WILEY Natural Resource Modeling

Impacts of altered disturbance regimes on community structure and biodiversity mediated by fecundity–tolerance interactions

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Abstract

We present an investigation of the effects of disturbance and fecundity–tolerance strategies on community composition. We develop a theoretical model and apply it to macrofaunal communities at deep-sea hydrothermal vents. We characterize community outcomes and find that dominance, coexistence, and alternative stable equilibria can all result from the interplay of disturbance regimes and fecundity–tolerance interactions. We show that fecundity–tolerance trade-offs can permit coexistence under disturbance, but a strict fecundity–tolerance trade-off is not required for coexistence to arise. We further describe how coexistence depends on habitat availability and disturbance regimes. Generally, our model elaborates on fecundity–tolerance strategies as a new axis of trait variation in coexistence theory. Natural disturbance regimes vary considerably across regions, and anthropogenic disturbance to vent communities will escalate with the advent of deep-sea mineral extraction. We demonstrate how anthropogenic changes to disturbance regimes may impact species diversity, pushing communities over thresholds leading to local species extinction.

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Recommendations for Resource Managers

- Conventional wisdom suggests that disturbance-adapted communities will not be strongly affected by novel perturbations associated with resource extraction or other human activities.
- We show that differing fecundity–tolerance strategies can mediate coexistence in disturbance-prone deep-sea environments, but that small changes to the disturbance regime can alter community composition and result in species extirpation.
- Natural disturbance should not be used as a rationale for expected low impacts of anthropogenic disturbance, for example, mining activities in management of deep-sea mineral extraction. Appropriate impact studies should be performed for all communities where disturbances, such as mining, are planned.

1 | INTRODUCTION

Hydrothermal vents are home to unique and productive communities. While there has been much interest in the physiology and ecology of vent species (Van Dover, 2000), research into how biodiversity is maintained in these multispecies communities is sparse, relative to terrestrial and shallow-water systems. The need for deep-sea stewardship has recently been highlighted in a flurry of prominent papers (Boetius & Haeckel, 2018; Dunn et al., 2018; Mengerink et al., 2014; Van Dover et al., 2018). Effective stewardship will demand a better understanding of species coexistence in these environments, in particular given the known and potential impacts of anthropogenic disturbance on vent ecosystems (Du Preez & Fisher, 2018; Mullineaux et al., 2018; Van Dover, 2014). Vent communities are dominated by sessile invertebrates that gain resources from vent fluids by means of endosymbiotic relationships (in which one symbiont lives inside the other) with chemoautotrophic microbes (which derive energy from inorganic compounds in the vent fluids). These communities persist in the face of regular disturbance, in the form of relatively frequent volcanic and tectonic events that can kill large numbers of individuals (Rubin et al., 2012). Mining licenses have been granted for resource extraction in some locations, and it is expected that these techniques will destroy vent habitat, and may even lead to species extinctions (Gena, 2013). While there are many theoretical models of coexistence under disturbance that have been developed for terrestrial and shallow-water communities, it is not clear that these explanations are meaningful for vent communities, and to our knowledge there is no existing theory on how disturbance regimes interact with coexistence in such systems.

One of the most commonly applied models of coexistence under disturbance is the competition–colonization trade-off (CCT), which describes how species with distinct ruderal (i.e., weedy) and competitive strategies can coexist in a successional mosaic across a variety of habitat types (Chesson & Huntly, 1997; Tilman, 1994). While the CCT is an important aspect of some systems, it depends crucially on trait distinctions that are not represented in some communities, because species do not compete directly, do not display competitive hierarchies, or have similar dispersal capabilities (Muller-Landau, 2010). The CCT does not provide a satisfactory explanation of sessile macrofaunal species diversity at hydrothermal vents, because dispersal abilities are not sufficiently distinct. While factors other than dispersal distance can affect colonization ability, there are also no known differences between our focal species in any fundamental aspect of colonization. Since species' similarity in dispersal distance does not support clear application of CCT, we here explore a new potential mechanism—fecundity–tolerance interactions (Muller-Landau, 2010)—as a mechanism for diversity maintenance and species coexistence.

Recently, new theory has been developed to describe the maintenance of species diversity in undisturbed tropical forest systems. Muller-Landau (2010) proposed that strongly differential competitive abilities have not been empirically established in tropical forests, and described how fecundity–tolerance trade-offs can theoretically promote coexistence in the absence of dispersal differences and competitive hierarchies. In that work, the fecundity–tolerance trade-off was defined as a negative correlation of fecundity and tolerance between species. In the case of forests, this displays as a contrast between species that have smaller, abundant seeds and those that have fewer, larger, seeds that can better establish in or "tolerate" low-resource habitats.

Motivated by the example of hydrothermal vent communities, which face novel threats from deep-ocean mineral extraction (Van Dover et al., 2017), we develop here a theoretical model to investigate how disturbance influences coexistence enabled by fecundity–tolerance strategies. Because we make few limiting assumptions about disturbance or species parameters, our model retains generality, and can be parameterized and adapted to study other systems. The present inquiry does not discuss other types of tolerance present in vent organisms, such as tolerance of high temperatures and toxic resources, which is a common subject of much physiological research (Childress & Fisher, 1992). Rather, we focus on a specific type of tolerance that confers the ability to establish in low-resource habitats (Muller-Landau, 2010). To add generality and breadth to our findings, we do not assume that high fecundity and high tolerance must strictly "trade-off" within species (i.e., the traits are negatively correlated, e.g., high fecundity implies low tolerance). Instead, we exhaustively examine community composition for all types of fecundity–tolerance strategies, and extend the analysis to perturbed environments, so that the effects of disturbance regimes, and alterations to disturbance regimes, can be explored. In our model, species compete for space in which to establish, but we make no assumptions of competitive hierarchy, or differences in dispersal distance (assumptions generally required by CCT, though more nuanced approaches are available [Calcagno, Mouquet, Jarne, & David, 2006; Yu & Wilson, 2001]. We also analyze the effects of a broad array of disturbance regimes, including the limiting case of no disturbance.

We generally find that fecundity–tolerance trade-offs can indeed allow for coexistence under disturbance, and that disturbance can act to increase the size of coexistence regions in parameter space. A key result of our analysis is that trade-offs per se are not necessary for coexistence to occur, and that shifts in disturbance regimes can quickly push communities over critical thresholds or "tipping points," that can lead to local species extinctions. Specific to the deep sea, our model provides a mechanistic basis for species coexistence at hydrothermal vents, without requiring

differences in dispersal abilities. It also can form a basis for future quantitative impact assessments. From a more general perspective, our work offers theoretical advances in our understanding of how species' life-history strategies interact with disturbance regimes and influence community composition, and how stochastic disturbance can enable alternative stable equilibria (ASE).

2 | METHODS AND MODEL

2.1 | Case study: Sessile invertebrates at hydrothermal vents

Our model is inspired by the community of sessile macrofauna found at hydrothermal vents on the East Pacific Rise (EPR). In particular, the mussel *Bathymodiolus thermophilus*, and the tubeworm *Riftia pachyptila* are known to co-occur at many sites along the EPR (referred to as mussels and worms or tubeworms henceforth). Though there are obvious biological differences between these species, they have broadly similar resource requirements, trophic status, and long-distance dispersal abilities (Childress & Fisher, 1992; Vrijenhoek, 2010).

From a theoretical perspective, stable coexistence of species depends on niche differences, but it is not clear a priori what traits distinguish these organisms sufficiently to provide for their coexistence. Both species have chemoautotrophic endosymbionts that obtain nutrients from vent fluids, but the species prefer different types of habitat (Fisher et al., 1988b, 1988c). The species (technically holobionts: The ensemble of host and symbiont species) can be loosely classified in terms of their resource demands. Mussels are broadly distributed, and can establish in a wide range of environmental conditions. Mussels can be considered tolerant to stresses related to low nutrient supply, because they are able to augment their symbiotic chemoautotrophic resources with filter feeding, and they can occupy habitats with low exposure to vent fluid that are never occupied by tubeworms (Fisher et al., 1988a; Page, Fiala-Médioni, Fisher, & Childress, 1991). In contrast, tubeworms cannot directly feed, have very high growth and metabolic rates, and are reliant on symbiotic chemoautotrophy for nutrition (Childress & Fisher, 1992; Lutz et al., 1994). Both species are limited to a relatively small region of the hydrothermal vent fields where they are exposed to dilute vent fluid issuing from the sea floor. In other locations, the vent fluid is too hot for these sessile invertebrates or chemical resource supply is too low to support these dense macrofaunal communities. Thus, we describe only the zone in which at least one of these species can establish, and ignore the habitat that is unavailable to either of the focal species. In general terms, the tubeworm species are thought to have higher base fecundity, though they are almost exclusively found in high-resource locations exposed to sources of rich vent fluid. In contrast, the mussel species are known to also establish in areas with exposure to very dilute vent fluid and much less exposure to vent resources (energy-rich reduced chemicals), and thus they are the more tolerant species using the present terminology. Thus, we consider this community as a key example of a community whose members may be coexisting via trade-offs in fecundity and tolerance. We construct our model to capture these ideas, and show how species' traits interact with detailed disturbance processes to determine competitive outcomes and community composition.

Though our model can be used to investigate many different species and life-history strategies, we focus here on how establishment abilities influence community structure through the outcomes of competitive and disturbance processes. Essentially, to explore how fecundity–tolerance strategies interact with disturbance, we focus on the more widely distributed and more generalist species (mussels), which then sets the competitive stage for the other species (tubeworms). First, we ask the question: Given a specific fixed fecundity–tolerance strategy used by the mussels, what other types

of strategies can coexist? We then examine an array of possible parameter combinations for a second species having high-resource demands, like the tubeworms. Finally, we consider an array of different establishment strategies for the mussel species, to more fully analyze the state space. We take this approach to show what the model predicts for a variety of different establishment abilities, and also to illustrate the differential effects of different strategies. This layer of generality will additionally be useful for applying our model to other ecological communities. To facilitate exact analytic results via stability analysis, we restrict our model to two species.

2.2 | Model design

We present a model representing two species that compete for space in which to establish. Our model is influenced by a recent model of forest communities (Muller-Landau, 2010), in that it uses lottery-type competition (in which the chance of an individual establishing in a given location is proportional to the total number of propagules available), has habitats of different qualities, and describes species with differing fecundities and tolerances (i.e., establishment abilities in stressful environments). However, our model is unique in a few key ways: We incorporate effects of detailed disturbance regimes, and we allow species to have a full spectrum of tolerances in each habitat, rather than a binary establishment rule.

Our model is formulated as a system of stochastic finite-difference equations, one for each species j. For convenience, all symbols are defined in Table 1. Let N_{jt} be the density of species j at time t. Habitat quality is distributed continuously, but for modeling purposes, we divide all available habitat into two types, a and b. In the EPR community example, we consider habitat type a to include the regions of high vent flow that are preferred by tubeworms (called "good" due to high-resource supply). Type b habitat represents the much larger region of cooler water and less concentrated vent chemicals (called "poor" due to lower resource supply). Because we are interested in two habitat types composing one area, the total population growth Λ comprises two growth rates (λ_{jat}, λ_{jbt}) for each species, depending on

TABLE 1 List of symbols

N_{jt}	Basic state variable, the proportional density of species j at time t
Λ_{jt}	Total finite rate of increase of species j, that is, "growth rate"
C_{kt}	Competition in habitat k at time t
λ_{jkt}	Growth rate of species j in habitat k
H_i	Ratio of the species' establishment abilities, weighted by habitat
r_{jt}	Growth rate on additive scale, $r_{jt} = \log\Lambda_{jt}$
$\bar{r}_i$	Long-term, low-density growth rate of the invading species i
h_k	Proportion of habitat of quality k, sum to 1
e_{jk}	Establishment modifier for species j in habitat k
δ_{jt}	Mortality of species j at time t. Encodes the effects of disturbance: δ_j^* is the constant parameter that reflects base mortality when no disturbance occurs, $\delta_{jt} = I$ when disturbance does occur
f_j	Fecundity of species j, does not vary in time
F	Disturbance frequency, controls probability of occurrence in Bernoulli process
I	Disturbance intensity, controls death rate induced by disturbance

habitat types a and b. The parameters h_k describe the relative proportion of each habitat type, with $h_a + h_b = 1$. Note that this model is most applicable at larger scales, where the populations are not strongly affected by immigration and emigration of propagules. The model is defined by the following equations:

$$N_{j,t+1} = \Lambda_{jt} N_{jt} = (h_a \lambda_{jat} + h_b \lambda_{jbt}) N_{jt}, \tag{1}$$

where

$$\lambda_{jkt} = (1 - \delta_{jt}) + \frac{\sum_l \delta_{lt} N_{lt}}{\sum_l e_{lk} f_l N_{lt}} (e_{jk} f_j) = (1 - \delta_{jt}) + \frac{e_{jk} f_j}{C_{kt}} \tag{2}$$

gives the general form of the local population growth rate, using competition C_{kt}:

$$C_{kt} = \frac{h_k \sum_l e_{lk} f_l N_{lt}}{h_k \sum_l \delta_{lt} N_{lt}} \tag{3}$$

and mortality δ_{jt}:

$$\delta_{jt} = \begin{cases} I, & \text{with probability } F, \\ \delta_j^*, & \text{with probability } (1 - F). \end{cases} \tag{4}$$

The model tracks adult densities at yearly time steps, and three processes occur within the year to contribute to the population at time $t + 1$: In each habitat, adults produce propagules ($f_j N_{jt}$), disturbance and mortality occur ($\delta_{jt} N_{jt}$), and finally, new propagules establish ($e_{jk} f_j / C_{kt}) N_{jt}$. Though populations can change fairly continuously, census efforts are often restricted to measurements once per year or less, and our model is not designed to capture within-year dynamics. Our goal is to understand long-term diversity outcomes, rather than make specific quantitative predictions in the short term.

We define competition as the ratio of propagules to free space, so that competition increases when the number of propagules increases, or when the amount of free space decreases. This is known as "lottery competition" (Chesson, 1994), meaning that the chance of a species establishing in a given "home" is proportional to the total number of that species' propagules in the pool. Lottery competition is used to model many different communities, and the original lottery model was developed for reef fishes, on the basis that they have a "home site" in which they establish (Chesson & Warner, 1981). Per capita fecundity is denoted f_j, and the establishment parameters e_{jk} describe the establishment ability of species j in habitat k. These parameters act to decrease propagules' establishment success, compared to an ideal environment, and thus by analyzing the range $0 < e_{jk} < 1$, we exhaust the state space of establishment strategies. Biologically, the model computes individuals present in year $t + 1$ as those that did not die in the previous year, added to those that were produced in the previous year, and were able to establish in the presence of inter- and intraspecific competition. While there are many parameters, the fecundity (f_j) and tolerance (ability to establish in low-resource habitat [e_{jb}]) are the key two features that describe a species' fecundity–tolerance strategy.

2.3 | Model assumptions

Our model is "space filling," meaning that space is an important limiting factor, and there is no empty space in the habitable zone that is described by the model. This is a reasonable assumption for any community where sessile individuals are densely packed in habitable zones, and space freed by disturbance is quickly colonized. Additionally, space-filling models provide very good approximations to population dynamics, even when the assumption is not strictly satisfied (Chesson, 1983). Formally, we consider the entire habitable zone to have area equal to one, and species densities sum to one. Initial densities must sum to one, and the growth rate Λ_{jt} is designed to preserve total density, so that $\sum_j N_{jt} = 1$ for any time t. Another consequence of the space-filling assumption is that our model does not include the extinction of both species as a possible outcome. Mortality is modeled as a uniform random variable: Deaths of species j in habitat k occur proportionally to the fraction of species j that is in habitat k, that is, deaths of species j in habitat k are given by $h_k \delta_{jt} N_{jt}$. Dispersal is also treated as a uniform random variable over space, so that propagules arrive in habitat k according to the fraction of total habitat that k comprises, that is, $h_k f_j N_{jt}$ propagules settle in habitat k.

2.4 | Disturbance model

The effects of disturbance are encoded in the model as variation in mortality terms, δ_{jt}. A Bernoulli process is created, with the probability of a disturbance event equal to the disturbance frequency, F. In years when a disturbance occurs, both species experience mortality equal to the mean disturbance intensity I, so that $\delta_{jt} = I$, and when no disturbance occurs species experience a background constant mortality rate, δ_j^*, which is also the constant value used when the model is applied to a system without disturbance. I represents mortality rate as a percent, and thus $I \in [0,1]$. Unless otherwise noted, we assume worm species have background mortality $\delta_2^* = 0.2$ and mussels have $\delta_1^* = 0.1$. Detailed longevity for vent species is not available, but it is thought that mussels can live much longer than worms if left undisturbed. Because we are interested in the volcanic disturbances at the EPR, we assume that species are affected equally by disturbance, though this assumption can easily be relaxed for other types of disturbance, such as grazing or flooding in terrestrial systems, where species will likely have very different sensitivities to disturbance. While we examine the effects of different mean intensities, for simplicity and tractability we do not at present address variation in I. This formulation gives us an independent, identically distributed disturbance process that we use to independently examine the different effects of disturbance frequency and intensity. It is important to separate these aspects of disturbance, because they can have different effects on diversity–disturbance relationships (Miller, Roxburgh, & Shea, 2011).

2.5 | Invasion analysis

Our primary tool for assessing stability of communities is invasion analysis (Bolker & Pacala, 1999; Chesson, 1994). This method utilizes the long-term, low-density growth rate to determine the eventual state of a community subject to environmental fluctuation and competition, and can discriminate between competitive exclusion, coexistence, and ASE, sometimes known as "alternative stable states" (Shurin et al. 2004). The basic idea is that, when each species can grow from low density (i.e., as an "invader") in the presence of the other (a well-established "resident"), then both species will coexist indefinitely. This method of establishing coexistence also guarantees that the coexistence is stable, meaning that no perturbation to species' densities

can cause extinction (provided that no density is multiplied by zero). Formally, to perform our invasion analysis, we compute $\bar{r}_i = \overline{\log(\Lambda_{it})}$, the long-term, low-density growth rate, for each species. We use the subscript i to denote either species when playing the role of the invader, that is, in the low-density limit. The overline indicates expected value with respect to t, and we take the logarithm to quantify the accumulated effects of the multiplicative growth rate Λ_{it} on an additive scale (Chesson, 1994). If both species have $\bar{r}_i > 0$, we conclude stable coexistence, but if the signs differ, the species with positive growth will tend to exclude the other. If both species have negative long-term low-density growth rates, the system operates under ASE dynamics, as the extinction equilibria are stable for both species. In this case, the identity of the species that goes extinct (i.e., it has a population size that tends towards zero) cannot be generally predicted based on species and disturbance parameters, because the outcome depends both on initial conditions and on the details of the specific sample of the stochastic disturbance process.

2.6 | Coexistence criteria

In this model, dynamic competition simulations are not necessary to determine the long-term outcome of competition and disturbance, because the long-term, low-density growth rates can be established exactly and analytically, in terms of the parameters describing species' life history and the disturbance regime. The conditions for stable coexistence via mutual invasibility are given by $\bar{r}_i > 0$ for each species as invader, which can be computed as

$$\bar{r}_i = F \cdot \log\left(1 - I + \frac{If_i}{f_r}H_i\right) + (1 - F)\log\left(1 - \delta_i^* + \frac{\delta_r^* f_i}{f_r}H_i\right) > 0, \qquad (5)$$

where i indicates the species acting as invader, and r indicates the established resident species. The term H_i describes the ratio of the species' establishment abilities, weighted by the relative amount of each habitat type:

$$H_i = \left(\frac{h_a e_{ia}}{e_{ra}} + \frac{h_b e_{ib}}{e_{rb}}\right). \qquad (6)$$

Note that in Equations 5 and 6, species' fecundity and establishment parameters appear only in invader/resident ratios. Thus, the raw fecundity and establishment abilities are not as important as the ability of one species relative to another. The form of H_i is also responsible for the boundaries of our coexistence regions, which are nearly linear in terms of invader establishment abilities, and near hyperbolic in terms of resident species' establishment. The formal derivation of the coexistence criteria is presented in Appendix A.

3 | RESULTS

We present analytic coexistence criteria for our model, and also several figures that illustrate the geometry of species coexistence, exclusion, and ASE. We display community outcomes in terms of the two-dimensional establishment space of a single species, but we also analyze the influence of many other factors on community stability. In particular, we show how changes to disturbance frequency and intensity have very different impacts on community composition, and we describe how habitat availability influences the types of fecundity–tolerance strategies that can coexist.

3.1 | Community composition, species establishment, and tolerance abilities

The result of an invasion analysis is a set of average growth rates for each species when introduced at low density in the presence of an established resident (5). When each species' growth is positive on average as an invader, then they will coexist. When the establishment parameters of the mussels are fixed, the establishment parameters for tubeworms describe an
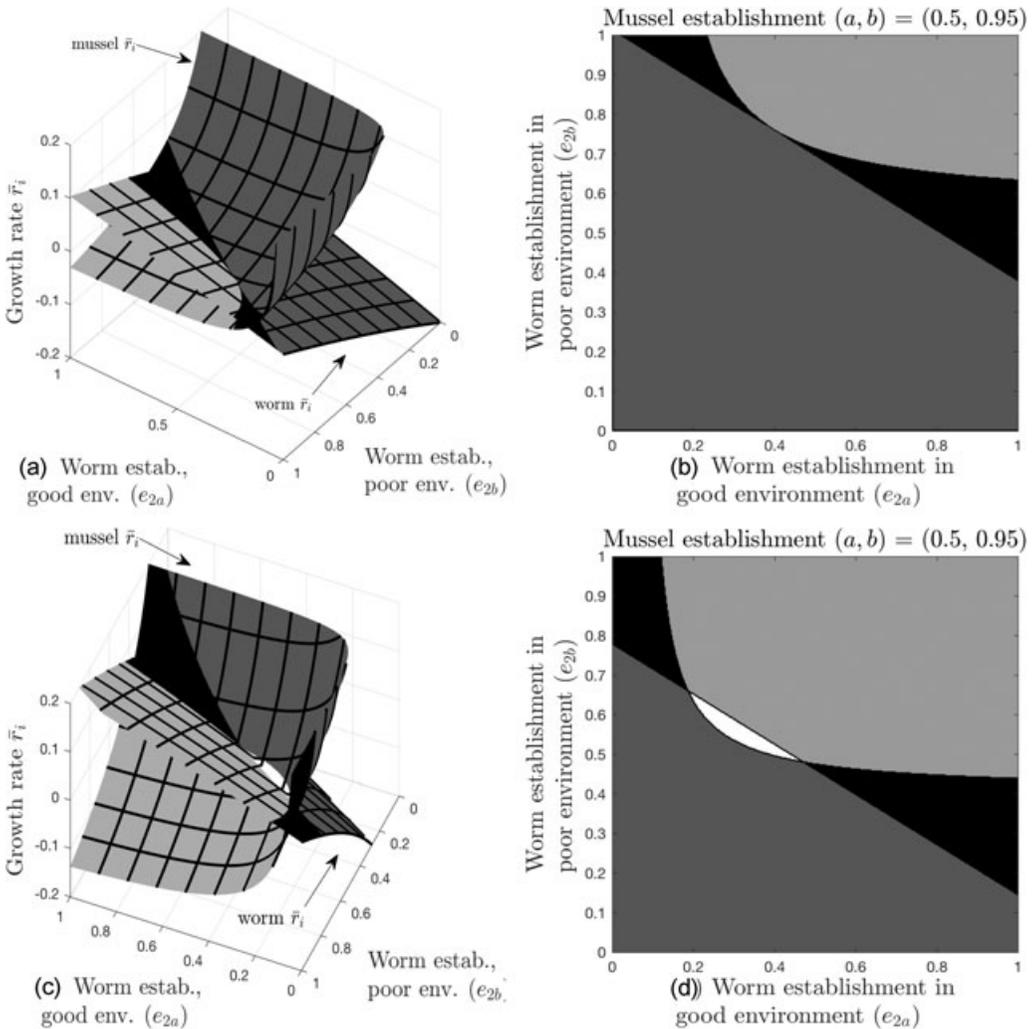

FIGURE 1 Growth rates and outcomes as a function of a single species' establishment abilities (hence tolerance). Black: coexistence, light gray: mussels extirpated, and dark gray: worms extirpated. Mussel growth rate is top sheet in the dark gray region. (a) Long-term low-density growth rates for each species without disturbance. (b) Competitive outcomes. Without disturbance, either species can extirpate the other, or they can coexist. (c, d) With a disturbance regime of $I = 0.99$, $F = 0.1$, the coexistence regions are shifted, such that lower establishment parameters allow for coexistence. Additionally, a new feature of alternative stable equilibria leading to conditional exclusion appears (white). The coexistence region is 36% larger when disturbance is added. Parameters: Mussels, f_1, δ_1, e_{1a}, $e_{1b} = 100, 0.1, 0.5, 0.95$; worms, f_2, $\delta_2 = 250$, 0.2 with e_{2a}, e_{2b} free. h_a, $h_b = 0.25, 0.75$

"establishment strategy," and this determines competitive outcomes in the model. In a temporally constant environment (no disturbance, fixed spatial variation), the possible outcomes are dominance of a single species (determined by fitness), or competitive coexistence, and these are generally the only possible results of an invasion analysis performed on a space-filling model (Chesson, 2000).

Mussels and tubeworms can coexist in the system by specializing on one of the habitat types (Figure 1a). Importantly, we can see from this figure that it is not necessary for species to display a fecundity–tolerance trade-off for species to coexist. While such a trade-off does lead to coexistence (lower right black region in Figure 1b), coexistence can occur for an establishment
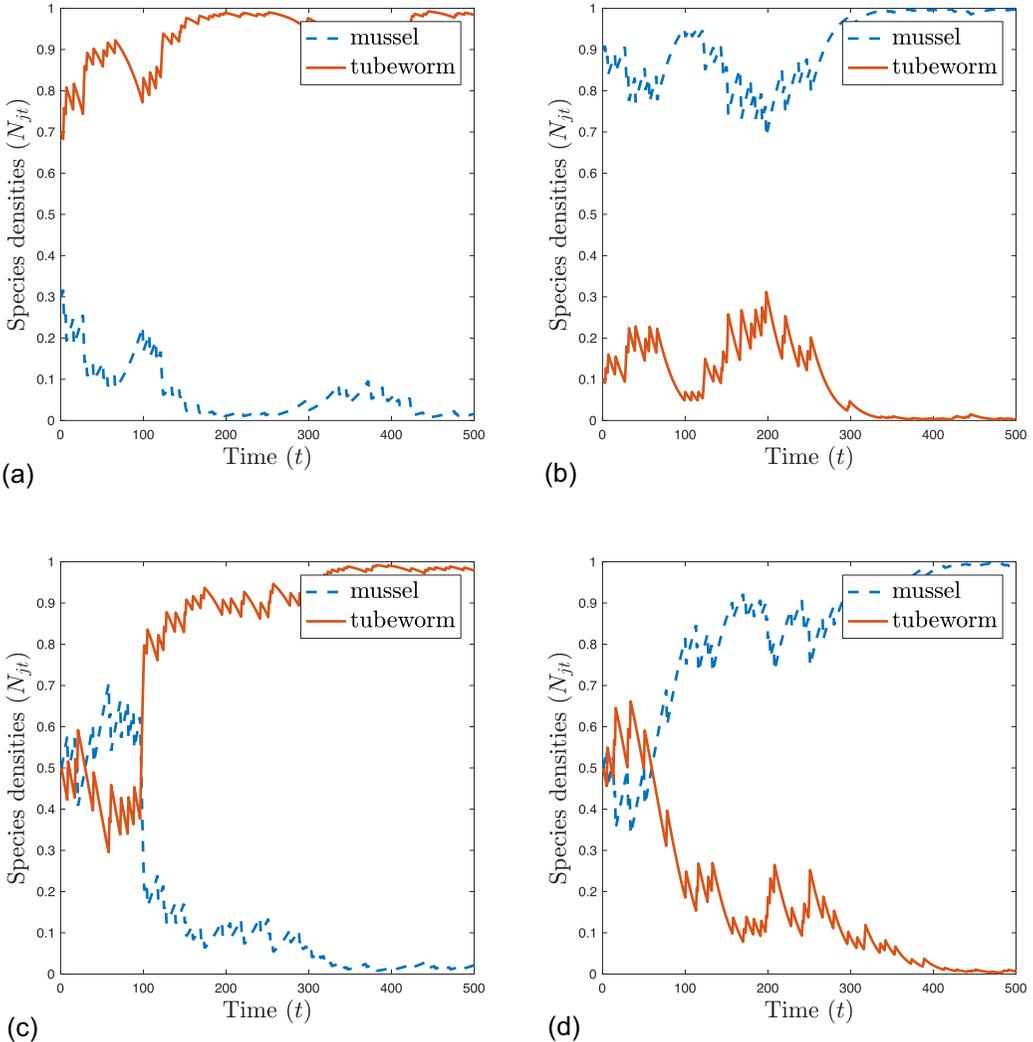

FIGURE 2 Density dynamics illustrating four possible outcomes in the scenario of alternative stable equilibria and conditional exclusion. One species will exclude the other, and the excluded species depends on both the initial densities and specific sample of the disturbance process. All parameters are as in Figure 1, with tubeworm establishment fixed at e_{2a}, $e_{2b} = 0.3, 0.55$, that is, in white region of Figure 1d. (a, b) Initial densities alter competitive outcomes when a sample of the disturbance process is fixed. (c, d) Specific sample of the stochastic disturbance process can alter outcomes, even when initial densities are fixed and equal at 0.5

strategy that has very high establishment in habitat b, very low establishment in habitat a, and high fecundity (the upper-left black region in Figure 1b). In this scenario, we do not consider the coexistence to be mediated by a fecundity–tolerance trade-off, because the species with the higher fecundity also has high tolerance, so fecundity and tolerance are not negatively correlated for all community members, even though the mussel species, with lower fecundity, does also have high tolerance. When disturbance acts in the model (Figure 1c,d), an additional outcome is available, called conditional exclusion. Here, this conditional exclusion is the result of both species having a negative long-term, low-density growth rate, meaning that both species have zero density as a stable state. In this case, growth rates $\bar{r}_i$ are not adequate to predict the community outcome, which additionally depends on the initial species densities, as well as the particular sample of the disturbance process, that is, the so-called luck of the draw (Figure 2). In the case of ASE causing conditional exclusion dynamics, both initial densities (Figure 2a,b) and disturbance history (Figure 2c,d) can influence which species will persist.

The shape of the coexistence regions displayed in Figure 1 depend on factors such as the disturbance regime parameters, as well as the ratio of habitat of type a and b available (Figure 3). Figure 3a shows how the ASE region changes with changes in habitat type. ASE dynamics are not often studied using invasion analysis (but see Miller, Thompson, Tepley, & Anderson-Teixeira, 2018); however, stochastic disturbance here provides a clear mechanism for nondeterministic community outcomes. Interestingly, the largest proportion of good habitat (h_a) leads to the largest area of ASE dynamics in the worm establishment plane, but it only covers a very narrow swath of worm establishment ability in that habitat type. ASE regions span the broadest span of total worm establishment strategies (i.e., a large range of both e_{2a} and e_{2b}) when habitats are distributed more evenly. When habitat type a increases in proportion, worm species need less establishment ability in that habitat type (e_{2a}) to coexist in the system. When
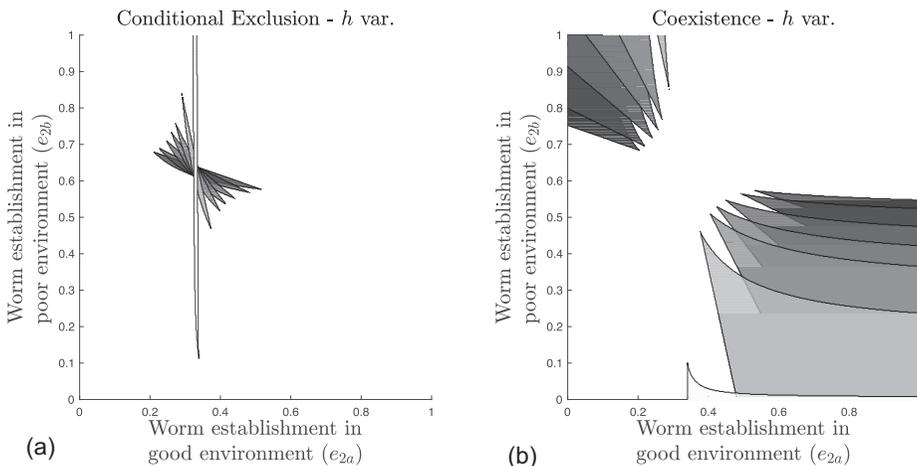
FIGURE 3 Effect of habitat proportions (h) on model outcomes. Regions with larger are shaded darker with proportion of poor environment $h_b = 0.15, 0.2, 0.3, 0.4, 0.5, 0.7, 0.99$. $I = 0.5$, $F = 0.1$, all other parameters as in Figure 1. (a) Increasing the proportion of good habitat h_a rotates the regions of conditional exclusion towards the vertical, while decreasing rotates the region toward horizontal, shifting the importance of specializing on establishment in each type. (b) Coexistence regions are similarly rotated, showing that less establishment ability is needed in a certain habitat as it becomes more available. Also, when there is very little poor habitat (white enclosed region), the worm strategy of high fecundity and high tolerance becomes unavailable as a means of coexistence
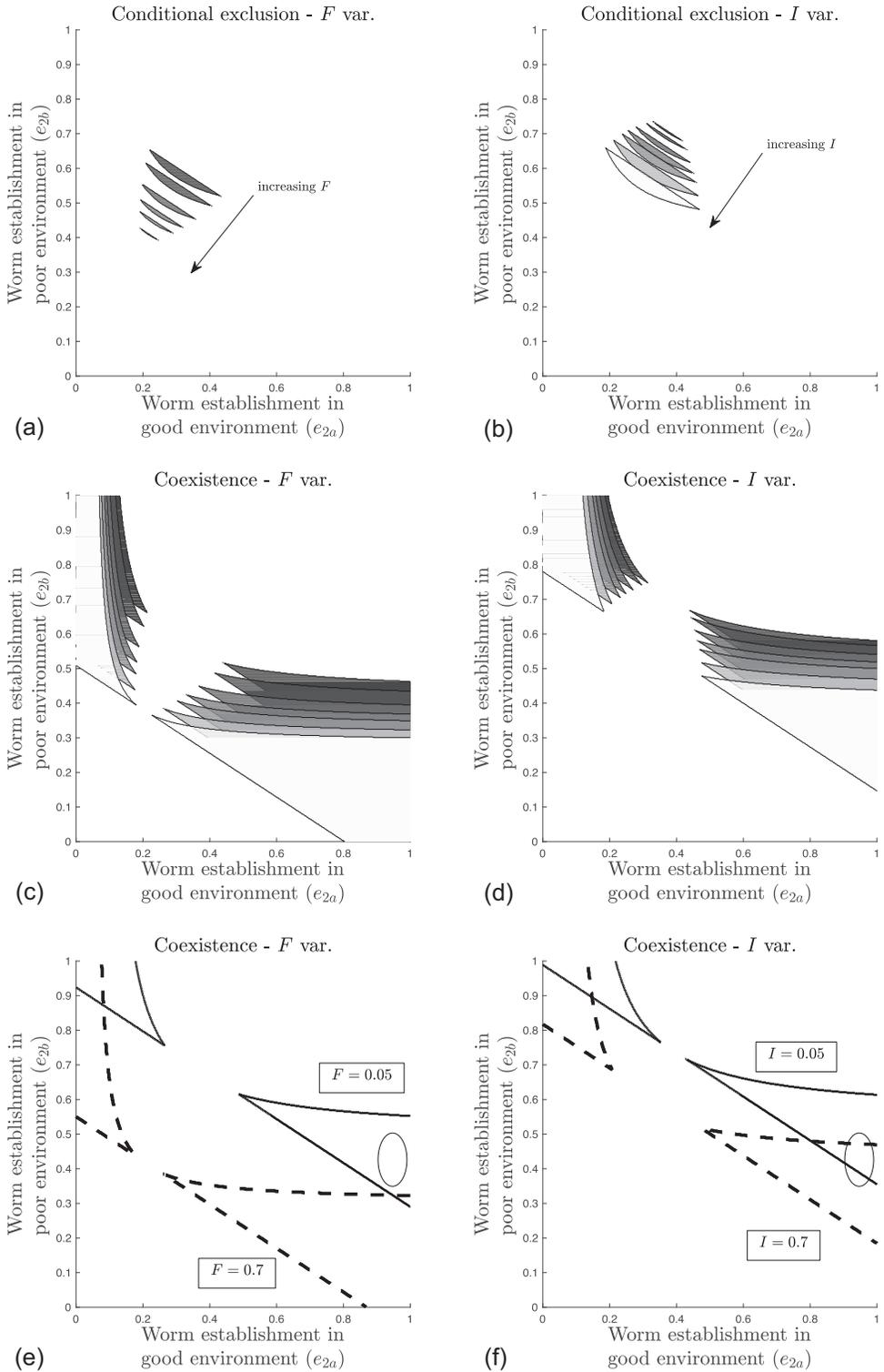
FIGURE 4 Continued.

habitat *b* is sufficiently rare, no amount of specialization in colonizing habitat *b* will allow for tubeworms to persist in the system (e.g., there are only six regions in the upper left of Figure 3b, but seven on the lower right).

The region of establishment strategies that lead to conditional exclusion depends on disturbance frequency and intensity (Figure 4a,b). Smaller frequencies lead to the largest regions of conditional exclusion, while larger disturbance intensities lead to larger regions of conditional exclusion, which matches well with intuition: Rare disturbance of high intensity induces more less predictable results than frequent, low-intensity disturbance. Put another way, while we are able to present deterministic results for long-term stability in a stochastic model, lower frequency of high-intensity stochastic disturbance makes this impossible for larger regions of the parameter space. Coexistence regions show a similar shift (Figure 4c,d). These figures illustrate the potential impacts on communities of changing otherwise stable disturbance regimes. For example, there is very little overlap between the high-frequency and low-frequency coexistence regions; however, changes to intensity cause less change to coexistence regions. (Figure 4e,f). Since real species' establishment parameters are essentially constant on the decadal timescale, changing disturbance frequency can easily cause one species to be excluded (i.e., driven locally extinct) relatively quickly. While a full analysis of transient behavior is outside the scope of the present work, our model does support the possibility of fast exclusion when frequency or habitat proportions are changed (Figures B.3–B.4). Interestingly, the community is more robust to changes in disturbance intensity. Figure 4d shows much larger overlap between the coexistence regions for different intensity parameters, meaning that changing intensity by a small amount is less likely to change the community membership than changing frequency in this situation. Our results so far have focused on a fixed set of fecundities. Since fecundities only appear in the coexistence criteria (Equation 5) as invader-resident ratios, it is only necessary to vary the fecundity of one species to assess sensitivity of community stability to species' fecundity. We include community outcome plots in the appendix (Figures B.1 and B.2), which show that shifting fecundity shifts coexistence regions in a fairly intuitive manner: Because the ratios of fecundity appear inside logarithms in Equation (5), changes to fecundity result in nearly linear transformations of the coexistence regions, and higher worm fecundity allows that species to persists with lower establishment abilities in either habitat type.

4 | DISCUSSION

The fecundity–tolerance trade-off constitutes an alternative to CCT models that can be applied to communities where the species traits necessary to form a CCT are not present. Our results demonstrate that, relative to a temporally constant environment, disturbance can increase the size of coexistence regions, and allow for ASE. Our findings show that a variety of

FIGURE 4 Regions of coexistence and conditional exclusion, for a range of disturbance frequencies and intensities. (a, c) Intensity is fixed at $I = 0.5$, frequencies range $F = 0.15, 0.2, 0.3, 0.4, 0.5\ 0.7, 0.99$, lower frequencies shaded darker. (b, d) Frequency is fixed at $F = 0.1$, intensities range $I = 0.15, 0.2, 0.3, 0.4, 0.5\ 0.7, 0.99$, lower intensities are shaded darker. All other parameters are as in Figure 1. Panels e and f show a comparison of how changes to I and F alter total diversity. Changing F has very little overlap in coexistence regions, indicating altered diversity is likely. In contrast, changes in I have larger overlap, particularly in the region of establishment space that worms are thought to occupy (elliptical regions)

fecundity–tolerance interactions can lead to coexistence, and that fecundity and tolerance need not trade-off to produce this stabilizing effect. Rather, species need only be sufficiently distinct in their establishment abilities to coexist. Additionally, we show that the long-term persistence of these strategies depends on habitat availability (Figure 3). Trade-offs certainly can occur in real systems, and they can provide a key theoretical concept for understanding how communities behave (Miller & Chesson, 2009; Tilman, 1994). Increasingly, researchers have been interested in studying life-history strategies that are not limited by a priori assumptions about how trait parameters interact (Seifan, Seifan, Jeltsch, & Tielbörger, 2012). Our work also advances this perspective and illustrates some cases in which the assumption of trade-offs artificially limits the explanatory power of a model. By considering the strategy space more
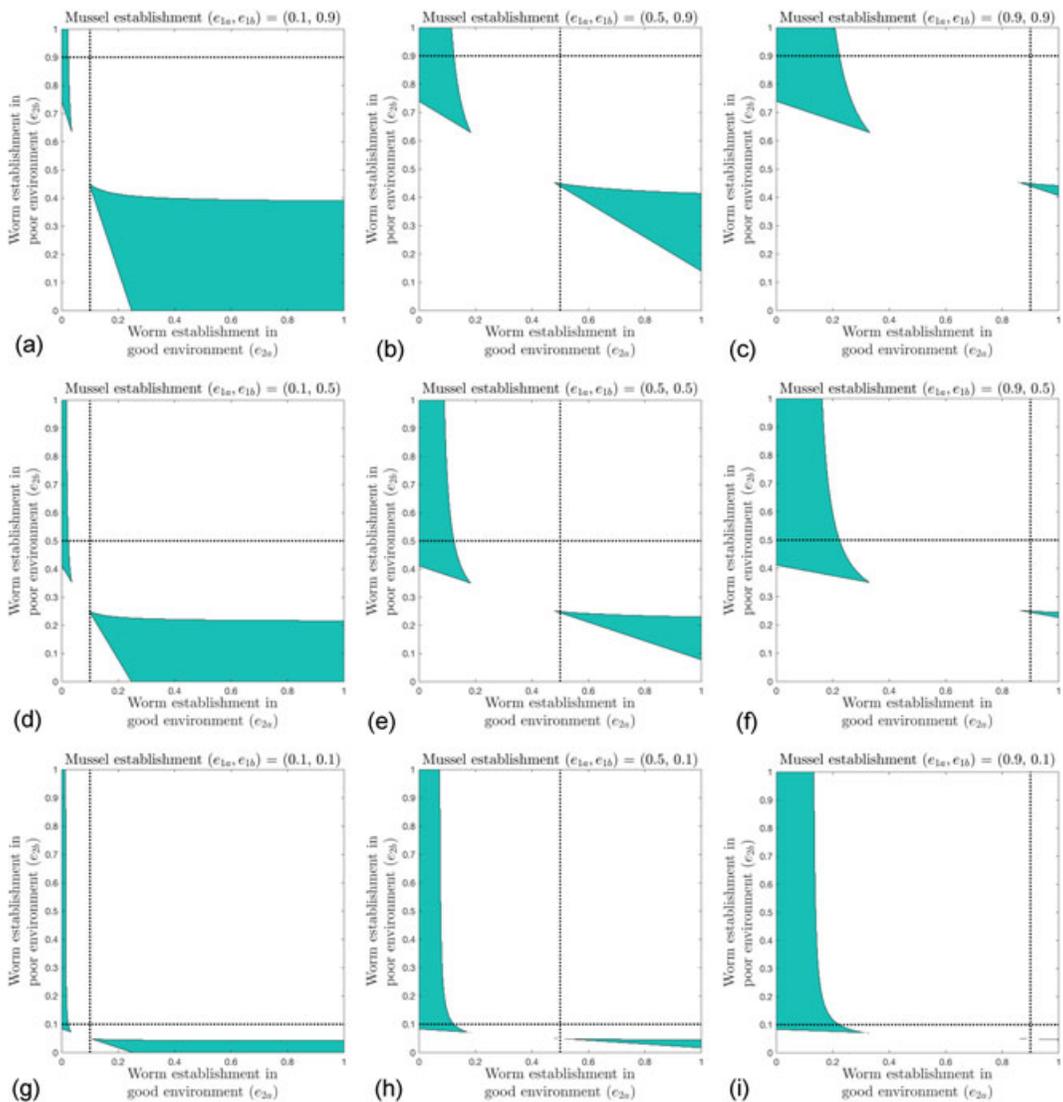
FIGURE 5 Coexistence regions across tubeworm establishment parameters, plotted for an array of mussel establishment parameters. Mussel establishment parameters are noted on each panel (a-i), with all other parameters as in Figure 1. Dashed crosshairs indicate point of mussel establishment strategy in the parameter space

broadly, we demonstrate how other types of fecundity–tolerance strategies can coexist. For example, Figure 5a–i shows how some coexistence scenarios are well described by a fecundity–tolerance trade-off: All the portions of coexistence regions in the lower right quadrant of the mussel establishment crosshairs satisfy the trade-off, because the worm species with higher fecundity has lower tolerance. However, portions of the coexistence regions that occur in the upper-left regions of the crosshairs are not well described by a within-species trade-off, because such a worm species would have both higher fecundity and higher tolerance. Nevertheless, where fecundity and tolerance do trade-off, our results are generally consistent with prior work (Muller-Landau, 2010).

Our work also illustrates how disturbance can affect the types of strategies that can lead to coexistence via fecundity–tolerance strategies. Compared to a constant environment (i.e., the no disturbance case), disturbance can promote coexistence, but also promote extinction, depending on species' traits. In communities that have been subject to relatively stable disturbance regimes over evolutionary timescales, changes to the disturbance regimes can have either mild or drastic consequences, depending on the aspects of disturbance that are altered, as well as species' life-history traits. For example, our results show that changes in disturbance frequency may be more likely to change community composition than equivalent changes in intensity.

While our model only considers two species at a time, it reflects some of the different strategies that are likely used by vent species. In fact, since our analyses are exhaustive with respect to establishment strategies, many parameters we investigate do not describe traits consistent with empirical descriptions of tubeworms (e.g., top left regions of Figure 1b,d). However, this strategy of very high establishment in low-resource habitat, coupled with very low establishment in high-resource habitat and high fecundity is consistent with a species of clam that co-occurs with *B. thermophilus* at the EPR, namely *Calyptogena magnifica* (Fisher et al., 1988a; see also Figure 5).

Compared to the case of a constant environment, disturbance in our model adds further potential coexistence mechanisms, and increases the number of strategies that can lead to coexistence. Our model is designed to disallow the well-studied mechanism of coexistence via competition–colonization trade-offs, so that effects of fecundity–tolerance strategies can be isolated. However, CCT and fecundity–tolerance trade-offs are potentially compatible mechanisms, further enriching possibilities for coexistence. Understanding the interactions between fecundity–tolerance and competition–colonization mechanisms will be a fruitful area of future research in the maintenance of high species diversity.

Our findings have direct implications for the mineral extraction industry's rapidly developing plans to exploit the rich mineral resources associated with hydrothermal vents (Van Dover, 2011). While vent species are adapted to live in disturbance-prone environments, anthropogenic disruption (removal) of substrate will change the effective disturbance frequency, and possibly habitat quality. In our model, changes to disturbance frequencies can change communities by causing local extinction, and the effect of changing disturbance frequency is generally stronger than that of changing intensity. Mining may also change the spatial autocorrelation of disturbance, which can affect community composition (Liao et al. 2016). Altered disturbance regimes are also generally believed to be a key factor in successful species invasions, which can further alter community structure (Moles et al., 2012; Moles, Gruber, & Bonser, 2008). Our present findings, and our other research on different aspects of disturbance (Garrison, Miller, Roxburgh, & Shea, 2012; Miller et al., 2011; Miller, Reilly, Bauman, & Shea, 2012; Miller, Roxburgh, & Shea, 2012), will be valuable for guiding

researchers and resource managers in determining the potential effects of such operations, and understanding the impacts of early mining operations.

While we have focused on hydrothermal vent communities at the EPR, our model can be applied to other systems as well. Communities at other hydrothermal vent systems, such as those found at the Lau basin, are characterized by different macrofaunal assemblages than the EPR, but the coexistence of mussels and the various snail species at Lau can also be explored with our model, because the species display different stress tolerances (Henry, Childress, & Figueroa, 2008; Podowski, Ma, Luther, Wardrop, & Fisher, 2010), and the system is similarly disturbance-prone. Though snails are motile, this does not pose a problem for our model given the lottery model was originally developed for coral reef fishes (Chesson & Warner, 1981; Sale, 1977). Some terrestrial plant communities also fit our model assumptions. For instance, oasis communities have plants with varying water requirements, and similar dispersal mechanisms (e.g., zoochory). Indeed, vent systems are often called oases of the deep sea, and this analogy is apt at the level of our model description. Additionally, riparian plant communities also display gradients in species' water demands, and are subject to flooding disturbance. Finally, the fecundity–tolerance model of coexistence was developed for tropical forests, and our extensions to study the effects of disturbance allow our model to address the effects of, for example, hurricane disturbance in those communities (Boucher, Vandermeer, Mallona, Zamora, & Perfecto, 1994). Thus, our model can be parameterized and extended to explore the effects of disturbance and fecundity–tolerance strategies on coexistence and diversity in a wide variety of ostensibly different communities, because species display conceptually similar trait patterns, and different disturbance types can have ecologically similar effects.

In conclusion, our model shows that communities of disturbance-adapted species are not immune to changes in disturbance regimes. Though many species have evolved to succeed in disturbance-prone environments, alterations to frequency and intensity of disturbances can cause significant changes to community structure and composition.

ACKNOWLEDGMENTS

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