascade context. Furthermore, we found that facilitation was strongly density-dependent, as shown for secondary habitat formers associated with trees (Ellwood and Foster 2004), seagrass (Thomsen 2010; Thomsen *et al.* 2012), mangroves (Bishop *et al.* 2012) and sessile invertebrates (Byers *et al.* 2012; Thomsen *et al.* 2013). Interestingly, density effects were stronger for *Notheia* than its host, which otherwise has been shown to be a direct driver of diversity patterns (Lilley and Schiel 2006; Schiel 2006; Bellgrove *et al.* 2010), even though biomass was one order of magnitude larger for the latter. Perhaps the finer structure and smaller interstitial spaces from the epiphyte provide a superior habitat for many small clients compared with the coarser *Hormosira* fronds (Hooper and Davenport 2006), a factor also suggested to be important in mimic experiments conducted in seagrass beds (Hall and Bell 1988; Schneider and Mann 1991; Bologna and Heck 1999). On the basis of our results (and as hypothesised in Thomsen *et al.* 2010), we suggest that habitat cascades become increasingly important when (1) there is more of the secondary habitat former (=amount, e.g. its size, abundance, longevity), (2) the secondary

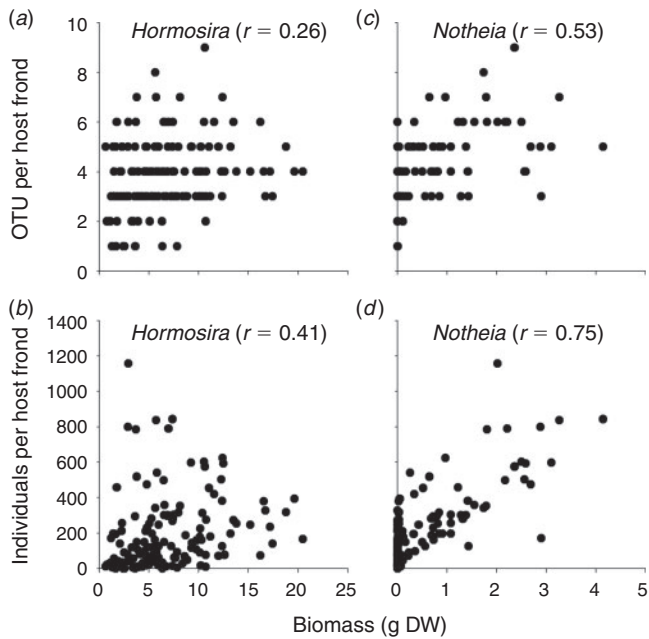


Fig. 7. Correlations between the biomass of the host *Hormosira* (a, b; the primary habitat former) and epiphytic *Notheia* (c, d; the secondary habitat former) against invertebrate richness (a, c) and abundances (b, d). $n = 153$; pooling samples shown on Figs 3–6. OTU, operational taxonomic units; r , Spearman's rank correlation coefficient; all correlations were significant ($P < 0.001$).

habitat former is form–functionally *different*, and (3) clients have high *host-specificity* (=affinity) for the secondary habitat former (this study; Bologna and Heck 1999; Thomsen 2010; Thomsen *et al.* 2010; Bishop *et al.* 2012). Whereas the ‘*more habitat*’ model should affect both client diversity and abundance patterns, combining ‘*different habitat*’ and ‘*client host-specificity*’ models could affect diversity more than abundances (because the combined two models represent the match between new and different empty niches and new clients with novel traits that can fill these niches). For example, aquatic invertebrate clients inhabiting bromeliad phytotelmata on host trees increase richness dramatically but barely affect total abundances of the client pool that inhabit the combined epiphyte–host tree complex (Frank and Fish 2008; Campos 2010). Interestingly, we also found several *Notheia* fronds that were heavily epiphytised by red filamentous algae, thereby potentially facilitating more and different clients through higher-order extended habitat cascades. Note that we here aimed to quantify the existence of a particular habitat cascade on general biodiversity responses. Currently, it is unclear whether these clients mainly inhabit *Notheia* to avoid enemies, to avoid stress, to find facilitators, to find resources or, more likely, a combination of these general mechanisms (Thomsen and Wernberg 2014). Clearly, future studies should aim to identify the underlying mechanisms whereby individual taxa are facilitated to provide stronger predictive insights into this facilitation cascade.

A growing number of studies has quantified habitat cascades in different ecosystems, but few studies have examined whether habitat cascades vary across ecological transition zones. We

targeted this research gap, documenting no differences across diurnal cycles, minor differences depending on whatever neighbours were intra- or interspecific canopy-formers, medium differences across seasons, and strong differences across tidal elevation levels. The lack of effects of diurnal cycling is perhaps not surprising for very small clients, many of which are slow moving, like microgastropods and some harpacticoid copepods. A similar lack of diurnal effects has been found for invertebrates associated with *Ascophyllum nodosum* (Pavia *et al.* 1999) whereas other studies have found larger and more mobile invertebrates to be more abundant on seaweeds at night (Taylor 1998; Sánchez-Jerez *et al.* 1999). Although we found a few minor effects of interspecific neighbours, these were mainly complex higher-order interactions that had inconsistent outcomes (e.g. in mensurative *v.* manipulative experiments), explained a low percentage of the data variability (sums of squares in Tables 4 and 5 were generally of less importance than elevation and *Notheia*), and was based on low replication levels and thereby increased possibility to be biased by outlier samples. For example, in the experiment, the *Cystophora* removal test factor explained slightly more data variability than *Notheia* removal on client richness but this discrepancy was partly driven by an outlier sample from the low-elevation zone where both *Cystophora* and *Notheia* was present (cf. the unusual high bar representing this treatment in Fig. 6a). Still, this outlier supported our general conclusions; clients were most diverse and abundant at low elevations and in the presence of *Notheia*. Thus, it remains a possibility that the identity of neighbours, like other landscape characteristics, modify client communities, for example by mediating different bottom-up propagule pressures or top-down consumer pressures (Bell *et al.* 2001; Roberts and Poore 2006), but more studies are needed to test if different neighbours modify this particular habitat cascade.

We also found strong seasonal effects with fewer clients in winter than summer, even though the abundances of the host or epiphyte were not affected by season. Such seasonality is common for invertebrates associated with temperate marine habitat formers (Gunnill 1983; Taylor 1997), probably reflecting effects of annual ontogenetic life history cycles and colder temperatures in winter. Still, our more specific habitat cascade tests (Figs 4–6) were all conducted in early winter, suggesting that *Notheia* is an important secondary habitat former in both summer and winter. We found strong and consistent effect of elevation on client biodiversity, with strongest positive epiphyte effects in the low zone and in the constantly submerged rock pools. This result likely reflects a combination of low desiccation tolerance for both the epiphyte and the client. Indeed, a re-analysis of client abundances standardized to unit *Hormosira* weights (without *Notheia*) showed fewer clients at high than low elevations (M. S. Thomsen, unpubl. data), suggesting that many clients are susceptible to desiccation stress. Similar patterns with fewer clients associated with primary habitat formers at high intertidal elevation levels have been documented many times, for example for clients associated with mussels (Silliman *et al.* 2011), seaweeds (Schiel and Lilley 2007; Cacabelos *et al.* 2010) and tunicates (Monteiro *et al.* 2002). Thus, we expect that habitat cascades within and across transition zones can be reduced by processes that create alternative pathways for clients to escape stress and enemies and find resources and facilitators

(compared to how the secondary habitat former provide these services).

We finally caution that some of our interpretations are based on low replication levels (e.g. a single collection event to represent seasonal and diurnal treatments) or low sample sizes for specific test-combinations (e.g. the 3-factorial treatment combination in the manipulative experiment is based on two replicates). Conclusions addressing these ecological transitions will require additional testing in more places and times and with improved replication. Still, our main finding that *Notheia* is a secondary habitat former that facilitates small mobile invertebrate clients across tidal zones and in proportion to its abundance, is based on well replicated treatments (e.g. $n = 12$, 12 and 8 for pooled single-factor epiphyte comparisons in Figs 4, 5 and 6 respectively), and was consistently found from both our ‘random’ and ‘targeted’ sampling schemes and mensurative and manipulative experimental data.

Conclusions

In past research, *Notheia* has been described as a ‘spurious thing’, as ‘anomalous in the extreme’, and as an ‘abnormal growth of the nobler species *Hormosira*’ (cited in Hallam *et al.* 1980). Here we conclude that *Notheia*, in addition to its ‘spurious anomalous, abnormal growth on its nobler host’, is a rare example of an obligate secondary habitat former that modifies biodiversity within and across ecological transition zones. Finally, we note that because *Notheia* is an obligate epiphyte, any anthropogenic threat to *Hormosira* (e.g. Doblin and Clayton 1995; Schiel and Taylor 1999; Bellgrove *et al.* 2010) is likely to have strong indirect cascading negative effect on invertebrate clients, as host switching by *Notheia* is simply not possible.

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References

Altieri, A. H., Silliman, B., and Bertness, M. D. (2007). Hierarchical organization via a facilitation cascade in intertidal cordgrass bed communities. *American Naturalist* **169**, 195–206. doi:10.1086/510603

Anderson, M. J., Gorley, R. N., and Clarke, K. R. (2008). ‘PERMANOVA for PRIMER: Guide to Software and Statistical Methods.’ (PRIMER-E Ltd: Plymouth, UK.)

Bell, S. S., Brooks, R. A., Robbins, B. D., Fonseca, M. S., and Hall, M. O. (2001). Faunal response to fragmentation in seagrass habitats: implications for seagrass conservation. *Biological Conservation* **100**, 115–123. doi:10.1016/S0006-3207(00)00212-3

Bell, J. E., Bishop, M. J., Taylor, R. B., and Williamson, J. E. (2014). Facilitation cascade maintains a kelp community. *Marine Ecology Progress Series* **501**, 1–10. doi:10.3354/MEPS10727

Bellgrove, A., McKenzie, P. F., McKenzie, J. L., and Sfiligoj, B. J. (2010). Restoration of the habitat-forming fucoid alga *Hormosira banksii* at effluent-affected sites: competitive exclusion by coralline turfs. *Marine Ecology Progress Series* **419**, 47–56. doi:10.3354/MEPS08843

Bertness, M., and Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology & Evolution* **9**, 191–193. doi:10.1016/0169-5347(94)90088-4

Bishop, M. J., Byers, J. E., Marcek, B. J., and Gribben, P. E. (2012). Density-dependent facilitation cascades determine epifaunal community structure in temperate Australian mangroves. *Ecology* **93**, 1388–1401. doi:10.1890/10-2296.1

Bologna, P. A., and Heck, K. L. (1999). Macrofaunal associations with seagrass epiphytes – relative importance of trophic and structural characteristics. *Journal of Experimental Marine Biology and Ecology* **242**, 21–39. doi:10.1016/S0022-0981(99)00092-1

Byers, J., Gribben, P., Yeager, C., and Sotka, E. (2012). Impacts of an abundant introduced ecosystem engineer within mudflats of the southeastern US coast. *Biological Invasions* **14**, 2587–2600. doi:10.1007/S10530-012-0254-5

Cacabelos, E., Olabarria, C., Incera, M., and Troncoso, J. S. (2010). Effects of habitat structure and tidal height on epifaunal assemblages associated with macroalgae. *Estuarine, Coastal and Shelf Science* **89**, 43–52. doi:10.1016/J.ECSS.2010.05.012

Campos, R. E. (2010). *Eryngium* (Apiaceae) phytotelmata and their macroinvertebrate communities, including a review and bibliography. *Hydrobiologia* **652**, 311–328. doi:10.1007/S10750-010-0364-Y

Cruz-Angon, A., and Greenberg, R. (2005). Are epiphytes important for birds in coffee plantations? An experimental assessment. *Journal of Applied Ecology* **42**, 150–159. doi:10.1111/J.1365-2664.2004.00983.X

Dalby, J. (1995). Consequences of aggregated living in the ascidian *Pyura stolonifera*: evidence for non-contact intraspecific competition. *Marine and Freshwater Research* **46**, 1195–1199. doi:10.1071/MF9951195

Díaz, I., Sieving, K., Peña-Foxon, M., and Armesto, J. (2012). A field experiment links forest structure and biodiversity: epiphytes enhance canopy invertebrates in Chilean forests. *Ecosphere* **3**, art5. doi:10.1890/ES11-00168.1

Doblin, M., and Clayton, M. (1995). Effects of secondarily-treated sewage effluent on the early life-history stages of two species of brown macroalgae: *Hormosira banksii* and *Durvillaea potatorum*. *Marine Biology* **122**, 689–698. doi:10.1007/BF00350691

Edgar, G. J., and Robertson, A. I. (1992). The influence of seagrass structure on the distribution and abundance of mobile epifauna: pattern and processes in a Western Australian *Amphibolis* bed. *Journal of Experimental Marine Biology and Ecology* **160**, 13–31. doi:10.1016/0022-0981(92)90107-L

Ellwood, M. D. F., and Foster, W. A. (2004). Doubling the estimate of invertebrate biomass in a rainforest canopy. *Nature* **429**, 549–551. doi:10.1038/NATURE02560

Frank, J., and Fish, D. (2008). Potential biodiversity loss in Florida bromeliad phytotelmata due to *Metamasius callizona* (Coleoptera: Dryophthoridae), an invasive species. *The Florida Entomologist* **91**, 1–8. doi:10.1653/0015-4040(2008)091[0001:PBLIFB]2.0.CO;2

Gartner, A., Tuya, F., Lavery, P. S., and McMahon, K. (2013). Habitat preferences of macroinvertebrate fauna among seagrasses with varying structural forms. *Journal of Experimental Marine Biology and Ecology* **439**, 143–151. doi:10.1016/J.JEMBE.2012.11.009

Gunnill, F. (1983). Seasonal variations in the invertebrate faunas of *Pelvetia fastigiata* (Fucaceae): effects of plant size and distribution. *Marine Biology* **73**, 115–130. doi:10.1007/BF00406879

Hall, M., and Bell, S. (1988). Response of small motile epifauna to complexity of epiphytic algae on seagrass blades. *Journal of Marine Research* **46**, 613–630. doi:10.1357/002224088785113531

Hallam, N., Clayton, M., and Parish, D. (1980). Studies on the association between *Noteia anomala* and *Hormosira banksii* (Phaeophyta). *Australian Journal of Botany* **28**, 239–248. doi:10.1071/BT9800239

Hooper, G. J., and Davenport, J. (2006). Epifaunal composition and fractal dimensions of intertidal marine macroalgae in relation to emersion.

- Journal of the Marine Biological Association of the United Kingdom* **86**, 1297–1304. doi:10.1017/S0025315406014329
- Lilley, S. A., and Schiel, D. R. (2006). Community effects following the deletion of a habitat-forming alga from rocky marine shores. *Oecologia* **148**, 672–681. doi:10.1007/S00442-006-0411-6
- Longtin, C. M., Scrosati, R. A., Whalen, G. B., and Garbary, D. J. (2009). Distribution of algal epiphytes across environmental gradients at different scales: intertidal elevation, host canopies, and host fronds. *Journal of Phycology* **45**, 820–827. doi:10.1111/J.1529-8817.2009.00710.X
- Martin-Smith, K. M. (1993). Abundance of mobile epifauna: the role of habitat complexity and predation by fishes. *Journal of Experimental Marine Biology and Ecology* **174**, 243–260. doi:10.1016/0022-0981(93)90020-O
- Monteiro, S. M., Chapman, M. G., and Underwood, A. J. (2002). Patches of the ascidian *Pyura stolonifera* (Heller, 1878): structure of habitat and associated intertidal assemblages. *Journal of Experimental Marine Biology and Ecology* **270**, 171–189. doi:10.1016/S0022-0981(02)00020-5
- Nesheim, I., and Økland, R. H. (2007). Do vine species in neotropical forests see the forest or the trees? *Journal of Vegetation Science* **18**, 395–404. doi:10.1111/J.1654-1103.2007.TB02552.X
- Norton, D. A., and Carpenter, M. A. (1998). Mistletoes as parasites: host specificity and speciation. *Trends in Ecology & Evolution* **13**, 101–105. doi:10.1016/S0169-5347(97)01243-3
- Pavia, H., Carr, H., and Åberg, P. (1999). Habitat and feeding preferences of crustacean mesoherbivores inhabiting the brown seaweed *Ascophyllum nodosum* (L.) Le Jol. and its epiphytic macroalgae. *Journal of Experimental Marine Biology and Ecology* **236**, 15–32. doi:10.1016/S0022-0981(98)00191-9
- Quinn, G. P., and Keough, M. J. (2002). 'Experimental Design and Data Analysis for Biologists.' (Cambridge University Press: New York.)
- Raven, J. A., Beardall, J., Chudek, J. A., Scrimgeour, C. M., Clayton, M. N., and McInroy, S. G. (2001). Altritol synthesis by *Notheia anomala*. *Phytochemistry* **58**, 389–394. doi:10.1016/S0031-9422(01)00286-2
- Roberts, D. A., and Poore, A. G. B. (2006). Habitat configuration affects colonisation of epifauna in a marine algal bed. *Biological Conservation* **127**, 18–26. doi:10.1016/J.BIOCON.2005.07.010
- Sánchez-Jerez, P., Barberá-Cebrián, C., and Ramos-Esplá, A. (1999). Daily vertical migrations in the epifauna associated with *Posidonia oceanica* meadows. *Journal of the Marine Biological Association of the United Kingdom* **79**, 971–977. doi:10.1017/S0025315499001204
- Schiel, D. R. (1988). Algal interactions on shallow subtidal reefs in northern New Zealand: a review. *New Zealand Journal of Marine and Freshwater Research* **22**, 481–489. doi:10.1080/00288330.1988.9516317
- Schiel, D. R. (2004). The structure and replenishment of rocky shore intertidal communities and biogeographic comparisons. *Journal of Experimental Marine Biology and Ecology* **300**, 309–342. doi:10.1016/J.JEMBE.2004.01.001
- Schiel, D. R. (2006). Rivets or bolts? When single species count in the function of temperate rocky reef communities. *Journal of Experimental Marine Biology and Ecology* **338**, 233–252. doi:10.1016/J.JEMBE.2006.06.023
- Schiel, D. R., and Lilley, S. A. (2007). Gradients of disturbance to an algal canopy and the modification of an intertidal community. *Marine Ecology Progress Series* **339**, 1–11. doi:10.3354/MEPS339001
- Schiel, D. R., and Taylor, D. I. (1999). Effects of trampling on a rocky intertidal algal assemblage in southern New Zealand. *Journal of Experimental Marine Biology and Ecology* **235**, 213–235. doi:10.1016/S0022-0981(98)00170-1
- Schneider, F. I., and Mann, K. H. (1991). Species specific relationships of invertebrates to vegetation in a seagrass bed. II. Experiments on the importance of macrophyte shape, epiphyte cover and predation. *Journal of Experimental Marine Biology and Ecology* **145**, 119–139. doi:10.1016/0022-0981(91)90009-L
- Silberfeld, T., Leigh, J. W., Verbruggen, H., Cruaud, C., de Reviers, B., and Rousseau, F. (2010). A multi-locus time-calibrated phylogeny of the brown algae (Heterokonta, Ochrophyta, Phaeophyceae): investigating the evolutionary nature of the 'brown algal crown radiation'. *Molecular Phylogenetics and Evolution* **56**, 659–674. doi:10.1016/J.YMPEV.2010.04.020
- Silliman, B. R., Bertness, M. D., Altieri, A. H., Griffin, J. N., Bazterrica, M. C., Hidalgo, F. J., Crain, C. M., and Reyna, M. V. (2011). Whole-community facilitation regulates biodiversity on Patagonian rocky shores. *PLoS ONE* **6**, e24502. doi:10.1371/JOURNAL.PONE.0024502
- Taylor, R. B. (1997). Seasonal variation in assemblages of mobile epifauna inhabiting three subtidal brown seaweeds in northeastern New Zealand. *Hydrobiologia* **361**, 25–35. doi:10.1023/A:1003182523274
- Taylor, R. B. (1998). Short-term dynamics of a seaweed epifaunal assemblage. *Journal of Experimental Marine Biology and Ecology* **227**, 67–82. doi:10.1016/S0022-0981(97)00262-1
- Thomsen, M. S. (2010). Experimental evidence for positive effects of invasive seaweed on native invertebrates via habitat-formation in a seagrass bed. *Aquatic Invasions* **5**, 341–346. doi:10.3391/AI.2010.5.4.02
- Thomsen, M. S., and McGlathery, K. (2006). Effects of accumulations of sediments and drift algae on recruitment of sessile organisms associated with oyster reefs. *Journal of Experimental Marine Biology and Ecology* **328**, 22–34. doi:10.1016/J.JEMBE.2005.06.016
- Thomsen, M. S., and Wernberg, T. (2014). On the generality of cascading habitat-formation. *Proceedings of the Royal Society B: Biological Sciences* **281**(1777), 20131994. doi:10.1098/RSPB.2013.1994
- Thomsen, M. S., Wernberg, T., Altieri, A. H., Tuya, F., Gulbrandsen, D., McGlathery, K. J., Holmer, M., and Silliman, B. R. (2010). Habitat cascades: the conceptual context and global relevance of facilitation cascades via habitat formation and modification. *Integrative and Comparative Biology* **50**, 158–175. doi:10.1093/ICB/ICQ042
- Thomsen, M. S., de Bettignies, T., Wernberg, T., Holmer, M., and Debeuf, B. (2012). Harmful algae are not harmful to everyone. *Harmful Algae* **16**, 74–80. doi:10.1016/J.HAL.2012.01.005
- Thomsen, M. S., Staehr, P. A., Nejrup, L. B., and Schiel, D. R. (2013). Effects of the invasive macroalgae *Gracilaria vermiculophylla* on two co-occurring foundation species and associated invertebrates. *Aquatic Invasions* **8**, 133–145. doi:10.3391/AI.2013.8.2.02
- Vaughn, K. C., and Bowling, A. J. (2011). Biology and physiology of vines. *Horticultural Reviews* **38**, 1–21.
- Wahl, M. (2009). Epibiosis ecology, effects and defences. *Ecological Studies – Marine Hard Bottom Communities, Part 1* **206**, 61–72. doi:10.1007/B76710_4
- Warren, R., Wells, R., and Blount, J. (1980). A novel lipid from the brown alga *Notheia anomala*. *Australian Journal of Chemistry* **33**, 891–898. doi:10.1071/CH9800891
- Watson, D. M., and Herring, M. (2012). Mistletoe as a keystone resource: an experimental test. *Proceedings. Biological Sciences* **279**, 3853–3860. doi:10.1098/RSPB.2012.0856
- Wernberg, T., Tuya, F., Thomsen, M. S., and Kendrick, G. A. (2010). Turban snails as habitat for foliose algae: contrasting geographical patterns in species richness explained by top-down control from limpets? *Marine and Freshwater Research* **61**, 1237–1242. doi:10.1071/MF09184
- Wright, P. J., Clayton, M. N., Chudek, J. A., Foster, R., and Reed, R. H. (1987). The carbohydrate altritol in *Bifurcariopsis capensis*, *Hormosira banksii*, *Notheia anomala* and *Xiphophora chondrophylla* (Fucales, Phaeophyta) from the Southern Hemisphere. *Phycologia* **26**, 429–434. doi:10.2216/I0031-8884-26-4-429.1
- Zotz, G., and Bader, M. Y. (2011). Sampling vascular epiphyte diversity – species richness and community structure. *Ecotropica* **17**, 103–112.