# The role of environmental generalist species in ecosystem function

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## Abstract

We constructed a Lotka–Volterra-like competition model to study the role of environmental generalists in maintaining ecosystem function under a range of species richnesses and environmental conditions. Ecosystem function was quantified as community biomass, proportion of initial species that coexist through time, and resilience and resistance to perturbation. Generalist and specialist species were created that differed in their realized growth rates under suboptimal environmental conditions. Generalists were more tolerant of suboptimal conditions but specialists grew faster when conditions were optimal. Model simulations were performed involving generalist-only and specialist-only communities comprised of 4–100 species under constant and cyclical environmental conditions. We used pulses applied to biomass to estimate resilience and pulses applied to the environment to estimate resistance. We also simulated 4-species and 100-species mixed communities of generalists and specialists under the same cyclical environmental conditions. Analysis of model predictions was performed after all simulations reached quasi-equilibrium. Comparisons of total community biomass, proportion of initial species coexisting through time, resilience, and resistance under constant and cyclical environmental conditions showed that, in some situations, a species-poor community of generalists can have equal or greater ecosystem function than a species-rich community of specialists. Results from the mixed community simulations confirmed these results. Our analyses suggest that the environmental tolerances of species can be an important consideration in determining ecosystem function, and should be considered in asking whether all species, or certain key species, drive the positive relationship between diversity and ecosystem function.
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## 1. Introduction

Ecologists have debated the relative benefits of generalization versus specialization for decades. Generalist and specialist species have been defined

in terms of the breadth of prey types they utilize or by the breadth of environmental conditions under which they thrive. Several studies have asserted that generalists could never outperform specialists due to the inherent extra costs associated with generalists being able to accommodate multiple prey types or variable environments (i.e., 'jack-of-all-trades is master of none') (Principle of Allocation, Levins, 1968; Pianka, 1978). The physiological plasticity that allows generalists to be tolerant of variable environmental conditions also has increased energetic costs (DeWitt et al., 1998; Coustau et al., 2000; Agrawal, 2000; van Kleunen et al., 2000). Thus, under optimal conditions specialists tend to outperform generalists. When the environment is variable or unpredictable, however, the costs associated with being a generalist may be small in comparison to the benefits of the increased behavioral, physiological, or phenotypic plasticity, and the generalist may be favored (Bergman, 1988; Parsons, 1994; Rutherford et al., 1995). Whether there is always a cost of being a generalist (cost of plasticity) is still under dispute; these costs have been demonstrated in certain instances (Wilson, 1988; Kawecki, 1994; Steinger et al., 2003) and refuted in others (Huey and Hertz, 1984; Relyea, 2002; Palaima and Spitze, 2004). The difficulty in measuring these costs reflects the complexity of organisms' responses to environmental conditions, which can include either expensive costs of producing and maintaining tolerance to a range of environmental conditions or inexpensive solutions such as the elimination of existing processes that prevent environmental tolerance (Bergelson and Purrington, 1996). Linkage disequilibrium may also confound the ability to accurately measure costs of plasticity.

The tradeoff between the costs and benefits of being a generalist can influence their performance relative to specialists. We might predict that a generalist will outperform a specialist under suboptimal environmental conditions in which the costs of generalization are small relative to the reduction in performance of the specialist. Measurement of competitive outcomes under variable environmental conditions is tractable in the laboratory (e.g., Kirk, 2002), but it is difficult to extrapolate the results to the natural system. Ideally, one would compare the relative performances of generalists and specialists when they co-occur in natural conditions. However, comparisons under natural conditions are confounded by the multitude of biotic and abiotic interactions, as well as indirect effects, that affect populations (Lawton, 2000; Wootton, 2002).

One way we can compare the performance of generalists and specialists is by using mathematical models to assess the ecosystem function of communities composed of various combinations of species types (e.g., Wilson et al., 2003). Ecosystem function is measured in a number of ways, including total biomass, temporal stability, and the nature and magnitude of the community response to perturbations (resilience and resistance) (Loreau et al., 2001). All of these measures are amalgams of the influences of both biotic characteristics of the community (e.g., species traits, species richness, strength of competitive interactions, complexity) and abiotic environmental conditions. Use of models allows for general understanding of the relative contribution of generalists and specialists to ecosystem function under controlled and contrived conditions. Models allow for the formulation of communities comprised of different numbers of species (richness) involving various mixes of generalists and specialists, and for these communities to be placed into a range of environmental (e.g., stable, cyclic, variable) conditions.

One mechanism that maintains ecosystem function under variable environmental conditions is the complementary responses of different species (Frost et al., 1995; Doak et al., 1998; Yachi and Loreau, 1999; Brown et al., 2001). In a species-rich community, different specialist species could dominate as the environment changes. However, complementary responses of specialist species may not be necessary to maintain ecosystem function under suboptimal or variable conditions. For example, if the cost of generalization is less than the cost of coping with the environmental fluctuations, generalist species may contribute to ecosystem function over all environmental conditions. In this situation, community composition would not change dramatically in the way we would expect from the complementary responses of specialists. Rather, the generalist species would dominate the community across a wide range of environmental conditions, such that not only community biomass but also community composition would be stable. The role of generalists in ecosystem function has not been fully explored, particularly in comparison to the performance of specialists under similar environmental conditions.

To investigate the influence of generalists on ecosystem function, we modeled and compared the ecosys-

tem function of communities comprised of generalist and specialist species. The model is based on a modified version of the Lotka–Volterra competition equations (May, 1974) where species performance was determined by their breadth of environmental tolerance (generalist versus specialist), environmental conditions, and the number and traits of the other species with which they compete. The costs of environmental tolerance were decomposed into constitutive costs (costs of plasticity, incurred regardless of conditions) and induced costs (incurred only when conditions deviated from optimal). We defined generalists as having higher constitutive costs and lower induced costs, while specialists had lower constitutive costs and higher induced costs.

We analyzed model communities comprised of only generalists, only specialists, and equal numbers of generalists and specialists for communities ranging from 4 to 100 species. Community dynamics were simulated under constant, pulsed, and cyclical environmental conditions until equilibrium or quasi-equilibrium conditions were obtained. We compared ecosystem function, as reflected in total biomass, proportion of initial species that coexist through time, and resilience and resistance to perturbation, for each of the three types of model communities in the different environments. Ecosystem function has been defined many different ways (e.g., Tilman, 1999; Symstad and Tilman, 2001). Our suite of ecosystem function response variables used in this paper are generally representative of the types of response variables commonly used in other studies.

Our general community model can be thought of in the context of marine phytoplankton. Marine phytoplankton are found in species-poor and species-rich communities, and individual phytoplankton species exhibit strategies for resource gathering and tolerances to suboptimal environmental conditions that could be likened to our treatment of generalists and specialists (Zeitzschel, 1978; Parsons, 1994; Reynolds, 1997).

## 2. Materials and methods

### 2.1. Model description

We modeled the growth of a multispecies phytoplankton community using a system of Lotka–Volterra-like competition equations. All species shared a global carrying capacity ($K$); species differed in their traits that affect their responses to environmental conditions. The traditional Lotka–Volterra competition equations for two species are:

$$\frac{dN_1(t)}{dt} = r_1 \cdot N_1 \cdot \left(1 - \frac{N_1 + \alpha_{12} \cdot N_2}{K_1}\right) - d_1 \cdot N_1 \tag{1}$$

$$\frac{dN_2(t)}{dt} = r_2 \cdot N_2 \cdot \left(1 - \frac{N_2 + \alpha_{21} \cdot N_1}{K_2}\right) - d_2 \cdot N_2 \tag{2}$$

This form of the equations includes the terms $r_i$ and $d_i$ as constants of proportionality for growth and death, respectively, and has been used in a number of Lotka–Volterra models (e.g., Doncaster et al., 2000; Pound et al., 2002).

We modified and expanded the traditional Lotka–Volterra model. We divided the growth term into two components: the maximum growth rate, $gb_i$, and the reduction in growth rate due to the constitutive cost of stress, $gc_i$. The latter term represents the cost of maintaining tolerance to a wide range of conditions, independent of environmental conditions. We also added a term for the constituent costs of coping with stress (i.e., dealing with suboptimal conditions), and we defined the carrying capacity as a global level shared by all species. Finally, we expanded the two-species model to simulate multiple species. In our modified model, the daily change in biomass of each species $i$ at time $t$ ($N_i(t)$) was:

$$\frac{dN_i(t)}{dt} = \left((gb_i - gc_i) \cdot N_i(t) \cdot \left(1 - \left(\frac{N_i + \left(\beta_{ij} \cdot \left(\sum N_i(t) - N_i(t)\right)\right)}{K_i(t)}\right)\right)\right) - (gs_i(t) \cdot N_i(t)) \tag{3}$$

where $\beta_{ij}$ is the interspecific competition coefficient representing the competitive effect of an individual of species $i$ on an individual of species $j$, $gs_i(t)$ is the induced cost of stress, and $K_i(t)$ is the carrying capacity of the environment for species $i$. The units of $gb_i$, $gc_i$, and

Table 1
Model parameters and values assigned to generalist and specialist species

| Variable or Parameter | Values | Descriptions and explanations |
| --- | --- | --- |
| $eo_i$ | Varies within 0.0–1.0 | *Optimal environmental condition:* when the environment is at the optimal value ($e = eo_i$) then species i experiences the lowest cost of stress; values for $eo_i$ were randomly assigned to species |
| $\beta_i$ | 0.50 | *Interspecific competition term:* $\beta_i = 0.5$ was used for all species; 0.5 was chosen as midpoint between no competition (0.0) and competition equivalent to conspecifics (1.0) |
| $K_i$ | Varies by species | *Carrying capacity of species I:* $K_i$ varies by species and time (day), depending on the global carrying capacity ($K = 1000$) and the biomasses of the other species in the community |
| $N_i$ | Varies over time | *Population size of species i:* initial values of $N_i$ were set to 0.1 for all species; low initial population size starts growth under density-independent conditions to allow all species a chance to establish |
| $gb_i$ | 1.75 | *Baseline phytoplankton growth rate:* $gb_i$ was set to 1.75 for all species; this is a typical near-maximum growth rate for phytoplankton (Parsons et al., 1984) |
| $gc_i$ | Varies by species | *Constitutive cost of stress:* values in the interval of 1.4–1.6 were used for generalists and values in the interval 0.0–0.1 were used for specialists; the maximum value of 1.6 was the largest value that still permitted positive population growth in all environmental conditions |
| $gm_i$ | Varies by species | *Induced cost of stress:* induced costs were always assigned so that they were higher for specialists than for generalists; three intervals were used*: low (0.0–0.05 for generalists and 0.5–1.25 for specialists), intermediate (0.05–0.1 for generalists and 0.75–1.5 for specialists), and high (0.15–0.2 for generalists and 1.25–2.0 for specialists) |

Three intervals of values (low, intermediate, and high) are shown for the induced cost of stress (gm).

$gs_i$ are 1/day, $N_i(t)$ and $K_i(t)$ are in units of population size (biomass), and $\beta_{ij}$ is unitless (Table 1).

All species were assigned the same gb and the same $\beta$ values. $gc_i$ was assigned species-specific values that did not vary over time. $gs_i(t)$ was species-specific and varied daily depending on the environmental conditions, while $N_i(t)$ and $K_i(t)$ varied daily due to the dynamics of other species. Values for all of the model parameters are listed in Table 1. We include the species subscript $i$ and time $t$ notation when needed for clarity. Simulations were performed for various combinations of environmental generalists and environmental specialists in communities comprised of 4–100 species, representing extremely low and moderate to high phytoplankton species richness (Makarewicz, 1993; Reynolds, 1997). All simulations were run for the longer of either 400 days or completion of 10 environmental cycles.

The induced cost of stress ($gs_i$) depended upon environmental conditions. The environment ($e$) was defined as a continuum between 0 and 1, and environmental conditions were specified in simulations as either constant or cyclical. The realized induced cost of stress for species $i$ at time $t$ ($gs_i(t)$) depended upon how much the specified environment deviated from the optimal environment ($eo_i$) for that species:

$$gs_i(t) = gm_i \cdot |e(t) - eo_i| \qquad (4)$$

where $gm_i$ is the slope of a line relating stress to the deviations of $e$ from $eo_i$. $gm_i$ can be considered the sensitivity of a species to stress; low values imply small responses to suboptimal environmental conditions. Suboptimal conditions are considered to be any conditions in which $e$ deviates from $eo_i$ for species $i$; the further the deviation, the greater the degree of suboptimality. The final term in the Lotka–Volterra competition equation (equation (3)) is therefore the reduction in growth due to poor environmental conditions.

Carrying capacity ($K$) was represented as a constant over time and was a global level shared by all species. At each time $t$, the carrying capacity of species $i$ ($K_i(t)$) was calculated to adjust for the biomass and competitive effects of all other species. We defined an interspecific competition term, $\beta_{ij}$, as the competitive influence of species $j$ on species $i$. For all simulations, $\beta_{ij}$ was set to 0.5 (Table 1), which implies that two individuals of another species affect the carrying capacity to a degree equivalent to one conspecific

individual. Given equal $\beta_{ij}$ values (denoted $\beta$), we computed the carrying capacity of species $i$ at time $t$ as:

$$K_i(t) = K - \sum_i N_i(t)\beta - N_i(t)\beta \qquad (5)$$

where $K$ is the global carrying capacity. The second term in equation (5) is the total effective biomass of the community, adjusted for interspecific competition, and the third term removes the effects of species $i$. The value of $K_i$ at any given time is the highest biomass that species $i$ could achieve (i.e., total community biomass would equal $K$), if all other species stayed at their current biomasses. Our definition of the global carrying capacity is slightly different from other treatments, where $K_i$ is more commonly calculated as the carrying capacity of species $i$ if it existed in isolation (i.e., no competition) (e.g., Doncaster et al., 2000; Byers and Noonburg, 2003). Our global carrying capacity is constrained such that the carrying capacities of all species present ($\sum K_i$) must sum to $K$, usually defined as a constant (e.g., Case, 1990).

## 2.2. Environmental generalists and environmental specialists

Three parameters (traits) described a species' response to the environment: the constitutive costs of stress (gc), the induced costs of stress (gm), and the species' optimal environmental condition (eo). Generalists were defined as having high gc values but low values of gm, while specialists were defined as having low gc values and high values of gm. A high gc value implies relatively high constant costs of maintaining the ability to tolerate many environmental conditions; a low gm value implies high relative tolerance or low sensitivity as the environment deviates from optimal conditions. Generalists had lower realized growth rates than specialists under optimal conditions, but incurred smaller reductions in growth rate when the environment deviated from optimal conditions. These parameters (gc and gm), and the presumed negative relationship between them, are in accordance with the theory that a fitness tradeoff exists between generalists and specialists (Sevenster and van Alphen, 1993; Egas et al., 2004; Palaima and Spitze, 2004). Our gc and gm correspond to the constitutive and induced costs (sometimes called mainte-

nance and production costs) reported in the literature on the costs of plasticity (e.g., DeWitt et al., 1998). It is important to note that there is also a competing theory in the literature (the resource breadth hypothesis), which states that resource generalists are able to both exploit a wide range of habitats and achieve higher densities in those habitats than specialists (Krasnov et al., 2004).

The costs of stress (gc, gm) were negatively correlated to each other for all species. The cost of being able to tolerate suboptimal environmental conditions (i.e., low gm value) was assumed to be higher constitutive costs (i.e., high gc value). These kinds of constitutive and induced costs of stress are considered to vary with the degree of phenotypic plasticity exhibited by a species (DeWitt et al., 1998).

For each simulation, values of the three traits (eo, gc, gm) were randomly assigned to each species from specified uniform probability distributions. To ensure adequate coverage of the possible trait values for differing number of species, we used a stratified sampling approach for assigning values of eo, gc, and gm to species. The range of possible values for a trait (Table 1) was divided into a number of intervals equal to the number of species in a simulation. For eo, an interval was randomly assigned (without replacement) to a species. A value was then randomly selected from within each interval. For gc and gm, the intervals were numbered, randomly assigned to first gc, and then the opposite interval was assigned to gm (e.g., for nine species, interval 2 assigned to gc implied interval 8 was assigned to gm). Once the intervals were assigned, values were randomly and independently selected from within the intervals for gc and for gm. Thus, the values of gc and gm assigned to a species were negatively correlated with each other but with some noise, and both were independent of the value of eo assigned to the species. We configured communities comprised of only generalists, only specialists, and an even mix of generalists and specialists.

By our definition of species types and traits, communities of specialists contained species with greater variability in their induced costs of stress (gm) than corresponding communities of generalists (Table 1). However, the ranges of values of gm did not overlap between specialists and generalists within any given simulation.

### 2.3. Environmental conditions

We performed simulations using constant and cyclical environmental conditions. Constant conditions maintained the environmental value (*e*) at a fixed value (between 0.0 and 1.0) throughout each simulation. Under cyclical conditions, the environment fluctuated in a sinusoidal pattern between the two environmental extremes of 0.0 and 1.0. We varied the period of the cycle from 0.1 days to approximately 820 days. The short period cycles correspond to much less than the 1–2 day turnover time of phytoplankton populations (Parsons et al., 1984). The longer period cycles correspond to seasonal, annual, and multi-year cycles in environmental conditions (Karentz and Smayda, 1998; Thomas and Strub, 2001).

As part of our analysis under constant environmental conditions, we used pulses on biomass to estimate resilience and used pulses on the environment to estimate resistance. Resilience is the ability for a community to recover from a perturbation; resistance is the degree to which a community withstands a perturbation (Grimm and Wissel, 1997). For estimation of resilience, the biomasses of all species in the community were reduced by a fixed percentage on day 100 of the 400-day simulations; resilience was defined as time (days) for the community biomass to regain 90% of its pre-pulse biomass. To estimate resistance, the 400-day simulations were run for 100 days with an environmental condition of zero. On day 100, a single 4-day pulse of new environmental conditions was imposed, after which the zero environmental condition was restored for the remaining 296 days of the simulation. We measured resistance as the proportion of unperturbed biomass, computed as the ratio of the lowest biomass (during or after the pulse) to the biomass on day 100. Values of the proportion unperturbed near one imply high resistance.

### 2.4. Design of simulations

Simulations were performed to address the following questions. (1) Under constant environmental conditions can a community of environmental generalists have greater ecosystem functioning (biomass, stability, maintenance of species richness) than a community of environmental specialists? (2) Do the results of simulations in cyclical environments differ from results obtained in a constant environment? (3) Are the results based on communities of either only generalists or only specialists robust when both species types coexist in a community? Three sets of simulations were performed to address these three questions.

#### 2.4.1. Question 1

Generalist-only and specialist-only communities comprised of 4, 9, 16, 25, 36, 49, 64, 81, and 100 species were simulated in a constant environment. We simulated environmental conditions ranging between 0.0 and 1.0. Because results were similar across environmental conditions, we show only the results of simulations with the environment (*e*) set to 0.0. The induced cost of stress (gm) was assigned from ranges that did not overlap between generalist and specialist types (intermediate intervals for gm in Table 1).

We report average community biomass (proportion of *K*), proportion of initial species coexisting, resilience, and resistance for the generalist-only and specialist-only communities. Biomass and proportion of species coexisting were computed from daily averages (over 20 replicate simulations) for days 51–400; total biomass of all communities reached equilibrium well prior to day 400. Resilience and resistance were computed for all levels of species richness; we show only the results from simulations with the extreme lowest level of 4 species and the highest level of 100 species. Resilience was computed from 10, 20, 30, 40, and 50% reductions in biomass on day 100. Resistance was computed from environmental conditions pulsed to 0.2, 0.4, 0.6, 0.8, or 1.0 for days 100–103.

#### 2.4.2. Question 2

Simulations were performed in a cyclical environment and with gm further subdivided into low, intermediate, and high intervals (Table 1). Communities of 4 species and 100 species, with each of the low, intermediate, and high intervals for gm, were used for both generalist-only and specialist-only communities. Each of these communities was simulated using cycle periods of 0.1–820 days. We report community biomass (proportion of *K*), averaged over day 51 to the end of the simulation, for each combination of species number and the three gm intervals. We also report the proportion of initial species coexisting, also averaged over the time from day 51 to the end of the simulation, for all cycle periods using the intermediate interval of gm.

### 2.4.3. Question 3

The third set of simulations involved the mixed-species communities under cyclical environmental conditions. All species used the intermediate interval for gm (Table 1), and the mixed community was composed of equal numbers of generalist and specialist species. Four-species and 100-species communities were simulated for cycle periods of 0.1–820 days. We report the community biomass and the proportion of generalist species, computed as the average from day 51 to the end of the simulation. We weighted the average proportion of generalist species by the biomasses of each species present at each time step.

### 2.5. Initial conditions, solution method, and replication

Initial biomass was set to 0.1 for all species in all simulations. If the biomass of a species dropped below 0.1, its biomass was reset to 0.1 in order to guard against complete extinction and to enable recolonization under possibly future favorable conditions. Setting densities to a minimum is realistic for communities that would likely experience immigration after local extinction. Species with biomass equal to 0.1 were ignored in all calculations of model outputs.

All statistics related to model simulations were based on daily values of species' biomasses. The model was coded in Fortran95 and the system of differential equations was solved using a fourth-order Runge–Kutta method. For constant environment and cyclic environments with period equal to or greater than 5 days, we used a daily time step to solve for daily biomasses. For cyclic environments with periods less than 5 days, we used a time step equal to one-fifth of the cycle period in order to ensure adequate sampling of the environmental cycles. We averaged predicted biomasses at each time step to predict daily values. We ran 20 replicate simulations for each combination of richness and environmental conditions. Each replicate differed in the values of traits (eo, gc, and gm) assigned to each species. In order to assure our results were robust to the numerical integration, we reran the model using finer time steps (e.g., 10 times per day, and 100 times per day) and confirmed that the model predictions exhibited the same behavior as with our daily time step.

We report mean values computed over the 20 replicate simulations. Between-replicate variability was generally small relative to the differences in mean values across different conditions. The within-replicate standard deviation of mean biomass was generally less than 5% of mean biomass for both generalist-only and specialist-only communities. The within-replicate standard deviation in the proportion of species coexisting was generally less than 8% of the mean species coexistence values in generalist-only communities, but varied much more (5–42% of mean species coexistence) in specialist-only communities. We examined a number of different levels of species richness and environmental conditions in order to be confident that any emergent patterns were real and reflected model behavior rather than chance effects.

## 3. Results

### 3.1. General patterns

Time series plots of species biomasses are shown in Fig. 1 for simulations with nine generalists species and nine specialist species under constant environmental conditions, a short (4-day) cycle period, and a long (200-day) cycle period. These results show the typical behavior of the model of a monotonic increase in individual species biomass to the global carrying capacity under constant environmental conditions (Fig. 1a and b), the coexistence of multiple species under short cycle period conditions (Fig. 1c and d), and the shifts in community composition and dominance under long cycle periods (Fig. 1e and f) as species track relatively slowly changing environmental conditions.

### 3.2. Question 1: generalist versus specialist communities in constant and pulsed environments

Under constant environmental conditions the generalist-only communities generated similar biomass (Fig. 2a), but maintained a higher proportion of coexisting species (Fig. 2b) than the specialist-only communities. Equilibrium biomass of both communities was nearly equal to the global $K$ value (Fig. 2a). The patterns shown in Fig. 2, based on the environment equal to zero, were consistent across the range of environmental conditions (0.0–1.0).
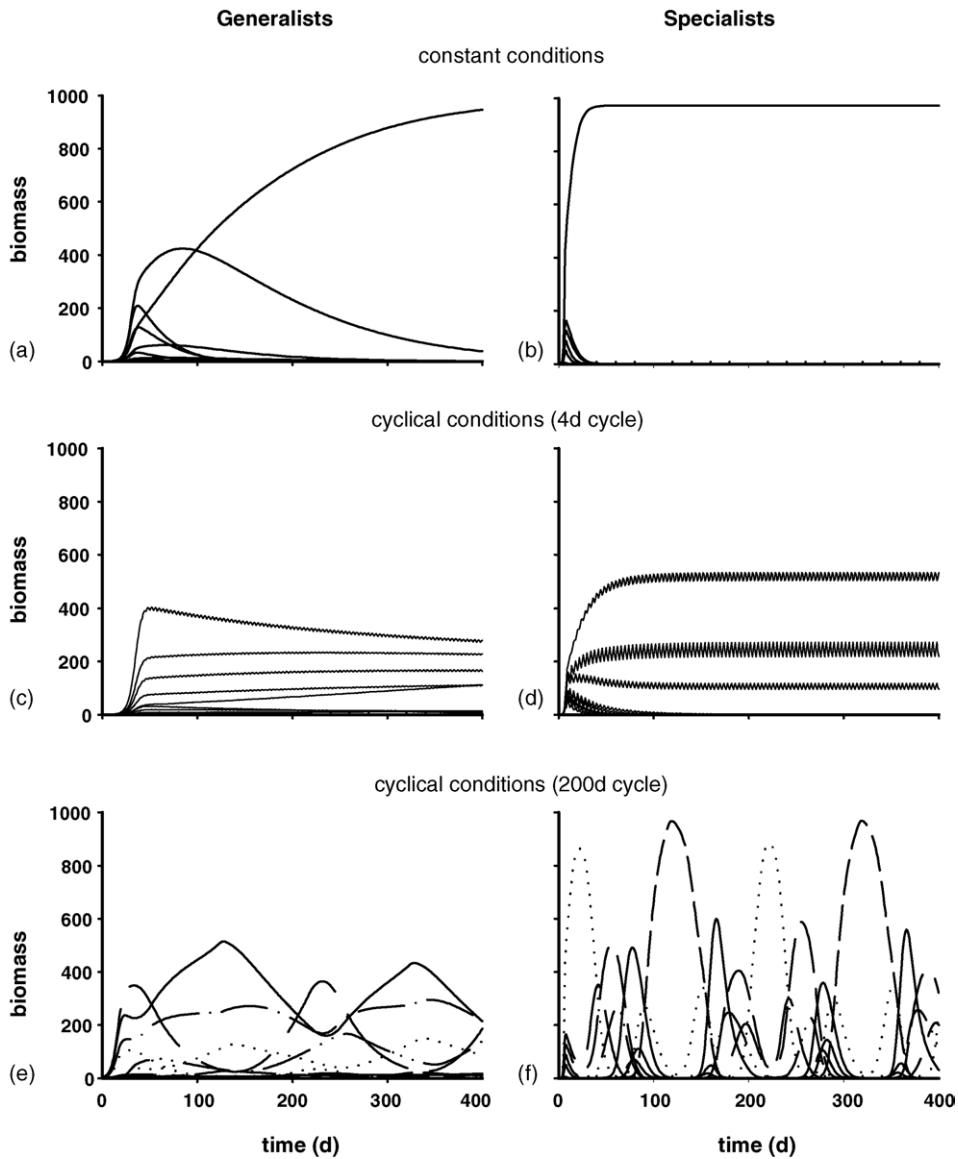
Fig. 1. Daily simulated biomass of individual species over a 400-day model run for nine species communities of generalists only and specialists only under constant environmental conditions, cyclical environmental conditions with a short (4-day) cycle period, and cyclical environmental conditions with a long (200-days) cycle period. (a) generalists in constant, (b) specialists in constant, (c) generalists in short cycle, (d) specialists in short cycle, (e) generalists in long cycle, and (f) specialists in long cycle.

The generalist-only community had a lower resilience (longer time to recovery), but a higher resistance (higher proportion of biomass unperturbed by pulse) compared to the specialist-only community (Fig. 3). These differences between community types increased with the magnitude of the biomass reduction (for resilience) and with the magnitude of the environmental pulse (for resistance). Species richness had little qualitative effect on the patterns of resilience and resistance, as the results were consistent between the 4-species and 100-species simulations.
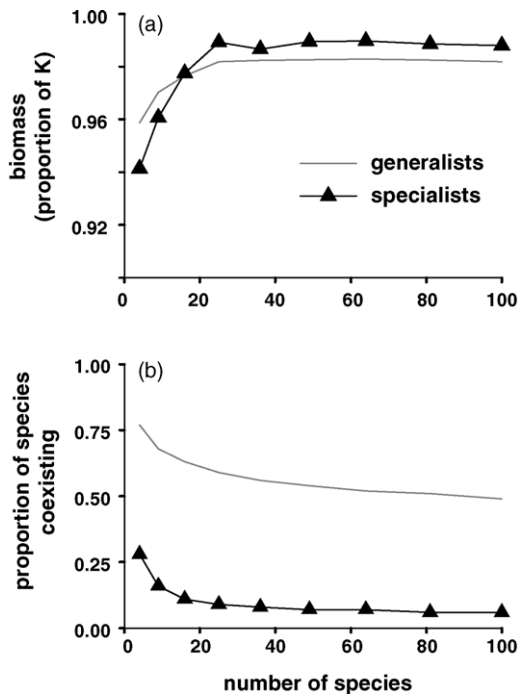
Fig. 2. Mean equilibrium biomass (a) and mean proportion of original species coexisting at equilibrium (b) for communities of generalists only (grey lines) and specialists only (black triangles) for increasing species richness. Environmental conditions were maintained at a constant value of zero. Mean equilibrium biomass was measured as the proportion of the global carrying capacity (*K*) realized.

### 3.3. Question 2: generalist versus specialist communities in a cyclical environment

While total biomass of the generalist-only and specialist-only communities was similar under constant conditions, generalists had higher biomass under some, but not all, of the cyclic environmental conditions. Whether the communities of generalists or specialists achieved higher average biomass was a complicated function of the values of the induced cost of stress (gm), the cycle period, and species richness. Average biomass of both community types generally increased with longer cycle periods (rising lines in Fig. 4a–c) and greater species richness (sold circles above open circles and solid triangles above open triangles in Fig. 4a–c). Average biomass also generally decreased with increasing intervals of gm for a given

cycle period (decreasing biomass from Fig. 4a–c for a fixed cycle period).

The biomass achieved by the specialist-only communities increased progressively more with longer cycle periods and with increasing values of gm than the biomass of the generalist communities (Fig. 4a–c). At low values of gm, average biomass was always higher for the generalist communities (solid lines above dotted lines in Fig. 4a). Even the species-poor (4-species) generalist communities achieved higher biomass than the species-rich (100-species) specialist communities (open circle line above solid diamond line in Fig. 4a). For intermediate values of gm (Fig. 4b), average biomass of the specialist community increased more rapidly with cycle period than the biomass of the generalist community, and became similar to the generalist community for periods of 400 days and longer. Up to cycle periods of approximately 200 days, the species-poor (4-species) generalist communities did at least as well as the species-rich (100-species) specialist communities (open circle similar to solid triangle for less than 200 day cycle periods in Fig. 4b) At high values of gm, biomass of the specialist-only communities exceeded the biomass of the same richness generalist-only communities for cycles longer than about 100 days (open triangle above open circle and solid triangle above solid circle for greater than 100 day cycle periods in Fig. 4c). Species-poor (4 species) generalist communities had equivalent biomass to species-rich (100 species) specialist communities for cycle periods shorter than 25 days (open circle similar to solid triangle near the abscissa in Fig. 4c).

Consistent with the results under constant environmental conditions, species coexistence was higher in the generalist-only community than in the specialist-only community at all levels of species richness (open circle line above open triangle line and solid circle line above solid triangle line in Fig. 4d). In both types of communities, the proportion of initial species coexisting decreased as the cycle period increased (i.e., stable conditions caused lower coexistence).

### 3.4. Question 3: mixed community in a cyclical environment

The proportion of generalists in mixed species communities depended upon both initial species richness and cycle period (Fig. 5a). The mixed community was
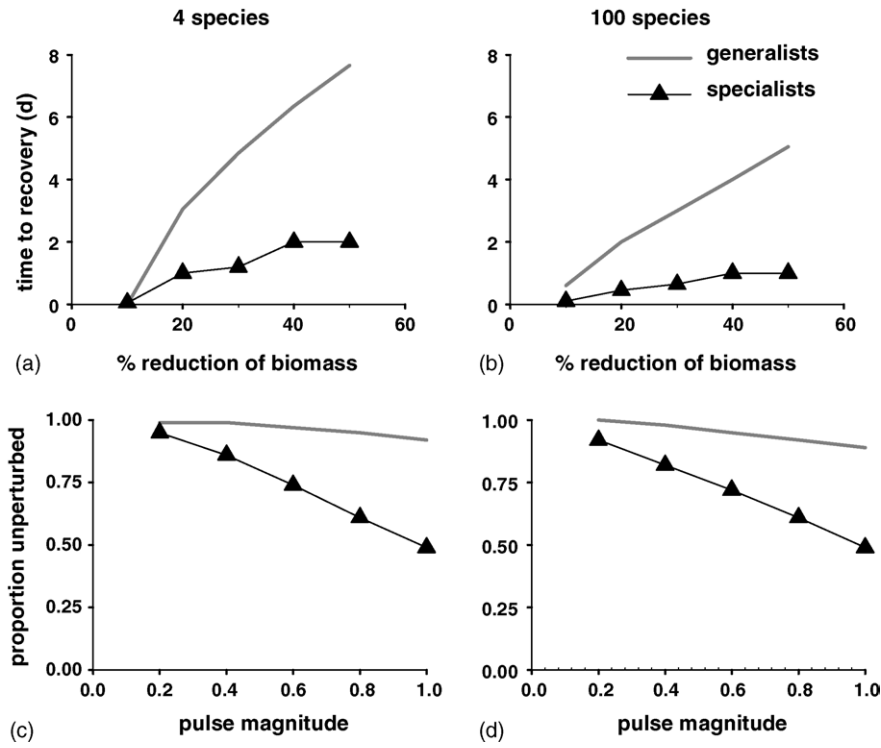
Fig. 3. Resilience and resistance of 4-species and 100-species generalist-only (grey lines) and specialist-only (black triangles) communities. Resilience was measured as the time in days for recovery to 90% of the pre-pulse biomass, and pulse strength is shown as the percent reduction in biomass. Resistance was measured as the proportion of pre-pulse biomass unperturbed by a 4-day long pulse, and pulse strength is shown as the magnitude of deviation in environmental conditions from a pre-pulse environment of zero. Resilience shown for (a) 4-species and (b) 100-species simulations; resistance shown for simulations with (c) 4 species and (d) 100 species.

dominated by generalists at virtually all cycle periods in the low richness (4-species) situation (open square line above 0.5 in Fig. 5a). In contrast, in the high richness (100-species) situation, generalists dominated only at cycle periods shorter than about 250 days (solid square line drops below 0.5 in Fig. 5a). For cycle periods of longer than 400 days, the 100-species mixed community was completely comprised of specialists (solid square line approaches zero in Fig. 5a). This shift in dominance from generalists to specialists as cycle period increased is consistent with the results obtained with generalist-only and specialist-only communities (i.e., increasing biomass of specialists with increasing cycle periods in Fig. 4a–c). Mean biomass of the mixed communities generally increased with species richness and cycle period (Fig. 5b), similar to the results of simulations with only one species type that used

the same (intermediate interval) induced cost of stress (Fig. 4b).

## 4. Discussion

### 4.1. Model predictions on the relative performance of generalists and specialists

We constructed this model to explore the conditions that could affect the relative contribution of generalists and specialists to the maintenance and stability of ecosystem function. We used total community biomass, species coexistence, resilience, and resistance to quantify ecosystem function. The model results indicate that generalists can disproportionately contribute to ecosystem function, especially
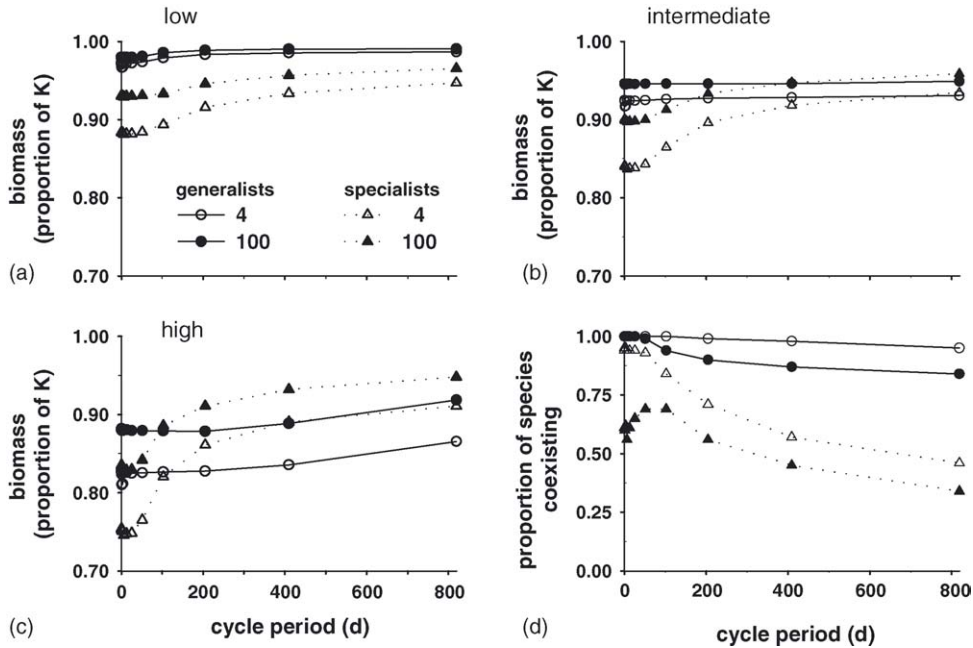
Fig. 4. Mean equilibrium biomass (a–c) and the mean proportion of the original species coexisting at equilibrium (d) in 4-species and 100-species communities of generalists only (solid lines and circles) and specialists only (dotted lines and triangles) for increasing cycle periods. Equilibrium biomass is shown for the low (a), intermediate (b), and high (c) intervals of the induced cost of stress (gm). Species coexistence in (d) is based on intermediate intervals of the induced cost of stress. Mean equilibrium biomass is measured as the proportion of carrying capacity ($K$) realized.

when environmental conditions fluctuate with short cycle periods. In addition, the presence of generalists can promote the coexistence of a greater number of species, both in constant and fluctuating environmental conditions, and across the range of species richness tested. Our analyses demonstrate that even with simple models of communities, the performance of generalists versus specialists in ecosystem function can be complicated.

We also showed that under highly variable environmental conditions a community comprised of generalists can outperform a similar richness community comprised of only specialists (Fig. 4). This was seen at short cycle periods as generalist communities having higher total biomass and a greater proportion of coexisting species compared to specialist communities for the 4-species case and the 100-species case. In some situations, the low species-richness (4-species) generalist-only community even outperformed the high species-richness (100-species) specialist-only community. For example, biomass of generalists was higher than specialists for all cycle periods for the low interval values

of gm (Fig. 4a), and for extremely short cycle periods for the intermediate and high interval gm values (Fig. 4b and c).

Species richness influenced the relative performance of generalists versus specialists. A larger number of species meant that, regardless of whether the species were generalists or specialists, there was a larger palette of traits from which to draw upon as environmental conditions fluctuated. High species richness in a community enabled that community to perform better under changing environmental conditions than a community with fewer species. Species richness affected biomass more strongly in specialist-only communities than in generalist-only communities (Figs. 2a and 4a–c). This result is consistent with empirical and theoretical work suggesting that system function increases with biodiversity (richness here) due to the increased likelihood that a more diverse community will contain at least one species that will perform well under any environmental conditions that arise (Hughes and Petchey, 2001; Loreau et al., 2002; Chesson et al., 2002).
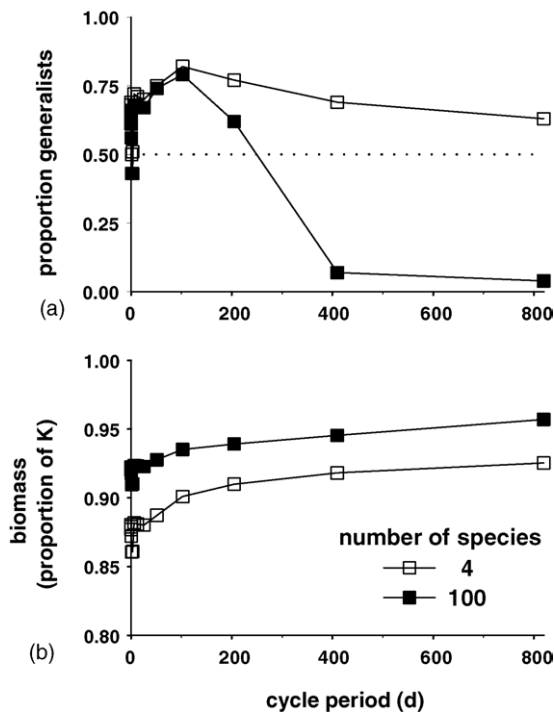
Fig. 5. Mean proportion of species that are generalists at equilibrium (a) and mean equilibrium biomass (b) for increasing cycle periods for mixed communities of 4-species (open squares) and 100-species (solid squares). All communities began with equal proportions of generalists and specialists (dotted horizontal line). Mean equilibrium biomass is measured as the proportion of carrying capacity ($K$) realized.

Our simulations with a mixed community composed of both species types paralleled the findings of simulations that included only generalists or only specialists. As the environmental cycle period increased (less variable conditions), community dominance shifted from generalists to specialists (Fig. 5a). In the species-rich community (100 species), this shift was more complete and occurred at a shorter environmental cycle period (less stable conditions) as compared to simulations with low species richness (4 species). However, under short environmental cycle periods, the community was dominated by generalists for both low and high species richness. Interestingly, the low richness simulations had a greater proportion of generalists than specialists even under more stable (longer cycle period) conditions. This result suggests that if generalists are present, even a low richness community may be able

to maintain system function (here, measured as total biomass; Fig. 5b).

Many of our results can be explained by comparing the performance of generalists and specialists under optimal versus suboptimal conditions. Neither species type incurs an induced cost under optimal conditions. As the environment strays further from the optimum, however, the induced costs incurred by the specialist increasingly offset its advantage over the generalist. In a fluctuating environment, a generalist incurs relatively constant costs because the generalist's costs are predominately constitutive. In contrast, a specialist in a fluctuating environment incurs potentially significant induced costs of stress, depending upon the magnitude and duration of deviations from optimal environmental conditions. The importance of the tradeoff between constitutive and induced costs was illustrated in our analysis of generalists and specialists in a fluctuating environment. As induced costs were increased (Fig. 4a–c), total biomass of specialist-only communities increased relative the biomass of the generalist-only communities. Thus, the performance of generalist versus specialist communities depends on the combination of constitutive and induced costs and the extent of suboptimal environmental conditions.

The generality of our conclusions depends on the robustness of the model results and the applicability of our model to natural communities. We tested the robustness of model predictions by constructing communities with a greater variety of traits among species, thereby relaxing our previous confinement of species types to only generalists or only specialists (i.e., relaxed the non-overlapping low, intermediate and high intervals of gm in Table 1). We randomly assigned species traits associated with the costs of stress (gc and gm) using the full range of possible values for both traits irrespective of species type (gc selected from 0.0 to 1.60 and gm selected from 0.0 to 2.0, see Table 1). We repeated the same simulations (cyclic environment) as performed with the mixed communities that used the more restrictive intervals for gm and gc (see Fig. 5). Model predictions using the full range were qualitatively similar to those obtained with the more restrictive intervals for gm and gc. While we no longer distinguished generalist- and specialist-species, the mean value of gm of the species persisting was generally lower (generalist-like) for short cycle periods and higher (specialist-like) for longer cycle periods, simi-

lar to the pattern predicted in Fig. 4. Also interesting is the shift from generalist species when species richness is low (4) to specialist species when species richness is high (100) as environmental conditions became more stable (longer cycle periods) (as in Fig. 5a). Total biomass for 4-species and 100-species communities using the full range of gc and gm values were similar to those obtained for the restrictive ranges shown in Fig. 5b.

We also evaluated the robustness of model results to several alternative assumptions. One alternative included assigning the trait eo from a normal (rather than uniform) probability distribution, which did little to change model predictions. In addition, we systematically explored different values for $\beta$ and various narrower and broader ranges of values of gm and gc that were assigned to generalist and specialist species. We repeated many of the simulations of specialist-only and generalist-only communities under constant environmental conditions. Different values of $\beta$ affect the degree of interspecific competition and therefore affected the total community biomass. All values of $\beta$ and the various intervals of gm and gc that we evaluated all generated community biomass and proportions of coexisting species results that were qualitatively similar to the results shown in Fig. 2.

Our model can be viewed as a modified version of the classic Lotka–Volterra competition model (May, 1974), where we explicitly define the costs of suboptimal environmental conditions with constitutive and induced costs and express a species' carrying capacity as part of a global carrying capacity. While others have explored and discussed the relevance of these classic models to niche breadth theory, we are unaware of other models that have explicitly incorporated ecological niche breadth (defined here as range of tolerance to environmental conditions) in a Lotka–Volterra multispecies competition model.

Lotka–Volterra competition models, and their closely related predator–prey (consumer–resource) versions, are widely used today in ecology to study food web and community dynamics (McCann et al., 1998; Chen and Cohen, 2001; Jordán et al., 2003; Wilson et al., 2003). Many of these have been theoretical analyses, leading some to argue that Lotka–Volterra, and similar simple models, do not reflect any actual natural systems (Hall, 1988). Despite their simplicity, many still acknowledge the utility and application of the

Lotka–Volterra approach to predicting the outcomes of ecological interactions (Case, 1990; Looigen, 1998; Pound et al., 2002; Vandermeer et al., 2002; Loreau, 2004). We view our analysis as providing theoretical results that are suggestive of mechanisms that may occur in real ecosystems. The next step is field-testing of model behavior and predictions using empirical data from natural systems to confirm or reject our results.

### 4.2. Generalists versus specialists: theoretical predictions

Our definitions of generalists and specialists are derived from a long history of ecological debate on the relative performances of generalist and specialist species (Kassen, 2002). Generalists have been defined a number of ways (McPeek, 1996): (a) species that maintain a variety of specialist genotypes that can be expressed depending upon the environmental conditions, (b) species in which each genotype has the ability to express various phenotypes depending upon environmental conditions (phenotypic plasticity), and (c) the "jack-of-all-trades"—a species with phenotypes intermediate to the range of environmental conditions experienced. We have designed our generalist species consistent with the phenotypic plasticity definition stated in (b), in order to explore the tradeoff between environmental tolerance and the costs of plasticity.

The cost of plasticity, while well-explored in the theoretical literature, has been notoriously difficult to measure empirically. Many explanations have been offered as to why empirical measurement of plasticity is so difficult. These explanations range from the possibility that there is little or no cost of plasticity (Kassen and Bell, 1998; Scheiner and Berrigan, 1998; Scheiner, 2002), to the possibility that generalists do well in a range of habitats because their niche is available in a wider range of habitats than the niche of a specialist (McPeek, 1996). Some studies have demonstrated costs of plasticity (Bergelson and Purrington, 1996; DeWitt, 1998; DeWitt et al., 1998; Semlitsch et al., 2000; Kassen, 2002), often measured as the costs of induced responses to environmental conditions (Agrawal et al., 1999; Strauss et al., 2002). Other studies have indicated that generalists can be outperformed by specialists in a given habitat not due to the cost of plasticity, but due to factors such as the accumulation of mutations in generalists experiencing many

environments—mutations that would be purged from a population of specialists remaining in one environment or habitat (Kawecki, 1994; Whitlock, 1996). Interestingly, some studies have demonstrated a cost of specialization, although this may be confined to a narrow set of circumstances (e.g., extreme conditions) in which the cost of performing well at extremes is a reduction in the range of conditions a species can tolerate (Miller and Castenholz, 2000). Finally, Vázquez and Simberloff (2002) suggested that generalists may not outcompete specialists under environmental disturbance, which is in contradiction to our results.

A number of ecological models have expanded upon the results of empirical studies comparing the performance of generalists and specialists. Models comparing ecological (or 'habitat') generalists and specialists have demonstrated how, despite the costs associated with generalization, generalists can be better invaders in degraded habitat conditions (Marvier et al., 2004) and can promote metapopulation stability (Sultan and Spencer, 2002). Reviews of empirical studies have failed to demonstrate conclusively that niche breadth influences invasion success, and it is likely that the outcome of a species introduction is the result of a complex array of variables, only one of which is a species' niche breadth (Vázquez, in press).

Our results are consistent with previous work suggesting that generalists are favored in fluctuating environments, while specialists excel under constant or slowly changing environmental conditions (Moran, 1992; Bowers and Harris, 1994; Gilchrist, 1995; Sultan, 2001; Van Buskirk, 2002). Our analysis also expands upon previous work that focused on single-species comparisons. We analyzed communities of only generalists, only specialists, and a mix of species types, in both low and high species-richness situations. We confirmed the general pattern that the relative performance of generalists and specialists is dependent upon environmental conditions, but our results also demonstrated that the success of generalists versus specialists can depend upon species richness.

There are many natural habitats where conditions are temporally variable and we would expect generalists to dominate. Estuaries are an example of a dynamic habitat in which the resident species are, by necessity, tolerant of a range of conditions (Teal, 1962; Day et al., 1989). These systems are also extremely productive despite the stress associated with environmental fluctuations, demonstrating how those species that excel under temporally variable conditions can effectively maintain ecosystem function (here, productivity). Estuaries are also relatively species-poor habitats, providing a concrete example of our model results: a species-poor community can still exhibit a high level of ecosystem function if the species present are environmental generalists. The environmental tolerance of a species may also play an important role in ecosystem function in regions where anthropogenic impacts are causing these fluctuations to be more severe or more common. Current global climate change models predict future environmental conditions to be increasingly unstable, with more frequent, abrupt, and extreme events (Committee on Abrupt Climate Change, 2002); in this light, generalist species may be particularly important in the maintenance of ecosystem functions in the future.

### 4.3. Relevance to biodiversity losses

Our results may have relevance to understanding the ecosystem consequences of species loss, which is occurring worldwide at an increasingly rapid rate (Chapin et al., 2000). Ecologists have focused considerable attention on predicting the repercussions of species losses, since depauperate ecosystems may not function as they did in their original states (Stachowicz et al., 1999; Tilman, 1999; Sala et al., 2000). The loss of species or functional types could interrupt food webs and destabilize systems, thereby making them more vulnerable to further stress or compromising their ability to provide essential ecosystem functions (e.g., nutrient recycling, decomposition) (Loreau et al., 2001). Our results suggest that the vulnerability of communities to perturbations is not a simple function of the number and types of species present, but can depend upon the mix of generalist and specialist species and the temporal dynamics of the environment.

There have been a number of mechanisms proposed to explain the positive relationship between biodiversity and ecosystem function. For example, the idea of species complementarity describes how system stability can be augmented by biodiversity (species richness) if the species in a community each excel under different environmental conditions. As conditions change, the proportional densities of individual species can be quite dynamic, but biomass of the overall community is maintained at a consistent level as different species

come to dominate under each new condition (Frost et al., 1995; Hughes et al., 2002). Biodiversity may also lead to greater system stability due to the sampling effect, where the presence of a greater number of species is associated with a greater probability that the system will include key species or functional types that will maintain essential functions (Huston, 1997; Díaz and Cabido, 2001; Tilman and Lehman, 2002). The degrees of complexity, connectivity, species co-tolerances, and species interactions within communities have also been proposed as important factors that affect system stability (Ives, 1995; Hughes and Roughgarden, 2000; Rozdilsky and Stone, 2001; Vinebrooke et al., 2004).

The results presented here point to a qualitatively different relationship between biodiversity and ecosystem function. Our results suggest that high biodiversity (here, species richness) is not a necessary prerequisite for the maintenance of ecosystem function, although species richness may affect the relative ability of generalist and specialist assemblages to maintain ecosystem function. While our model results confirm previous findings that under stable or slowly changing environmental conditions, ecosystem function (here, biomass) is highest in species-rich communities, there are conditions under which low diversity (species-poor) communities of generalists can outperform more diverse specialist communities. In light of the combination of species losses and predictions of increasingly variable environmental conditions in the future, our model results suggest that attempts to predict how ecosystem function will be impacted should include a consideration of the range of environmental tolerances (generalists versus specialists) of the component species.

## Acknowledgements

## References

Agrawal, A.A., Strauss, S.Y., Stout, M.J., 1999. Costs of induced responses and tolerance to herbivory in male and female fitness components of wild radish. Evolution 53, 1093–1104.

Agrawal, A.A., 2000. Benefits and costs of induced plant defense for *Lepidium virginicum* (Brassicaceae). Ecology 81, 1804–1813.

Bergelson, J., Purrington, C.B., 1996. Surveying patterns in the cost of resistance in plants. Am. Nat. 148, 536–558.

Bergman, E., 1988. Foraging abilities and niche breadths of two percids, *Perca fluviatilis* and *Gymnocephalus cernua*, under different environmental conditions. J. Anim. Ecol. 57, 443–453.

Bowers, M.A., Harris, L.C., 1994. A large-scale metapopulation model of interspecific competition and environmental change. Ecol. Modell. 72, 251–273.

Brown, J.H., Whitham, T.G., Ernest, S.K.M., Gehring, C.A., 2001. Complex species interactions and the dynamics of ecological systems: long-term experiments. Science 293, 643–650.

Byers, J.E., Noonburg, E.G., 2003. Scale dependent effects of biotic resistance to biological invasion. Ecology 84, 1428–1433.

Case, T.J., 1990. Invasion resistance arises in strongly interacting species-rich model competition communities. Proc. Natl. Acad. Sci. U.S.A. 87, 9610–9614.

Chapin, F.S.I., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C., Diaz, S., 2000. Consequences of changing biodiversity. Nature 405, 234–242.

Chen, X., Cohen, J.E., 2001. Transient dynamics and food-web complexity in the Lotka–Volterra cascade model. Proc. R. Soc. Lond. B 286, 1–10.

Chesson, P., Pacala, S., Neuhauser, C., 2002. Environmental niches and ecosystem functioning. In: Kinzig, A.P., Pacala, S.W., Tilman, D. (Eds.), The Functional Consequences of Biodiversity. Princeton University Press, Princeton, pp. 213–245.

Committee on Abrupt Climate Change, National Research Council, 2002. Abrupt Climate Change: Inevitable Surprises. National Academy Press, Washington, DC.

Coustau, C., Chevillon, C., French-Constant, R., 2000. Resistance to xenobiotics and parasites: can we count the cost? Trends Ecol. Evol. 15, 378–383.

Day Jr., J.W., Hall, C.A.S., Kemp, W.M., Yáñez-Arancibia, A., 1989. Estuarine Ecology. John Wiley and Sons, New York.

DeWitt, T.J., 1998. Costs and limits of phenotypic plasticity: tests with predator-induced morphology and life history in a freshwater snail. J. Evol. Biol. 11, 465–480.

DeWitt, T.J., Sih, A., Wilson, D.S., 1998. Costs and limits of phenotypic plasticity. Trends Ecol. Evol. 13, 77–81.

Díaz, S., Cabido, M., 2001. Vive la différence: plant functional diversity matters to ecosystem processes. Trends Ecol. Evol. 16, 646–655.

Doak, D.F., Bigger, D., Harding, E.K., Marvier, M.A., O'Malley, R.E., Thomson, D., 1998. The statistical inevitability of stability–diversity relationships in community ecology. Am. Nat. 151, 264–276.

Doncaster, C.P., Pound, G.E., Cox, S.J., 2000. The ecological cost of sex. Nature 404, 281–285.

Egas, M., Dieckmann, U., Sabelis, M.W., 2004. Evolution restricts the coexistence of specialists and generalists: the role of trade-off structure. Am. Nat. 163, 518–531.

Frost, T.M., Carpenter, S.R., Ives, A.R., Kratz, T.K., 1995. Species compensation and complementarity in ecosystem function. In: Jones, C.G., Lawton, J.H. (Eds.), Linking Species and Ecosystems. Chapman and Hall, New York, pp. 224–239.

Gilchrist, G.W., 1995. Specialists and generalists in changing environments. I. Fitness landscapes of thermal sensitivity. Am. Nat. 146, 252–270.

Grimm, V., Wissel, C., 1997. Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confuion. Oecologia 109, 323–334.

Hall, C.A.S., 1988. As assessment of several of the historically most influential theoretical models used in ecology and of the data provided in their support. Ecol. Modell. 43, 5–31.

Huey, R.B., Hertz, P.E., 1984. Is a jack-of-all-temperatures a master of none? Evolution 38, 441–444.

Hughes, J.B., Roughgarden, J., 2000. Species diversity and biomass stability. Am. Nat. 155, 618–627.

Hughes, J.B., Petchey, O.L., 2001. Merging perspectives on biodiversity and ecosystem functioning. Trends Ecol. Evol. 16, 222–223.

Hughes, J.B., Ives, A.R., Norberg, J., 2002. Do species interactions buffer environmental variation (in theory)? In: Loreau, M., Naeem, S., Inchausti, P. (Eds.), Biodiversity and Ecosystem Functioning: Synthesis and Perspectives. Oxford University Press, Oxford, pp. 92–101.

Huston, M.A., 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. Oecologia 110, 449–460.

Ives, A.R., 1995. Predicting the response of populations to environmental change. Ecology 76, 926–941.

Jordán, F., Scheuring, I., Molnár, I., 2003. Persistence and flow reliability in simple food webs. Ecol. Modell. 161, 117–124.

Kassen, R., 2002. The experimental evolution of specialists, generalists, and the maintenance of diversity. J. Evol. Biol. 15, 173–190.

Kassen, R., Bell, G., 1998. Experimental evolution in *Chlamydomonas*. IV. Selection in environments that vary through time at different scales. Heredity 80, 732–741.

Karentz, D., Smayda, T.J., 1998. Temporal patterns and variations in phytoplankton community organization and abundance in Narragansett Bay during 1959–1980. J. Plankton Res. 20, 145–168.

Kawecki, T.J., 1994. Accumulation of deleterious mutations and the evolutionary cost of being a generalist. Am. Nat. 144, 833–838.

Kirk, K.L., 2002. Competition in variable environments: experiments with planktonic rotifers. Freshwater Biol. 47, 1089–1096.

Krasnov, B.R., Poulin, R., Shenbrot, G.I., Mouillot, D., Khokhlova, I.S., 2004. Ectoparasitic "jacks-of-all-trades": relationship between abundance and host specificity in fleas (Siphonaptera) parasitic on small mammals. Am. Nat. 164, 506–516.

Lawton, J.H., 2000. Community Ecology in a Changing World. Ecology Institute, Oldendorf/Luhe, Germany.

Levins, R., 1968. Evolution in Changing Environments. Princeton University Press, Princeton.

Looigen, R.C., 1998. The reduction of the Lotka/Volterra competition model to modern niche theory. In: Holism Reductionism in Biology and Ecology: The Mutual Dependence of Higher Lower Level Research Programmes. University Library Groningen, Groningen, Netherlands, pp. 177–198 www.ub.rug.nl/eldoc/dis/fil/r.c.looijen/.

Loreau, M., 2004. Does functional redundancy exist? Oikos 104, 606–611.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M., Raffaelli, D., Schmid, B., Tilman, D., Wardle, D.A., 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294, 804–808.

Loreau, M., Downing, A., Emmerson, M., Gonzalez, A., Hughes, J., Inchausti, P., Joshi, J., Norberg, J., Sala, O., 2002. A new look at the relationship between diversity and stability. In: Loreau, M., Naeem, S., Inchausti, P. (Eds.), Biodiversity and Ecosystem Functioning: Synthesis and Perspectives. Oxford University Press, Oxford, pp. 79–91.

Makarewicz, J.C., 1993. Phytoplankton biomass and species composition in Lake Erie, 1970–1987. J. Great Lakes Res. 19, 258–274.

Marvier, M., Karieva, P., Neubert, M.G., 2004. Habitat destruction, fragmentation, and disturbance promote invasion by habitat generalists in a multispecies metapopulation. Risk Anal. 24, 869–878.

May, R.M., 1974. Stability and Complexity in Model Ecosystems. Princeton University Press, Princeton.

McCann, K., Hastings, A., Huxel, G.R., 1998. Weak trophic interactions and the balance of nature. Nature 395, 794–798.

McPeek, M.A., 1996. Trade-offs, food web structure, and the coexistence of habitat specialists and generalists. Am. Nat. 148, S124–S138.

Miller, S.R., Castenholz, R.W., 2000. Evolution of thermotolerance in hot spring cyanobacteria of the genus *Synechoccus*. Appl. Environ. Microbiol. 66, 4222–4229.

Moran, N.A., 1992. The evolutionary maintenance of alternate phenotypes. Am. Nat. 139, 971–989.

Parsons, P.A., 1994. The energetic cost of stress. Can biodiversity be preserved? Biodiv. Lett. 2, 11–15.

Parsons, T.R., Takahashi, M., Hargrave, B., 1984. Biological Oceanographic Processes, third ed. Pergamon Press, New York.

Palaima, A., Spitze, K., 2004. Is a jack-of-all-temperatures a master of none? An experimental test with *Daphnia pulicaria* (Crustacea: Cladocera). Evol. Ecol. Res. 6, 215–225.

Pianka, E.R., 1978. Evolutionary Ecology, second ed. Harper and Row, New York.

Pound, G.E., Doncaster, C.P., Cox, S.J., 2002. A Lotka–Volterra model of coexistence between a sexual population and multiple asexual clones. J. Theor. Biol. 217, 535–545.

Relyea, R.A., 2002. Costs of phenotypic plasticity. Am. Nat. 159, 272–282.

Reynolds, C.S., 1997. Vegetation Processes in the Pelagic: A Model for Ecosystem Theory. Ecology Institute, Oldendorf/Luhe, Germany.

Rozdilsky, I.D., Stone, L., 2001. Complexity can enhance stability in competitive systems. Ecol. Lett. 4, 397–400.

Rutherford, M.C., O'Callaghan, M., Hurford, J.L., Powrie, L.W., Schulze, R.E., Kunz, R.P., Davis, G.W., Hoffman, M.T., Mack, F., 1995. Realized niche spaces and functional types: a framework for prediction of compositional change. J. Biogeogr. 22, 523–531.

Sala, O.E., Chapman, F.S.I., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzing, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. Science 287, 1770–1774.

Scheiner, S.M., 2002. Selection experiments and the study of phenotypic plasticity. J. Evol. Biol. 15, 889–898.

Scheiner, S.M., Berrigan, D., 1998. The genetics of phenotypic plasticity. VIII. The cost of plasticity in *Daphnia pulex*. Evolution 52, 368–378.

Semlitsch, R.D., Bridges, C., Welch, A., 2000. Genetic variation and a fitness tradeoff in the tolerance of gray treefrog (*Hyla versicolor*) tadpoles to the insecticide carbaryl. Oecologia 125, 179–185.

Sevenster, J.G., van Alphen, J.J.M., 1993. A life history trade-off in *Drosophila* species and community structure in variable environments. J. Anim. Ecol. 62, 720–736.

Stachowicz, J.J., Whitlatch, R.B., Osman, R.W., 1999. Species diversity and invasion resistance in a marine ecosystem. Science 286, 1577–1579.

Strauss, S.Y., Rudgers, J.A., Lau, J.A., Irwin, R.E., 2002. Direct and ecological costs of resistance to herbivory. Trends Ecol. Evol. 17, 278–285.

Steinger, T., Roy, B.A., Stanton, M.L., 2003. Evolution in stressful environments. II. Adaptive value and costs of plasticity in response to low light in *Sinapis arvensis*. J. Evol. Biol. 16, 313–323.

Sultan, S.E., 2001. Phenotypic plasticity for fitness componenets in *Polygonum* species of contrasting ecological breadth. Ecology 82, 328–343.

Sultan, S.E., Spencer, H.G., 2002. Metapopulation structure favors plasticity over local adaptation. Am. Nat. 160, 271–283.

Symstad, A.J., Tilman, D., 2001. Diversity loss, recruitment limitation, and ecosystem functioning: lessons learned from a removal experiment. Oikos 92, 424–435.

Teal, J.M., 1962. Energy flow in the salt marsh ecosystem of Georgia. Ecology 43, 614–624.

Thomas, A., Strub, P.T., 2001. Cross-shelf phytoplankton pigment variability in the California Current. Cont. Shelf Res. 21, 1157–1190.

Tilman, D., 1999. The ecological consequences of changes in biodiversity: a search for general principles. Ecology 80, 1455–1474.

Tilman, D., Lehman, C., 2002. Biodiversity, composition, and ecosystem processes: theory and concepts. In: Kinzing, A., Pacala, S.W., Tilman, D. (Eds.), The Functional Consequences of Biodiversity: Empirical Progress and Theoretical Extensions. Princeton University Press, Princeton, pp. 9–41.

Van Buskirk, J., 2002. A comparative test of the adaptive plasticity hypothesis: relationships between habitat and phenotype in anuran larvae. Am. Nat. 160, 87–102.

Vandermeer, J., Evans, M.A., Foster, P., Höök, T., Reiskind, M., Wund, M., 2002. Increased competition may promote species coexistence. Proc. Natl. Acad. Sci. U.S.A. 99, 8731–8736.

van Kleunen, M., Fischer, M., Schmid, B., 2000. Costs of plasticity in foraging characteristics of the clonal plant *Ranunculus reptans*. Evolution 54, 1947–1955.

Vázquez, D.P. Exploring the relationship between niche breadth and invasion success. In: Cadotte, M.W., McMahon, S.M., Fukami, T., (Eds.), Conceptual Ecology and Invasions Biology: Reciprocal Approaches to Nature. Kluwer Academic Press, in press.

Vázquez, D.P., Simberloff, D., 2002. Ecological specialization and susceptibility to disturbance: conjectures and refutations. Am. Nat. 159, 606–623.

Vinebrooke, R.D., Cottingham, K.L., Norberg, J., Scheffer, M., Dodson, S.I., Maberly, S.C., Sommer, U., 2004. Impacts of multiple stressors on biodiversity and ecosystem functioning: the role of species co-tolerance. Oikos 104, 451–457.

Whitlock, M.C., 1996. The red queen beats the jack-of-all-trades: the limitations on the evolution of phenotypic plasticity and niche breadth. Am. Nat. 148, S65–S77.

Wilson, J.B., 1988. The cost of heavy-metal tolerance: an example. Evolution 42, 408–413.

Wilson, W.G., Lundberg, P., Vázquez, D.P., Shurin, J.B., Smith, M.D., Langford, W., Gross, K.L., Mittelbach, G.G., 2003. Biodiversity and species interactions: extending Lotka–Volterra community theory. Ecol. Lett. 6, 944–952.

Wootton, J.T., 2002. Indirect effects in complex ecosystems: recent progress and future challenges. J. Sea Res. 48, 157–172.

Yachi, S., Loreau, M., 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. Proc. Nat. Acad. Sci. U.S.A. 96, 1463–1468.

Zeitzschel, B., 1978. Why study phytoplankton? In: Sournia, A. (Ed.), Phytoplankton Manual. Monographs on Oceanographic Methodology, vol. 6. Musée National d'Histoire Naturelle, Paris, pp. 1–5.