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Loss of predator species, not intermediate consumers, triggers rapid and dramatic extinction cascades

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Abstract

Ecological networks are tightly interconnected, such that loss of a single species can trigger additional species extinctions. Theory predicts that such secondary extinctions are driven primarily by loss of species from intermediate or basal trophic levels. In contrast, most cases of secondary extinctions from natural systems have been attributed to loss of entire top trophic levels. Here, we show that loss of single predator species in isolation can, irrespective of their identity or the presence of other predators, trigger rapid secondary extinction cascades in natural communities far exceeding those generally predicted by theory. In contrast, we did not find any secondary extinctions caused by intermediate consumer loss. A food web model of our experimental system—a marine rocky shore community—could reproduce these results only when biologically likely and plausible nontrophic interactions, based on competition for space and predator-avoidance behaviour, were included. These findings call for a reassessment of the scale and nature of extinction cascades, particularly the inclusion of nontrophic interactions, in forecasts of the future of biodiversity.

KEYWORDS
algae, consumers, ecological stability, field experiment, food web, intertidal, nontrophic interactions, rocky shore, secondary extinctions, structural robustness

1 | INTRODUCTION

There is growing recognition that the unprecedented rates of biodiversity loss seen worldwide comprise a key threat to a sustainable future for humanity (Hooper et al., 2012; Pimm et al., 2014). The ecological networks that make up the living world around us are tightly interlinked (Montoya, Pimm, & Solé, 2006; Williams, Berlow, Dunne, Barabási, & Martinez, 2002), such that changes in the abundance of species—a common consequence of human exploitation of natural populations and habitats (e.g., Millennium Ecosystem Assessment, 2005; Myers & Worm, 2003)—can propagate through intermediaries to affect other species many links away (McClean et al., 2015; Montoya et al., 2006; Sanders, Sutter, & van Veen, 2013; Säterberg, Sellman, & Ebenman, 2013). Thus, the extinction of even

a single species can have dramatic consequences for the structure and dynamics of whole ecosystems (Dunne & Williams, 2009; Estes, Burdin, & Doak, 2016; Estes & Palmisano, 1974; Estes et al., 2011; Koh et al., 2004; O'Connor & Donohue, 2013; Paine, 1966).

Species loss can trigger a breakdown in the mechanisms that support coexistence of interacting species, resulting in a sequence of additional species extinctions (Brodie et al., 2014; Sanders, Kehoe, & van Veen, 2015). Theory (Borrvall & Ebenman, 2006; Dunne & Williams, 2009; Dunne, Williams, & Martinez, 2002; Ebenman, Law, & Borrvall, 2004; Eklöf & Ebenman, 2006; Fowler, 2010, 2013; Pimm, 1980), supported by empirical studies in natural systems (Estes & Palmisano, 1974; Paine, 1966; Springer et al., 2003; Terborgh et al., 2001), predicts that such secondary extinctions are likely to be a common consequence of species loss. Both static (topological) and

dynamic food web models, covering a wide variety of web structures, interaction strengths and connectivities, indicate that the probability of secondary extinctions is greatest following the loss of species from intermediate or basal trophic levels and that they are relatively unlikely following the loss of predator species (Ebenman et al., 2004; Eklöf & Ebenman, 2006; Petchey, Eklof, Borrvall, & Ebenman, 2008). In contrast, most cases of secondary extinctions recorded from natural systems have been attributed to the loss of predators (Estes & Palmisano, 1974; Estes et al., 2016; Paine, 1966; Springer et al., 2003; Terborgh et al., 2001). While some studies focus on how species loss can cause net changes in diversity, there are very few empirical studies that quantify secondary extinctions explicitly (Donohue et al., 2016). Further, most of those are either observational (e.g., Estes & Palmisano, 1974; Springer et al., 2003; Terborgh et al., 2001) or experiments that lacked replication of treatments at the plot scale (Paine, 1966), with consequently limited capacity to elucidate mechanisms (but see Sanders et al., 2013, 2015). Nonetheless, the apparent disparity between theory and the results of empirical research may be a consequence of the fact that the empirical studies consistently involved the loss of all top predators and therefore the effective removal of an entire trophic level (Ebenman et al., 2004). No studies have, to our knowledge, compared experimentally the effects of loss of individual predator species, as distinct from the removal of all predation, with that of species from intermediate trophic levels on secondary extinctions simultaneously in the field.

To address this, we established a field experiment in a marine benthic system where we caused the loss of consumer species from multiple trophic levels and quantified rates of subsequent local extinctions of macroalgal species in natural rocky shore communities comprising primary producers, primary consumers (prey) and predators. Specifically, we simulated the extinction of one of two predator species (the whelk [*Nucella lapillus*] and crab [*Carcinus maenas*]) and one of two groups of their primary consumer prey (mussels [*Mytilus edulis*] and gastropod grazers [comprising principally *Patella vulgata*, *Littorina littorea* and *Gibbula umbilicalis*]), both separately and together, over 14 months (Figure 1). Many of the manipulated species are heavily exploited around the globe (Martins, Thompson, Neto, Hawkins, & Jenkins, 2010) and are extremely susceptible to disturbance caused by human activities (Thompson, Crowe, & Hawkins, 2002), making them highly pertinent for use in species loss experiments.

We quantified the direct and indirect effects of our experimental species removals on rates of subsequent loss of macroalgal taxa from our experimental plots (our measure of secondary extinctions at the plot scale). We used wire-mesh cages to manipulate target consumers. These allowed immigration and recruitment of primary producers and many epibenthic consumers (including primary consumers and small predators, e.g., amphipods, polychaetes and Nemertea) and their presence caused no detectable experimental artefacts (Table S1 in Supporting Information). Our experiment thereby caused the local extinction of key components of a larger intertidal food web (Figure 1) in an open experimental system,
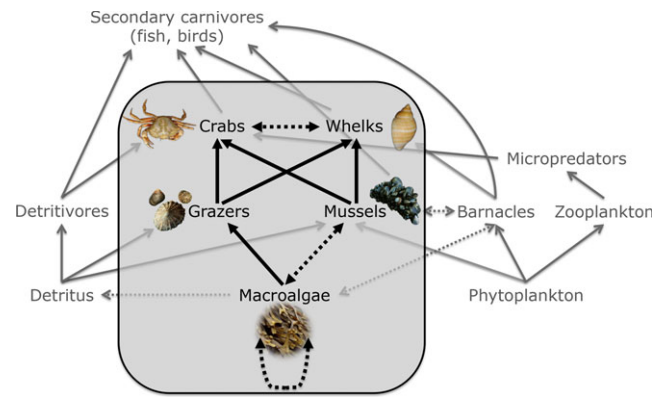

FIGURE 1 Simplified network highlighting the key trophic (closed arrows) and nontrophic (dashed arrows) interactions between species on rocky shores. Organisms manipulated and quantified in our study are highlighted in the grey box. Both competition for space (among algal species and between algae and mussels) and altered consumer foraging behaviour in the presence of predators (such as crabs and whelks) comprise important nontrophic interactions on rocky shores that can have strong influence on overall assemblage structure (see Section 2 for more information). In addition, mussel beds provide a key predation refuge at the experimental site. We manipulated the presence of both predators (crabs and whelks) and primary consumers (mussels and gastropod grazers), both separately and together, and quantified the effects of these experimentally simulated species extinctions on rates of subsequent loss of macroalgal species from our experimental plots (our measure of secondary extinctions) [Colour figure can be viewed at wileyonlinelibrary.com]

subject to fluctuations in both environmental conditions and recruitment dynamics of dispersing species, without removing all consumers from a given trophic level.

The aims of our experiment were to test whether: (i) loss of individual predator species, as distinct from the complete loss of predation, triggers more secondary extinctions than the loss of intermediate consumer species; (ii) trophic position plays a more important role than species identity in determining rates of secondary extinctions; and (iii) given the need to understand the factors regulating the identity of species that go secondarily extinct (Petchey et al., 2004), we also tested whether the identity of those species was determined by the identity of the species that was initially lost from the system.

Although logistically challenging, field removal experiments are an ideal counterpart to other experimental methods for investigating the functional consequences of extinctions. Field removals make minimal model assumptions and maximize realism, primarily by incorporating natural environmental fluctuations, biotic dispersal and established natural assemblages structured by a diverse range of trophic and nontrophic interactions (Díaz, Symstad, Chapin, Wardle, & Huenneke, 2003; Naeem, 2008). On moderately exposed rocky shores, mussels have strong nontrophic interactions with macroalgae arising primarily from competition for space on the shore (O'Connor, 2010; Figure 1), which can interact with the presence of grazers (Crowe, Frost, & Hawkins, 2011). Alterations to consumer foraging

patterns and growth rates as a consequence of predator avoidance behaviour can also comprise important drivers of community dynamics in marine benthic systems (Trussell, Ewanchuk, & Bertness, 2002, 2003; Figure 1). At our experimental site, mussel beds provide a key refuge for reducing exposure to predators. Such strong nontrophic interactions are largely absent from current theoretical frameworks (Bruno, Stachowicz, & Bertness, 2003; Kéfi et al., 2012), yet they are recognized as important for ecological dynamics in many ecosystems (Kéfi, Miele, Wieters, Navarrete, & Berlow, 2016; McClean et al., 2015; Suraci, Clinchy, Dill, Roberts, & Zanette, 2016), including coastal shores (Bertness & Leonard, 1997; Hartnoll & Hawkins, 1985; Hawkins & Hartnoll, 1983b; O'Connor, Bracken, Crowe, & Donohue, 2015; O'Connor & Donohue, 2013; Trussell et al., 2002, 2003). For example, Paine's (1966) argument for the influence of predation on species diversity was built fundamentally around the importance of competition for space, and there is a broad literature on trait-mediated indirect effects (Banerji et al., 2015; Bukovinszky, van Veen, Jongema, & Dicke, 2008; Sanders et al., 2013; Schmitz, 1998; Werner & Peacor, 2003). Because of this, we explored whether any disparities between the general predictions of theory regarding the factors that regulate the secondary loss of species from ecosystems and the results of our field experiment could be reconciled by incorporating explicit nontrophic interactions into a classical food web model of our experimental system.

2 | MATERIALS AND METHODS

2.1 | Field experiment

Our experimental site was located on the mid to low shore at Rush (53°31.4′N, 6°04.9′W) on the east coast of Ireland on a moderately exposed flat rocky reef containing networks of patches of bare rock, mussels, barnacles and macroalgal stands (Mrowicki, O'Connor, & Donohue, 2016; O'Connor, Emmerson, Crowe, & Donohue, 2013). Each of our experimental plots contained approximately 50% mussel cover prior to the random allocation of treatments (range 45%–55%). There was no difference in the taxon richness (ANOVA; $F_{9,30} = 0.75$, $p = .66$) or overall multivariate structure (PERMANOVA; Pseudo-$F_{9,30} = 0.81$, $p = .82$) of algal assemblages (Table S2) among treatments at the commencement of the experiment.

Our fully crossed experimental design comprised two fixed factors: "predators removed" and "primary consumers removed," each comprising three levels (predators removed: no removal, whelks removed and crabs removed; primary consumers removed: no removal, grazers removed and mussels removed). Comparison of the resulting nine treatments enabled us to quantify the individual and combined effects of consumer species loss across multiple trophic levels on rates of subsequent loss of macroalgal taxa (our measure of secondary extinctions) and to elucidate the relative importance of species identity and trophic position as regulatory factors. Each of our ten experimental treatments (nine caged, one uncaged procedural control) was replicated four times. Mussels and molluscan grazers were removed manually from treatments to simulate loss of these

species. Predators were present at a density of one individual per plot where required for the treatment. Densities of each of the manipulated consumers within our plots were within the range found naturally on the shore. Thus, our experimental manipulations mimicked as closely as possible natural patterns at the experimental site. In treatments where species were removed, there was no experimental compensation for the loss of species, or artificial increase in biomass of remaining species, similar to an additive design (Byrnes & Stachowicz, 2009). Crabs found on the shore and used in the experiment had a carapace width of 3–6 cm. This size range feeds mainly on mussels and small grazers (Rangeley & Thomas, 1987). Although larger crabs have been found to feed on whelks, no predation by crabs upon whelks was observed during our experiment.

The stainless steel mesh cages used to manipulate the presence of target consumers (0.9 mm wire diameter, 3.33 mm aperture, 61% open area) measured 35 × 35 cm and were 12 cm high, allowing for algal growth and recruitment. This cage design has been used extensively and successfully to manipulate consumer presence on rocky shores with no consequences for algal assemblage structure or stability (Donohue et al., 2013; O'Connor & Donohue, 2013; O'Connor, Donohue, Crowe, & Emmerson, 2011). The fences were attached to the shore by drilling holes into the rock and securing them with stainless steel screws and washers. Roofs were also made from the stainless steel mesh and were fixed to the tops of the fences with cable ties. Cages and treatments were checked and maintained regularly (approximately every two weeks), and cages were scrubbed routinely with a wire brush to remove any algae. Juveniles of species that were being excluded were removed from the appropriate treatments as they became visible while settlement and recruitment of all other species was left intact. Comparison of unmanipulated (i.e., with all consumers present) caged and uncaged communities over the duration of the experiment demonstrated that there were no experimental artefacts associated with the presence of the experimental cages, the associated exclusion of some larger consumers (such as fish and birds) or with enclosing our target consumers (Table S1).

Algal communities on rocky shores are highly dynamic and can change dramatically within a few months, particularly at the scale of individual plots, driven by dynamic interactions between environmental fluctuations and biological interactions (Hawkins & Hartnoll, 1983a,b). Consequently, by focusing our efforts on primary producers, we maximized the probability of detecting relatively rapid local extinctions (Borrvall & Ebenman, 2006). We quantified the extent of cover and composition of macroalgal assemblages on each plot with a 25 × 25 cm double-strung quadrat four, seven, ten and fourteen months after the commencement of the experiment. The quadrat was placed in the middle of each plot to avoid sampling edge effects and the cover and composition of algae estimated by identifying all species present under each of 64 intersections. Species of algae present within the quadrat but not recorded under an intersection point were noted and assigned a value of 1% cover. Rates of secondary extinctions were quantified from each experimental plot as the number of

macroalgal taxa that were present in the plots at the commencement of the experiment but that were lost after experimental manipulation. We waited four months before commencing our measurements to ensure establishment of experimental treatments.

We tested for effects of species loss using analysis of variance (ANOVA) and permutational multivariate analysis of variance (PERMANOVA; with PRIMER® Version 6.1.13; PRIMER-E Ltd., Plymouth, UK) after first ensuring data homoscedasticity. Variables were transformed where necessary to homogenize variances. The Student–Newman–Keuls procedure was used to make post hoc comparisons among levels of significant terms in univariate analyses. Generalized linear models (GLMs) with binomial errors were used to test for effects of species loss on the proportion of macroalgal species that went secondarily extinct from experimental plots. SIMPER (Similarity of Percentages; Clarke & Warwick, 2001) analyses were used to identify which algal taxa contributed most to pairwise dissimilarities between treatments, while permutational analysis of multivariate dispersions (PERMDISP; Anderson, 2006) was used to test for differences in compositional heterogeneity of algal assemblages among treatments. Multivariate analyses were based on Jaccard similarity matrices calculated from the presence-/absence-transformed algal compositional data and were based on 9,999 permutations of the residuals under a reduced model.

2.2 | Dynamical model

We developed a dynamic ecological network model to explore the conditions that qualitatively reproduce the results of our field experiment—specifically, those that enable secondary extinctions of basal species to occur after the loss of one predator in isolation, but not after the loss of any intermediate consumer species. Our allometric-scaling dynamic interaction web model comprised a simplified version of the trophic network studied in the field experiment and included two top predators (whelks and crabs), two sets of intermediate consumers (mussels and grazers) and four algae taxa at the base of the network (highlighted in the grey box in Figure 1). In addition to the trophic links, we also included two types of nontrophic interactions that are known to be important on rocky shores: competition for space between mussels and algae (Crowe et al., 2011; O'Connor, 2010) and shifts in foraging behaviour as a consequence of the presence of predators (McKillup, 1981; Nakaoka, 2000; Trussell et al., 2002, 2003; Figure 1). Although there are clearly many more nontrophic interactions that occur between species on rocky shores (e.g., both limpet "bulldozing" and sweeping of *Fucus* hinders barnacle recruitment: Hawkins, 1983; Hawkins & Hartnoll, 1983a,b and the presence of large fucoids can increase mussel mortality: Wangku-langkul, Hawkins, & Jenkins, 2016), we chose to incorporate only what we perceived as the most important interactions based on our experience at the site into our simplified modelled interaction web.

We used an allometric-scaling dynamic food web model derived from Yodzis and Innes (1992), updated with more recent allometric coefficients (see Table S3 for parameter values) and using a different functional response (see Supporting Information for model derivation

and references). The change in biomass density B_i of a primary producer species i is described by:

$$\frac{dB_i}{dt} = \left(1 - \frac{B_i}{K_i}\right)B_i - \sum_j \frac{x_j y h_j}{1 - \delta} F_{ij}(B)B_j \tag{1}$$

The change in biomass density B_i of a consumer species i is described by:

$$\frac{dB_i}{dt} = \sum_k x_i y h_i F_{ik}(B)B_i - \sum_j \frac{x_j y h_j}{1 - \delta} F_{ij}(B)B_j - x_i B_i \tag{2}$$

where K is the carrying capacity, δ is the proportion of nutrients that are not assimilated, x_i is the metabolic rate, y is the maximum ingestion rate of consumers, h_i is the handling time of species I and F_{ij} is a functional response (see Equation 3). Note that we use j to refer to the set of consumers of i and k to refer to its set of prey. The functional response of species i consuming species j is defined as a multiprey Holling-type functional response (Holling, 1959):

$$F_{ij} = \frac{p_{ij}(B)a_{ij}B_j^q}{1 + h_i \sum_k a_{ik} p_{ik}(B)B_k^q} \tag{3}$$

where a_{ij} is the foraging intensity (attack rate) of species i on j, q is the exponent of the response (set at 0.5 in our study [Table S3], corresponding to a form intermediate between Holling type II and type III) and $p_{ij}(B)$ is the realized foraging preference of species i on j. The latter depends on the abundance of all prey of a predator, as follows:

$$p_{i,j}(B) = \frac{w_{ij}B_j}{\sum_k w_{ik}B_k} \tag{4}$$

where w_{ij} is the "raw" foraging preference of species i on j. It is equal to one when summed over all j. This model has a reduced number of free parameters, as x_i, y and h_i are constrained using empirical relationships.

Attack rates were considered to scale with the product of a predator and its prey sizes, the latter scaling with body mass to the power of 0.25. This models the increase in probability of encounter as body mass increases (Peters, 1983):

$$a_{i,j} = a_0 m_i^{0.25} m_j^{0.25} \tag{5}$$

where a_0 is set to 0.05 and m_i is the body mass of species i. We implemented nontrophic interactions in the model (Figure 1) as follows:

1. Algae compete with mussels for space on the shore. This was modelled through an additive mortality term for algae that varied with the abundance of mussels. To explore the effect of space competition from mussels on algal extinctions, we considered that only one of the four groups of algae in the model competed for space with mussels. Equation (1) then becomes:

$$\frac{dB_i}{dt} = \left(1 - \frac{B_i}{K_i}\right)B_i - \sum_j \frac{x_j y h_j}{1 - \delta} F_{ij}(B)B_j - \sum_i c_{li}B_l \tag{6}$$

with l the set of space competitors of species i and c_{li} the competition strength from species l to species i.

2. The predators affect each other's foraging preference. When both predators are present, their diet switches from a preference for grazers to a more balanced contribution between both grazers and mussels (i.e., both crabs and whelks eat proportionally more mussels when together than alone). This altered foraging behaviour, a common consequence of the presence of other predators, including crabs and whelks (McKillup, 1981; Nakaoka, 2000; Trussell et al., 2002, 2003), on rocky shores reflects greater use of refugia for predator avoidance, which tends to be within mussel beds at the experimental site (I. Donohue pers. obs.). In the model, we implemented this by modulating the raw foraging preferences of predators for each of their resources by the abundance of the other predator (described by a saturating "rational function"; Kéfi et al., 2012):

$$w'_{ij} = \frac{(w_{ij} + \delta w_{kij})B_k + w_{ij}B_0}{B_k + B_0} \quad (7)$$

where δw_{kij} is the intensity of the nontrophic effect of species k on the raw foraging preference of i for j. B_0 is the shape parameter of the rational function (set to 0.25). A predator has no preference for any of its N prey when all w'_{ij} are equal to $1/N$. It has a positive preference when w_{ij} is above $1/N$. We defined the strength of the predator foraging modulation s_{fp} to summarize the strength of this nontrophic effect into one value. The raw foraging preference of predator i was in favour of grazers through the relationships:

$$w_{i,mussels} = \frac{1}{N_{preys}} - s_{fp} \quad (8)$$

and

$$w_{i,grazers} = \frac{1}{N_{preys}} + s_{fp} \quad (9)$$

However, the presence of the remaining predator j countered this preference of predator i for grazers through the nontrophic coefficients

$$\delta w_{j,i,mussels} = -\delta w_{j,i,grazers} = 2 * s_{fp} \quad (10)$$

We set s_{fp} to 0.3 so that predators had a lesser foraging preference for mussels of 0.2 when the other predator was absent, and a greater preference for mussels of 0.8 when the other predator was very abundant (i.e., biomass close to unity).

All species abundances were set to 0.5 at the beginning of the simulation. Simulations were run until $t = 5,000$, at which point one or more species were removed from the network in accordance with the experimental design. The run was then continued until $t = 10,000$. Both of these time thresholds were sufficient to allow the system to reach a steady state before and after species removal.

3 | RESULTS

3.1 | Field experiment

The removal of either of the two manipulated predator species in isolation resulted in the loss of about five macroalgal taxa from experimental plots compared to less than one from plots that experienced no experimental species removals (Figure 2a). This large effect occurred only when the intermediate consumer trophic level was intact; concurrent removal of grazers or mussels resulted in rates of loss of algal taxa that were similar to background levels (Figure 2a; ANOVA interaction term, $F_{4,27} = 7.51$, $p = .0003$). In contrast, the removal of only primary consumer species caused few if any, local extinctions of macroalgae from plots (i.e., rates of loss of algal taxa from plots were similar to the treatment with no consumer manipulations; Figure 2a).

These results were consistent for both the absolute and proportional number of local algal extinctions that occurred within experimental plots [AIC of GLMs for proportional data with and without interactions, was, respectively, 92.69 and 107.22] and across all of our field surveys, with experimental treatments generally having highly consistent effect sizes throughout the duration of the experiment (Figure 2b). Thus, observed local extinctions of macroalgal species from experimental plots occurred relatively rapidly, less than four months after predator species removal.

Removal of either predator species in isolation increased mussel cover, while the removal of grazers, either in isolation or in combination with the removal of either predator species, reduced mussel cover (ANOVA; interaction between loss of predators and loss of grazers; $F_{2,18} = 10.02$, $p = .001$; Figure 3a). This indicates that both predator species had direct negative effects on mussel biomass, while the presence of grazers facilitated mussels, likely indirectly through the consumption of algal propagules that compete with mussels for space on the shore and/or by being consumed preferentially by the predators. Further, the removal of either predator species, but only when in combination with the removal of mussels, increased the biomass of gastropod grazers (ANOVA; $F_{2,18} = 22.1$, $p \leq .0001$; square-root transformed data; Figure 3b). The fact that grazer biomass did not increase when either predator species was removed in isolation suggests a shift in the foraging behaviour of the remaining predator towards a stronger preference for grazers. Simultaneous removal of mussels likely benefited grazers by reducing feeding rates of remaining predators through increasing their own perceived exposure to predation coupled with freeing up space on the shore and facilitating increased biomass of their algal food. Taken together, these results indicate clearly that nontrophic interactions comprise key mechanisms underpinning the observed secondary extinctions of macroalgal taxa in our experiment.

Even though the removal of primary consumer species in isolation did not affect rates of loss of macroalgal taxa from experimental plots (Figure 2), we found that the identity of the algal taxa that were lost from experimental plots was determined solely by primary consumers, irrespective of the presence or absence of their
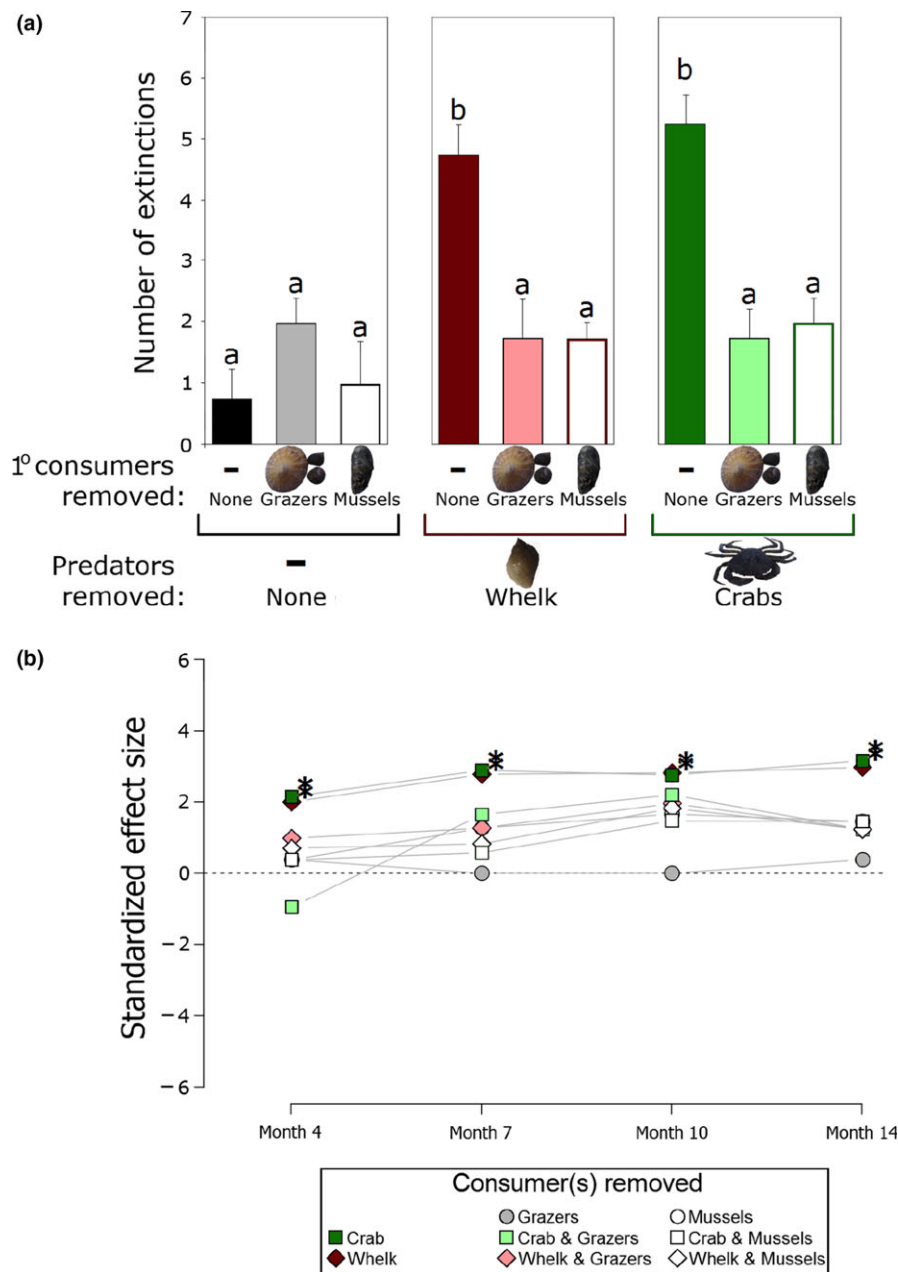
FIGURE 2 (a) The number of macroalgal taxa lost (mean + *SEM*, *n* = 4) from experimental plots in each of our experimental treatments over the course of the experiment. Letters (a, b) indicate groups of treatments that are statistically indistinguishable from each other (*p* > .05). (b) Standardized effect sizes of our experimental manipulations based on the difference between experimental treatments and the corresponding treatment with no species removals for each algal survey. Treatments that differed significantly (*p* < .05, based on post hoc comparisons among levels of significant terms in ANOVAs) from the latter are highlighted with asterisks

predators (PERMANOVA, pseudo-$F_{2,27}$ = 3.62, *p* ≤ .0001). Pairwise post hoc tests showed that the removal of grazers enhanced the likelihood of loss of different algal taxa compared with the removal of mussels (*p* = .0004) and both treatments differed significantly from the treatment where no primary consumers were removed (grazers lost-no primary consumers lost: *p* = .005; mussels lost-no primary consumers lost: *p* = .004). Removal of grazers enhanced primarily the local extinction of the red alga *Lithothamnion* spp., whereas removal of mussels increased the probability of loss of ephemeral algae such as *Ulva lactuca* and *Porphyra umbilicalis*

(Table 1). This preferential loss of different taxa after the removal of different primary consumers led to distinct shifts in algal assemblage composition in experimental plots by the end of the experiment (PERMANOVA, pseudo-$F_{2,27}$ = 7.27, *p* ≤ .0001; grazers removed-no primary consumers removed: *p* = .038; mussels removed-no primary consumers removed: *p* ≤ .0001; grazers removed-mussels removed: *p* ≤ .0001). Moreover, it also homogenized the composition of algal assemblages in space (PERMDISP, $F_{2,33}$ = 24.65, *p* ≤ .0001; grazers removed-no primary consumers removed: *p* ≤ .0001; mussels removed-no primary consumers removed: *p* ≤ .0001; grazers
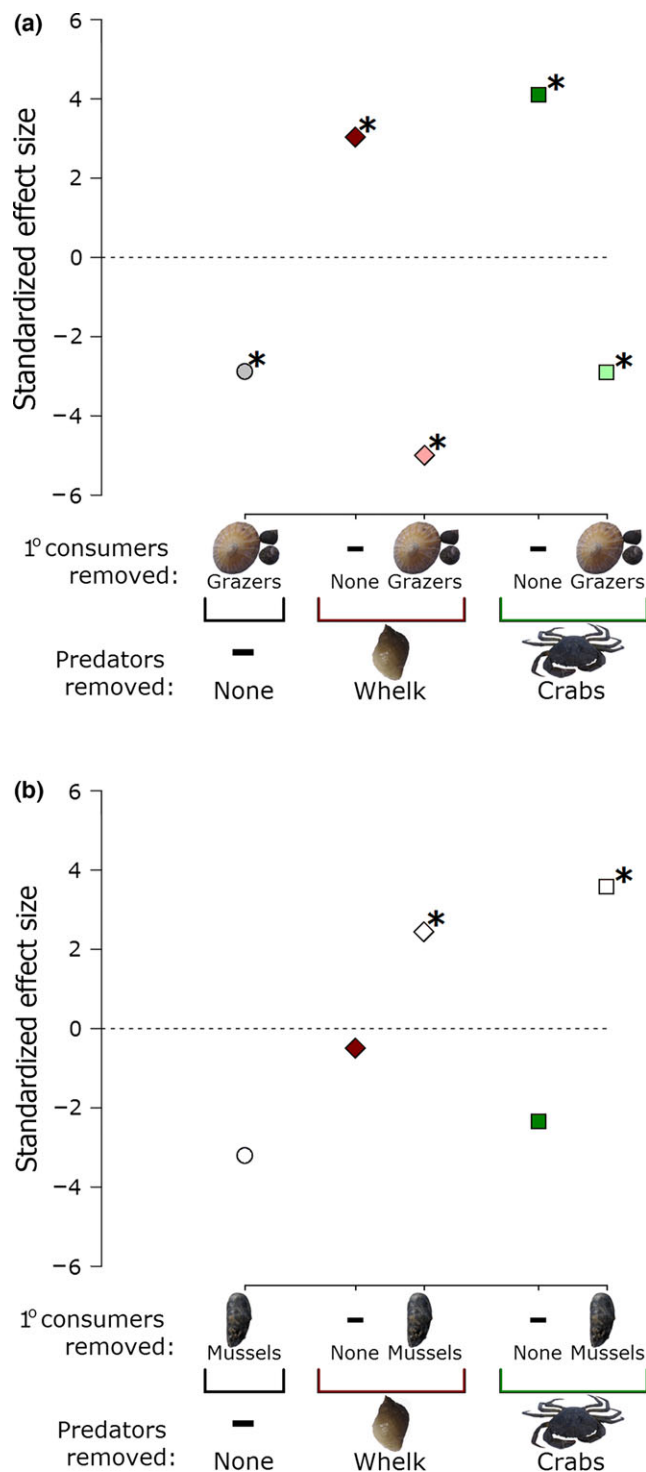
FIGURE 3 Standardized effect sizes of our experimental manipulations on the biomass of (a) mussels and (b) grazers at the end of the experiment based on the difference between experimental treatments and the corresponding treatment with no species removals. Treatments that differed significantly ($p < .05$, based on post hoc comparisons among levels of significant terms in ANOVAs) from the latter are highlighted with asterisks. Positive and negative values correspond to, respectively, increases and reductions in biomass in treatments relative to the treatment with no species removals. Treatment symbols as in Figure 2b

TABLE 1 Results of SIMPER analyses identifying the five taxa contributing most strongly to differences in the composition of algal taxa lost from experimental plots following the removal of primary consumer species, shown as proportions of experimental plots in treatments from which algal taxa went locally extinct

| Primary consumer removed | Taxon | Local algal extinctions (proportion of plots) | | % Contribution |
		Consumer present	Consumer absent	
Grazers	*Lithothamnion* spp.	0.58	0.67	17.8
	Corallina officinalis	0.5	0.75	14.2
	Ulva lactuca	0.42	0.08	12.1
	Chondrus crispus	0.42	0.33	12
	Osmundea pinnatifida	0.5	0	9.7
Mussels	*Ulva lactuca*	0.42	0.5	16.8
	Porphyra umbilicalis	0.25	0.33	12.5
	Corallina officinalis	0.5	0.08	11.8
	Lithothamnion spp.	0.58	0	11.2
	Fucus serratus	0.33	0.17	10.2

% Contribution corresponds to the percentage contribution of each algal taxon to the overall dissimilarity between assemblages with and without grazers or mussels.

removed-mussels removed: $p = .36$). Plots from which grazers were removed contained primarily ephemeral and brown algae such as *Polysiphonia* spp., *Fucus serratus*, *U. lactuca* and *P. umbilicalis*, whereas those from which mussels were removed were dominated by red algae such as *Osmundea pinnatifida*, *Chondrus crispus*, *Lithothamnion* spp. and *Corallina officinalis* (Table S4).

3.2 | Dynamical model

We found that no secondary extinctions of algal species occur when the ecological network comprises only trophic interactions (bottom-left corner of all panels in Figure 4). Rather, secondary extinctions of algal species occur only when competition for space between mussels and algae is incorporated into the model at intermediate levels of intensity (green area in Figure 4a). However, both types of non-trophic interactions (i.e., competition for space and shifts in predator foraging behaviour in response to predator densities) are necessary to reproduce the patterns of consumer biomass observed in the field experiment, in particular that predator species removal not only triggers subsequent extinctions of algae, but also an increase of 20%–60% in mussel biomass while simultaneously leaving grazer biomass unaltered (Fig. S1). These key results of the field experiment occur at intermediate levels of competition for space and high levels of foraging preference modulation (orange area in Figure 4b).
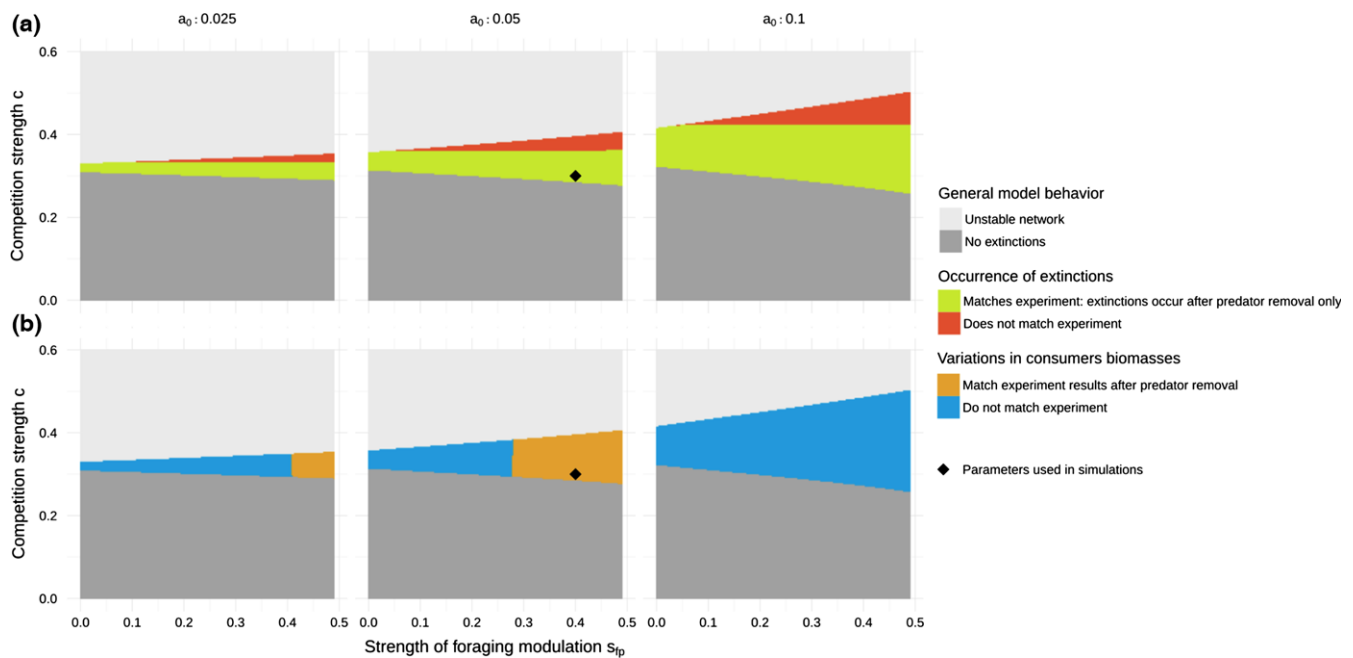
FIGURE 4 (a) Ranges of parameters leading to extinctions of algae (red and green areas) after species removal from the network. We distinguish the cases where extinctions were caused by the removal of one predator (red area) from the cases where extinctions occurred when removing one predator in isolation but not when a predator and a consumer were removed (green area, i.e., what was observed in the experiment). Y-axis: intensity of competition c for space between algae and mussels. X-axis: strength of foraging modulation. Note that the point at which both competition for space and forging modulation are null (i.e., bottom left corner of the graph) corresponds to a classic food web (i.e., a network with no nontrophic interactions). (b) Ranges of parameter values leading to biomass variations as observed in the experiment following the removal of one predator. The orange area indicates the range of parameters that qualitatively reproduce what was observed in the experiment (i.e., for which we observe extinctions of algae, an increase in mussel cover and no increase in abundance of grazers)

4 | DISCUSSION

The removal of predator species in isolation triggered cascading loss of basal species from our experimental plots, whereas the removal of primary consumers did not. This finding not only contrasts markedly with most theoretical predictions (Ebenman et al., 2004; Eklöf & Ebenman, 2006; Petchey et al., 2008), but also demonstrates that the loss of individual predator species can, even when other predators remain, trigger secondary extinction cascades in natural communities. Overall, 30%–33% of the 16 macroalgal taxa found in our study were lost from our experimental plots following the removal of either predator species. This level of secondary extinction is an order of magnitude greater than obtained for entire food webs from many theoretical studies (Ebenman et al., 2004; Eklöf & Ebenman, 2006; Quince, Higgs, & McKane, 2005), yet is consistent with the dramatic extinction cascades recorded after the removal of all predators from comparable natural systems (Paine, 1966). Our results therefore indicate that most existing theoretical models not only fail to capture adequately the mechanisms leading to secondary extinctions from real ecosystems but that they also underestimate the frequency of those extinctions. This supports strongly recent assertions (Donohue et al., 2016; Fowler, 2010; Kéfi et al., 2012; O'Connor & Donohue, 2013) that current theoretical understanding, which is based almost entirely on trophic interaction networks, may not provide a particularly accurate model of natural systems.

Exploration of the conditions that enabled secondary extinctions to occur in our dynamic network model highlights clearly the importance of both trophic and nontrophic interactions in explaining the outcome of the field experiment. The main results of the experiment were reproduced only when both competition for space and predator avoidance behaviour were incorporated into the model. Note that only one of the four algal taxa was subject to competition for space with mussels in our relatively simple model and only that specific taxon went extinct following the removal of one of the predators. However, in principle, any algal taxon could be considered to compete for space with mussels and other algae and so go to extinction. Thus, in a more complex ecological network with several algal taxa competing for space, many would be driven to extinction following removal of a predator.

Our results demonstrate that loss of individual predator species, as distinct from complete release from predation, is sufficient to trigger dramatic extinction cascades in natural communities. This is consistent with the theoretical predictions of Säterberg et al. (2013), who found that even reductions in the abundance of species can trigger the extinction of other species. Moreover, the threshold for causing such "functional extinctions" was lower for species at higher trophic levels. In our study, even though total predator biomass was reduced when either crabs or whelks were removed, and even though the two manipulated predator species differ considerably in the biomass of individuals, feeding preferences and modes of feeding—their loss thus likely affecting different parts of the foodweb (e.g., crabs eat limpets [Silva, Hawkins, Boaventura, & Thompson, 2008], key grazers in this system [Coleman et al., 2006; O'Connor & Crowe, 2005], whereas whelks tend not to)—subsequent rates of loss of algal taxa were

remarkably similar. Although these findings may be driven by features specific to our study system, the fact that they are consistent with the theoretical prediction that trophic position, rather than species identity, is the key determinant of the impact of a species on rates of secondary extinctions (Allesina & Pascual, 2009) would suggest that they may be generalizable to other systems. Moreover, because we found similarly high rates of loss of algal taxa irrespective of the identity of the predator species that was removed, our results also indicate a more general importance of loss of predator species in triggering cascading extinctions than was appreciated previously.

The cascading effects of predator species removal on macroalgal local extinctions occurred only when the intermediate trophic level was intact, disappearing when either grazers or mussels were lost in tandem with either predator. Observed shifts in the biomass of grazers and mussels after predator removal indicate clearly that this result was likely driven by the level of competition for space on the shore—removal of either predator species increased competition for space indirectly via increasing mussel biomass, triggering local extinctions of macroalgal taxa. However, because grazers facilitated mussels indirectly by reducing algal cover, removal of either primary consumer, irrespective of the presence or absence of either predator species, reduced competition for space on the shore—as a consequence of reductions in mussel biomass—and thus failed to cause any secondary extinctions of algal taxa.

Not only did intermediate consumers moderate the number of macroalgal taxa that went locally extinct due to predator species loss, but they also determined the identity of those taxa that were lost, independently of the presence or absence of their predators. Loss of indirect interactions therefore triggered cascading local extinctions of basal species in our experiment, but the identities of those extinctions were determined by the direct interactions between macroalgal taxa and primary consumers. Moreover, the preferential loss of algal taxa also homogenized the composition of algal assemblages remaining on the experimental plots, which may, in turn, reduce functional diversity and resistance to perturbations by narrowing the range of species-specific responses (Donohue, Jackson, Pusch, & Irvine, 2009; Olden, Poff, Douglas, Douglas, & Fausch, 2004). Taken together, these results highlight an importance of all species to the maintenance of structural robustness in ecosystems and underscore the significance of management approaches that conserve the integrity of whole ecosystems and, thus, all of the biodiversity contained therein.

The majority of algal species losses in our field experiment occurred relatively rapidly, within four months of predator removal. This is likely a consequence of the fact that we focused on algal populations with relatively rapid turnover (Borrvall & Ebenman, 2006). The magnitude of the effect of predator species loss was remarkably consistent over the duration of the experiment, indicating strongly that our experiment was of adequate duration to capture the top-down effects of consumer species loss on algal assemblages. Theory predicts, however, that most secondary extinctions are due to bottom-up effects (Eklöf & Ebenman, 2006; Schleuning et al., 2016), with the secondary loss of basal species recorded in our experiment potentially triggering, in turn, a sequence of further species losses (Quince et al., 2005). Unfortunately, it was

not possible to quantify this in our experiment given the nature of our experimental design. There remains therefore a pressing need to examine experimentally the bottom-up effects of species loss on secondary extinctions in natural communities.

As with all ecological experiments, the generality of our findings may be constrained by the ecological context in which our experiment took place. Changes in interaction web structure through the addition of a particularly strong interactor might be expected to alter our findings, for example. Although the removal of predation by fish and birds did not affect algal communities in our experiment, likely because crabs and whelks maintained strong predator avoidance behaviour within the cages, the presence of strong predation by tertiary consumers could potentially alter our conclusions regarding the importance of primary consumers in causing secondary extinctions. Our plots encompassed the significant range of spatial heterogeneity and patchiness found across the experimental site, however, and were exposed to significant large-scale variation in environmental conditions, movement and feeding patterns of small mobile consumers and recruitment dynamics of dispersing species for the duration of the experiment. In spite of this significant spatiotemporal variation in both biotic and abiotic conditions, the effects of our experimental treatments remained highly consistent. Moreover, our results indicating an importance of predator loss in driving secondary extinctions are consistent with those of both observational (Estes & Palmisano, 1974; Springer et al., 2003; Terborgh et al., 2001) and experimental (Sanders et al., 2013, 2015) studies from other ecosystems. This suggests that our general findings are likely to be applicable across a range of ecological contexts beyond those of our experiment.

In addition to triggering secondary extinctions, the loss of species from ecosystems also provides opportunities for others to invade. For example, in Paine's classic 1966 experiment (Paine, 1966), the removal of *Pisaster* ultimately caused a net increase in species richness, largely as a consequence of the invasion of many new species associated with the mussel beds that expanded after the removal of predation by the sea star (Lafferty & Suchanek, 2016). Our theoretical understanding of the factors that regulate secondary extinctions is, however, based almost entirely on closed systems that lack the capacity to model invasions by new species. Given the pressing need to test these theoretical predictions, and the inherent importance to both conservation and management of improving our understanding of the factors that determine the identity of the species that are lost from ecosystems (Petchey et al., 2008), our study focused solely on secondary extinctions. It may have come to very different conclusions regarding the factors that drive net changes in diversity after species loss.

Our findings demonstrate an importance of both predator species and intermediate consumers, as well as trophic and nontrophic interactions, in maintaining the structural robustness of ecological communities. We conclude that holistic knowledge of interaction networks, incorporating both direct and indirect nontrophic and trophic interactions (Kéfi et al., 2016), and their ecological context is key to predicting the effects of species loss on not only rates of secondary extinctions but also the identities of the species that are likely to be lost. With human exploitation of natural resources set to

intensify further around the globe, secondary extinctions are likely to comprise a major source of biodiversity loss now and in future (Koh et al., 2004; Montoya et al., 2006), with notable consequences for both ecosystem functioning and stability (Donohue et al., 2013; Hooper et al., 2012; Petchey et al., 2004). There remains therefore a critical need for more experiments in natural communities to test the generality of our findings and the predictions of theory in a variety of ecological contexts and help us understand the true magnitude of the extinction crisis that we face.

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