

LETTER

Scaling up keystone effects from simple to complex ecological networks

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Abstract

Predicting the consequences of species loss requires extending our traditional understanding of simpler dynamic systems of few interacting species to the more complex ecological networks found in natural ecosystems. Especially important is the scaling up of our limited understanding of how and under what conditions loss of ‘keystone’ species causes large declines of many other species. Here we explore how these keystone effects vary among simulations progressively scaled up from simple to more complex systems. Simpler simulations of four to seven interacting species suggest that species up to four links away can strongly alter keystone effects and make the consequences of keystone loss potentially indeterminate in more realistically complex communities. Instead of indeterminacy, we find that more complex networks of up to 32 species generally buffer distant influences such that variation in keystone effects is well predicted by surprisingly local ‘top-down’, ‘bottom-up’, and ‘horizontal’ constraints acting within two links of the keystone subsystem. These results demonstrate that: (1) strong suppression of the competitive dominant by the keystone may only weakly affect subordinate competitors; (2) the community context of the target species determines whether strong keystone effects are realized; (3) simple, measurable, and local attributes of complex communities may explain much of the empirically observed variation in keystone effects; and (4) increasing network complexity *per se* does not inherently make the prediction of strong keystone effects more complicated.

Keywords

Competition, complexity, food web, interaction strength, networks, population dynamics, predation, resource enrichment, species removal, trophic cascades.

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INTRODUCTION

One of the most important challenges in ecology and environmental sciences is to better understand how losing certain species may subsequently lead to the loss of many other species (Graedel *et al.* 2001). Perhaps the best known example involves ‘keystone’ predators that maintain biodiversity in a variety of ecosystems by preferentially consuming competitively dominant prey species and thus preventing the competitive exclusion of many other subordinate competitors – hereafter called the ‘keystone effect’ (Paine 1969; Morin 1983; Brown & Heske 1990; Grover 1994; Power *et al.* 1996). Reviews of empirical studies suggest that, while this keystone effect is mechanistically simple and intuitive, its manifestation in complex natural communities is context-dependent and difficult to predict (Mills *et al.* 1993; Menge *et al.* 1994; Power *et al.*

1996). Most studies seeking to explain this troublesome context-dependency focus on variation in keystone consumption of the competitive dominant as a function of productivity, recruitment, environmental stress, etc. (Menge *et al.* 1994; Sanford 1999). To our knowledge, none have examined how the myriad species ‘peripheral’ to the keystone system might regulate the strength of the keystone effect. Empirically addressing the influence of the larger system on keystone effects is logistically difficult due the intractably large number of species interactions. Theoretically, when connected to a realistically complex web of interactions, keystone effects on any given species could be (1) essentially indeterminate because of the many potentially strong influences of distant species (Yodzis 2000); or (2) relatively uninfluenced by distant species if long chains of effects are buffered in complex webs (Strong 1992; Schoener 1993; Polis & Strong 1996). Here we address

these hypotheses by simulating keystone removal experiments in communities that are progressively scaled up from simple systems of four to seven species to 32 species networks with up to 195 trophic interactions.

MATERIALS AND METHODS

Population and resource dynamics

We use a bioenergetic consumer–resource model for the species’ trophic interactions (Yodzis & Innes 1992; McCann *et al.* 1998; Brose *et al.* 2003; Williams & Martinez 2004b) that describes the biomass density changes over time *t* in an *n*-species system by

$$B'_i(t) = G_i(\bar{R}) - x_i B_i(t) + \sum_{j=1}^n x_j y_{ij} \alpha_{ij} F_{ij}(\bar{B}) B_i(t) - x_j y_{ji} \alpha_{ji} F_{ji}(\bar{B}) B_j(t) / e_{ji} \tag{1}$$

where $G_i(\bar{R})$ describes the growth of producer species; x_i is the mass-specific metabolic rate; y_{ij} is species *i*’s maximum ingestion rate of resource *j* per unit metabolic rate of species *i*; α_{ij} is species *i*’s per capita rate of consuming species *j*, which is equal the fraction of resource *j* in the diet of consumer *i* when all *i*’s resources are equally abundant and is normalized to one for consumers and zero for producers, and e_{ji} is the biomass conversion efficiency of species *j* consuming *i*. The flow of biomass from resource *j* to consumer *i* follows a type II functional response (Holling 1959):

$$F_{ij}(\bar{B}) = \frac{B_j(t)}{\sum_{k=1}^n \alpha_{ik} B_k(t) + B_{0ji}} \tag{2}$$

where B_{0ji} is the half saturation density. In contrast to the original model (Yodzis & Innes 1992), the producer species’ growth follows a well-known model of shared resource consumption by plants:

$$G_i(\bar{R}) = r_i \text{MIN} \left(\frac{R_1}{K_{1i} + R_1}, \frac{R_2}{K_{2i} + R_2} \right) B_i(t) \tag{3}$$

that depends on the concentrations of two limiting physical resources R_l (Tilman 1977; Huisman & Weissing 1999). In eqn 3, r_i is the maximum growth rate of species *i* that is non-zero only for producer species, K_{li} is the half saturation constant for resource *l*, and MIN is the minimum operator, which causes the most limiting resource to determine producers’ growth rates. The variation of resource *l*’s density with time $[R'_l(t)]$ is given by

$$R'_l(t) = D(S_l - R_l) - \sum_{i=1}^n [c_{li} G_i(R)] \tag{4}$$

where c_{li} is the content of resource *l* in species *i*, D is the system’s turnover rate, S_l is the supply rate of resource *l*. Note that we did not correlate the species’ loss rates to the system turnover, which assumes that species are not passively drifting out of the system. Based on previous empirical estimates (Yodzis & Innes 1992), we use parameter values meant to characterize invertebrate communities ($y_{ij} = 10$, $e_{ji} = 0.45$ for herbivores and $e_{ji} = 0.85$ for carnivores, $B_{0ji} = 0.5$). We assume resource–consumer body size ratios, L , of 0.1 (consumers are thus 10 times larger than the average body size of their resources). This value coincides with the mean over 13 101 invertebrate consumer–resource body size ratios in a global empirical data base (Brose *et al.* 2005). We calculate consumer metabolic rates by

$$x_i = d [L^{0.25}]^{T-1} \tag{5}$$

where d is a constant that equals 0.54 for invertebrates and T is the consumer’s trophic level. The parameters of the growth model are $D = 0.25$, $r_i = 1$,

$$K_{li} = \begin{pmatrix} 0.11 & 0.12 & 0.12 & 0.12 & 0.12 \\ 0.06 & 0.20 & 0.16 & 0.10 & 0.02 \end{pmatrix} \tag{6}$$

$$C_{li} = \begin{pmatrix} 1.0 & 1.0 & 1.0 & 1.0 & 1.0 \\ 0.5 & 0.5 & 0.5 & 0.5 & 0.5 \end{pmatrix} \tag{7}$$

where rows represent two resources and columns represent five producer species. The first resource, R_1 , is most needed by all producer species for their growth as indicated by the higher content in producers’ biomasses. As all producer species have similar r_i and x_i , species 1 with the lowest K_{li} consumes R_1 at the highest rate per unit biomass (hereafter, ‘*per capita*’) (Huisman & Weissing 1999). In a community of five producer species, D quickly competitively excludes the other four producer species, S_1 to S_4 , whereas the addition of an herbivore to each of the producer species promotes coexistence (Brose *et al.* in press). D and S_1 to S_4 are the competitively dominant and subordinate producers, respectively. Note that in the food-web simulations the producer species S_1 to S_4 are identical to columns two to five in (6) and (7). Resource supply rates, S , of 0.5, 1 and 2 are called low, intermediate and high, respectively.

Keystone effects and community structure

We used model communities consisting of a generalist keystone species, K , which preferentially consumes D as well as up to all four subordinates, S_1 – S_4 (Fig. 1). All of the producers consume two abiotic resources, and are consumed by up to 26 additional ‘non-keystone’ consumers, NK_n (Fig. 1). The generalist keystone K dedicated 90% of its

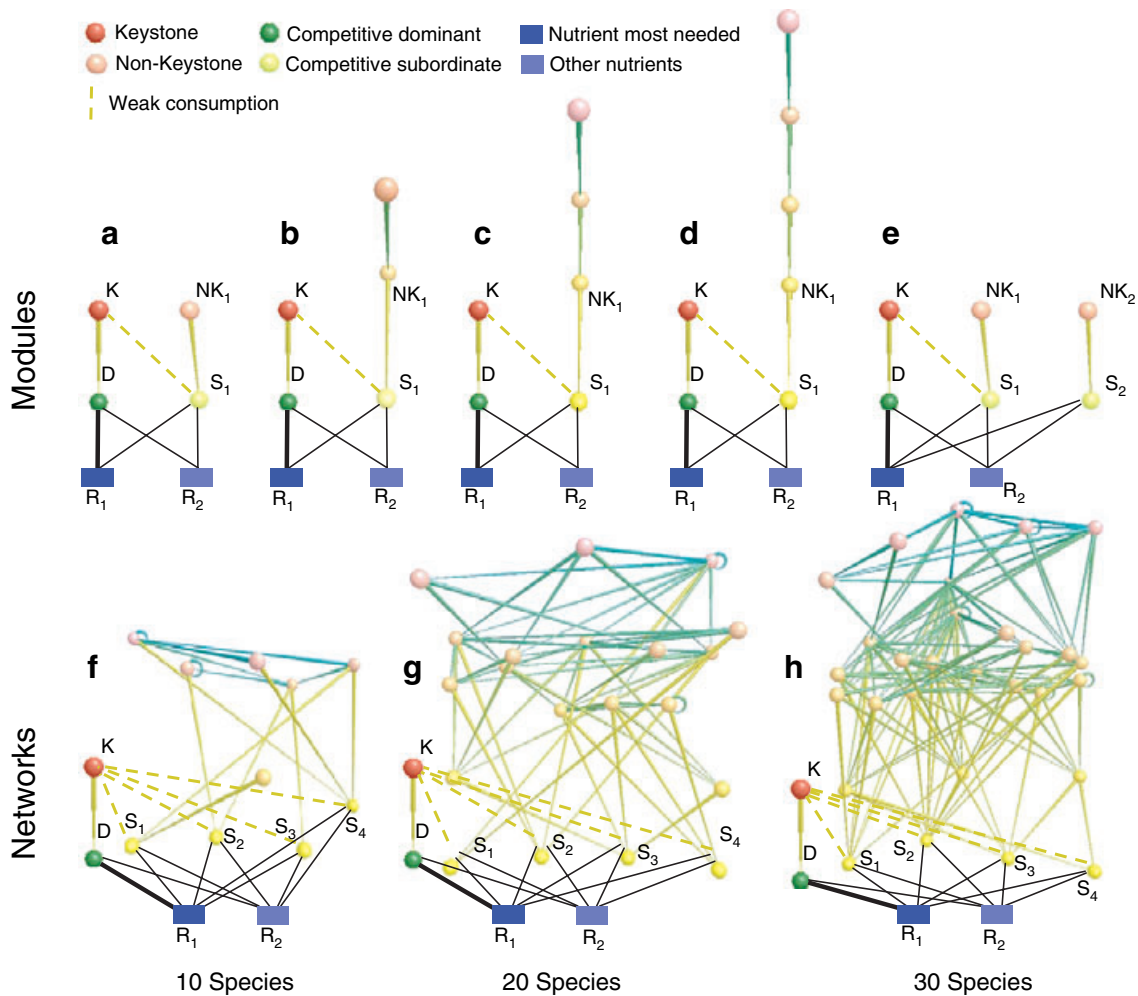


Figure 1 Model food webs with keystone (K) and non-keystone consumers (NK_n), a competitive dominant (D) and one to four subordinate producer species (S_1 – S_4). (a) Simple keystone module; (b–d) food chain on top of NK_1 ; (e) additional subordinate producer, S_2 , and its consumer NK_2 ; (f–h) complex peripheral food webs with 10 (f), 20 (g) and 30 (h) species and connectance = 0.15.

per capita consumption rate, α_{ij} , to D ($\alpha_{KD} = 0.9$) and the remaining 10% was evenly distributed amongst the coexisting S -species. For all other consumers, we assumed that *per capita* consumption rates are uniformly distributed amongst their resource species such that consumption is allocated according to the relative biomass of prey species.

For each simulation, we assigned random initial biomass densities to the populations, $B_i(0) = 0.05$ – 1 , and measured the mean biomass densities of each species between $t = 50$ and $t = 200$. Choosing biomass densities over this time period allows initial transient dynamics to settle down, captures the inherent variability among runs, and thus increases consistency with empirical studies. Simulations until $t = 2000$ indicated similar average biomass densities but smaller variation (results not shown). Model runs were replicated after keystone removal resulting in mean biomass

densities with and without keystone (B_i^+ and B_i^-). As the body masses of K , D and the S -species are constant across all simulations, changes in the biomass densities reflect variation in abundances. The strength of keystone effects on a given species was measured as the *per capita* log response ratio (Navarrete & Menge 1996; Navarrete 1996; Laska & Wootton 1998; Berlow *et al.* 1999; Hedges *et al.* 1999; Berlow *et al.* 2004):

$$IS = \log[(B_i^+ + 1)/(B_i^- + 1)]/(B_k + 1), \quad (8)$$

where B_k is the biomass density of the keystone species. Adding one to the biomass densities prevents very low keystone abundances from generating ‘artificially’ large variation in IS. Since the body sizes of the focal species (K , D , S_1 – S_4) did not vary, IS is directly proportional to *per capita* interaction strength.

We explored how this ‘keystone effect strength’, IS, on individual subordinate producer species (e.g. S_1) depends on factors that potentially constrain the latter’s growth such as ‘bottom-up’ physical resource supply, ‘top-down’ predation on S_1 by NK_1 , and ‘horizontal’ exploitation and ‘apparent’ (Holt 1977) competition with S_1 by additional basal species (S_n). Here, ‘predation’ generically refers to trophic consumption of organisms including parasitism, herbivory and filter feeding. We first address variation of IS in simple systems with few species (Fig. 1a–e).

We then compare these results to simulations where this simple keystone ‘module’ (*sensu* Paine 1980: Fig. 1a) is connected to food webs of varying (1) species richness (10, 20, and 30 species: Fig. 1f–h); (2) connectance, or the proportion of possible links that are realized (0.10, 0.15, and 0.20); and (3) resource supply (‘low’, ‘medium’, and ‘high’). For each combination of species richness, connectance, and resource supply, we use the Niche Model (Williams & Martinez 2000) to randomly generate 100 different ecologically realistic food-web networks that were constrained to have four basal species. The number of trophic interactions excluding the keystone interactions and the consumption of R_1 and R_2 in these networks ranges from 10 to 195. Each of these 2700 different food webs was simulated with and without K to quantify keystone effect strengths on D and each of the four subordinate basal species, S_1 to S_4 (Fig. 1f–h) under a wide range of conditions.

Explaining variation in keystone effects

In all the model scenarios described above, the parameters determining keystone consumption of D and S_n , as well as the competitive hierarchy among D and S_n , were held constant. This ensures that variation among scenarios in the keystone effect was because of variation in resource supply and a combination of structural attributes of the community. We used Regression Trees (De’ath & Fabricius 2000) to explore the relative importance of multiple attributes of network structure and resource supply in explaining variation in the keystone effect on each S_n . Regression Trees explain variation in the *per capita* keystone interaction strength by repeatedly splitting the data (starting with 2700 observations) into more homogeneous groups, using combinations of explanatory variables that can be both discrete (e.g. resource supply) and continuous (e.g. mean biomass of competitors). Unlike multiple linear regressions, Regression Trees are flexible analytical methods which are robust to non-normally distributed data, non-linear relationships, and high-order interactions (De’ath & Fabricius 2000).

To explore what aspects of web structure best explain variation in the keystone effect strength, for each of the 2700 simulated food webs, we calculated several global web

structure variables: species richness, connectance, the number of top species (Top Spp), the fraction of omnivores (Omnivory), the number of links from top to intermediate (T-I), top to basal (T-B) and amongst intermediate species (I-I), the standard deviations of species’ generality (SD Gen, or the standard deviation of the number of prey species consumed by each consumer), vulnerability (SD Vuln, or the standard deviation of the number of predator species that consume each resource), and connectivity (SD Links, or the standard deviation of the total number of consumer and resource species connected to each species), the food web’s mean prey averaged trophic level (Mean TL; Williams & Martinez 2004a), cluster coefficient (Clust Coeff; Williams *et al.* 2002), and the maximum length of the shortest chain between each species and a basal species (Max Chain). We chose these global predictors from a larger set of commonly used structural food web attributes (Dunne *et al.* 2004) by omitting predictors that were highly correlated with (> 0.75 or < -0.75 Pearson product-moment correlation coefficient), and therefore statistically dependent on, the selected 13 predictors. To explore the relative contribution of ‘local’ vs. more ‘distant’ effects of network structure on keystone effect strength, we also calculated, for each of the S -species, the number (no. Spp), biomass density (Biom), vulnerability (Vuln, mean number of predators), and generality (Gen, mean number of prey) of primary (1°), secondary (2°), and tertiary (3°) consumer species.

We ran separate trees for each S -species using the following explanatory variables that fall into seven categories: (1) bottom-up: resource supply; (2) keystone biomass; (3) competition: mean biomass of all producer (D and all S_n) species with K present; (4) one degree predation: no. Spp, Biom, Vuln, Gen of the primary consumers; (5) two degree predation: no. Spp, Biom, Vuln, Gen of the secondary consumers; (6) three degree predation: no. Spp, Biom, Vuln, Gen of the tertiary consumers; and (7) global web structure: the 13 topological attributes described above. For each S_n , the data were split until additional splits explained $< 1\%$ of the residual variation in keystone effect strength. From the Regression Tree results, we then selected three of the best predictor variables (both categorical and continuous) for an Analysis of Covariance (ANCOVA). We then used the Akaike Information Criteria (AIC) to select the simplest model that best explained variation in keystone effects across all the conditions examined.

RESULTS

Keystone effects in simple systems

We start with a simple four-species two-trophic-level ‘keystone module’ (*sensu* Paine 1980: Fig. 1a). In the absence of K , D eventually competitively excludes S_1 which

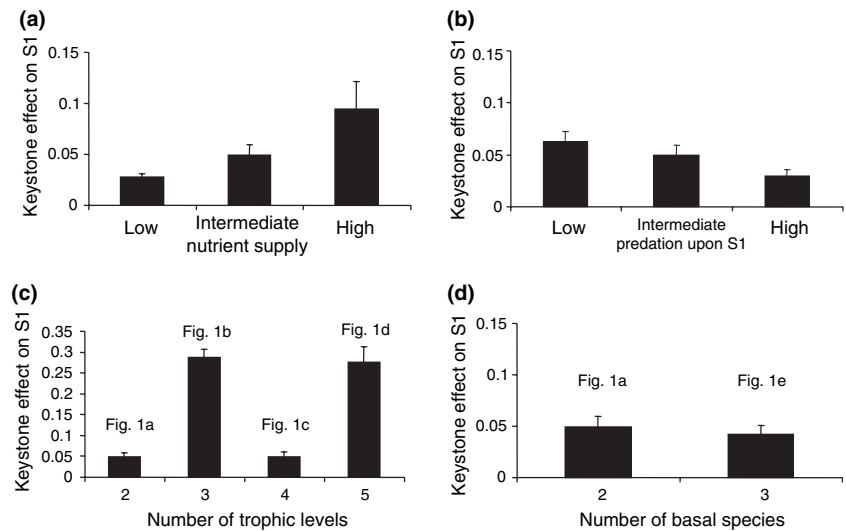


Figure 2 Keystone effects in modules (Fig. 1a–e) on the subordinate producer S_1 (Fig. 1) as a function of (a) resource supply; (b) predation on S_1 ; (c) the number of trophic levels in a food chain on top of S_1 (Fig. 1b–d); and (d) the number of producer species in the network (Fig. 1a vs. Fig. 1e).

consequently starves and excludes NK_1 . In all simulations, the presence of K facilitates coexistence of all four species. Here, a ‘keystone effect’ is defined as K ’s strong indirect positive effect on S_1 (and consequently NK_1 as well) because of K ’s strongly negative direct effect on D . Increasing resource supply to this simple module strengthens the keystone effect on S_1 (Fig. 2a, ANOVA $P < 0.001$) by disproportionately increasing S_1 ’s biomass when K is present. Increasing the maximum consumption rate of NK_1 on S_1 weakens the keystone effect on S_1 (Fig. 2b, ANOVA $P < 0.001$) by limiting how much S_1 can increase in biomass when K is present. Addition of the secondary consumer of NK_1 (Fig. 1b) lowers predation upon S_1 and strengthens the keystone effect relative to that in the 2-level system in Fig. 1a (Fig. 2c). Similarly, tertiary and quaternary consumers (Fig. 1c,d) predictably increase and decrease the predation on S_1 through trophic cascades thus leading to weaker and stronger keystone effects, respectively (Fig. 2c, ANOVA $P < 0.001$). We increase competition amongst the producer species by adding a producer species (S_2) with its own specialist consumer (NK_2) to the keystone module (Fig. 1e). The resulting increase in competition on S_1 slightly but significantly (ANOVA $P < 0.001$) weakens the keystone effect on S_1 again by constraining how much K can facilitate S_1 by consuming D (Fig. 2d). Overall, in the simpler systems: (1) the strength of K ’s negative effect on D is highly correlated with K ’s indirect positive effect on S_1 ($r = -0.825$, $P < 0.001$); (2) negative constraints on S_1 growth – by resource depletion, predation, or competition – consistently weaken the keystone effect; (3) large variation in K ’s effect on S_1 (CV = 97%) occurs in simple modules of four to seven species (Fig. 1a–e) despite constant parameters describing the fundamental characteristics of K , D , or S_1 ; and (4) species up to four links away from S_1 greatly modify K ’s effect on S_1 .

Keystone effects in complex food webs

Similar to the simpler systems, K promotes coexistence of all four producers (S_{1-4}) and the consumers that depend on them in 97% of the complex network simulations. Of the remaining 3%, never more than one S_n goes extinct in any given run while K is present. In the absence of K , D always excludes all S_n and their consumers. Despite this remarkable consistency in keystone-facilitated coexistence, K ’s effect on S_1 is highly variable (CV = 97% across all 2700 simulations). This variability in the more complex 10–30 species networks is surprisingly similar to variability in the simpler four to seven species modules and variability in K ’s effect on any S_n in the complex networks does not systematically change with either species richness or connectance. Similar to the simpler systems, the strength of K ’s negative effects on D in the complex networks is largely determined by resource supply and K ’s density (ANCOVA model with resource supply and K biomass: $R^2 = 0.97$, $P < 0.001$). However, much less of the variation of K ’s effects on any S_n in the complex networks is explained by these variables (ANCOVA with resource supply, K biomass, and their interaction: $R^2 = 0.08–0.12$ for S_{1-4}).

The Regression Trees contained 17–24 splits and explained on average 60% of the total variation in *per capita* keystone effect strength on any given S_n . The global web descriptors such as species richness and connectance explain essentially none of the variation in K ’s effects on any S_n (Fig. 3a). Instead, variation in K ’s effects on any given S_n is best explained by factors local to S_n . In general, K ’s effect on any given S_n strengthens with increasing resources, decreasing biomass of competitors, decreasing predation of S_n by primary consumers, and increasing predation of primary consumers by secondary consumers of S_n (Fig. 3a). While all of the primary predation predictors are important, only one

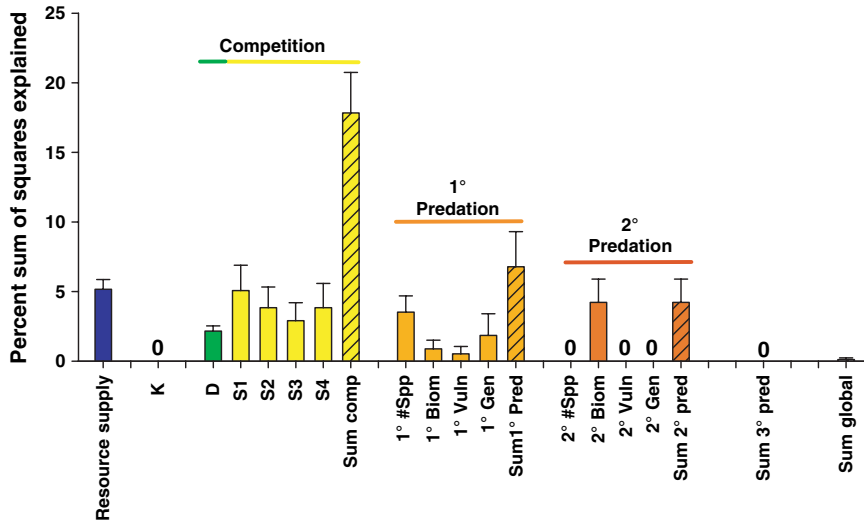


Figure 3 Mean (\pm SE) per cent variation in keystone effect strength explained by each predictor variable included in the four Regression Trees (one for each of four S_n species). Hatched bars indicate the sum of the variation explained by each group of predictors. Bar colours indicate the types of nodes in Fig. 1 associated with the predictor variables. In all cases where a predictor was selected for multiple splits, the sign of the relationship stayed the same. Predictors that were positively correlated with keystone effect strength when selected for a split included: resource supply, 1° Biom, 1° Vuln, 1° Gen, and 2° Biom (i.e. the biomass, vulnerability, and generality of primary consumers, and the biomass of secondary consumers of S_1 , respectively). Predictors that were negatively correlated with keystone effect strength when selected for a split included 1° no. Spp (i.e. the number of primary consumers of S_1) and the biomasses of all five competitors (D and S_{1-4}).

secondary predictor, the biomass of the secondary consumers, is important (Fig. 3a). Predictors associated with tertiary level consumers do not explain any of the variation in K 's effect on any S_n .

These results suggest that the many potential community attributes that might predict variation in keystone effects can be reduced a very important and small subset local to the target S_n . These predictors fall into three categories of local constraints on S_n growth: (1) predation intensity on S_n (i.e. 'top down' constraints); (2) exploitative or 'apparent' competition with S_n (i.e. 'horizontal' constraints); and (3) and resource supply (i.e. 'bottom up' constraints). The large number of splits (17–24) in the Regression Trees makes it difficult to characterize how these key variables interact to regulate the strength of K 's effect. To explore this interaction, we collapsed the 10 most important explanatory variables into three functionally distinct predictors: (1) a compound indicator of local top-down pressure on S_n (*Predation*); (2) a compound indicator of local horizontal constraints on S_n (*Competition*); and (3) direct bottom-up constraints on S_n (*Resource Supply*). *Predation* on S_n equals 1° Spp/(1°Gen \times 2°Biom). Thus, *Predation* is high when S_n has many direct, specialist consumers that are not themselves limited by a high biomass of secondary consumers. *Competition* equals the total biomass density of competing producers that share resources (D and all non-target S_n). *Predation* is uncorrelated with both *Competition*, and *Resource Supply* for all four S_n ($R^2 < 0.05$). *Competition* includes

exploitative and apparent competition and is thus not a simple surrogate of *Resource Supply*, in fact the two were only weakly correlated ($R^2 < 0.49$ for every S_n).

Together *Predation*, *Competition*, *Resource Supply*, and their interactions explain on average 71% of the variation in keystone effect strengths on a given S_n (ANCOVA's, $P < 0.0001$ for all effects and for each S_n). Similar to simpler systems, negative constraints on S_n by *Predation*, *Competition*, or low *Resource Supply* decrease keystone effect strength in complex systems (Fig. 4a,b). Release from any of these individual constraints on S_n growth leads to a large increase in the variance of keystone effects. *Predation* and *Competition* define triangular 'envelopes' of possible keystone effect strengths, with the size of the envelope generally increasing with increasing *Resource Supply* (Fig. 4a,b). Thus each separate predictor alone explains on average $< 14\%$ of the variation in the keystone effects on any given S_n (mean $R^2 = 0.11, 0.14,$ and 0.07 for the independent effects of *Predation*, *Competition*, and *Resource Supply*, respectively). Rather than explaining the size of the effect, these single independent predictors better explain the upper bound, while the interplay of the predictors best explains the individual effects (Fig. 4a,b).

A similarly triangular envelope of possible keystone effects on S_n is defined by the strengths of K 's suppression of D (Fig. 4c). Strong suppression of D allows for potentially strong positive keystone effects on S_n , but the realized magnitude of K 's effect on S_n depends on *Predation*

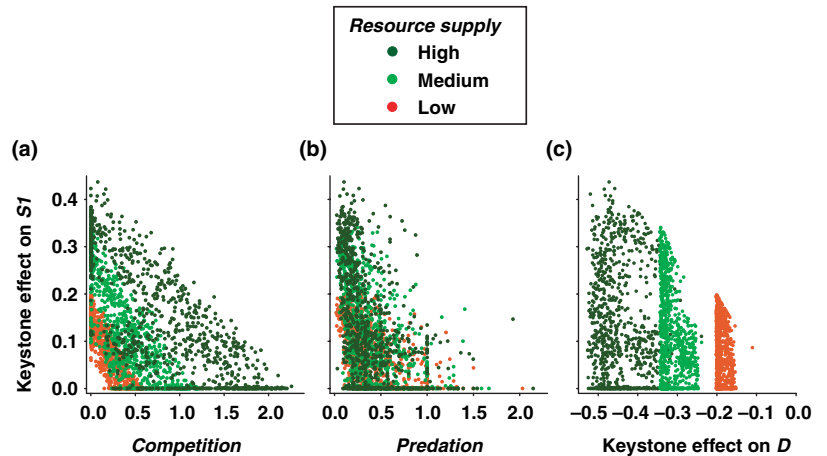


Figure 4 The relationships between keystone effects on S_1 and (a) competition, (b) Predation, and (c) keystone suppression of D . The patterns for S_{2-4} (not shown) were qualitatively identical to those for S_1 .

and *Competition*. In contrast to the simpler systems, K 's suppression of D is only weakly correlated with indirect positive effects of K on S_n in the complex systems (Fig. 4c, $r = -0.285$, $P < 0.001$).

DISCUSSION

Our results demonstrate how resource supply and peripheral network structure may systematically influence the magnitude of a classic keystone effect that involves the facilitation of competitively subordinate basal species (S_n) through keystone (K) consumption of the competitive dominant (D) (Paine 1969; Morin 1983; Brown & Heske 1990; Grover 1994; Power *et al.* 1996; Davic 2003). The simulations predict stronger keystone effects on a specific basal species when it is not constrained by predation, competition, or resource availability. Any one of these constraints on the target S_n species has the potential to weaken the keystone effect or to decouple keystone facilitation of S_n species from the direct keystone suppression of the competitive dominant (D). Our approach assumes: (1) similar type II functional responses for all consumers; (2) competition for limiting resources amongst the basal species; (3) basal species growth that depends on two limiting resources; (4) consumers that are 10 times larger than their resources; and (5) a generalist keystone consumer that dedicates 90% of its *per capita* consumption rate to D . However, qualitatively similar results not shown here were obtained when simulating (1) type III functional responses; (2) logistically growing basal species that compete via linear Lotka-Volterra competition terms – which might be considered more representative of animal basal species competing for space (Paine 1969); (3) up to five limiting resources; (4) predator–prey body size ratios that ranged from 1 : 1 to 1000 : 1, and that span the naturally occurring range in predator–prey body size ratios (Brose *et al.* 2005); and (5) keystone species that dedicate between 100% and 60% of its *per capita* consumption rate to D . Taken

together, our findings suggest remarkably robust predictions that deserve field tests quantifying the effects of keystone species on both dominant and subordinate species across natural or manipulated variation in productivity and web structure surrounding the target species.

Equilibrium-based analyses of simple systems have shown that specialized consumers that control the competitively dominant basal species facilitate coexistence of competitively subordinate basal species (Grover 1994). Generalist consumers behave similarly as long as basal species trade resource exploitation for consumer tolerance abilities (Holt *et al.* 1994; Leibold 1996). Under non-equilibrium conditions, multiple basal species can coexist on few resources without keystone consumers (Huisman & Weissing 1999; Huisman *et al.* 2001) but this coexistence breaks down when basal species exhibit a strong competitive hierarchy (Brose *et al.* in press). Our non-equilibrium approach corroborates the equilibrium-based conclusions on keystone mediated coexistence in simple systems. Beyond corroboration, we have extended these studies by scaling up to much more complex systems and quantifying how the broader ecological context may regulate the presence and strength of keystone interactions.

Species up to four links away from our target S_n radically alter the keystone effect within our simpler systems with four to seven species. This suggests that consumers several degrees (links) away from S_n can greatly modify keystone effects through trophic cascades (Oksanen *et al.* 1981; Estes *et al.* 1998). This variability in keystone effects observed in simple modules (Fig. 1b–e), supports the idea that keystone effects could be essentially indeterminate in more realistically complex networks (Yodzis 2000). The ecological realization of this indeterminate potential depends on the actual realization of strong long-chain effects in complex networks.

In contrast to the suggestions both from simpler systems and from general complex systems analysis, our results

demonstrate that increasing network complexity (both size and connectance) *per se* does not inherently make the prediction of strong keystone effects more complicated. When the simple four-species keystone module is connected to 32-species webs with up to 195 links, distant influences, such as long trophic cascades, appear to be of minor importance. This lack of ‘distant’ influences could be because of either dampening effects in long chains (Schoener 1993; Menge 1995), or to multiple pathways of effects with opposite sign cancelling each other out (Berlow 1999). Thus in contrast to the simpler systems, trophic cascades of more than two links appear to be buffered by more complex network structures in realistic food webs (Strong 1992; Schoener 1993; Polis & Strong 1996). These results are consistent with other theoretical studies demonstrating that additional links can act to stabilize the dynamics of more complex networks (McCann *et al.* 1998; Fussmann & Heber 2002).

Thus, what is probable appears to be a small subset of what is possible, and most of the large variability in keystone effects may be explained by a measurable, local sphere of influence around the focal interaction. While quantifying the consumption intensity on *D* is critical to establishing the potential for a strong keystone effect (Paine 1969, 1992; Menge *et al.* 1994; Sanford 1999; Sala & Graham 2002; Grantham *et al.* 2004), our simulations indicate that this direct suppression can be decoupled from the indirect facilitation of competitively subordinate species in complex systems. The community context of the target species (e.g. S_n in our simulations) determines whether this potential is realized (Navarrete & Castilla 2003) – a condition consistent with the troublesome context-dependency of keystone effects observed in naturally complex communities (Brown & Heske 1990; Power *et al.* 1996). However, our simulations suggest that the most relevant community context may be a measurable set of ‘bottom-up’, ‘top-down’, and ‘horizontal’ constraints within one or two degrees of separation from target species of interest. More generally, our findings suggest that potentially indeterminate effects of species loss in complex ecological networks (Yodzis 2000) may be reduced to, and explained by, surprisingly simple ecosystem attributes.

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