



The context dependency of species keystone status during food web disassembly



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ABSTRACT

Global change continues to push individual species towards extinction and in many cases these species cannot be expected to disappear silently, without a trace, from the communities in which they reside. Importantly, the loss of certain species can trigger a cascade of secondary extinctions, resulting in further degradation of a system with potential effects on ecosystem functioning. It is thus crucial to better our understanding of the types of species which, if lost, will affect community structure the most, because in this context they are analogous to keystone species. Here, using a dynamical approach and simulating species loss in model communities, we study whether the importance of species changes as the structure of the food web changes by analyzing the potential importance of 11 species traits during food web collapse following simulated extinctions. We find that the keystone status of species traits is context dependent, with the identity of the most important trait changing during food web collapse. The relative importance of two trait categories tend to be inversely related, with body size based traits being important in intact to moderately degraded webs and interaction strength based species traits being important in highly collapsed food webs. The results of our study furthermore suggest that the response of communities to small and large perturbations may be related in the sense that the same kinds of species are important in both situations.

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1. Introduction

Global change such as habitat loss, overexploitation, invasive species and climate change have forced species to extinction and continue to do so at an accelerating rate (Barnosky et al., 2011; Wake and Vredenburg, 2008). This rapid loss of biodiversity is expected to affect the structure and functioning of ecosystems (Hooper et al., 2012; Isbell et al., 2011) and their ability to recover from future perturbations (Ives and Cardinale, 2004; Myers and Worm, 2003). Furthermore, due to the interdependencies among species, the loss of one can change predation pressure and/or resource availability for others and thus, conditions for coexistence among species within a community. The consequence of this can be additional species loss due to so called secondary extinctions (Borrvall and Ebenman, 2006; Borrvall et al., 2000; Colwell et al., 2012; Estes and Palmisano, 1974; Estes et al., 2011; Ives and Carpenter, 2007; Sanders et al., 2013; Terborgh et al., 2001).

The response of ecological communities – in terms of the number of secondary extinctions – to the primary loss of one species depends in an intricate way on factors such as the structure of the community (e.g. network topology, connectance, proportion of species at different trophic levels, Dunne and Williams, 2009; Dunne et al., 2002; Mikkelsen, 1993; Thébault et al., 2007), species dynamics (Curtsdotter et al., 2011; Dunne et al., 2002; Ebenman and Jonsson, 2005), as well as on properties of the species going extinct (Berg et al., 2015; de Visser et al., 2011; Jacob et al., 2011; Pimm, 1980; Sole and Montoya, 2001; Srinivasan et al., 2007; Staniczenko et al., 2010). Theoretical studies of species loss from food webs suggest that highly connected species, top predators and/or trophically unique species could reflect potential keystone roles or positions within food webs, affecting community persistence (Borrvall and Ebenman, 2006; Eklöf and Ebenman, 2006; Petchey et al., 2008) in the sense that loss of such species tend to cause many secondary extinctions. Empirical studies, although not explicitly studying the number of secondary extinctions, support some of these suggestions (e.g. showing how the loss of top predators can result in mesopredator release and radical changes in species composition, Beschta and Ripple, 2009; Estes et al., 2011; Reisewitz et al., 2006; Terborgh et al., 2001), while indicating that plants, parasites and species

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at intermediate trophic levels can be keystone species too (Cottee-Jones and Whittaker, 2012). Previous theoretical studies have usually simulated the loss of just one species from an initial web topology and have to the best of our knowledge never quantified the effects of subsequent species extinctions, either applied randomly or according to some trait value. Consequently, they have only identified important species for a particular community state, that is, a relatively intact community. As species are sequentially lost from food webs the structure of the community is altered which could affect the stability and behavior of the remaining community. Kaneryd et al. (2012), for example, found that communities affected by extinctions in the past are more robust against further species loss, compared to communities that have not been subjected to previous extinctions. They suggested that this finding (also supported by Jonsson et al., 2015) occurred because the loss of species tended to clean out fragile interaction patterns present in the intact community. In contrast, structures promoting robustness, such as asymmetric links connecting specialist species to generalist species, are more likely to be preserved during the disassembly process (Kaneryd et al., 2012). The changes in food web topology and interaction patterns that occur during food web disassembly lead to a range of different ecological contexts by changing the ecological milieu in which species are embedded. This could alter the role of a focal species from one context to another, as some of its traits change as a function of web structure (e.g., as species are lost the trophic position or linkage density of remaining species can change). If traits such as trophic position and linkage density determine the 'keystoneness' of a species then the role of a species might change as the web collapses around them. For practical and ethical reasons this possibility is difficult to address empirically, but also from a theoretical point of view this has yet not been given thorough attention in a realistic setting.

By successively deleting species from a food web model the response of the system can be monitored as it gradually collapses. Previous studies of repeated species removals – focused on topological descriptions of food webs with no dynamics – have identified ecological communities to be robust against the sequential removal of specialist species or species with large body size, low abundance and/or high trophic position, but very sensitive to the sequential removal of generalist species or species close to the bottom of food webs (Bascompte and Stouffer, 2009; de Visser et al., 2011; Dunne et al., 2002; Jacob et al., 2011; Sole and Montoya, 2001; Srinivasan et al., 2007). In these topological studies species dynamics are ignored and a species only goes secondarily extinct if it loses its entire set of prey species. These studies have also not considered species removals beyond 50% of the original number of species in a web. However, because species dynamics are important and can affect conclusions regarding the effects of species extinctions in food webs (Berg et al., 2015; Curtsdotter et al., 2011), and because extinctions have been shown to affect the response of food webs to further species loss (Kaneryd et al., 2012), there is a need to know more about important species traits at different stages during web collapse and when indirect species interactions are taken into account. We here use a dynamical approach and remove species randomly from model food webs until no species remain in the community – reflecting the range of ecological contexts that occur from an intact to a fully collapsed community – and investigate whether traits associated with the keystone status of species are consistently the same during different degrees of food web collapse. More specifically, we focus on the following questions: i) which species traits best explain variation in the secondary extinction rate (proportion of species present in a web that goes secondarily extinct after a primary extinction) during different phases of web collapse, ii) does the identity of important traits change as the structure of the food web becomes degraded, iii) does initial web connectance affect the explanatory power of species traits, iv) are food webs more sensitive to species loss during different phases of food web collapse, and v) are species

identified as keystone species using community sensitivity analysis (Berg et al., 2011) the same species that trigger many secondary extinctions when lost through extinction, i.e., does the community level effect of a small perturbation to a species correlate with the response of a large perturbation to the same species?

2. Methods

2.1. Food web structure and dynamics

We use a set of 100 model food webs, each containing 50 species distributed across multiple trophic levels. These webs were generated using a sequential community assembly algorithm where predator–prey body size ratios are used to predict the existence of trophic interactions (Säterberg et al., 2013). The resulting structure of these food webs mimics' structural properties (e.g. connectance, generality, vulnerability, omnivory, length of food-chains) found in empirical systems (see Table S1 for a comparison with real food web data). The set of 100 webs have been used in previous studies (Berg et al., 2015; Jonsson et al., 2015; Säterberg et al., 2013) but not for the purpose described here (see Supplementary Methods for a summary of the relevant steps of the algorithm, and Säterberg et al., 2013 for full details).

2.2. Simulations of web disassembly

All species initially live in a stable deterministic environment with starting densities given by the equilibrium point of the system with all 50 species present. These equilibrium communities are then subjected to species removal and hence, all secondary extinctions will be directly or indirectly due to the primarily removed species. The first species, selected at random, was removed from the community and the dynamical response of the species in the remaining community (described by a generalized Lotka–Volterra model, Supplementary Methods Eq. S2) was monitored. This primary extinction may result in other species going secondarily extinct, or the system may oscillate or settle down to a new equilibrium but without any secondary extinctions. If species abundances after a species deletion (primary extinction) fell below a predefined extinction threshold, here 0.1% of its equilibrium abundance, they were removed from the system and recorded as secondary extinctions, after which the simulation continued. The biological rationale for this was that a 99.9% decline in a species' abundance was likely to reflect a trajectory towards extinction from which a species would not recover. If no (new) secondary extinctions occurred for a period of 10,000 time steps after a species deletion (or the most recent secondary extinction) the simulation was halted and the new equilibrium point was analyzed. If all remaining species were within a distance of 10% of a new equilibrium (corresponding to the time averaged abundance in the case of oscillations, Hofbauer and Sigmund, 1988) and this equilibrium was feasible and locally stable then the system was considered to be persistent and the simulation was terminated and the next, randomly selected species, was deleted. This process continued until there were no species left to remove. Two sets of random deletion sequences were simulated, one where only consumer species were allowed to go primarily extinct, i.e., basal species could only go secondarily extinct, and another where any species could be directly removed. One hundred replicate random removal sequences were performed on each food web for each of the two deletion sequence scenarios (any species and only consumer species respectively), where one replicate represents random deletions of species until there were no species left to remove.

Loss of basal species can in our models, all else being equal (such as the number of consumer species, interaction strengths to other species etc.), be expected to be more devastating (lead to more secondary extinctions) than the loss of consumer species, simply because it decreases the total energy input into the system. Thus, to study the downright

effect of species traits on secondary extinctions (and not have it confounded by a primary producer effect), we focus below on results from simulations where only consumer species could be deleted. Results from simulations where basal species could be removed are however described and discussed briefly in the main text and are presented in full in the Supplementary material.

2.3. Species traits

The number of secondary extinctions that followed after each random species removal was correlated to the characteristics of the removed species. We focus on 11 “species traits” that can be extracted from our models and analyze whether these traits can be used as indicators of the importance of species for community structure during different degrees of food web collapse. The traits included are: 1) body size, 2) numerical abundance, 3) biomass abundance, 4) trophic position, 5) generality (or in-degree, i.e., the number of prey of a species), 6) vulnerability (or out-degree, i.e. the number of predators of a species), 7) connectivity (or total degree, i.e. the number prey and predators of a species), 8) predation pressure (π_j), a measure of how strongly a consumer species j interacts with its entire set of resource species (R_j), defined as the sum of its per capita trophic interactions with its prey (α_{ij} , Supplementary Methods Eqs. S2–S3): $\pi_j = \sum_{i \in R_j} \alpha_{ij}$, 9) predation

stress (σ_i), a measure of how exposed a resource species i is to predation from its entire set of consumer species (C_i), defined as the sum of its trophic interactions with its predators: $\sigma_i = \sum_{j \in C_i} \alpha_{ij}$, 10) sensitivity of equilibrium abundances (S_x) and 11) sensitivity of resilience (S_λ). The two sensitivity measures (10 and 11) indicate how sensitive community structure (distribution of species equilibrium abundances) and community resilience (rate of return after a temporary perturbation) is to a small permanent change in the mortality rate (b) of species k and is given by: $S_x(b_k) = \sum_i |\gamma_{ik}|$ and $S_\lambda(b_k) = \text{Re} \sum_{i,j} \frac{\bar{v}_i w_j}{\langle \mathbf{w}, \mathbf{v} \rangle} \alpha_{ij} \gamma_{ik}$, respectively

(see Berg et al., 2011). Here α_{ij} is an element (per capita interaction strength, Supplementary Methods Eqs. S2–S4) of the interaction matrix \mathbf{A} , γ_{ik} is element ik in the inverse interaction matrix (\mathbf{A}^{-1}), \mathbf{v} and \mathbf{w} are the left and right eigenvectors (corresponding to the dominant eigenvalue of the Jacobian matrix), v_i and w_j are elements i and j of the respective vectors, \bar{v}_i is the complex conjugate of v_i , and $\langle \mathbf{w}, \mathbf{v} \rangle$ is the scalar product of \mathbf{w} and \mathbf{v} . All species traits, except body size, can change when the food webs become degraded through primary and secondary extinctions, and the ecological context changes. Therefore, with each new species deletion the traits of species were updated.

2.4. Statistical analyses

We analyzed whether the extent of secondary extinctions resulting from primary species extinctions could be explained by different species traits as the food webs sequentially collapsed. Four disassembly groups (DG_x , representing different levels of food web collapse) were considered in the analysis below: $DG_1 = 75$ –100% of the initial number of species remaining, $DG_2 = 50$ –75% of species remaining, $DG_3 = 25$ –50% of species remaining and $DG_4 = 0$ –25% of species remaining. Furthermore, we considered four treatment groups for food web connectance ($C = L/N^2$, where L is the initial number of trophic links in the food web and $N = 50$ is the number of species) when analyzing the response of species loss: $C_1 = 0.084$ –0.12 ($n = 31$ food webs), $C_2 = 0.12$ –0.14 ($n = 32$ food webs), $C_3 = 0.14$ –0.16 ($n = 27$ food webs) and $C_4 = 0.16$ –0.2 ($n = 10$ food webs). These groups were constructed to include roughly the same number of webs (although we acknowledge that the sample size for C_4 is significantly smaller than for the other groups).

Regression tree analysis (De'ath and Fabricius, 2000) was used to analyze the importance of traits within each treatment group

(combination of food web collapse (DG_1 – DG_4) and connectance group (C_1 – C_4), see above). We extracted the *explanatory power* of each of the different traits identified by the best tree (as well as the total explanatory power of all traits together), as the proportion of the total variance in secondary extinction rate that was explained by each trait (or all traits together). Furthermore, to assess the direction of any association between a species trait and the risk of secondary extinctions, i.e., whether a high trait value was associated with an increased or decreased secondary extinction rate, we first grouped all removed species into regularly spaced bin classes (based on trait value) and for each bin class calculated the geometric mean proportion of secondary extinctions that occurred when a species in this bin class was removed. Next, we correlated this geometric mean secondary extinction rate for species with a similar trait value to the average trait value of these species. Finally, to compare the average proportions of secondary extinctions among food webs with different degrees of food web collapse, a multiple comparison of the means was performed (using Tukey–Kramer criteria with a significance level of 0.05).

3. Results

In the following we focus on simulations where only consumer species could be deleted (see Section 2.2 above for motivation) and only briefly note results from simulations where basal species could be removed (all figures from simulations where basal species could be deleted can be found in the Supplementary material). In general, as the food webs collapsed we did not observe the appearance of isolated subunits of interacting species, rather, each food web held together as one interacting part (see Figs. 1 & S1 for two examples of the gradual collapse of a food web, as a result of primary and secondary extinctions, where basal species were not allowed to and could be deleted, respectively).

The route to total food web collapse is highly variable among food webs and replicates when viewed only as a function of the total number of primary extinctions (Fig. 2A). On average however, absolute species loss from communities (number of species, Fig. 2B) is high in rather intact webs, then slows down with increasing level of web collapse. Furthermore, the gradual decrease in the slope of the collapse trajectory (dotted line in Fig. 2A) implies that the extinction rate could be more or less constant during web collapse. This is corroborated by data on the average proportion of species going secondarily extinct in the different collapse groupings that show no clear trend (Fig. 2C).

3.1. Accounting for variation in secondary extinctions using individual species traits

Across all random removals, irrespective of the level of food web collapse and food web connectance, the studied species traits explained approximately 30% of the variation in secondary extinctions. However, when dividing the data into treatment groups (representing different degrees of food web collapse and food web connectance), the explanatory power of species traits was in general considerably higher, exceeding 50% for some combinations (Fig. 3B, D, F and H). Here, the total variation explained by species traits increased with connectance and there was a tendency for it to peak at intermediate levels of food web collapse.

The importance of individual species traits for explaining secondary extinctions and the direction of the association also varied, depending on the level of food web collapse and food web connectance (Fig. 3A, C, E and G, Table 1). Very broadly, body size and trophic position dominated strongly as important traits, with a high explanatory power in general and each being identified as the single most important trait in around one third of the treatment groups (4×4 combinations of degrees of food web collapse and food web connectance). Structural sensitivity, numerical abundance, predation stress and predation pressure followed as moderately important traits in general, being identified as

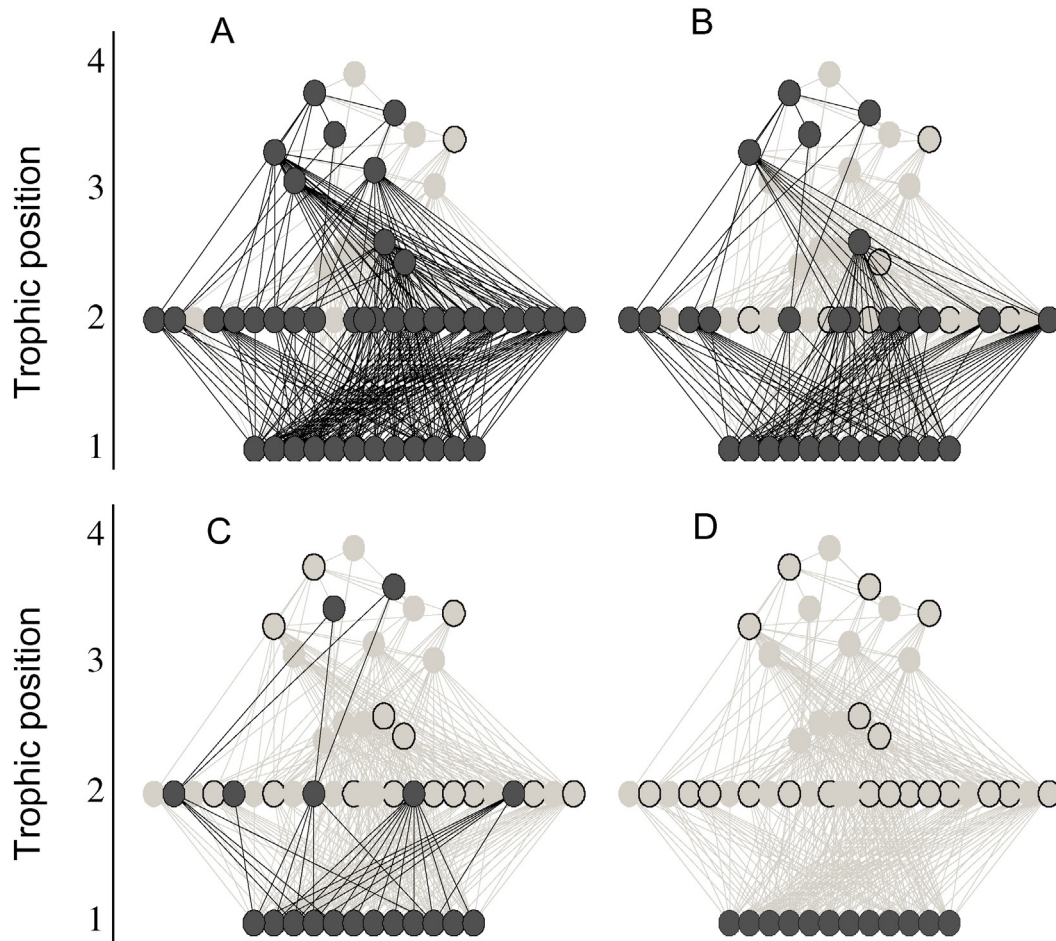


Fig. 1. Snapshots of food web structure during four stages of food web disassembly due to primary and secondary extinctions when basal species were not allowed to go primarily extinct. Dark shaded nodes and links denote extant species and interactions. Light shaded nodes with a black border denote species that have been removed (primary extinction) and light shaded nodes without a border and shaded links denote extinct species and their interactions. Fraction of remaining species: A) 41/50 (82%), B) 29/50 (58%), C) 19/50 (38%) and D) 12/50 (24%).

the single most important in a few cases. The other five traits (biomass abundance, generality, vulnerability, connectivity and dynamical

sensitivity) played a minor role in explaining variation in secondary extinctions.

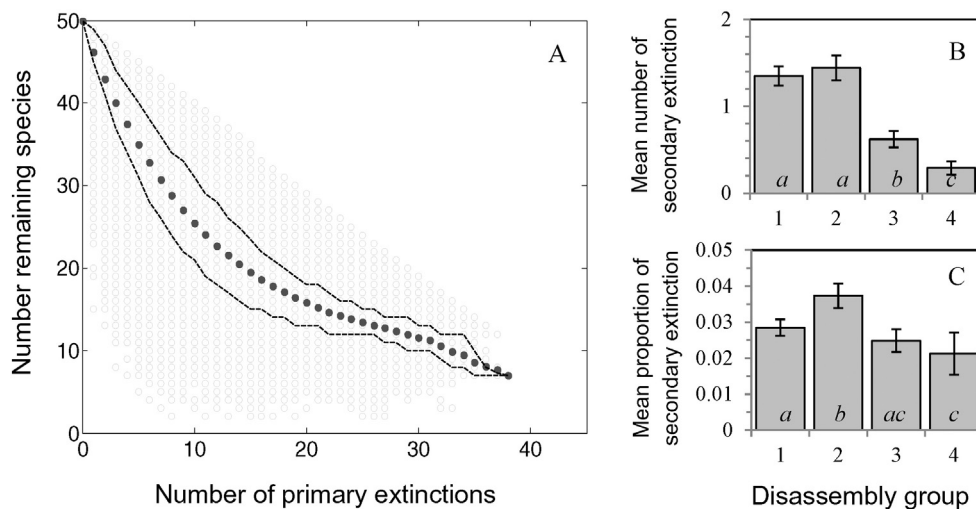


Fig. 2. (A) Decreasing web size (number of remaining species) with increasing number of forced primary extinctions (causing cascades of secondary extinctions) in model food webs where basal species were not allowed to be deleted. Light gray circles show the number of remaining species after each primary extinction, from all replicates and all food webs, and dark gray circles show the mean number of remaining species after each primary extinction. Dashed lines are the upper (75%) and lower (25%) percentiles respectively. Average number (B) and proportion (C) of secondary extinctions resulting from one random species removal in model food webs varying in the degree of disassembly (1 [75–100%], 2 [50–75%], 3 [25–50%] and 4 [0–25%] species remaining). Error bars show the 95% CI and letters within bars group treatments in each subplot that are not significantly different (at $P < 0.05$). There were significant differences in number ($F = 12.28$, $P < 0.0001$) and proportion ($F = 105.64$, $P < 0.0001$) of secondary extinctions among the different disassembly groups.

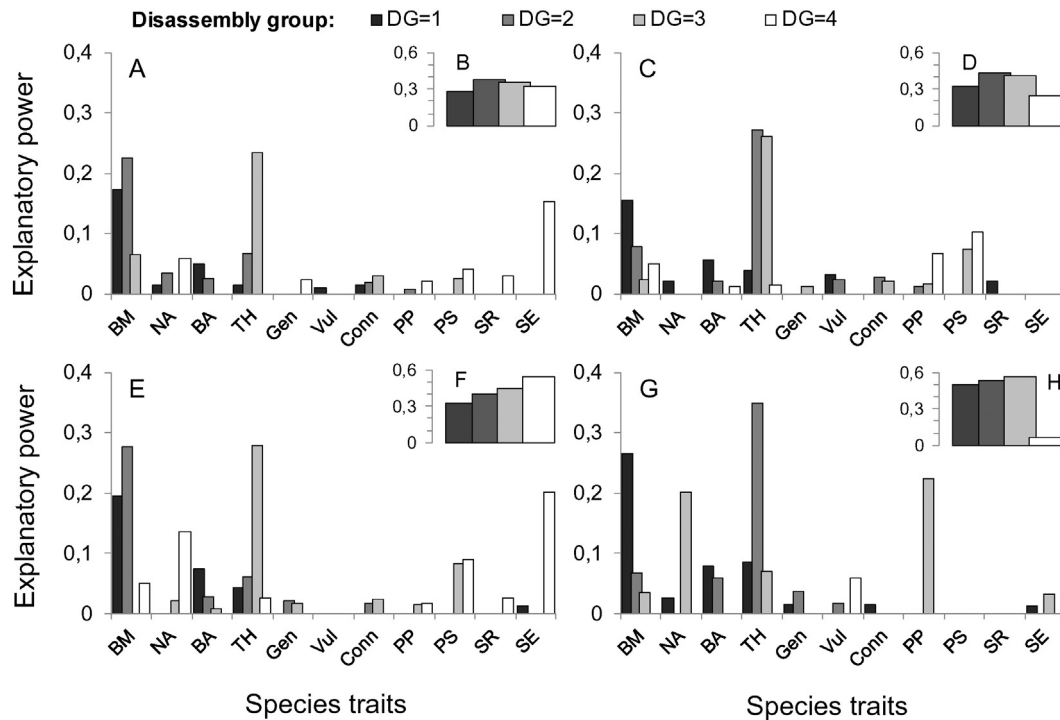


Fig. 3. Explanatory power of species traits (amount of variation in the proportion of secondary extinctions, as a result of random species deletions, that can be explained by traits of the deleted species, according to regression tree analyses) in model food webs with increasing level of disassembly (DG₁–DG₄, dark shaded to light bars), and where basal species were not allowed to be deleted. Large bar charts (subplots A, C, E and G) show explanatory power for each species trait in the four disassembly groups, while small bar charts (subplots B, D, F and H) show the total (summed) explanatory power of all species traits in each disassembly group. Initial connectance of the webs were in the range of (A, B): [0.084 0.12], (C, D): [0.12 0.14], (E, F): [0.14 0.16] and (G, H): [0.16 0.2]. Proportion of initial number of species remaining: DG₁ = [0.75 1], DG₂ = [0.5 0.75], DG₃ = [0.25 0.5], DG₄ = [0 0.25]. BM: Body mass, NA: Numerical abundance, BA: Biomass abundance, TH: Trophic height, Gen: Generality, Vul: Vulnerability, Conn: Connectivity, PP: Predation pressure, PS: Predation stress, SR: Sensitivity of resilience (structural sensitivity), SE: Sensitivity of equilibrium abundances (structural sensitivity).

More specifically, the explanatory power of body size was high initially (6–28% in rather intact webs), but it decreased with increasing web collapse (Fig. 3) and body size was in general positively correlated to the proportion of secondary extinctions (significantly so for intermediate levels of web collapse, Table 1), suggesting that the relative importance of body mass changed with ecological context during sequential web collapse. The explanatory power of trophic position was relatively high for intermediate levels of web collapse (6–35%), but not for intact and highly collapsed webs (Fig. 3) and, like body size, trophic position tended to be positively correlated to the proportion of secondary extinctions (significantly so for intermediate levels of web disassembly, Table 1). The effects of body mass and trophic level combined suggest that when species are large and lost from high trophic levels in intact to moderately degraded webs a greater proportion of secondary extinctions will occur (than if small species are lost from low trophic levels). For numerical abundance explanatory power was in general low (0–4%), except for highly connected and collapsed webs (Fig. 3), and there was no clear pattern in the direction of the association with secondary extinction rate (although both significant correlations were negative). The explanatory power of biomass abundance was moderate (3–8%) for rather intact food webs and decreased further with increasing web collapse (Fig. 3), although in general the association with secondary extinction rate was positive (for low to intermediate levels of web disassembly the correlations tended to be significantly positive). For generality the explanatory power was low (0–4%, Fig. 3) and the direction of the association seemed to change with increasing web collapse (significant positive correlations for intermediate levels of web disassembly, but significant negative correlations for high levels). The explanatory power of vulnerability was low in general (0–6%) and the direction of the association was not consistent (Table 1, although the

relationship tended to be significantly positive for low to intermediate levels of web connectance and with low to intermediate levels of web collapse). For connectivity the explanatory power was low in general (0–3%, Fig. 3) and there was a tendency for the direction of the association to change with increasing web collapse (significant positive correlations for low to intermediate levels of web collapse, but significant negative correlations for highly collapsed webs, Table 1). The explanatory power of predation pressure was low in general (0–2%), except for highly connected and collapsed webs (Fig. 3), and in general there was a positive correlation between predation pressure and secondary extinction rate (although rarely significantly so, Table 1). For predation stress the explanatory power was moderate (0–10%), but tended to increase with increasing levels of web collapse (Fig. 3) and there were mixed results with regard to the direction of the association (although the significant correlations tended to be positive, Table 1). The explanatory power of the dynamical sensitivities was in general very low (0–3%, Fig. 3), although the secondary extinction rate tended to increase significantly as the sensitivity value of a species increased (Table 1). This pattern occurred for many combinations of web connectance and web collapse. Finally, for structural sensitivity the explanatory power was low in most cases (0–3%), except for highly collapsed webs with a low to intermediate level of connectance (where the explanatory power was high, 15–20%, Fig. 3), and in general the direction of the association was positive (with significant positive correlations between structural sensitivity values of species and the proportion of secondary extinctions for intermediate to high levels of web disassembly, Table 1). This suggests that there was a correspondence between the importance of species revealed by local sensitivity analyses and global species deletions, but that this was only manifest when overall diversity in the system was low.

Table 1
Correlation statistics for the relationship between traits of removed (primarily extinct) species and the proportion of secondary extinctions following the loss of that species, in model food webs varying in the degree of disassembly (DG) and connectance (C), and where basal species were not allowed to go primarily extinct. Ranges in the proportion of initial number of species remaining: DG_1 : [0.75 1], DG_2 : [0.5 0.75], DG_3 : [0.25 0.5], DG_4 : [0 0.25]. Ranges in food web connectance: C_1 : [0.084 0.12], C_2 : [0.12 0.14], C_3 : [0.14 0.16], C_4 : [0.16 0.20].

Species trait		DG_1	DG_2	DG_3	DG_4
Body size	C_1	$R = 0.79 P = 0.003$	$R = 0.88 P < 0.001$	$R = 0.91 P < 0.001$	$R = 0.24 P = 0.476$
	C_2	$R = 0.54 P = 0.086$	$R = 0.87 P < 0.001$	$R = 0.91 P = 0.001$	$R = 0.75 P = 0.007$
	C_3	$R = 0.50 P = 0.119$	$R = 0.82 P = 0.002$	$R = 0.85 P = 0.001$	$R = 0.13 P = 0.698$
	C_4	$R = -0.06 P = 0.854$	$R = 0.82 P = 0.001$	$R = 0.77 P = 0.005$	$R = 0.33 P = 0.320$
Numerical abundance	C_1	$R = 0.39 P = 0.163$	$R = -0.39 P = 0.209$	$R = -0.78 P = 0.002$	$R = 0.34 P = 0.339$
	C_2	$R = 0.15 P = 0.634$	$R = -0.19 P = 0.556$	$R = -0.32 P = 0.301$	$R = -0.44 P = 0.232$
	C_3	$R = 0.26 P = 0.421$	$R = -0.45 P = 0.163$	$R = -0.26 P = 0.400$	$R = 0.26 P = 0.411$
	C_4	$R = 0.39 P = 0.206$	$R = -0.08 P = 0.808$	$R = -0.89 P = 0.001$	$R = -0.45 P = 0.183$
Biomass abundance	C_1	$R = 0.87 P = 0.002$	$R = 0.96 P < 0.001$	$R = 0.95 P = 0.001$	$R = 0.83 P = 0.081$
	C_2	$R = 0.88 P = 0.009$	$R = 0.965 P < 0.001$	$R = 0.79 P = 0.061$	$R = 0.93 P = 0.066$
	C_3	$R = 0.98 P < 0.001$	$R = 0.86 P = 0.027$	$R = 0.80 P = 0.053$	$R = 0.76 P = 0.076$
	C_4	$R = 0.88 P = 0.019$	$R = 0.93 P = 0.005$	$R = 0.60 P = 0.155$	$R = 0.08 P = 0.869$
Trophic height	C_1	$R = 0.94 P = 0.012$	$R = 0.99 P = 0.002$	$R = 0.91 P = 0.033$	$R = -0.99 P = 0.042$
	C_2	$R = 0.79 P = 0.105$	$R = 0.85 P = 0.069$	$R = 0.90 P = 0.036$	$R = 0.89 P = 0.298$
	C_3	$R = 0.58 P = 0.302$	$R = 0.89 P = 0.042$	$R = 0.93 P = 0.001$	$R = 0.70 P = 0.295$
	C_4	$R = -0.05 P = 0.941$	$R = 0.94 P = 0.017$	$R = 0.89 P = 0.040$	$R = -0.01 P = 0.990$
Generality	C_1	$R = -0.14 P = 0.411$	$R = 0.68 P < 0.001$	$R = -0.02 P = 0.917$	$R = -0.89 P = 0.001$
	C_2	$R = -0.24 P = 0.180$	$R = 0.72 P < 0.001$	$R = 0.69 P = 0.001$	$R = -0.72 P = 0.007$
	C_3	$R = 0.49 P = 0.003$	$R = 0.82 P < 0.001$	$R = 0.70 P < 0.001$	$R = -0.33 P = 0.291$
	C_4	$R = 0.28 P = 0.094$	$R = 0.75 P < 0.001$	$R = 0.80 P = 0.001$	$R = -0.58 P = 0.046$
Vulnerability	C_1	$R = 0.78 P = 0.023$	$R = 0.79 P = 0.033$	$R = 0.81 P = 0.027$	$R = -1 P = NA$
	C_2	$R = 0.16 P = 0.689$	$R = 0.76 P = 0.028$	$R = 0.81 P = 0.028$	$R = -0.87 P = 0.323$
	C_3	$R = -0.89 P < 0.001$	$R = -0.10 P = 0.805$	$R = -0.47 P = 0.341$	$R = -0.24 P = 0.846$
	C_4	$R = -0.04 P = 0.901$	$R = 0.33 P = 0.382$	$R = -0.72 P = 0.103$	$R = -1 P = NA$
Connectivity	C_1	$R = 0.31 P = 0.066$	$R = 0.55 P < 0.001$	$R = 0.08 P = 0.714$	$R = -0.96 P < 0.001$
	C_2	$R = -0.16 P = 0.367$	$R = 0.75 P < 0.001$	$R = 0.74 P < 0.001$	$R = -0.81 P < 0.001$
	C_3	$R = 0.46 P = 0.006$	$R = 0.79 P < 0.001$	$R = 0.69 P < 0.001$	$R = -0.66 P = 0.013$
	C_4	$R = 0.35 P = 0.029$	$R = 0.71 P < 0.001$	$R = 0.73 P < 0.001$	$R = -0.53 P = 0.061$
Predation pressure	C_1	$R = 0.73 P = 0.040$	$R = 0.65 P = 0.079$	$R = 0.43 P = 0.287$	$R = 0.96 P = 0.001$
	C_2	$R = 0.53 P = 0.221$	$R = 0.38 P = 0.346$	$R = 0.37 P = 0.359$	$R = 0.72 P = 0.044$
	C_3	$R = 0.52 P = 0.187$	$R = 0.37 P = 0.357$	$R = 0.28 P = 0.503$	$R = -0.17 P = 0.675$
	C_4	$R = 0.41 P = 0.362$	$R = 0.47 P = 0.281$	$R = 0.96 P = 0.001$	$R = 0.64 P = 0.125$
Predation stress	C_1	$R = 0.81 P = 0.008$	$R = -0.29 P = 0.45$	$R = 0.65 P = 0.056$	$R = 0.44 P = 0.270$
	C_2	$R = -0.56 P = 0.118$	$R = 0.72 P = 0.029$	$R = 0.07 P = 0.844$	$R = 0.09 P = 0.860$
	C_3	$R = 0.54 P = 0.135$	$R = 0.05 P = 0.894$	$R = -0.54 P = 0.132$	$R = 0.47 P = 0.241$
	C_4	$R = 0.76 P = 0.046$	$R = 0.57 P = 0.108$	$R = -0.26 P = 0.501$	$R = -0.32 P = 0.482$
Dynamical sensitivity	C_1	$R = 0.89 P < 0.001$	$R = 0.61 P = 0.003$	$R = 0.39 P = 0.091$	$R = 0.04 P = 0.890$
	C_2	$R = -0.40 P = 0.127$	$R = 0.23 P = 0.359$	$R = 0.49 P = 0.037$	$R = 0.82 P = 0.001$
	C_3	$R = 0.84 P < 0.001$	$R = 0.62 P = 0.011$	$R = 0.24 P = 0.312$	$R = 0.37 P = 0.157$
	C_4	$R = 0.19 P = 0.487$	$R = 0.58 P = 0.013$	$R = 0.04 P = 0.892$	$R = 0.66 P = 0.004$
Structural sensitivity	C_1	$R = 0.60 P = 0.032$	$R = 0.81 P < 0.001$	$R = 0.83 P < 0.001$	$R = 0.77 P = 0.002$
	C_2	$R = 0.57 P = 0.065$	$R = 0.82 P = 0.001$	$R = 0.81 P < 0.001$	$R = 0.90 P < 0.001$
	C_3	$R = 0.25 P = 0.512$	$R = 0.79 P = 0.001$	$R = 0.81 P < 0.001$	$R = 0.85 P < 0.001$
	C_4	$R = 0.85 P = 0.003$	$R = 0.75 P = 0.003$	$R = 0.69 P = 0.009$	$R = 0.81 P = 0.002$

Note: R is the Pearson product moment correlation coefficient and P the probability of no relationship between the trait value of a removed (primarily extinct) species and the proportion of secondary extinctions following the loss of that species. A constant = 0.001 was added to all proportions of secondary extinctions to include proportions = 0 in the geometric mean and correlation. For plots of the relationships see Figs. S5–S8.

3.2. Importance of and relationship between species trait categories

Some of the species traits used here are correlated and/or represent different facets of a more general feature. More specifically, (i) generality, vulnerability and connectivity are all aspects of the number of links (hereafter termed *Degree*) of a species, (ii) trophic position and abundance are highly correlated to the *Body mass* of a species, and (iii) predation pressure, predation stress, dynamical and structural sensitivity of a species are different facets of how strongly a species interacts (trophically) with other species, hereafter termed *Interaction strength*. When grouping the species traits into these main categories (Fig. 4) the relative explanatory power of *Degree* was in general very low (except in highly collapsed and initially highly connected food webs) and appears not to be affected by web collapse. The importance of the two categories *Body size* and *Interaction strength*, instead, tended to be negatively correlated to each other (Fig. 4). In intact and moderately collapsed webs secondary extinction rate was mainly affected by traits highly correlated to the body mass of a species, while the importance of traits related to how strongly a species interacts with other species increased with web disassembly and dominated in highly collapsed webs.

4. Discussion

Using a dynamical approach and simulating species loss in complex model communities we have studied the context dependency of species keystone status by analyzing the potential importance of 11 species traits and four trait categories during food web disassembly. The few previous dynamical studies of sequential extinctions analyzing the importance of consumer species traits have identified the loss of large-bodied species with a high trophic position and low numerical abundance (Berg et al., 2015), as well as species with many trophic links at low trophic levels (Curtisdotter et al., 2011), to result in a fast food web collapse. However, these studies only focused on the risk that sequences of different kinds of primary extinctions would cause a 50% decrease in species richness and did not analyze whether the importance of different species traits changed during the disassembly process. Concentrating on the latter question we here find that the identity of important consumer traits (i.e. those with the highest explanatory power for the number of secondary extinctions, Fig. 3) indeed depends on the degree of food web collapse, but also on the connectance of the web, supporting the conclusion that the keystone status of species is

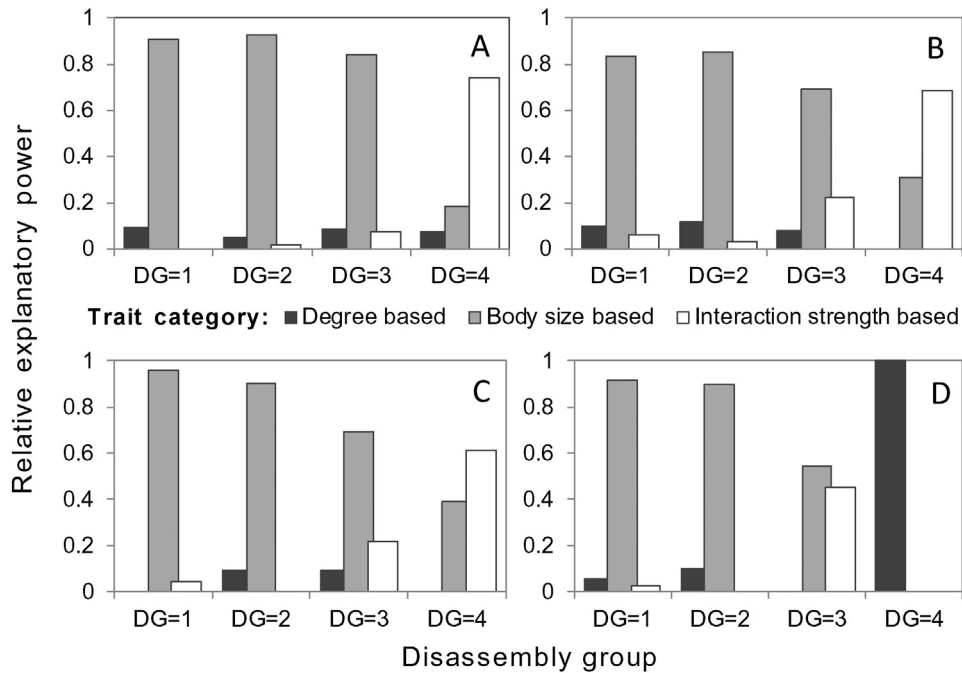


Fig. 4. Relative explanatory power of different categories of species traits (proportion of total explanatory power of all species traits that can be attributed to different categories of traits of the deleted species, according to regression tree analyses) in model food webs with increasing level of disassembly (DG = 1 – DG = 4), and where basal species were not allowed to be deleted. Initial connectance of the webs were in the range of (A) [0.084 0.12], (B) [0.12 0.14], (C) [0.14 0.16] and (D) [0.16 0.2]. Proportion of initial number of species remaining: DG = 1: [0.75 1], DG = 2: [0.5 0.75], DG = 3: [0.25 0.5], DG = 4: [0 0.25]. Degree = Relative explanatory power of (Generality + Vulnerability + Connectivity), Body size = Relative explanatory power of (Body mass + Trophic height + Numerical abundance + Biomass abundance), Interaction strength = Relative explanatory power of (Predation pressure + Predation stress + Sensitivity of resilience + Sensitivity of equilibrium abundances).

context dependent and influenced by how much species loss a food web has experienced. Our results furthermore reveal an interesting pattern: as food webs become degraded by species loss there is a change in the relative importance of different species trait categories: from body size based to interaction strength based traits (Fig. 4). This suggests a previously unrecognized possibility: that large-bodied species with a high trophic position and low numerical abundance are the most important for upholding the structure of rather intact communities, while species with high trait values for predation pressure, predation stress, dynamical and/or structural sensitivity could be keystone species in highly degraded food webs. Other studies (Otto et al., 2007) have sometimes found the distribution of trophic links among species (regardless of their strength) to be important, but in our systems traits related to the distribution of trophic links (here represented by the category *Degree*) appear to be unimportant for explaining the extent of secondary extinctions after primary species loss.

4.1. Large and small perturbations

Ecological perturbations can be classified along two important dimensions (although we acknowledge that many more are possible), representing duration (pulse vs press perturbations) and strength (small vs large perturbations). The response of ecological communities to large press perturbations, such as species loss, has been studied both empirically in natural ecosystems using accidental or controlled experiments (e.g., Estes and Palmisano, 1974; Jackson et al., 2001; O’Gorman and Emmerson, 2009; Paine, 1966; Terborgh et al., 2001) and in the laboratory using micro- or mesocosm experiments (e.g., Petchey et al., 1999; Sanders et al., 2013), as well as theoretically in real and model food webs (e.g., Berg et al., 2015; de Visser et al., 2011; Ebenman et al., 2004; Pimm, 1980; Sole and Montoya, 2001). At the other end of the perturbation spectrum, a number of studies (e.g. Berg et al., 2011; Montoya et al., 2005; Montoya et al., 2009) have

used theoretical approaches based on linear and matrix algebra to study the response of community structure and function resulting from perturbations to species that are assumed to be small. However, the extent to which effects on community properties, resulting from small perturbations to a species’ vital rates or abundance, are correlated with the effects resulting from the permanent loss of the same species is largely unknown. When species are the targets of small perturbations, community sensitivity analysis (Berg et al., 2011; Ebenman and Jonsson, 2005) indicates which species will affect the distribution of species equilibrium abundances and community resilience, respectively, the most. Although easy to calculate, it has been suggested that these metrics cannot be used to infer the effects of larger perturbations (Berlow et al., 2004). However, O’Gorman et al. (2010) found just this: coefficients that describe the effect of small perturbations to species could be used to approximate empirically estimated effects of predators on prey from enclosure experiments (large perturbations). This suggests that the response of communities to small and large perturbations might be related. The results of our simulations, where we perform large press perturbations on species (removals) and simultaneously calculate the effect on community structure and dynamics of small perturbations to these species, provide additional support for this (Table 1). More specifically, of the 16 treatment combinations of level of food web collapse and food web connectance, there is a significant positive relationship between *i*) proportions of secondary extinctions and sensitivity of equilibrium abundances in 14 groups, and *ii*) proportions of secondary extinctions and sensitivity of resilience in 8 out of 16 groups (while there are no significant negative relationships, Table 1). The binomial probability of observing 14 and 8 successes in 16 independent trials, where the probability of success in any given trial is 0.05, is 6.6×10^{-17} and 3.3×10^{-7} respectively. Thus, there is strong support for a positive relationship between proportions of secondary extinctions and (the value of) both sensitivity traits. This is perhaps not surprising when it comes to sensitivity of equilibrium abundances since it means

that species causing a large change in community structure, when subjected to a small perturbation in growth or mortality rate, also will cause many secondary extinctions if lost entirely. Notably however, there is also a tendency for species that cause a relatively large change in community resilience, when subjected to a small perturbation, to also cause many secondary extinctions if lost entirely. These results are potentially important since they suggest that community sensitivity analysis could also be used to predict which species will have the largest negative effects on community structure through cascading secondary extinctions.

4.2. The explanatory power of species traits

In our simulations, the total explanatory power of species traits rarely exceeds 50% for the observed variation in secondary extinctions. Furthermore, the explanatory power of the single most important trait rarely exceeds 30%. There are a number of competing explanations for why species traits do not explain more of the variation in secondary extinctions. One obvious explanation is that the response of food webs is highly complex and the response cannot fully be explained by species traits alone. As suggested in a recent study (Curtsdotter et al., 2014), food web resistance to species loss could be determined by an interaction between species traits and community properties (such as food web topology and community dynamic characteristics). Taking both of these into account, Curtsdotter et al. (2014) were able to explain 35–55% of the variance in extent of secondary extinctions previously observed in Curtsdotter et al. (2011). Interestingly, these figures are on the same magnitude as the explanatory power of species traits in our study where we are able to explain 30–60% of the variance in the proportion of secondary extinctions, after taking food web connectance and level of web collapse into account. Taken together, this suggests that species traits are situated in a dynamical community context and if we increase our understanding of the interaction between species traits and community properties we should increase our ability to predict the consequences of species loss. An additional explanation regarding why the explanatory power of species traits is not higher (even when community properties are taken into account) has to do with the fact that some secondary extinctions in our study probably are tertiary extinctions, i.e., extinctions that are the results of secondary extinctions. More precisely, when relatively “unimportant” species (based on species traits) are the targets of primary removals, their loss is, by definition, expected to result in only a few secondary extinctions. However, these few secondary extinctions could sometimes involve one or more “important” species, which in turn cause a significant number of tertiary extinctions. In other words, when such important species go secondarily extinct (due to the primary extinction of an “unimportant” species) this will in turn cause additional species losses (i.e. tertiary extinctions) and boost the number of extinctions that result from the loss of the “unimportant” species. In the present study, we cannot differentiate between secondary and tertiary extinctions and this will likely inflate variation in the number of secondary extinctions. Consequently, the predictive ability of species traits might be limited. This furthermore underscores the need to go beyond species traits alone and consider interactions between species traits and community properties, e.g., the characteristics of the species connected to focal species which is the target of an extinction or perturbation. These approaches might in future studies help us to gain a better mechanistic understanding of the consequences of primary species loss.

4.3. Primary extinction of basal species

Here, we have focused on sequential extinctions of consumers, i.e., basal species could only go secondarily extinct, but were not allowed to be directly removed. The reason for this is that both basic biology and previous studies (Berg et al., 2015; Curtsdotter et al., 2011) indicate that loss of basal species will be fundamentally different

in mechanism from and more devastating (lead to more secondary extinctions) than the loss of consumer species simply because they are the primary producers in a system and, as such, their loss will lead to a decrease in the total energy input into the system. Thus, to avoid confusing the effects of species traits on secondary extinctions with a primary producer effect, we focused on results from simulations where basal species were not deleted. However, we have also performed simulations where basal species could go primarily extinct (Table S2, Figs S1–S4) that the results discussed above can be compared with. Confirming previous studies (Berg et al., 2015; Curtsdotter et al., 2011), we found that when basal species were directly removed (and not only went secondarily extinct) food webs collapsed faster (Fig. 2 vs. S2), due to a higher secondary extinction rate that increased with increasing food web collapse (instead of being unrelated or negatively related to food web collapse, as when only consumers could be directly removed). Although there were some differences in which traits were identified as important (vulnerability and predation stress were e.g. more often identified as important while body mass and trophic position had a less prominent position in terms of explanatory power), the general results still hold: the explanatory power of traits varied with the level of food web collapse and connectance (Figs 3 and 4 vs. S3–S4), and the direction of the association between trait values and secondary extinction rate was in general the same as when only consumer species could be removed (Table 1 vs. S2).

5. Conclusions

As food webs undergo species loss structural properties of the network are bound to change (Kaneryd et al., 2012; Mikkelsen, 1993; Saavedra et al., 2008), with potential effects on stability and function of ecosystems (Borrval et al., 2000; Eklöf and Ebenman, 2006; Kaneryd et al., 2012; Stouffer and Bascompte, 2010, 2011; Thébault and Fontaine, 2010). The structure of food webs has also been shown to affect the extinction risk of species (Jonsson et al., 2006; Karlsson et al., 2007), implying that food web structure and species loss are interconnected. This means that we need to increase our understanding of the role of species and their trait combinations in mediating changes to food web structure and/or dynamics. Importantly, this will reduce the uncertainty over the consequences of species loss and will help us to identify trait combinations that, when lost in a range of contexts, lead to the largest cascades of secondary extinctions (Borrval et al., 2000; Ebenman and Jonsson, 2005). Many studies have focused on identifying key attributes of species that are of high importance for the persistence of communities (e.g., Berg et al., 2011; Borrval and Ebenman, 2006; Jordán et al., 2009; Libralato et al., 2006; Saavedra et al., 2011). However, the extent to which key attributes of species remain the same, or change in a predictable way, as a food web becomes degraded through species loss is unclear. Here we addressed this important question, using complex model food webs, and exposed those webs to the reverse process of assembly, i.e. forced collapse via random primary species extinctions and the cascades of secondary extinctions resulting from these. We found that the most important trait changes during food web collapse and is affected by connectance (Fig. 3), and that the relative importance of two trait categories – body size based and interaction strength based species traits – tend to be inversely related (Fig. 4). Furthermore, our study suggests that the response of communities to small and large perturbations may be consistent so that the same kinds of species are important in both situations. Although preliminary, our study illustrates how the keystone status of species in ecological communities can be context dependent. This could provide a way out of two extremes of viewpoints – “every species is important” vs “species of type X are the ones that really matter” – to a more nuanced view of species importance: “species of type X_1 , X_2 and X_3 are important in situations Y_1 , Y_2 and Y_3 respectively”. To further advance our understanding of the context dependency of species keystone status (during food web disassembly) we have suggested that future studies should focus on the interaction between species traits and

various community properties. Furthermore, when species go locally extinct from a community this affects more than just the species composition and link structure of the food web; to compensate for lost prey consumers may (i) adjust feeding efforts on their remaining resources (e.g. due to switching, Murdoch, 1969) and/or (ii) start to feed on entirely new prey species (so called trophic rewiring). Here, we have only used linear functional responses of consumers and include no opportunity for trophic rewiring. This means that our study could represent a worst-case scenario under the dynamical approach, since switching and trophic rewiring can be expected to lower the risk of bottom-up extinctions (because consumers can compensate for lost prey). At the same time, trophic rewiring might increase the risk of some top-down extinctions (because predation pressure on some prey might increase), making the net effect of switching and trophic rewiring uncertain. If it can be established how and under what circumstances interaction strength modifications and trophic rewiring occur in real systems, future studies should analyze the consequences of this for the context dependency of species keystone status during food web disassembly. Finally, we acknowledge that all traits analyzed here, but body size, are to varying degrees network dependent (either being simple and direct functions of trophic structure, as traits 4–7, or being indirectly affected by trophic structure, as traits 2–3 and 8–11, which change dynamically with trophic structure). Currently, our knowledge of how other potentially relevant, but network independent, species traits than body size (e.g. mobility, feeding mode, predator defenses etc.) affect species interactions and dynamics in general is poor, rendering a study similar to ours, of the importance and context-dependency of such traits, difficult. Once we know more about how a diversity of such truly network independent traits affect species interactions and dynamics we call for other studies to analyze the importance and context dependency of such traits.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.fooweb.2015.07.002>.

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