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Not all disturbances are created equal: disturbance magnitude affects predator–prey populations more than disturbance frequency

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Disturbance plays a key role in ecological structure and function. Two important and often studied components of disturbance are frequency and magnitude. Despite the potential for non-linear interactions between frequency and magnitude, their effects are often assumed to combine in a linear manner. Additionally, studies of disturbance have mainly examined effects on species diversity and competitive interactions within a single trophic level, with less focus on exploitative interactions across trophic levels. Furthermore, while the effects of disturbance are often viewed in terms of reducing population abundance, disturbances can also alter demographic processes, 'indirectly' changing abundances. We analyzed several classic dynamic models of species interactions to examine the effects of varying disturbance frequency and magnitude on population persistence in predator–prey and competition systems. Our analysis revealed the potential for non-linear interactions between frequency and magnitude and their effect on population persistence. Effects differed depending on the form of population dynamics and whether disturbance affected abundance or demographic rates. It is critical to management efforts aiming to improve chances of population persistence to further understand the effects of varying disturbances on interacting populations.

Keywords: competition, disturbance, frequency, magnitude, non-linearity, population modeling, predator–prey

Synthesis

Ecological disturbances can be described in terms of both their frequency and their magnitude. Often, disturbance frequency and magnitude are assumed to interact linearly. That is, increases in either frequency or magnitude have equivalent consequences for the effects of the disturbance. Whether this is the case has important implications for understanding how populations respond to disturbances. Furthermore, disturbances can affect systems directly by reducing abundance or indirectly by altering demographic rates (or both), though the latter is rarely investigated. Our paper reveals the surprising potential for non-linear effects in the interaction of disturbance frequency and magnitude on predator-prey systems, particularly when disturbance affects predation rates. Our results reveal that disturbances may affect interacting populations in unexpected ways.

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Introduction

The effects of environmental disturbances on populations have been well studied in ecology (Sousa 1984, Dayton et al. 1992, Connell et al. 1997, Wilson et al. 2006, Pollack et al. 2011). Disturbance can be decomposed into many components, including distribution, area, frequency and magnitude (White and Pickett 1985). Changes to disturbance regimes, such as changes in frequency and magnitude, can alter community composition or resources, which in turn impacts ecosystem function (Connell 1978, Noble and Slatyer 1980, White and Pickett 1985, Hobbs and Huenneke 1992, MacDougall et al. 2013). However, much of this work has focused on the dynamics of single species, or guilds of species at the same trophic level (e.g. tree communities). Less is known about how varying disturbance regimes affect the dynamics and persistence of populations linked by predator–prey or consumer–resource interactions.

While there are many aspects of disturbance, it is often studied in the context of frequency and magnitude. A crucial step to understanding the consequences of varying disturbances on population persistence is elucidating the relationship between disturbance frequency and magnitude, and whether their interaction is linear (technically log-linear, i.e. effect proportional to magnitude × frequency, but for brevity we refer to this as 'linear'; Fig. 1a) or non-linear (e.g. effect proportional to magnitude × frequency^2, or some other non-linear combination; Fig. 1b). Despite the potential for non-linear interactions between the frequency and magnitude of disturbances, it is commonplace to treat their effects as linear. Stress metrics such as degree heating weeks (DWH; Gleeson and Strong 1995, Donner 2011) are one example of this approach. Designed to monitor thermal stress on coral reefs, a DHW is defined as one week that is 1°C greater than the climatological average for that week (Donner 2011). Two-degree heating weeks can represent, for example, a 1°C increase that persists for two weeks or a 2°C increase for one week. This metric has good predictive success in this system (Kayanne 2017), but this type of linear approach may not be universally applicable. For example, Fabina et al.'s (2015) model analysis showed that infrequent, severe disturbances would be more detrimental than frequent, small disturbances for the persistence of coral populations in competition with macroalgae. Thus, there is potential for non-linear interactions between disturbance frequency and intensity.

The ecological effects of disturbances are usually studied in the short-term, measuring the changes after a single disturbance event (Martin et al. 2011, Lourenço et al. 2013, Parks et al. 2014). In empirical studies, this is due to practical and logistical considerations. However, models reveal that the effects of short-term disturbances can extend over longer time scales, with additional disturbances potentially exacerbating both short-term and long-term dynamic effects of the original disturbance (Connell 1978, Syms and Jones 2000, Pollack et al. 2011). Thus, further investigation is needed into not only the consequences of single large disturbances but also the subtle effects of repeated, high frequency, low-intensity disturbances that would keep a system away from equilibrium (Hastings 2004, 2010).

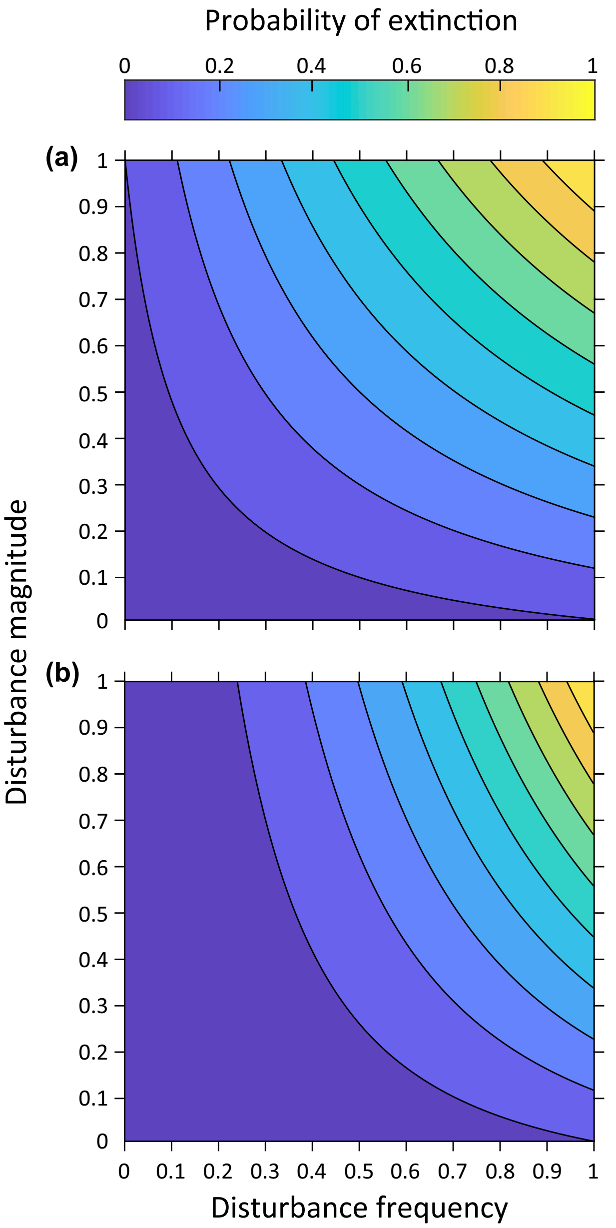

Figure 1. A conceptual illustration of a hypothesized linear (a) and non-linear (b) interaction between disturbance frequency and magnitude and the effects on probability of population extinction.

An additional consideration is that typically the effects of disturbance are thought of in terms of eliminating habitat or reducing population abundance. However, particularly in the context of interacting species, one could also consider environmental disturbances that temporarily alter the strength or rate of interspecific interactions, without directly changing abundances (this is consistent with the definition of 'disturbance' proposed by White and Pickett 1985, and amplified by van der Maarel 1993). For example, the eastern oyster *Crassostrea virginica* is a sessile, estuarine bivalve that can tolerate a wide range of salinities, often withstanding prolonged high salinity events due to drought or low river flow (Menzel et al. 1966, Kennedy et al. 1996). However, while such high-salinity disturbance events may not directly affect oyster abundance they can increase the local abundance and predation rate of gastropod oyster predators (Garton and Stickle 1980, Kennedy et al. 1996, Pusack et al. 2018), indirectly causing steep reductions in oyster density (Garland and Kimbro 2015, Kimbro et al. 2017). Such effects will likely also depend on the degree of nonlinearity in interspecific interactions (e.g. type II versus type III predator functional responses; Holling 1959). In a consumer–resource content, type III functional responses generally lead to more stable dynamics than type II functional responses (at low prey densities; Murdoch and Oaten 1975a), so it is reasonable to expect that they would also produce different responses to environmental disturbances. Additionally, the relative importance of disturbance magnitude and frequency may depend on whether the disturbance affects population abundance directly (i.e. by killing individuals), or indirectly through demographic processes (i.e. predation rate is increased so prey are killed), or both. For example, effects on population abundance may be more sensitive to disturbance magnitude, while effects on demographic processes, such as predation rates, could be more sensitive to low-intensity, high-frequency disturbances.

Here, we examine the effects of varying disturbance frequency and magnitude on predator–prey populations using classic, dynamic models with well-understood behavior (in the absence of disturbance). We focus on two types of species interactions: predator–prey (more broadly this could be considered consumer–resource), and competition (between species at the same trophic level), for comparison. We sought to address three questions: First, how does predator–prey response to disturbance compare to previous studies examining the response of horizontal diversity. Second, if interactions between components of disturbance over time exhibit non-linear or linear characteristics. Third, if the non-linear impact is directly on prey abundance versus indirectly via interaction rates.

Our analysis reveals that not all disturbances are created equal, that certain patterns hold across multiple types of interspecific dynamics, and that it would be inappropriate to view the interaction between disturbance frequency and magnitude as being linear in these systems.

Methods

We centered our analysis on the dynamics of two well-understood models: the Rosenzweig–MacArthur predator–prey model (Rosenzweig and MacArthur 1963) and the Lotka–Volterra competition model. For the predator–prey models, we examined models with both type II and type III predator functional responses (Holling 1959) to compare results across predator–prey systems with different consumer strategies. A type II functional response is characteristic of a specialist predator, with per capita predator consumption reaching a maximum, limited by handling time, as prey density increases; whereas a type III response is more characteristic of a predator electing not to forage or switching prey at low prey densities, with consumption initially increasing exponentially with prey density then leveling off due to handling constraints (Murdoch and Oaten 1975b, Oaten and Murdoch 1975). The Rosenzweig–MacArthur family of models can describe populations with deterministic dynamics that span a stable, constant equilibrium, stable limit cycles or unstable oscillations, depending on parameter values (Gurney and Nisbet 1998). We compared the effects of disturbance (both to numerical abundance and demographic rates) on populations with both stable non-cyclic equilibria and stable limit cycle dynamics. For the competition models, we examined the effects of disturbance on systems that exhibited both stable coexistence and competitive exclusion dynamics.

The original Rosenzweig–MacArthur model includes logistic prey growth, a type II predator functional response, predator growth that is entirely dependent on prey consumption, and density-independent predator mortality. The dynamics of the population density of prey, *N* and predator, *P*, are described by a pair of differential equations:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \frac{aNP}{1 + hN} \tag{1a}$$

$$\frac{dP}{dt} = e\frac{aNP}{1 + hN} - dP \tag{1b}$$

where r is the prey intrinsic growth rate, K is the prey carrying capacity, a is the predator attack rate, h is the predator handling time, e is the predator biomass conversion efficiency and d is the predator mortality rate (Table 1).

The type III model is similar, with the addition of a type III predator functional response that differs in dynamics from a type II at lower prey densities.

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \frac{aN^2P}{1 + hN^2} \tag{2a}$$

$$\frac{dP}{dt} = e\frac{aN^2P}{1 + hN^2} - dP \tag{2b}$$

The competition model describes population dynamics by logistic growth and the per capita effect of each species on the population growth of the other. The dynamics of population density for species 1 (N_1) and species 2 (N_2) are described by the differential equations:

$$\frac{dN_1}{dt} = r_1N_1\left(K_1 - N_1 - \frac{a_{12}N_2}{K_1}\right) \tag{3a}$$

$$\frac{dN_2}{dt} = r_2N_2\left(K_2 - N_2 - \frac{a_{21}N_1}{K_2}\right) \tag{3b}$$

Table 1. Model parameters.

Parameter	Value	Model type	Definition
Predator–prey model			
a	5	all	predator attack rate
	0.9	type III cyclic	
r	0.1	all	prey per capita growth rate
d	0.1	all	predator mortality rate
	0.6	type III cyclic	
h	1	all	predator handling time
e	0.1	all	predator biomass conversion efficiency
	1	type III cyclic	
K	0.7	type II non-cyclic	prey carrying capacity
	2	type II cyclic	
	5	type III non-cyclic	
	15	type III cyclic	
N_{eq}	0.25	type II non-cyclic	prey equilibrium population size
	0.32	type II cyclic	
	0.5	type III non-cyclic	
	3.57	type III cyclic	
P_{eq}	0.02	all	predator equilibrium population size
	0.04	type III non-cyclic	
	0.34	type III cyclic	
Competition model			
r_1	0.1	all	species 1 per capita growth rate
K_1	2	all	species 1 carrying capacity
a_{12}	0.4	all	per capita effect of species 2 on the population growth of species 1
r_2	0.2	all	species 2 per capita growth rate
K_2	1	all	species 2 carrying capacity
a_{21}	0.6	all	per capita effect of species 1 on the population growth of species 2
N_{1eq}	1.69	coexistence	species 1 equilibrium population size
	1.93	exclusion	
N_{2eq}	0.66	coexistence	species 2 equilibrium population size
	0.04	exclusion	

where r is the species intrinsic growth rate, K is the species carrying capacity, a_{12} is the per capita effect of species 2 on the population growth of species 1 and a_{21} is the per capita effect of species 1 on the population growth of species 2 (Table 1).

Disturbance regimes

To apply disturbances to the models, we created a series of disturbance regimes covering a range of frequencies and magnitudes. To implement disturbance using continuous-time models, we simulated model dynamics for 500 model years. For a given simulation, disturbances were randomly distributed among those 500 years, at a specified frequency between 0% and 100% (at intervals of 10%). This approach allows for disturbance frequency to on average have a specific frequency (over long-time horizons) without having a deterministic periodicity. When disturbances were applied to population abundance, an instantaneous population reduction was applied at the start of the model year. When disturbances were applied to demographic rates, the rate took on its 'disturbed' value for the entire model year. Other options would be possible, such as a disturbance that had an initial peak in effect then decayed over time (cf. McMullen et al. 2017). In practice the general patterns we report are not particularly sensitive to this detail but one would want to choose an appropriate pattern of disturbance effect if one were modeling a specific study system. Numerically, this procedure was achieved by solving the differential equations in a piecewise manner over time intervals in which demographic rates were constant (e.g. for 'abundance disturbances', the population density immediately prior to disturbance, multiplied by the amount of reduction, was used as the initial conditions for solving the next time interval (cf. Sorte and White 2013); for 'rate disturbances', separate solutions were obtained for disturbed and non-disturbed years, with the ending solution in one time interval providing the initial conditions for the next). All model simulations were conducted in MATLAB R2016a (MathWorks Inc.) using the ode45 ordinary differential equation solver.

In the predator–prey models, we applied disturbances to both prey and predator population abundances (abundance disturbances), as well as two demographic rates affecting the predator–prey dynamics: the predator attack rate a and the predator mortality rate d (rate disturbances). For abundance disturbances, we varied magnitude as an instantaneous 0–90% decrease in abundance. For rate disturbances, we varied magnitude as a 0–100% increase (predator attack rate) or decrease (predator mortality rate) above/below the baseline parameter value (a reasonable range that reflects disturbances that would have a negative effect on prey population dynamics).

For all models, parameter values corresponding to equilibria with different stability conditions (stable equilibrium or stable limit cycle for the predator–prey models; stable coexistence or unstable exclusion for competition model) were found through local stability analysis (Supplementary material Appendix 1 Fig. A1, A2). All simulations were then started at the deterministic equilibrium for the given set of parameter values (Table 1). Twenty-five hundred simulations were performed for each disturbance frequency and magnitude combination. Probabilities of prey 'extinction' (i.e. population collapse) were calculated as the percentage of simulations in which populations fell below 5% of the initial population abundance (Fig. 2). This threshold was chosen as the lowest value that did not produce 'extinctions' when the system underwent deterministic limit cycles. Extinction thresholds are commonly used in population viability

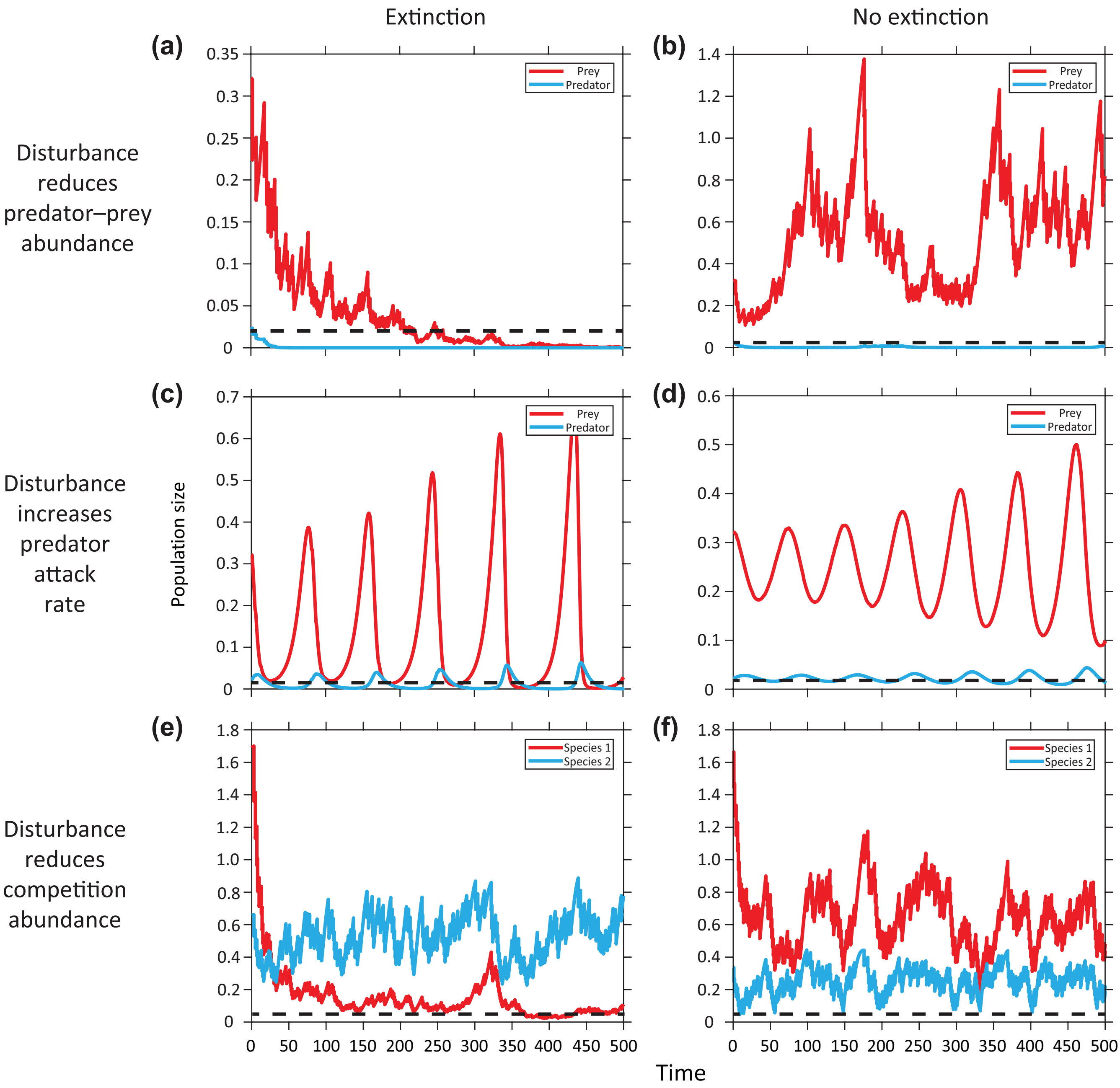

Figure 2. (a–d) Population time series of predator–prey models with type II predator functional response and cyclic dynamics with disturbance applied to population abundance (a–b) or predator attack rate (c–d). (a) magnitude = 0.3, frequency = 0.3; (b) magnitude = 0.2, frequency = 0.3; (c) magnitude = 0.9, frequency = 0.9; (d) magnitude = 0.1, frequency = 0.1. (e–f) Population time series of competition models with coexistence dynamics and disturbance applied to population abundance. (e) magnitude = 0.2, frequency = 0.4; (f) magnitude = 0.1, frequency = 0.4. Dashed line denotes extinction threshold (i.e. 5% of equilibrium prey or species 1 population size).

analysis (Lande 1987, Boyce 1992) in determining probability of extinction. While both predator and prey probabilities of extinction were calculated, we chose to focus our analysis on the prey results.

Similar steps as the predator–prey models were followed for the simulations of the competition models (Table 1). For disturbance magnitude, disturbances were applied to competition coefficient parameter a_{12} and population abundances and ranged from 0 to 100% increase above the steady state parameter value (or 0–90% decrease in population size in the case of population abundance). Probabilities of extinction were generated by calculating the percentage of simulations where populations fell below 5% of the equilibrium population size. While both species 1 and species 2 probabilities of extinction were calculated, we chose to focus our analysis mostly on the species 1 results.

One of our central questions was the relative influence of disturbance frequency and magnitude on the probability of extinction. Because we varied those two factors over different scales (frequency has units of time^{-1} while magnitude is a dimensionless proportional change in abundance or rate), we calculated elasticities (*e*) to determine the proportional increase in extinction probability (*E*) for a given proportional increase in frequency (*F*) or magnitude (*M*):

$$e_F = \frac{\Delta E / \bar{E}}{\Delta F / \bar{F}} \tag{4a}$$

$$e_M = \frac{\Delta E / \bar{E}}{\Delta M / \bar{M}} \tag{4b}$$

Given a discrete grid of combinations of frequencies and magnitudes, we calculated the value of e_F for each adjacent pair of frequency values, for a given value of the magnitude. For that pair of frequencies, we calculated the change in extinction probability (ΔE) as frequency increased and scaled ΔE by the mean of the extinction probabilities, $\bar{E}$, at those two frequencies. We then divided by the change in frequency, ΔF, scaled to the mean of the two frequencies, $\bar{F}$. The equivalent calculations were performed for changes in magnitude to obtain e_M. These calculations are similar to the typical way ecologists calculate the elasticity of a population growth rate (λ) to small changes in a demographic parameter, such as an element of a Leslie projection matrix (Caswell 2019).

We then aimed to summarize the relative influence of frequency and magnitude for each combination. We did this by treating each pair of elasticities (i.e. e_F, e_M) as orthogonal vectors in the Cartesian plane (frequency along the abscissa and magnitude along the ordinate), and calculated theta (θ), the angle of their vector sum relative to the abscissa. Assuming extinction probability increased monotonically with both frequency and magnitude (which it did), this angle has the interpretation that if $\theta < 45°$, an increase in disturbance frequency has a greater relative effect than an increase in disturbance magnitude on extinction probability, for the given values of frequency and magnitude (and vice versa). Elasticity analysis was performed only on disturbance scenarios which produced non-zero extinction probabilities.

An important utility of the elasticity analysis is in evaluating whether disturbance regimes reflect a linear or non-linear interaction of frequency and magnitude (Fig. 1). In the former case, the null expectation is that elasticities are equivalent along both axes, and $\theta = 45°$. In the latter case, the null expectation is that elasticity is greater for the variable with greater non-linearity (e.g. it would be greater in the direction of frequency in Fig. 1b, and θ would be $<45°$).

Data deposition

Model code available at <https://github.com/cjccommander/disturbance-models>.

Results

Predator–prey models

Of our twelve predator–prey model disturbance scenarios (two dynamic types, two functional response types, and disturbance applied to predator attack rate, mortality, and population abundances), results from nine scenarios produced prey extinctions while three did not. All of these three non-extinction scenarios had non-cyclic dynamics and disturbances were applied to a demographic rate (i.e. type II predator functional response, disturbance applied to predator attack rate; type III, attack rate; type III, predator mortality rate); for these three scenarios, we had to increase disturbance magnitude to 150% to start to see extinctions. In Fig. 2 we show representative examples of population dynamics from each type of model (predator–prey; competition), disturbance scenario (abundance disturbance; rate disturbance), and population outcome (extinction; no extinction). Of the scenarios that produced extinctions, the results revealed that disturbance frequency and magnitude exhibited non-linear interactions in their effect on the probability of prey extinction (Fig. 3, 4). In all cases, patterns of predator extinction matched those of prey extinction (as one would expect in a system with a specialist predator), and we present results for the prey only.

For the four scenarios in which disturbances were applied to population abundances (both functional response types and cyclic/non-cyclic), extinction probabilities followed a pattern like that shown in Fig. 3a–b. In these simulations, the narrow band of increasing isoclines indicates that extinction probabilities rapidly climbed from 0 to 100% as frequency increased slightly (at high magnitude) or as magnitude increased slightly (at high frequency) or for small changes in either disturbance component across a wide range of intermediate values. In these scenarios, the elasticity analysis revealed instances of non-linearity. Specifically, when disturbances reduced population abundance, frequency had a greater proportional effect when magnitude was high and frequency low; and magnitude had a greater proportional effect across almost all frequency levels when magnitude was low (Fig. 4a–b).

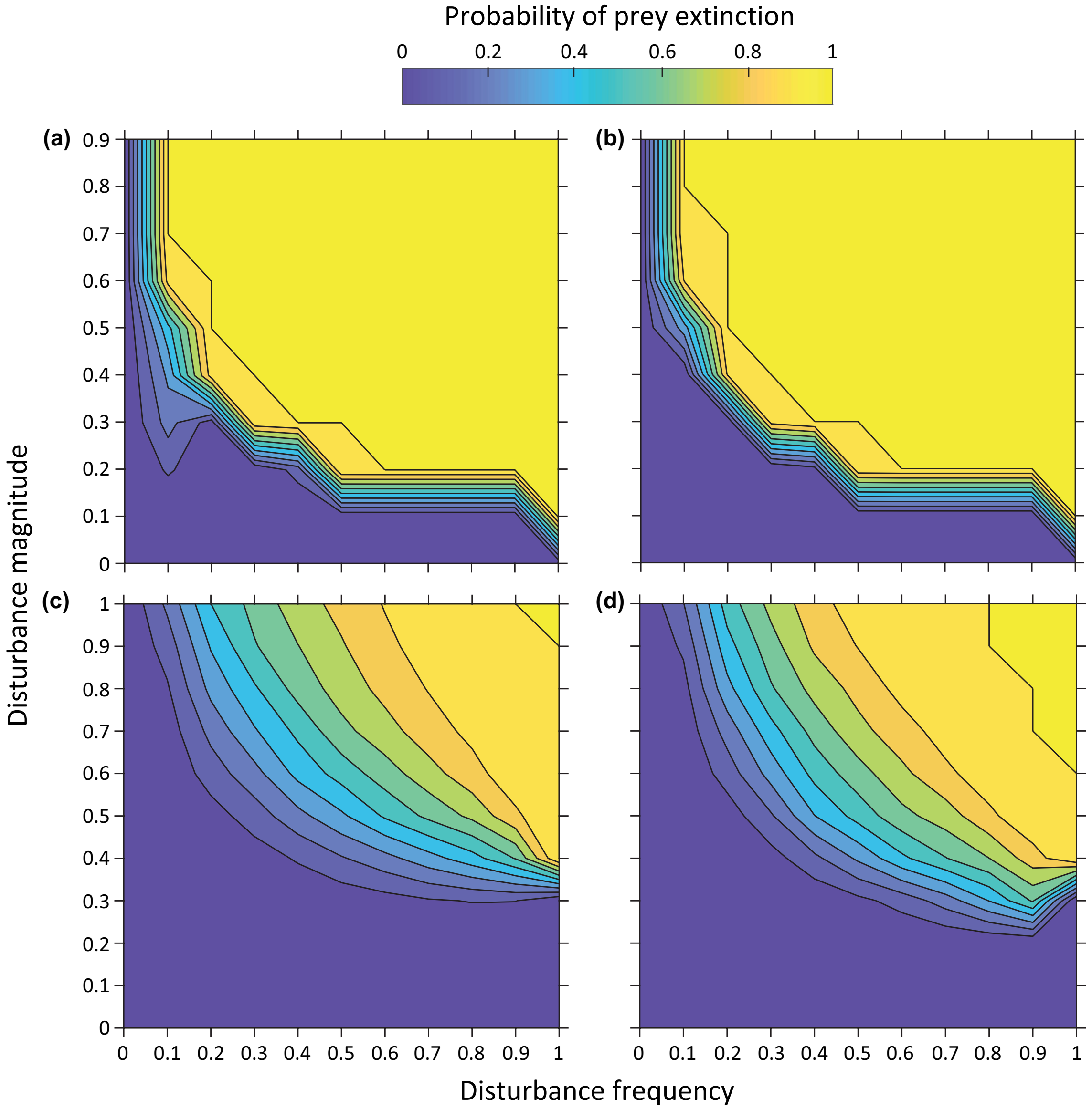

Figure 3. Probability of prey extinction in predator–prey models with (a) type II predator functional response, cyclic dynamics and disturbance applied to population abundance; (b) type III functional response, non-cyclic dynamics and disturbance applied to population abundance; (c) type II functional response, cyclic dynamics and disturbance applied to predator attack rate; and (d) type II functional response, cyclic dynamics and disturbance applied to predator mortality rate. Frequency is the proportion of time intervals experiencing disturbance (e.g. 50%), and magnitude is the proportional intensity of disturbance (e.g. 90% population reduction).

Similar to the scenarios with disturbance applied to abundance, when disturbance affected a demographic process, the isoclines showed a similar shape but had broader bands (Fig. 3c–d). Additionally, while the region of 100% extinction in these scenarios was not as large as those like Fig. 3a–b, this could be due to the arbitrary range of magnitudes. Furthermore, as in the abundance disturbance scenarios, the elasticity analysis of the rate disturbance scenarios showed disturbance frequency and magnitude interactions that displayed non-linear behavior. When disturbances increased a demographic rate (predator attack and mortality rates), magnitude had a greater proportional effect across almost all magnitude and frequency levels (Fig. 4c–d). However, at high magnitude and high frequency, frequency had a greater proportional effect (Fig. 4c–d).

Competition models

Of our four competition model disturbance scenarios (two dynamic types and disturbance applied to competition coefficient parameter a_{12} and population abundances), results from two scenarios produced extinctions while two did not. These two scenarios that did not produce extinctions were cases where disturbances were applied to a demographic

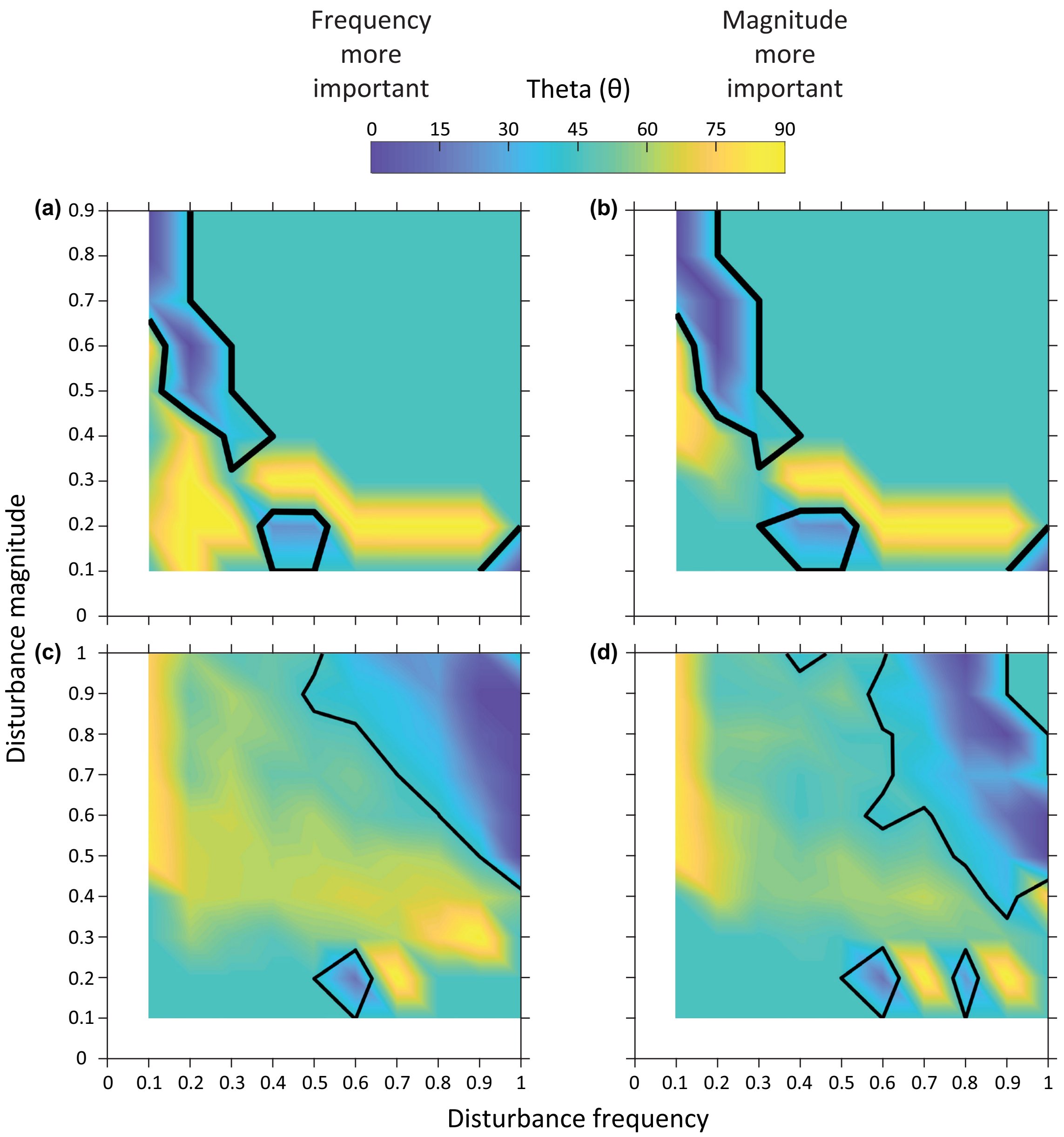

Figure 4. The relative elasticity of extinction probability relative to disturbance frequency and magnitude. The relative elasticity is measured as θ, the angle in degrees relative to the x-axis of the elasticity vectors for frequency and magnitude. Results (prey) are shown for predator–prey models with (a) type II functional response, cyclic dynamics and disturbance applied to population abundance; (b) type III functional response, non-cyclic dynamics and disturbance applied to population abundance; (c) type II functional response, cyclic dynamics and disturbance applied to predator attack rate; and (d) type II functional response, cyclic dynamics and disturbance applied to predator mortality rate. θ values closer to 0° indicate greater proportional effect of frequency on probability of prey extinction; values closer to 90° indicate magnitude is more important in affecting probability of prey extinction. White areas denote space for which there are no values. Black lines separate regions where $\theta < 45°$ from regions where $\theta \geq 45°$.

rate (i.e. coexistence and exclusion dynamics, respectively, and disturbance applied to competition coefficient a_{12}). Of the competition model scenarios that did produce extinctions (coexistence and exclusion dynamics, respectively, and disturbance applied to population abundances), the results were consistent with the predator–prey model results shown in Fig. 3a–b (Fig. 5a–b). Indeed, the pattern of elasticities in the competition model (Supplementary material Appendix 1 Fig. A3a–b) matched those of the corresponding predator–prey model nearly exactly (Fig. 4a–b). In the case of the competition model with competitive exclusion dynamics and disturbance applied to population abundances, under low to moderate disturbance magnitude and frequency the dynamics changed, with the 'winner' (species 1) becoming the 'loser' and species 2 no longer being excluded (Fig. 5c–d).

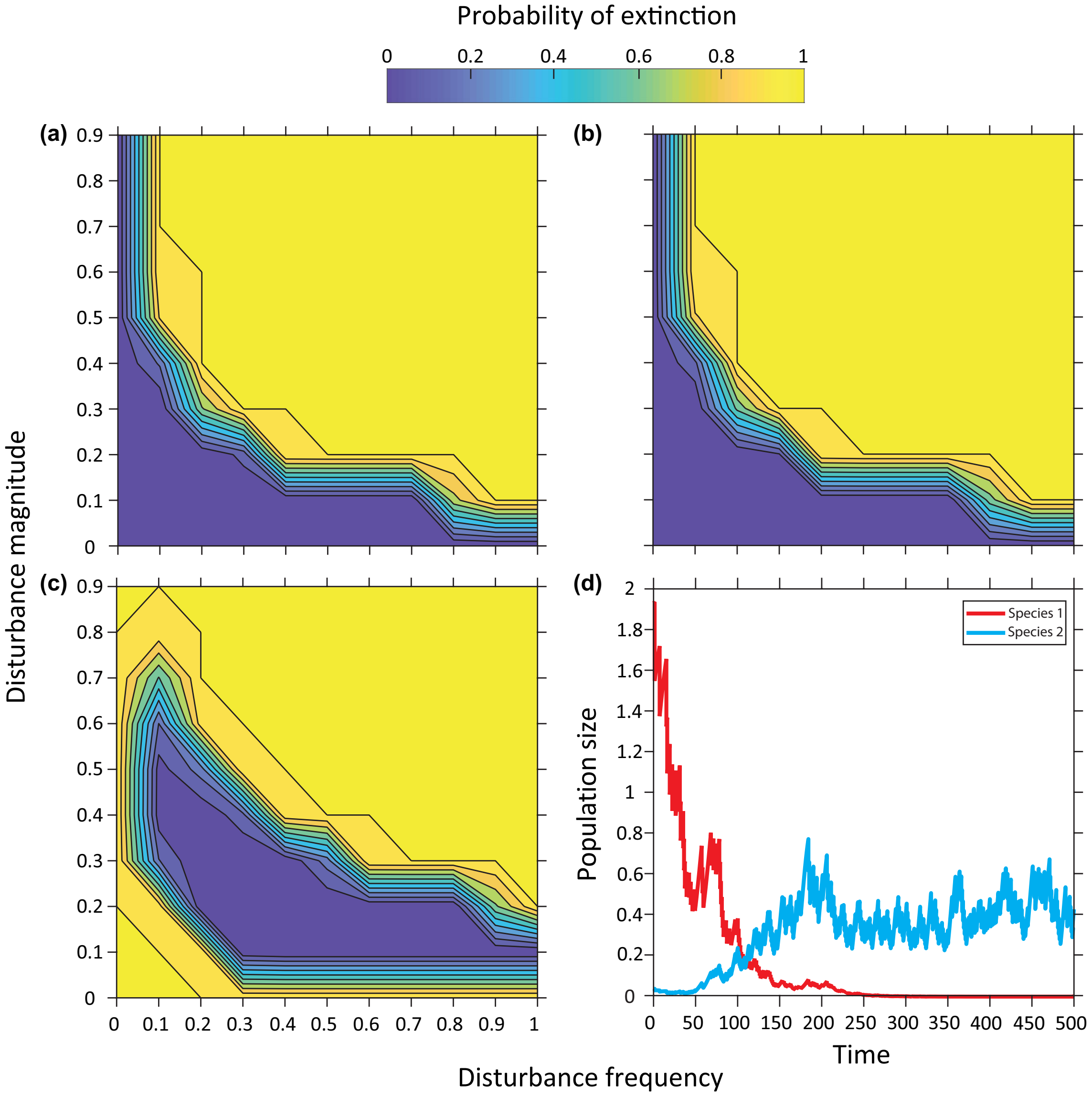

Figure 5. Probability of extinction for competition models with (a) coexistence dynamics and disturbance applied to abundance (results for species 1); (b) exclusion dynamics and disturbance applied to abundance (species 1); (c) exclusion dynamics and disturbance applied to abundance (results for species 2); (d) a representative population time series (population size (y-axis) over time (x-axis)) from a competition model with exclusion dynamics and disturbance applied to abundance (i.e. the model that yielded results for Fig. 5b–c).

Discussion

Our results indicate that disturbance frequency and magnitude may exhibit non-linear behavior in their effect on interacting populations. All the predator–prey model scenarios that produced extinctions exhibited non-linear interactions between disturbance frequency and magnitude. That is, magnitude had a greater proportional effect than did frequency at particular disturbance levels (and vice versa), as if their effects were non-linear (Fig. 1b) rather than linear (Fig. 1a). Furthermore, whether disturbance magnitude or frequency had a greater proportional effect depended on how disturbance affected the system (i.e. abundance disturbance versus rate disturbance). For example, when disturbance reduced population abundances, small increases in frequency had a greater proportional effect when magnitude was high and frequency was low, while small increases in magnitude had a greater proportional effect when magnitude was low and frequency was high (Fig. 4a–b). This is somewhat intuitive, that the variable with the lower value would have a greater effect of marginal increase, yet it does depart from the typical assumption of linearity. In contrast, when disturbance was applied to demographic rates (predator attack and mortality rates), magnitude had an overall greater proportional effect than frequency on prey population persistence (Fig. 4c–d). This result is congruent with the finding of Fabina et al. (2015) that bleaching magnitude had a greater effect on coral population persistence than bleaching frequency in a model of competitive interactions with macroalgae. The implications of these results are that high magnitude, low frequency disturbances may not have the same effect on population persistence as low magnitude, high frequency disturbances; and the differences in these disturbance regimes and their effect on interacting populations likely depends on if the disturbances affect demographic processes or population abundance directly. As shown when disturbances affected the rate of an interspecific interaction, the outcome will likely be much more sensitive to the change in magnitude of that rate than to the frequency of the disturbance.

The finding that disturbance frequency and magnitude have a non-linear, rather than linear, effect on population persistence in predator–prey systems can also be examined in the context of our understanding of the dynamics of stochastic single-species population models. In a stochastic linear population model (e.g. $N_{t+1} = r_t N_t$), variability in the annual growth rate r_t has a multiplicative effect, such that the expected distribution of population densities after a long time period is log-normal (Tuljapurkar 1990). In that type of model, the variance in the logarithm of population abundance is proportional to the variance in the growth rate, so increases in the frequency or magnitude of variability (assuming they make an equal contribution to the variance of the growth rate) would have a linear effect on the log scale. Thus deviations from that linear expectation (primarily at extreme values of either disturbance magnitude or frequency) reflect conditions under which the single-species small-fluctuation approximations (Tuljapurkar 1990) do not apply because of the effects of species interactions.

To understand the difference in the marginal effects of disturbance frequency and magnitude when disturbances affect abundance versus interaction rates, it is useful to think of the classic 'marble-in-a-basin' metaphor for stable equilibria. When disturbance affects abundance, it is akin to pushing the marble out to the edge of the basin, moving it further from equilibrium. However, when disturbance changes a demographic rate, the marble is not pushed out of the basin, rather the shape of the basin is itself being changed. Increasing the frequency of small changes (low magnitude perturbations) has less effect (particularly if the system remains at stable equilibrium) than drastic change of shape (potentially to an unstable solution) at the same frequency.

The general result that disturbance frequency and magnitude had a non-linear effect on population persistence when disturbance affected abundance applied to both predator–prey and interspecific competition systems. The key difference between those systems is that for a competitive system for which the deterministic equilibrium is one of competitive exclusion, some disturbance regimes can lead to coexistence. This is, of course, an example of the well-known relationship between disturbance and species diversity (Levin and Paine 1974, Connell 1978, Sousa 1984, White and Pickett 1985, Roxburgh et al. 2004, Miller et al. 2011). This effect was originally described as the intermediate disturbance hypothesis (Connell 1978), but like Miller et al. (2011) we found a U-shaped region of coexistence (i.e. higher diversity) spanning a range of disturbance frequencies and magnitudes, rather than merely at intermediate levels of either.

Empirically, there has long been an appreciation of the need to understand the contributions of disturbance frequency and magnitude to community and population dynamics, particularly in the context of understanding diversity–disturbance relationships (Levin and Paine 1974, Miller 1982, McCabe and Gotelli 2000, Miller et al. 2011). Our model results, like those of Miller et al. (2011), provide an important warning to empirical studies: because of the non-linear interaction between disturbance frequency and magnitude, the results of any study investigating the univariate effect of one factor (e.g. disturbance magnitude) on a system will depend heavily on the level of the other factor (e.g. frequency) that is held constant.

More recently, there has been an increasing appreciation of the potential effects of disturbances that affect interspecific interactions, rather than population abundances directly.

In a consumer–resource system comprised of the periwinkle snail *Littoraria irrorata* and the cordgrass *Spartina alterniflora*, Silliman et al. (2005) showed that increasing drought intensity can lead to consumer outbreaks (likely by drought decreasing one of *Littoraria*'s major predators), driving down the resource population. Even if both factors of drought and consumer outbreak separately are sublethal, together their combined effects on prey populations can be lethal (Silliman et al. 2005, Bertness and Silliman 2008). A similar example is that of the eastern oyster *Crassostrea virginica* and one of its major predators the southern oyster drill *Stramonita haemastoma* on the coast of northern Gulf of Mexico. In this system, periods of high salinity can lead to drill outbreaks (Menzel et al. 1966), and the duration and intensity of the salinity disturbances affect the degree of predation (Pusack et al. 2018), with high salinity disturbances decimating oyster populations (Kimbro et al. 2017). Like the disturbances to the predator attack rate in our models, in these cases of *Littoraria* and *Stramonita*, there is a disturbance-induced change in consumer behavior which causes a decline in the resource population. Other examples of population crashes mediated indirectly by disturbance effects on consumer–resource interactions include: outbreaks of crown-of-thorns starfish *Acanthaster planci*, induced in part by episodic nutrient run-off events, which can locally decimate scleractinian coral populations (Brodie et al. 2005, Fabricius et al. 2010); and urchins consuming kelp forests barren after changes in local water conditions decrease kelp productivity, causing urchins to change foraging strategies and increase grazing rates (Harrold and Reed 1985). In these cases, changes in environmental conditions lead to changes in demographics (likely higher birth rates or survival rates in juvenile stages) that, like the change to the predator death rate parameter in our model, benefit the consumer, which in turn leads to the consumer outbreak. Disturbance-induced changes in interspecific interactions like these cases highlight the need to understand the interplay of intensity and duration of disturbance and the effect on interacting population dynamics.

Our approach should serve as a foundation to examine if the patterns shown here (e.g. non-linear interactions between disturbance frequency and magnitude) hold in more sophisticated models with disturbances more reflective of natural regimes. Future work should also incorporate disturbance regimes that more realistically represent the full spectrum of frequencies and magnitudes (e.g. by using time series of real environmental data) rather than the single combinations of those two values we used here. For example, environmental variability often has a 'pink' or 'red' distribution, with both small, frequent and large, infrequent disturbances and some degree of temporal autocorrelation (Ripa and Lundberg 1996, Vasseur and Yodzis 2004). Autocorrelated disturbances have been shown to either increase or decrease extinction risk, depending on the model being analyzed (Ovaskainen and Meerson 2010), so this is a topic in need of additional investigation. Additionally, particular frequencies of environmental variability may excite resonant modes of variability in coupled or age-structured systems (Nisbet and Gurney 1976), though we did not observe that phenomenon in our model results.

Our model results have important implications for the way we quantify disturbance regimes. Specifically, linear metrics such as the degree heating week calculation may not be transferable to systems such as those we modeled in which the interaction of disturbance frequency and magnitude is non-linear. In these cases, a frequency × intensity metric of sorts may be more appropriate. In today's changing environments (Steffen et al. 2007), it is imperative that researchers and decision makers are well-informed of how environmental disturbances, both natural and human-induced, will impact systems of concern. As climate changes, so too are disturbance regimes expected to change (Dale et al. 2001, Fischlin et al. 2007), so understanding the interplay of varying disturbances and species interactions is critical to addressing present as well as future ecological challenges.

Speculations

Any study using mathematical models to represent ecological systems is vulnerable to the criticism that it explores biologically unrealistic states of nature. For example, ecological models are often analyzed at steady-state equilibria, even though most natural systems are rarely at equilibrium (Hastings et al. 2018). In our study, one could point out that no natural system will have a single combination of disturbance frequency and magnitude. As we mention in the discussion, disturbance regimes typically follow a distribution, often with frequency inversely correlated with magnitude (Denny et al. 2004). This distribution would appear as a declining-to-the-right, concave-up band of values in our contour figures. Thus one way to interpret our results might be to ask whether (and where) that distribution overlaps with the persistence frontier on those contour plots. However, there are also examples of human-managed systems in which the disturbance regimes could be managed with effectively a single combination of disturbance frequency and magnitude. Fire-managed forests and flow-controlled waterways are two examples. Our study was inspired by the latter type of system (Kimbro et al. 2017), and we propose that our results could be valuable in determining what sort of disturbances would be advantageous in that type of system.

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Author contributions – CC and JW designed the study and constructed the models. CC performed the analyses. Both authors discussed the results. CC wrote the first draft of the manuscript, and both authors revised it.

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Supplementary material (available online as Appendix oik-06376 at <www.oikosjournal.org/appendix/oik-06376>). Appendix 1.