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Ecological impact of changes in intrinsic growth rates of species at different trophic levels

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Decreased and increased intrinsic growth rate and abundance of a single species can severely and negatively impact other species in the same food web. Here we compare the wider system effects of decreased and increased intrinsic growth rates of species occupying different trophic levels. Specifically, we derive the change in growth rate of a single (focal) species necessary to cause a 90% reduction in the abundance – a quasi-extinction – of another species in model communities. We find that even relatively small changes, negative as well as positive, in the growth rate of the focal species can cause quasi-extinctions of others. Furthermore, the magnitude of change needed to cause a quasi-extinction depends on the trophic level of the perturbed species. The potential ecosystem impact of such 'negative' and 'positive' changes is largely unknown. We argue that such a targeted decrease or increase could be induced by human interference, such as hunting or harvesting, but also by an outbreak or fade-out of an infectious disease. As ecosystems maintain many and diverse infectious agents, these results suggest that these agents may play an important role in the structure and balance of ecosystems.

Keywords: ecosystems, infection, intrinsic growth rate, quasi extinction

Introduction

It is well-known that decreased intrinsic growth rate in a species (that is, increased mortality rate and/or decreased birth rate) can lead to its functional/ecological extinction which can, in turn, cause extinctions of other species in the ecosystem (Soulé et al. 2003, Estes et al. 2011, Wollrab et al. 2012, Sanders et al. 2013, 2015, Säterberg et al. 2013, Sellman et al. 2015). Likewise, a positive change in the intrinsic growth rate leading to increased abundance can turn a species into a so called natural invader, with negative effects on the persistence of other species (Carey et al. 2012). Decreases as well as increases in the growth rates and abundances of species in ecosystems can be driven by a multitude of abiotic and biotic factors. Exogenous changes can occur at long or short time scales and affect a broad or a narrow range of species. Effects of some factors,

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like climate change (Amarasekare and Coutinho 2013, Poloczanska et al. 2013), nutrient stress, pollution and other slow-acting antropogenic disturbance, mostly strike broadly and gradually, directly affecting the vital rates in many species simultaneously. Other drivers could be the invasion of new species into an ecosystem, gradually affecting a broad or a narrow range of resident species, or natural disasters affecting a broad range of species on shorter time scales, or almost immediately. In this paper, we are concerned with changes that initially affect only a very narrow range of species and that have a fast effect. As a thought experiment, we focus on the scenario where an exogenous change directly affects the intrinsic growth rate of only one species (to be referred to as focal species) and we study the ecosystem consequences of such changes. This could for example be imposing or lifting species-specific human interference (hunting, harvesting) of the focal species. Here, we take a general approach, but our motivation is the influence of an outbreak or fade-out of a pathogen or parasite with a narrow host range directly influencing a limited number of (its host) species, in particular limiting this direct effect, in our thought experiment, to a single focal species (Anderson 1965, Weste and Marks 1987, Dobson and Crawley 1994, Houston 1994).

Although an outbreak or fade-out of an infectious agent or another exogenous force may affect the intrinsic growth rate and abundance of only one focal species directly, the indirect effects can be far-reaching. Specifically, changed abundance in the focal species may alter the interactions among species with potentially important consequences for community structure and stability and ultimately for biodiversity (Carpenter 1990, Dobson and Crawley 1994, Wilmers et al. 2006, Lafferty et al. 2008, Getz 2009, Holdo et al. 2009, Sato et al. 2012, Hollings et al. 2013, Selakovic et al. 2014, Buhnerkempe et al. 2015, Miner et al. 2018). For example, an exogenous change decreasing intrinsic growth rate of a keystone predator can trigger an extinction cascade (Tansley and Adamson 1925, Wilmers et al. 2006, Hollings et al. 2014, Menge et al. 2016, Schultz et al. 2016, Cerny-Chipman et al. 2017, Miner et al. 2018). The same effect on a dominant competitor, however, can potentially promote biodiversity by allowing the persistence of subdominant competitors (Hatcher et al. 2006, Bagchi et al. 2014). Conversely, changes leading to increasing intrinsic growth rate and abundance of a dominant competitor might result in competitive exclusion of sub-dominant species. These examples show that changes in the infection prevalence in a host species can alter the structure and composition of the ecological community of which it and the infectious agent are a part. Furthermore, they suggest that the direction of effects on biodiversity depends on both the direction of the change in growth rate and the ecological position of the focal species.

Motivated by such potential effects, we derive the change in the intrinsic growth rate of a focal species necessary to cause a quasi-extinction (defined here as a 90% decline in abundance) of another species in model food webs. We find that the robustness of the community depends on the direction of the change, the size of the change and the trophic level of the focal species. We also find that the trophic level most affected by the change depends on the direction of change and the trophic level of the focal species. We discuss the potential implications of our results for the ecological role of parasites and pathogens, as one of the potential underlying explanations for a change in focal-species' growth rate.

Methods

We generate 1000 feasible (i.e. with all species having positive abundance) and locally stable pyramidal food webs consisting of 12 species, using the approach in Kaneryd et al. (2012). These food webs have three trophic levels; primary producers (six species), herbivores (four species) and carnivores (two species). Pyramidal topology and relatively discrete trophic levels are commonly observed in natural food webs (Jonsson et al. 2005). The number of consumer–resource links, L, in the systems is based on an empirically observed range of connectance, C (defined as L/S^2, where S is the number of species in the web) (Dunne et al. 2002, Digel et al. 2011). The links are randomly distributed with two restrictions: consumers must have at least one prey and carnivores must have at least one herbivore prey species. We analyse two scenarios: one where consumer species show strong preference for one of their prey species (specialists) and one where consumers show equal preference for each of their prey species (generalists). Community dynamics are described by generalized Lotka–Volterra equations (see Kaneryd et al. 2012 and the Supporting information for details and parameterization):

$$dN_i / dt = N_i \left(r_i + \sum_j a_{ij} N_j \right) \tag{1}$$

Here dN_i/dt is the population growth rate of species i, N_i the density of species i, r_i the intrinsic growth rate of species i and a_{ij} the per capita interaction strength that species j exerts on species i. The per capita interaction strengths, a_{ij}, represent different types of interactions: interspecific competition if j and i are at the same trophic level, trophic interactions if j is a consumer (resource) and i its resource (consumer) and intraspecific competition if $i=j$. In matrix notation:

$$d\mathbf{N} / dt = \mathbf{D}(\mathbf{r} + \mathbf{A}\mathbf{N}) \tag{2}$$

where $\mathbf{D}$ is a matrix with population densities on the diagonal and zeros elsewhere, $\mathbf{N}$ is a vector of population densities, $\mathbf{r}$ is the vector of intrinsic per capita growth rates and $\mathbf{A}$ is the interaction matrix with elements a_{ij}. We follow Säterberg et al. (2013) in the analysis of this system. The unique interior equilibrium, if it exists, is given by the vector:

$$\hat{\mathbf{N}} = -\mathbf{A}^{-1}\mathbf{r} \tag{3}$$

To mimic an increase or a decrease in the infection prevalence in a focal species *j*, we decrease or increase its intrinsic growth rate, respectively, by an amount ε_j:

$$r'_j = r_j + \varepsilon_j \tag{4}$$

keeping the growth rates of all other species unchanged. Thus, if infection prevalence is increased $\varepsilon_j < 0$ while if it is decreased $\varepsilon_j > 0$. The new equilibrium for any species *i*, given a change in the intrinsic growth rate of focal species *j*, is:

$$\hat{N}'_i = \hat{N}_i - \varepsilon_j \gamma_{ij} \tag{5}$$

where $\gamma_{ij} = -\partial N_i / \partial r_j$ is the (i, j)'th element of $\mathbf{A}^{-1}$. We are interested in the change of r_j needed to cause a predetermined proportional decrease in $\hat{N}_i$. We set $\hat{N}'_i = p\hat{N}_i$ in Eq. 5 giving $\varepsilon_j(i) = \hat{N}_i(1-p)/\gamma_{ij}$, where $0 \le p < 1$. This quantity is the change in the intrinsic growth rate of species *j* that would lead to a $(1-p)$-proportional decrease in the equilibrium abundance of species *i*. We are interested in a substantial reduction in equilibrium abundance and therefore set $p = 0.1$, imposing an abundance reduction of 90% (results for 50% decline in abundance, i.e. $p = 0.5$, are given in the Supporting information). Such a substantial reduction in the abundance of a species is here considered as a quasi-extinction. For each species *j*, we wish to find the largest negative (closest to zero) and smallest positive ε_j causing such a quasi-extinction in one of the species in the system. To this end, we calculate $\varepsilon_j(i)$ for all species *j* and *i*, and record the maximum negative value and minimum positive value, respectively:

$$\varepsilon_j^{dec} = \max_i\left(\varepsilon_j(i) : \varepsilon_j(i) < 0\right) \tag{6}$$

$$\varepsilon_j^{inc} = \min_i\left(\varepsilon_j(i) : \varepsilon_j(i) > 0\right) \tag{7}$$

Thus, ε_j^{dec} is the smallest decrease in focal species *j*'s intrinsic growth rate that will lead to a $(1-p)$-proportional decrease in the equilibrium abundance of a species in the community. Likewise, ε_j^{inc} is the smallest increase in focal species *j*'s growth rate that will lead to a $(1-p)$-proportional decrease in the equilibrium abundance of a species in the community.

These minimal changes in intrinsic growth rate required to reach the desired effect are evaluated relative to the initial, baseline intrinsic growth rate of the focal species. Additionally, for each focal species, we record the ratio of smallest decrease and smallest increase in its intrinsic growth rate needed to cause a quasi-extinction. These data are then compared for species at different trophic levels in the food webs.

Some degree of self-limitation is likely to be present in all populations but the strength of this will be species and context-dependent and is difficult to quantify. To visualise the influence of self-limitation, we give all our results for two scenarios: one where we include self-limitation only for the basal species and one where all species experience self-limitation (but consumers less so than the basal species), see the Supporting information for the parameter values chosen.

Further details of the model and choices made for the parameters are given in the Supporting information.

Results

Overall, increased as well as decreased intrinsic growth rate of a focal species in our in-silico experiments, frequently leads to quasi-extinction of other species in the community.

Pattern of quasi-extinctions

In communities where only basal species experience self-limiting growth, decreased growth rate of single species often leads to quasi-extinctions of other species rather than the focal species themselves (Fig. 1a, c). For these systems, decreased growth rate often has bottom–up effects when the growth rate is changed at the basal and herbivore level, and top–down effect when the growth rate is changed at the carnivore level. Species at the same trophic level are less affected than species at other trophic levels. On the contrary, for communities where all species experience self-limiting growth it is more often so that the focal species itself, rather than another species in the community, goes quasi-extinct following a decreased growth rate (Fig. 1b, d).

Increased growth rates in basal focal species lead most frequently to quasi-extinctions in herbivores, increased growth rates in focal herbivores lead to quasi-extinction of mostly basal species, and increased growth rate in focal carnivores lead mostly to quasi-extinction of herbivore species. To summarize, increased growth in a focal species usually leads to quasi-extinction of a species at the trophic level below it, except, of course, in the case of basal focal species.

We do not present the corresponding results for the case $p = 0.5$. The reason is that they are identical to the results in Fig. 1 for the case $p = 0.1$. This can be understood because of the choice we made in quantifying the effects of a change in the focal species. We regard the first species, and its trophic level, that is affected by the change, and it is likely that the species that is the first to be reduced by 50% is the same species that is the first to be reduced by 90%. In the analyses in the next section, we do expect an influence because there we regard the magnitude of changes needed, both absolute and relative to the growth rate.

Community robustness to increased/decreased growth rate of species

The change in growth rate in a focal species needed to cause a quasi-extinction in the community is shown in Fig. 2 sub-panels (a) to (h) for $p = 0.1$ (see the Supporting information for $p = 0.5$). We first describe the case with self-limitation in the basal species only. Overall, communities

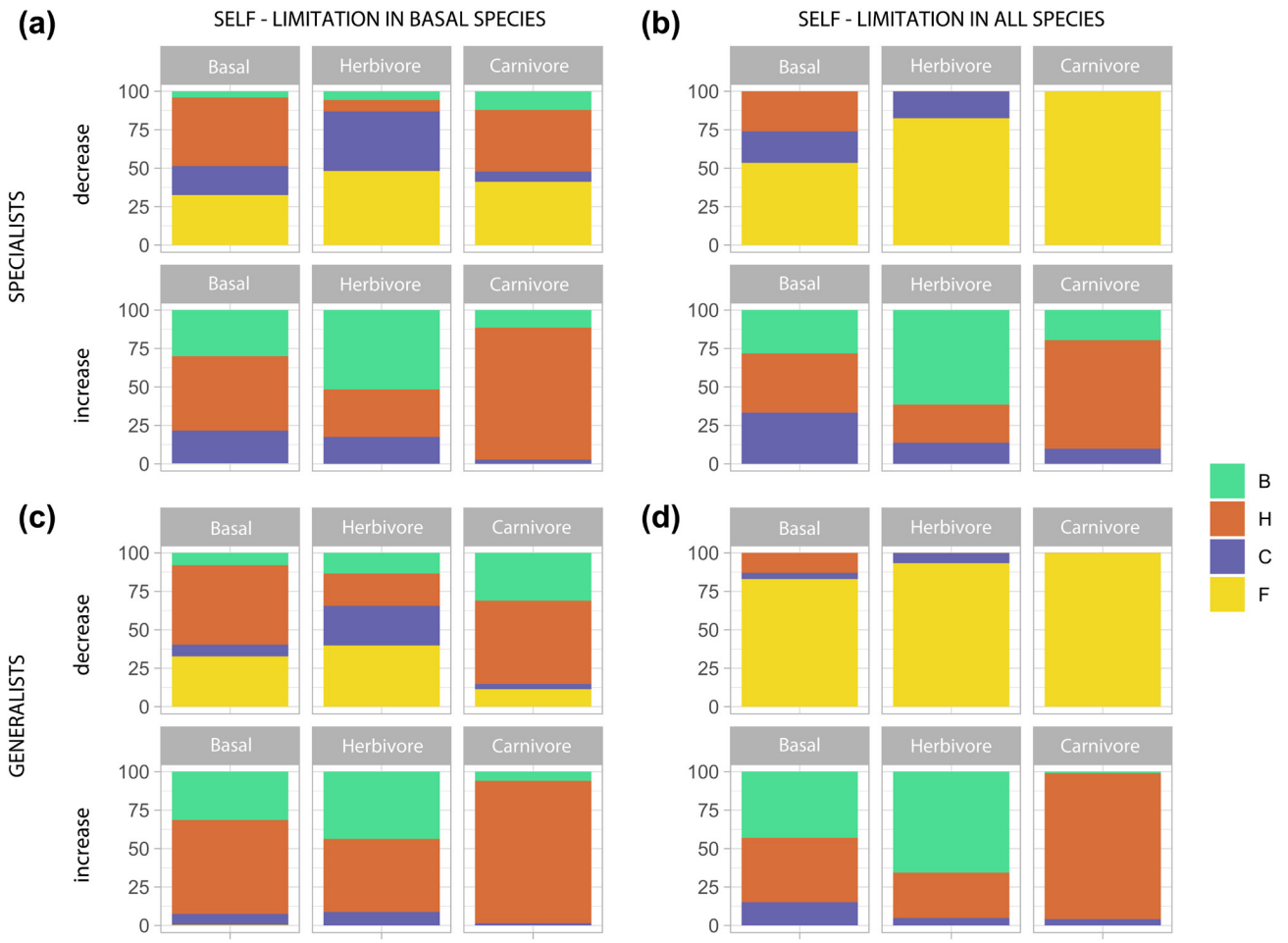

Figure 1. Patterns of quasi-extinctions. This figure shows the proportion of quasi-extinctions ($p = 0.1$) affecting a basal (green), herbivore (orange), carnivore (blue) or the focal species (yellow) following a change in growth rate of basal, herbivore and carnivore focal species, respectively. Shown are decreased or increased intrinsic growth rate of the focal species, in communities with specialist or generalist consumers, with distinction between cases with self-limitation only in basal species (a, c) and with self-limitation in all species (b, d).

with generalist consumers are less robust to changes in the growth rate of focal species, than communities with specialist consumers, as suggested by the observation that larger changes are needed in the growth rates of specialists than generalists for quasi-extinctions to occur. For both specialist and generalist focal species, the relative decrease in growth rate, as measured by $|\varepsilon/r|$, needed to cause a quasi-extinction in the community increases with increasing trophic level of the focal species (Fig. 2c–d, g–h, Supporting information). This is in contrast to the effects of absolute decrease in growth rate, as measured by $|\varepsilon|$, where the absolute change needed decreases with increasing trophic level of the focal species (Fig. 2a–b, e–f). The relative *increase* $|\varepsilon/r|$ needed seems hardly correlated with trophic level of the focal species. In general, these communities are most robust to relative changes in the growth rate ($|\varepsilon/r|$), of focal species at the top trophic level, and least robust when these changes apply to focal species at the bottom trophic level (Fig. 2c, g).

The results for the case with self-limitation in all species are qualitatively similar to the case with self-limitation in basal species only when viewed in terms of absolute changes that are needed to cause a quasi-extinction (Fig. 2a–b, e–f). When looking at relative changes, we observe that in the case of self-limitation in all species, the increase needed rises with increasing trophic level, where this is much less pronounced, or absent, when self-limitation affects basal species only (Fig. 2c–d, g–h). For a relative decrease needed, the qualitative patterns are the same in the basal and all-species self-limitation cases.

The ratios of increase to decrease in the growth rate of focal species at different trophic levels needed to cause a quasi-extinction are shown in Fig. 3. Overall, larger ratios of increases to decreases in the growth rate of species are needed to cause a quasi-extinction in specialist than in generalist food webs (Fig. 3a), in systems with self-limitation in basal species only. Furthermore, for systems where all species experience self-limiting growth, larger increases than decreases are needed to cause a quasi-extinction in the food web (Fig. 3b). Thus, self-limitation among consumers strongly determines the magnitude needed to cause quasi-extinctions in the communities.

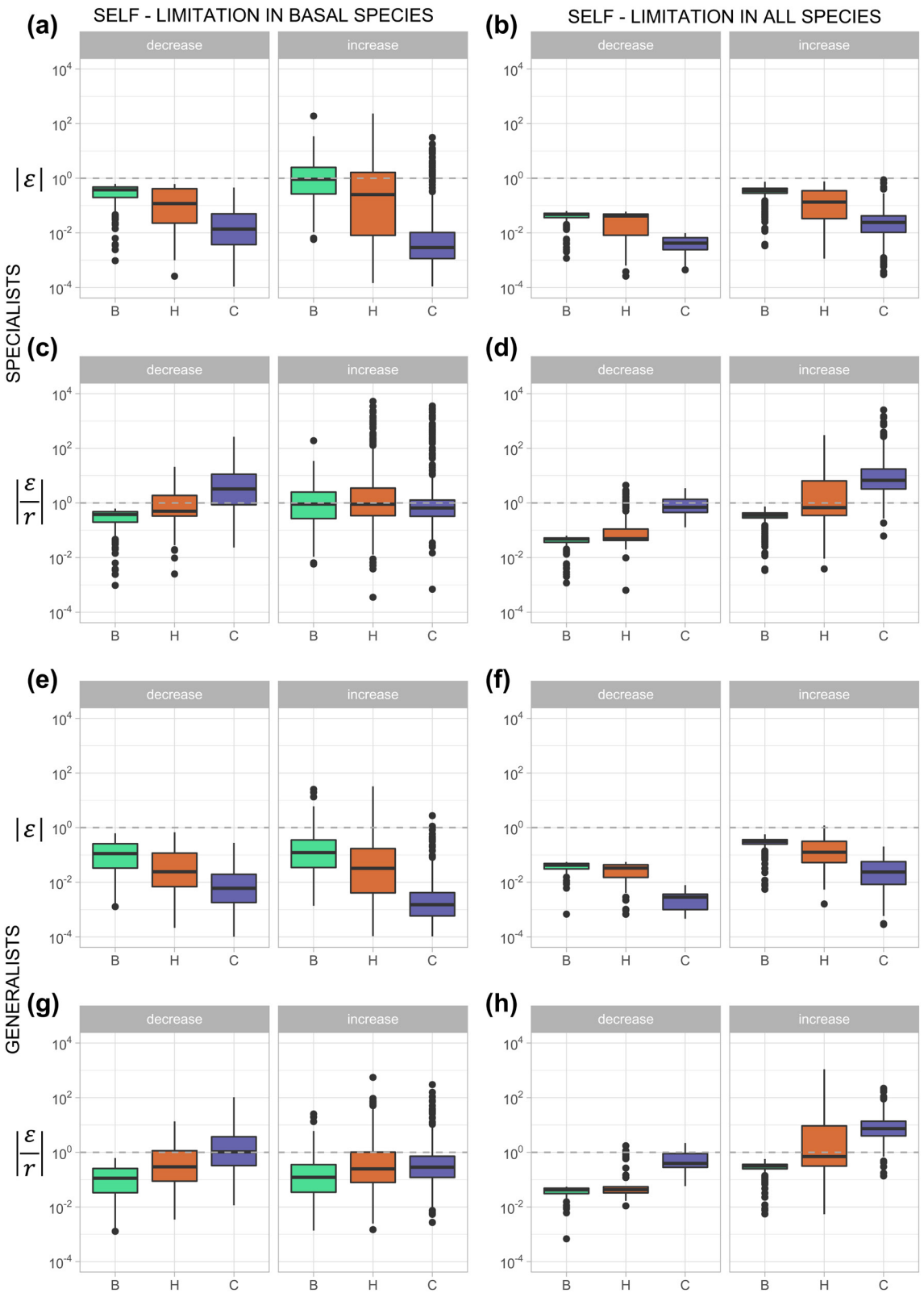

Figure 2. Boxplots showing the absolute (|ε|; a, b, e, f) and relative (|ε/*r*|; c, d, g, h) decrease and increase of intrinsic growth rate, for basal (B), herbivore (H) and carnivore (C) species, respectively, needed to cause quasi-extinction (p = 0.1) in the community. The left column of panels is the case with self-limitation in basal species only, the column on the right is for the case with self-limitation in all species. The top four panels are for specialist systems, the bottom four panels are for generalist systems.

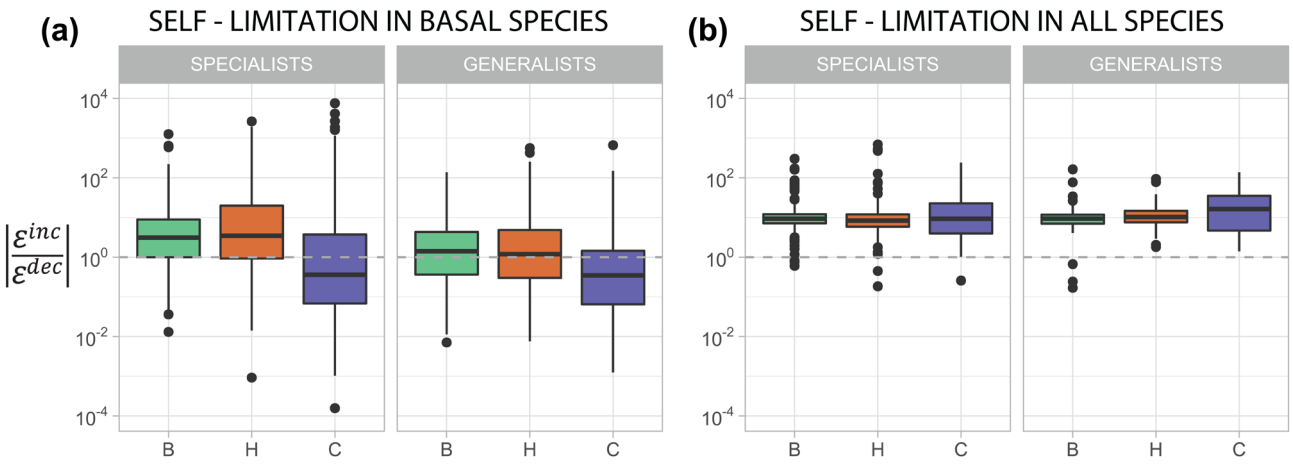

Figure 3. Boxplots comparing the decrease and increase of intrinsic growth rate, needed to cause quasi-extinction in the community, for basal (B), herbivore (H) and carnivore (C) species. (a) shows the results for the case with self-limitation in basal species only, (b) shows the results for the case with self-limitation in all species. Note that this result does not depend on p as ε^{inc} and ε^{dec} both change proportionally with p.

Discussion

We find that small decreases or increases in the intrinsic growth rate in a single (focal) species can trigger quasi-extinction of species elsewhere in the same food web, often at other trophic levels than that of the focal species. These observations hold for both specialists and generalists communities, and are most pronounced for systems where self-limitation is included only among basal species.

More specifically, decreased intrinsic growth rate in a basal or herbivore focal species frequently caused quasi-extinction of species at a higher trophic level – suggestive of bottom–up trophic cascades. Decreased growth rate in a carnivore focal species frequently caused quasi-extinctions of herbivore species. Here the mechanism involved may be a disruption of consumer-mediated coexistence. Decreased carnivore abundance leads to decreased predation pressure on herbivores, which in turn increase the intensity of competition among the herbivore species causing the quasi-extinction of sub-dominant competitors. Similar patterns have been found in recent studies focusing on true extinctions following decreased growth rate of a species (Säterberg et al. 2013, Sellman et al. 2015). Likewise, even relatively small increases in the growth rates of herbivore and carnivore focal species, can trigger quasi-extinctions at the trophic level immediately below, suggestive of increased consumption pressure on subdominant species (Gilljam et al. 2015). The most frequent outcome of increased growth rate in a basal species is quasi-extinction of herbivore species. This result is somewhat counter-intuitive – a possible explanation is that an increase in the abundance of the focal basal species causes a decrease in the abundance of basal species competing at the same trophic level, with negative consequences for the herbivores feeding on them. Increased growth rate in a basal species can also lead to quasi-extinction of other basal species. Here, the likely mechanism is also increased interspecific competition among basal species. In both the specialist and the generalist case, the relative decrease in growth rate that causes a quasi-extinction in the community is larger for top predators than for primary producers. Investigating the absolute decrease in the growth rate of a given species, Säterberg et al. (2013) found that the decrease in growth rate needed to cause a quasi-extinction in the community was smaller for top predators than for primary producers. Thus, when evaluating the robustness of a community to perturbations to different types of species, like top predators and primary producers, the conclusions might differ depending on whether the focus is on relative or absolute changes needed to change the state of the community Säterberg et al. (2019). This problem is related to the question whether to use sensitivity or elasticity analysis when comparing the effects of small changes in ecological parameters on community structure or stability (Berg et al. 2011).

Various choices had to be made that could influence the outcome and the interpretation. This holds for structural aspects such as species diversity and functional responses, as well as for parameter values, such as drawing the strength of interspecies competition from a uniform distribution for each species independently and the strength of self-limitation. It is also possible that the type of changes we have imposed and the resulting conclusions on quasi-extinctions depend on the relatively small size of our food webs and that much larger food webs are more robust to these changes. This robustness may be because species potentially have broader and more diverse ranges of interactions and interaction strengths in larger webs, which can dissipate detrimental effects arising from a target species they are directly or indirectly connected to. Studying larger webs also makes additional characterisations of food web complexity and dynamics, such as nestedness, modularity and connectance, become sufficiently relevant to quantify potential ecosystem effects of the small changes to growth rates in our set up (Landi et al. 2018, Kéfi et al. 2019). The wider consequences for ecological communities likely depend on patterns in the strength of interactions among species as the distribution of interaction strengths has important links to ecosystem structure and stability (McCann et al. 1998, Borrvall et al. 2000, Kokkoris et al. 2002, Neutel et al. 2002,

Emmerson and Yearsley 2004, Christianou and Ebenman 2005, Tang et al. 2014, Landi et al. 2018, Kéfi et al. 2019).

As explained in the introduction, the motivation for our study came from furthering the understanding of the role of infectious agents in ecosystems. However, the underlying cause for the changes in growth rate that we study could lie in other factors with a sudden impact on a narrow range of species. Examples are species-specific human interference, such as harvesting a species, or sudden changes in the abundance of a prey, predator or competitor of the focal species (due to some internal of exogenous factor). Our rudimentary way of exploring the influence of infection at least suggests that infectious agents may play an important role in maintaining food web diversity and structure as small changes can have large effects in species that are not even hosts to the infectious agent, or at the same trophic level as the focal host species. The large majority, and possibly all, species are likely to be hosts to at least one infectious disease agent (Rossiter 2013). Changes in disease prevalence will directly affect the behaviour and life-history traits, such as mortality and reproduction, of their host species. Our study suggests that owing to dependencies among species these direct effects may in turn lead to indirect changes in the abundance of other species with potentially far-reaching consequences for the system at large. Indeed, a number of studies show that the direct effects of infectious disease agents on host species can lead to large declines in the abundance, even extinctions, of other species in ecological communities (Anderson 1965, Weste and Marks 1987, Carpenter 1990, Duffy and Sivars-Becker 2007, Getz 2009, Holdo et al. 2009, Sato et al. 2012, Hollings et al. 2013). In contrast, infectious agents have also been suggested to promote coexistence of species, and thus upholding diversity in ecosystems (Bagchi et al. 2014). In that case, increased intrinsic growth rate and abundance of a dominant competitor following decreased disease prevalence is hypothesised to cause competitive exclusion of sub-dominant competitors. That is, the disease agents fulfil the same ecological role as a keystone predator, suppressing the abundance of the dominant competitor (Paine 1966). Our study shows that increased intrinsic growth rate and abundance of basal host species can lead to quasi-extinction of other basal species, thus supporting this hypothesis. Explicit epidemiological dynamics of the infectious agent in the target population directly linking to reproduction and mortality, and hence growth rate, needs to be incorporated in a next step in larger and more realistic food webs such as those considered here. In toy systems with only a few species, it has been shown that non-host species influence, through ecological interaction, the relation between infection level and biodiversity (Roberts and Heesterbeek 2018) and whether or not a (group of) host species acts as a reservoir of infection or is a maintenance community for a given pathogen (Roberts and Heesterbeek 2020).

In conclusion, our results show that sudden, even relatively small, decreases as well as increases in the intrinsic growth rate of single species can have far-reaching consequences for other species in an ecological community. Because there can be many causes for such sudden and small changes, this finding suggests that it is important for our understanding of ecosystem dynamics and stability that the mechanisms behind such changes in intrinsic growth rates are investigated in more detail. This would hold, for example, for ecosystem-level studies of hunting and harvesting. We argue that also infectious agents can be an important mechanism behind sudden changes in species intrinsic growth rates and thus that changes in infectious prevalence may have important consequences for the dynamics and stability of ecological communities.

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Author contributions

Sanja Selaković: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (supporting); Project administration (lead); Resources (equal); Software (equal); Visualization (lead); Writing – original draft (equal); Writing – review and editing (supporting). **Torbjörn Säterberg**: Conceptualization (equal); Methodology (lead); Software (equal); Writing – original draft (equal); Writing – review and editing (supporting). **Hans Heesterbeek**: Conceptualization (equal); Funding acquisition (lead); Investigation (supporting); Project administration (supporting); Supervision (equal); Writing – original draft (equal); Writing – review and editing (lead).

Data availability statement

This paper contain no original data.

Supporting information

The supporting information associated with this article is available from the online version.

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