

LETTER

Species dynamics alter community diversity–biomass stability relationships

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Abstract

The relationship between community diversity and biomass variability remains a crucial ecological topic, with positive, negative and neutral diversity–stability relationships reported from empirical studies. Theory highlights the relative importance of Species–Species or Species–Environment interactions in driving diversity–stability patterns. Much previous work is based on an assumption of identical (stable) species-level dynamics. We studied ecosystem models incorporating stable, cyclic and more complex species-level dynamics, with either linear or non-linear density dependence, within a locally stable community framework. Species composition varies with increasing diversity, interacting with the correlation of species' environmental responses to drive either positive or negative diversity–stability patterns, which theory based on communities with only stable species-level dynamics fails to predict. Including different dynamics points to new mechanisms that drive the full range of diversity–biomass stability relationships in empirical systems where a wider range of dynamical behaviours are important.

Keywords

Complex dynamics, dynamical instability, environmental stochasticity, intrinsic growth rate, portfolio/insurance effect, synchrony, species–environment interactions, species–species interactions.

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INTRODUCTION

How the size of total biomass fluctuations varies with species diversity in ecosystems is a fundamental ecological issue, with empirical evidence pointing to a positive relationship between biodiversity effects and ecosystem services (Balvanera *et al.* 2006). Field and laboratory experiments report the full range of qualitatively different diversity–biomass stability relationships, i.e., positive, negative or neutral, whereas theoretical work highlights conditions under which different relationships can be expected (Ives & Carpenter 2007; Gonzalez & Loreau 2009; Campbell *et al.* 2011).

Previous theoretical work has emphasised the relative importance of Species–Species (*SS*) and Species–Environment (*SE*) interactions in determining the direction of diversity–biomass stability patterns (Ives *et al.* 2000; Ives & Hughes 2002; Ives & Carpenter 2007), which has become a popular paradigm for understanding observed patterns in natural systems (Fig. 1). Mathematical approaches were developed to predict how changes in community diversity will affect biomass stability (Hughes & Roughgarden 1998; Ives *et al.* 1999, 2000; Ives & Hughes 2002). A general outcome, based on simple dynamical models, is that increased diversity is associated with reduced variability in total biomass fluctuations when species respond differently to environmental fluctuations (Ives *et al.* 1999, 2000; Ives & Hughes 2002). The same result comes from statistical, rather than dynamical approaches, termed the Insurance or Portfolio effect (Doak *et al.* 1998; Tilman *et al.* 1998; Yachi & Loreau 1999; Lehman & Tilman 2000; Lhomme & Winkel 2002). This positive diversity–stability relationship can be reversed by varying the relative importance of *SS* or *SE* interactions: biomass variability

should increase (biomass stability decreases) when increasing diversity increases the relative importance of *SS* interactions (Ives *et al.* 2000).

Much of the above theoretical work is based on simple dynamical models coupled with stochastic environmental fluctuations, assuming locally (asymptotically) stable deterministic population dynamics at both the species and community levels: communities are composed of populations that return to their equilibria following a small perturbation, or fluctuate around their equilibria under continued environmental forcing. Early models assumed that species were equivalent in all aspects, e.g., strength of competition, intrinsic growth rates and carrying capacities, although relaxing some of these assumptions (e.g., allowing asymmetric, randomised between-species interactions) was not found to qualitatively alter predictions (Hughes & Roughgarden 1998; Ives *et al.* 1999, 2000; Ives & Hughes 2002). Later work developed methods that accounted for species differences, predicting community Variance–Covariance matrices and demonstrating the utility of these mathematical tools in simple two or three species (or life-history stage) systems (Greenman & Benton 2005). However, finding general mathematical descriptions of diversity–stability patterns is not straightforward based on these more flexible approaches. Introducing species differences makes algebraic manipulation overly complex to derive simple, easily interpretable analytical results.

Species differences are an integral part of natural communities, including variation in intrinsic growth or return rates (Sibly *et al.* 2007). Species with undercompensatory density dependence tend to return slowly to equilibrium, whereas species with overcompensatory density dependence will overshoot their equilibrium following a

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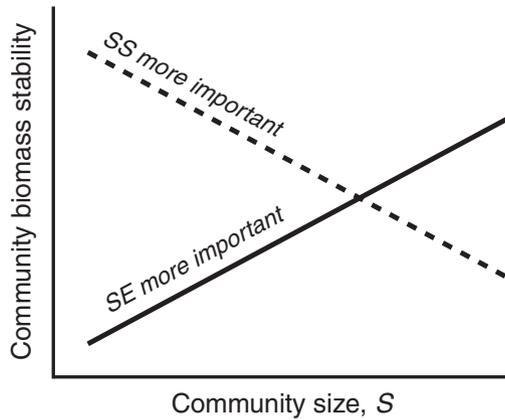


Figure 1 A schematic representation, illustrating how the direction of community diversity–biomass stability relationships have been predicted to be influenced by the relative importance of Species–Species (negative relationship) and Species–Environment (positive relationship) interactions.

disturbance. These fluctuations can eventually dampen to a stable equilibrium, or grow with a tendency to cyclic or more complex dynamics (May & Oster 1976). Insects are common examples of species capable of showing high intrinsic growth rates and unstable dynamics, e.g. in laboratory (e.g., Constantino *et al.* 1995; Dey & Joshi 2006) and natural systems (Ives *et al.* 2008). There is also evidence of cycles and other complex dynamics from plant populations (Crone & Taylor 1996; Buckley *et al.* 2010). Zipkin *et al.* (2008) recently reported overcompensatory responses of invasive small-mouth bass in a freshwater fish community following harvesting, suggesting high intrinsic growth rates, whereas Mata *et al.* (2012) and Lawrence *et al.* (2012) have demonstrated wide ranges in within-guild maximum growth rates in microcosm communities.

Here, we investigate the direction of diversity–stability relationships in a model describing an ecosystem based on a single trophic level (guild). Such models have formed the basis of much theoretical research on diversity–stability questions (Ives & Carpenter 2007) and are often incorporated within trophically structured food webs as the primary producer (basal) level. We take a novel approach by allowing differences in species' intrinsic growth rates or their shape of density dependence. These differences can qualitatively alter deterministic dynamics at the species level, in the absence of species interactions, from under- and overcompensating stable equilibrium dynamics to cyclic and more complex (chaotic) dynamics (May & Oster 1976), while maintaining the assumption of locally stable community dynamics in the presence of species interactions (Fig. 2; see also Fowler 2009). Maintaining this assumption allows us to compare our results with earlier studies based on locally stable communities, composed only of species with qualitatively similar (stable) dynamics.

We show that both positive and negative diversity–stability patterns can arise across matched communities, depending on the correlation structure (always less than perfectly correlated) and scaling of species responses to environmental variation. Theoretical work based on similar models has only demonstrated positive (or neutral) diversity–stability patterns (Ives *et al.* 1999; Ives & Hughes 2002). We highlight the deterministic and stochastic effects that underlie these opposing stochastic patterns and discuss our results in relation to the relative importance of *SS* and *SE* interactions. Diversity–biomass stability relationships in communities composed of species with dif-

ferent dynamical behaviours are more nuanced than previous work has suggested, with negative diversity–stability patterns possible contrary to predictions from earlier work on similar models.

METHODS

We used simple, multispecies models to simulate dynamics in discrete time: the multispecies Ricker (1954; May & Oster 1976) and Maynard-Smith & Slatkin (1973) models with linear (Lotka–Volterra) between-species interactions. The basic formulation is one of the most commonly used ecosystem models (in continuous or discrete time), and often forms the foundation for more complex, trophically structured dynamical food web models. Population density of each species (N_i) in the Ricker model is found across consecutive time steps (t) as

$$N_{i,t+1} = N_{i,t} \exp\left(r_i \left[1 - \frac{\sum_{j=1}^m \alpha_{ij} N_{j,t}}{K_i}\right]\right) \exp(\varepsilon_{i,t}), \quad (1)$$

where r_i and K_i give species-specific intrinsic growth rates and carrying capacities respectively, while α_{ij} is the *per-capita* effect of species j on the *per-capita* growth rate (*pgr*) of species i . Species responses to stochastic fluctuations in the environment are given by $\varepsilon_{i,t}$, defined below.

We also considered a model that incorporates non-linear density dependence, based on Maynard-Smith & Slatkin (1973):

$$N_{i,t+1} = \frac{N_{i,t} r_i}{1 + (1 - r_i) \left(\sum_{j=1}^m \alpha_{ij} N_{j,t} / K_i\right)^{b_i}} \exp(\varepsilon_{i,t}), \quad (2)$$

where b_i describes the form of competition for each species, based on the shape of density dependent *pgr*. Values of $b_i < 1$ produce convex (stabilising) density dependence, whereas $b_i > 1$ is associated with concave (destabilising) density dependence.

Deterministic equilibria for both these systems of coupled equations are found as $\mathbf{N}^* = \mathbf{A}^{-1} \mathbf{K}$, where \mathbf{N} and \mathbf{K} are m -by-1 vectors of population densities and carrying capacities, respectively, and \mathbf{A} is an m -by- m square matrix with intraspecific interaction strengths (within species competition) on the main diagonal ($\alpha_{ii} = 1$) and interspecific interactions (α_{ij}) in the off-diagonal elements. We initially examined the simple case of diffuse competition, where all $\alpha_{ij} = \alpha = 0.5$ ($i \neq j$). We also examined asymmetric interactions, by drawing the α_{ij} values ($i \neq j$) from a uniform distribution with limits $[0, 2\alpha]$, but including asymmetries did not qualitatively alter our results. Species-carrying capacity (K_i) values varied with community size, maintaining total average community biomass over different community sizes as $X^* = \sum N_i^* = 1$, by setting $\mathbf{K} = \mathbf{A} \mathbf{N}^*$. K_i is found by setting $N_i^* = 1/m$, giving $K_i = (1 + [m - 1]\alpha)/m$, when all $\alpha_{ij} = \alpha$. This approach increases the relative strength of competition with diversity: as communities increase in size, K_i values decline. We also tested the effect of maintaining $K_i = 1$ across all community sizes, which asymptotically increases total biomass with increasing community size (Overyielding), but this did not qualitatively alter our results.

A novel aspect of our approach is that we drew intrinsic growth rates (r_i) randomly from a uniform distribution with limits $r_i \sim [0.5, 3.5]$ for eqn 1, or the shape of density dependence $b_i \sim [0, 2r_i/(r_i - 1)]$ for eqn 2, where $r_i = 4$ ($i = 1 \dots m$). We also examined the case where $r_i \sim [1, 2b_i/(b_i - 2)]$ and $b_i = 5$ ($i = 1 \dots m$; see Supporting Information for derivations), but this approach did not affect our

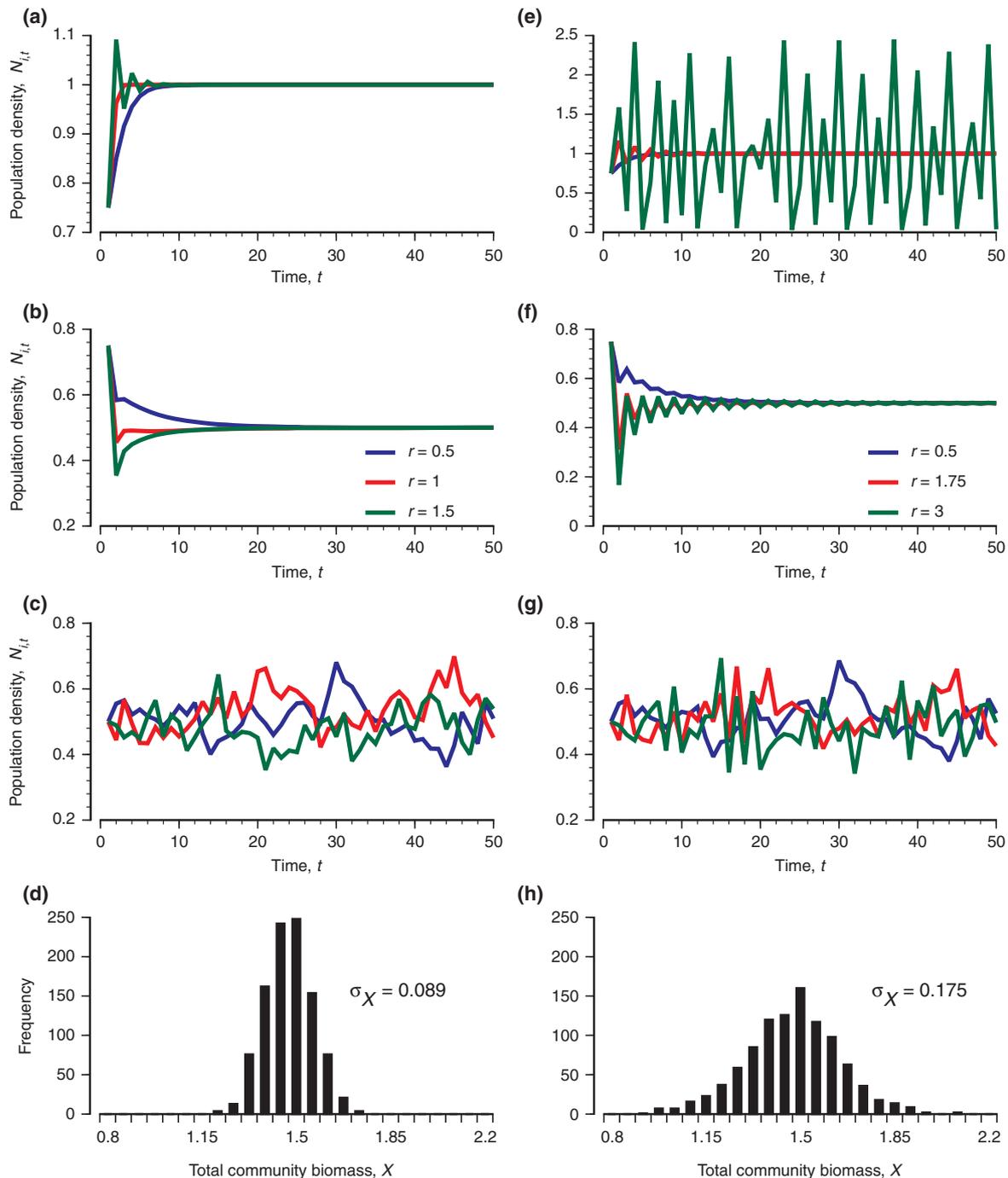


Figure 2 Species- and community-level dynamics in deterministic and stochastic systems with or without complex dynamics. Based on the multispecies Ricker model *eqn 1*. Left panels illustrate communities composed of species with only stable species-level dynamics (all $r_i < 2$). Right panels show a community including species with stable ($r_i = 0.5, 1.75$) and chaotic ($r_i = 3$) species-level dynamics. (a, e) deterministic populations without interspecific competition ($\alpha = 0$); (b, c, f, g) between-species competition ($\alpha = 0.5$) generates feasible and locally stable deterministic (b, f) or stochastic (c, g) community-level dynamics. Both communities were forced by identical, uncorrelated environmental variation ($\sigma_{\varepsilon(t)} = 0.1$). (d, h) Frequency distributions from 1000 steps of total biomass fluctuations (X_t) from each community.

main results or conclusions. These decisions relax the common assumption that all community members will have stable equilibrium dynamics in the absence of species interactions. Drawing r_i or b_i values from these ranges allows species to be included in the community that show anything from slow, undercompensating stable equilibrium dynamics, to rapid, cyclic or chaotic (unstable) dynamics in the absence of interspecific interactions (May & Oster 1976; Fig. S1).

Communities were assembled and selected for simulation by testing for deterministic feasibility (all $N_i^* > 0$) and local stability (the absolute value of the dominant eigenvalue [λ_1] of the Jacobian matrix of eqns 1 and 2 evaluated at equilibrium, $|\lambda_1| < 1$, eqns S4 and S5). We only considered communities that were feasible and locally stable, for comparison with previous results based on simulation and analytical approaches. We also restricted our analyses to communities with $|\lambda_1| < 0.95$, rather than $|\lambda_1| < 1$ (the

deterministic bifurcation point/stability boundary), to avoid influencing our results with systems close to the stability boundary that might behave in different ways when forced by noise (Greenman & Benton 2005). We recorded r_i , b_i and λ_i values from each community selected for further analyses. These were pooled for each community size and used to generate empirical probability distributions, to examine how they varied with diversity.

Species-specific responses to stochastic fluctuations in the environment were introduced to the *per-capita* growth rate through $\varepsilon_{i,t}$, generated as

$$\varepsilon_{i,t+1} = \kappa \varepsilon_{i,t} + \frac{(\varphi_{i,t} + \delta \omega_t)}{\sqrt{1 + \delta^2}} \quad (3)$$

$$\delta = \sqrt{\frac{1 - |\rho|}{|\rho|}}$$

Here, κ defines how much influence past environmental conditions have on the current state. We present results based on $\kappa = 0$ (a white-noise process), but note that results did not change qualitatively when $|\kappa| < 1$. Parameters $\varphi_{i,t}$ and ω_t are random variables, independently drawn from a Gaussian distribution (mean 0, standard deviation 1). Species responses to environmental fluctuations can be correlated by varying ρ . We examined two cases, of independent ($\rho = 0$) or positively correlated ($\rho = 0.9$) environmental responses. The mean of ε_i was 0 and we standardised the variance in two different ways (Ives *et al.* 2000): (1) each ε_i series was scaled to $\sigma_{\varepsilon(i)} = \gamma$ independently of community size, which maintains the relative importance of environmental fluctuations at the species level, although the total variability entering the system at the community level increases with community size and (2) each ε_i series was scaled so that $\sigma_{\varepsilon(i)} = \gamma N_i^* / \sum N_i^*$, which decreases the relative importance of environmental fluctuations at the species level as community size increases, while it remains constant at the community level ($\sum \sigma_{\varepsilon(i)} = \gamma$). The second approach models a guild competing for a stochastically fluctuating common (but not necessarily limiting) resource. If species have a saturating rate of resource intake, or have different performance optima along an environmental gradient, increasing community size increases the net intake of the resource, leading to a decline in resource availability. Assuming that the variance of resource availability scales with its mean availability, increasing community size would reduce the environmental variance each species experiences through the resource fluctuations, coupled with the observed increase in the mean density of each species. The same deterministic communities were used for a single replicate of each of the environmental treatments. We varied γ from 1×10^{-10} to 1, but this did not qualitatively alter our results.

Community size, m , varied between 2 and 12 species, with total community biomass recorded at each time step $X_t = \sum N_{i,t}$. Larger communities were increasingly time-consuming to assemble, especially for asymmetric interaction values. Populations were initiated at equilibrium \mathbf{N}^* , and simulated for $T = 1000$ time steps. We recorded the sample mean and standard deviation of the time series of X_t ($t = 501 \dots T$), to calculate the inverse of the Coefficient of Variation of the biomass fluctuations for a given community size (m),

$$\frac{1}{CV_X} = \frac{\mu_X}{\sigma_X}, \quad (4)$$

a measure commonly termed 'biomass stability' (Lehman & Tilman 2000) that increases as the size of biomass fluctuations decreases,

i.e., larger values of $1/CV_X$ describe a more 'stable' community in terms of lower biomass variability. To facilitate comparison with the analytical methods outlined in the Supporting Information, we also examined variability in the sum of deviations from the stochastic equilibrium, $1/\sigma_n$, where $n_t = \sum (N_{i,t} - \sum N_{i,t}/T)$, noting that results based on $1/CV_X$ and $1/\sigma_n$ did not differ qualitatively. We therefore only present results here based on $1/\sigma_n$. These statistical biomass stability results should not be confused with the mathematical concept of local (asymptotic) stability ($|\lambda_1| < 1$) mentioned above.

The two different environmental scenarios described above: species-level environmental variance is either: (1) independent of m , or (2) declines with increasing m ; allow us to test the idea that the direction of diversity–biomass stability relationships depends upon the relative importance of *SS* vs. *SE* interactions (Ives *et al.* 2000). A positive diversity–biomass stability relationship (increasing m increases $1/\sigma_n$) is predicted when adding species makes *SE* more important; a negative diversity–biomass stability relationship is predicted when adding species makes *SS* more important (Fig. 1). Under this view, we expect a negative diversity–stability pattern when species-level environmental responses weaken with increasing diversity ($\sum \sigma_{\varepsilon(i)} = \gamma$), or a positive diversity–stability pattern when competition increases in the community through the addition of species or when species-carrying capacities decline with increasing diversity ($\sum N_i^* = 1$).

To summarise, we consider the effect of three factors on the relationship between community size and total biomass stability: stochastic environmental fluctuations ($\varepsilon_{i,t}$) were either: (1) independent ($\rho = 0$) or positively correlated ($\rho = 0.9$) across species; (2) were scaled to have a constant species-specific standard deviation across all community sizes ($\sigma_{\varepsilon(i)} = \gamma$) or a standard deviation (at the species level) that declined with increasing community size, such that the total of the standard deviations remained constant with m , $\sum \sigma_{\varepsilon(i)} = \gamma$. Finally, (3) we also test whether the functional form of density dependence (either linear or non-linear) has any effect on the observed patterns. Feasible, locally stable communities were replicated 10 000 times for each community size and set of conditions, with the results presented as the median $1/\sigma_n$ as well as the component elements (μ_X , v_{ij}) recorded across these replicates.

RESULTS

Increasing diversity in locally stable communities containing species drawn from a range of different characteristic dynamics (stable, cycling or chaotic in the absence of between-species interactions), generates both positive and negative diversity–biomass stability relationships (Fig. 3). The direction depends on the correlation of species responses to environmental fluctuations and how species responses to environmental variation change with community size (scaled or unscaled). When the addition of species to the community has no effect on the species-level response to environmental variance (unscaled; $\sigma_{\varepsilon(i)} = \gamma$), uncorrelated responses produce a positive diversity–stability pattern, whereas correlated responses ($\rho = 0.9$) produce a negative pattern: increasing variability of total biomass fluctuations with increasing community size (Fig. 3a). These results hold for models with either linear or non-linear density dependence (eqns 1 and 2).

If species-level environmental responses scale with increasing community size ($\sum \sigma_{\varepsilon(i)} = \gamma$), the correlation in species environmental responses has no qualitative effect: increasing diversity is always

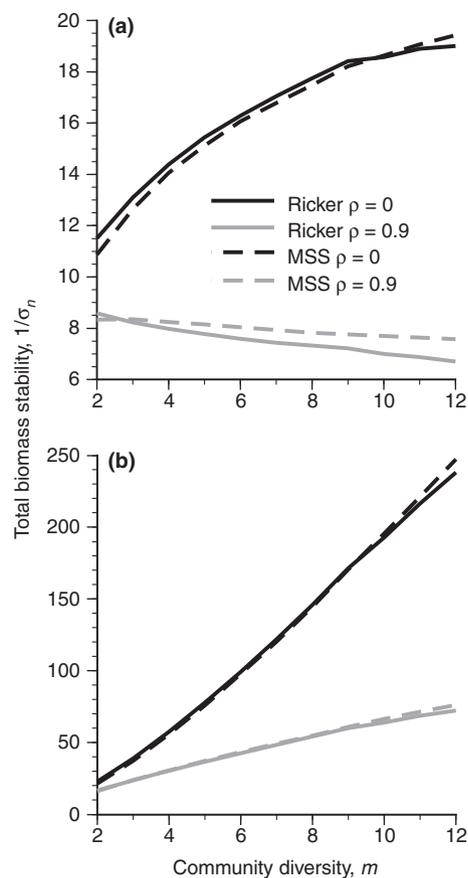


Figure 3 Diversity–stability patterns in locally stable communities including species with a range of dynamics. Species have uncorrelated ($\rho = 0$, black) or strongly correlated ($\rho = 0.9$, grey lines) environmental response, according to linear (solid) or non-linear density dependence (dashed lines). (a) Communities composed of species that do not change the variance of their response to environmental fluctuations with community size ($\sigma_{e(i)} = \gamma$). (b) Communities that always show the same level of environmental response at the community level, regardless of community size ($\sum \sigma_{e(i)} = \gamma$). In all cases, $\gamma = 0.1$, $\alpha = 0.5$. Results based on the median of 10 000 replicate communities for each community size.

associated with increased biomass stability (Fig. 3b). Simulation results are captured by algebraically derived numerical results (eqn S6, Fig. S2; Supporting Information), however, species differences in r_i or b_i values mean that finding a simple, general algebraic solution with these methods is not possible.

Increasing diversity is always associated with a reduction in summed species-level variability ($\sum v_{ij}$; Fig. 4a, b), regardless of species' responses to the environment (scaled, unscaled, correlated or uncorrelated). When species show correlated responses and do not change the variance of their responses to environmental fluctuations with increasing diversity (unscaled responses), summed covariances ($\sum v_{ij}$, $i \neq j$) increase with increasing diversity (Fig. 4c). If species experience weaker environmental variation with increasing diversity (scaled responses), summed covariances decline with increasing diversity (Fig. 4d).

Diversity–stability patterns are driven by the interaction of deterministic and stochastic effects. While r_i and b_i values were generated randomly during community assembly, examining only feasible, locally stable communities limits the parameter ranges selected for further analysis, which did not match the underlying uniform distri-

butions used to generate parameters (Fig. 5). Smaller communities are on average composed of species with lower intrinsic growth rates (r_i ; eqn 1), or weaker, more convex density dependence (b_i ; eqn 2), than larger communities (Fig. 5a, b). The proportion of species that would show stable dynamics in the absence of competition decreases with increasing diversity, $P(r_i < 2) = 0.79, 0.65, 0.60$; $P(b_i < 8/3) = 0.78, 0.64, 0.59$ in 2, 6 and 12 species communities respectively. Stronger total between-species competition in larger communities (more α -values) permits the retention of species with higher r_i or b_i values by dampening the deterministic fluctuations that would otherwise dominate community dynamics in the absence of species interactions. The distribution of eigenvalues also changes with diversity, indicating a shift towards slower (undercompensating) dynamics in larger communities (Fig. 5c, d).

This eigenvalue shift may appear counterintuitive, as higher r_i values are associated with more rapid (overcompensating) fluctuations and larger communities contain relatively fewer species with low r_i or b_i values (Fig. 5a, b). However, the increased effects of competition associated with larger community sizes dampen deterministic population fluctuations and are also associated with a shift to positive eigenvalues.

Increasing community size affects the proportions of compensating or synchronised fluctuations among species, with large differences between uncorrelated or correlated environmental responses when the environmental variation is unscaled (Fig. 6). For example, the proportion of negative between-species correlations (compensating fluctuations) increases strongly with diversity for uncorrelated environmental responses: $P[\rho(N_b, N_j) < 0] = 0.0067; 0.1049; 0.4297$; for 2, 6 and 12 species based on Ricker dynamics (eqn 1). The equivalent values for correlated environmental responses are close to zero and only increase slightly with diversity: $P[\rho(N_b, N_j) < 0] = 0; 0.0002; 0.0036$. The proportions of synchronised dynamics among species show the opposite patterns: $P[\rho(N_b, N_j) > 0.5] = 0.0006; 0.0073; 0.0101$; i.e., very few and increasing only slightly for uncorrelated environments, whereas there are more, which increase rapidly with diversity under correlated environments $P[\rho(N_b, N_j) > 0.5] = 0.0126; 0.1792; 0.7592$.

Correlations between species pairs therefore show different response patterns to increasing diversity under different environmental correlations, relating to their intrinsic growth rates (r_i). Increasing community size in uncorrelated environments leads to changes in the correlation responses of species with a given pair of r_i values (Fig. 6a–c). Relatively high correlations only occur between species with the highest r_i values present in any community. The composition of r_i values varies with community size (Fig. 5a), resulting in changes in the correlation (synchrony or compensation) of species pairs with a given r_i combination. These changes do not occur under correlated environments: species pairs with similar intrinsic dynamics (e.g., both undercompensating or both chaotic) fluctuate synchronously with each other, whereas species pairs with different intrinsic dynamics fluctuate asynchronously, independently of community size (Fig. 6d–f).

The methods outlined by Greenman & Benton (2005; their eqns 5 and B3; eqn S6 Supp Info) numerically confirm our simulation results (Fig. S2) and have the potential to provide understanding of other mechanisms driving these patterns. However, even the algebraic solutions for the two species systems we study are highly complex (in part due to the eigenvector products in their eqn 5, or the matrix inverse of Kronecker products in their eqn B3,

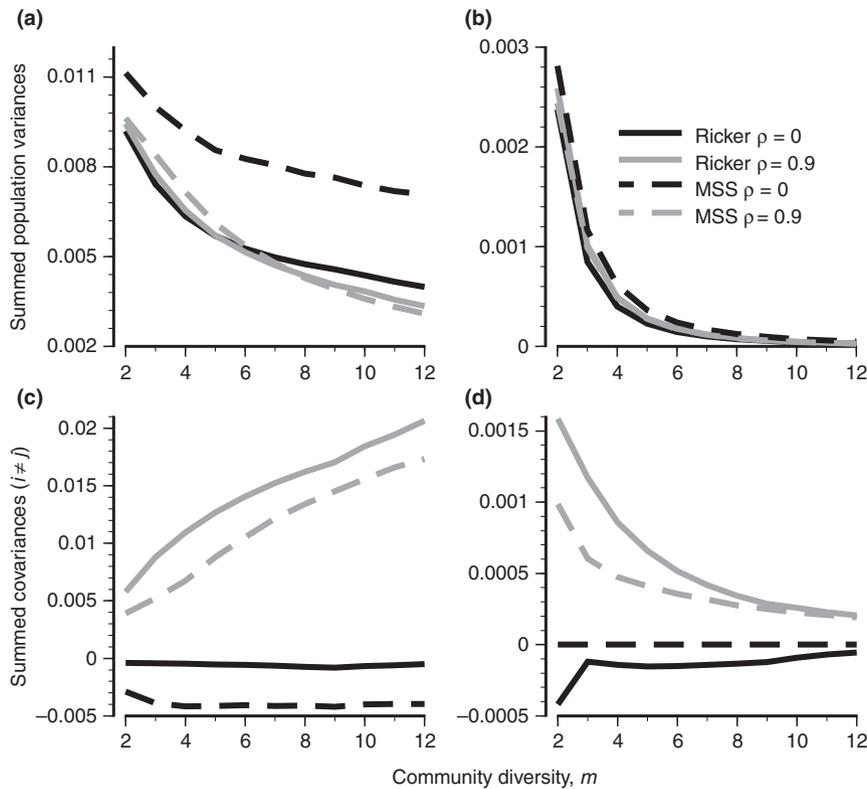


Figure 4 Statistical components of total biomass stability vary with diversity. Summed species-level variances (a, b) and covariances (c, d) for communities with uncorrelated ($\rho = 0$, black lines) or strongly correlated ($\rho = 0.9$, grey lines) environmental responses, according to linear (solid lines) or non-linear density dependence (dashed lines). (a, c) Communities composed of species that do not change the size of their response to environmental fluctuations as community size varies ($\sigma_{v(i)} = \gamma$). (b, d) Communities that always show the same level of environmental response at the community level, regardless of community size ($\sum \sigma_{v(i)} = \gamma$). In all cases, $\gamma = 0.1$, $\alpha = 0.5$. Results based on the median of 10 000 replicate communities for each community size.

$\Phi = (\mathbf{I} - \mathbf{B} \otimes \mathbf{B})^{-1}$, see eqns S4 - S6), therefore do not offer straightforward insight into the qualitative differences in diversity–biomass stability patterns between correlated and uncorrelated environments.

The only elements in eqn S6 that differ for a given community size are the off-diagonal elements of the environmental covariance matrix, \mathbf{S} , which have greater absolute values in correlated than uncorrelated environments. This offers an intuitive explanation for understanding the numerical differences between uncorrelated and correlated environments in our study: biomass stability is expected to be lower under correlated environments due to the combination of non-zero elements of \mathbf{S} with Φ , with the addition of these extra values resulting in relatively larger values for the variance of total biomass. However, considering only the elements of \mathbf{S} does not help us understand why negative diversity–stability relationships can arise in systems that include species with $r_i > 2$ (e.g., Fig. 3a), but only positive or neutral diversity–stability patterns occur when all community members have $r_i < 2$, as shown in previous analyses. Understanding how the elements of Φ , which incorporates information on within- and between-species interactions, change with community size is not straightforward, especially as the distribution of r_i or b_i values also varies with m (Fig. 5). A new challenge that may offer further insight into these problems will be to provide an intuitive biological interpretation of the elements in the matrix Φ . Until then, simulations have proven to be a useful and necessary tool in demonstrating our results.

DISCUSSION

Simple, competitive communities assembled from a wider range of species-level dynamics than previously considered (stable, cyclic and more complex) show positive or negative diversity–biomass stability patterns when species respond to environmental fluctuations in an uncorrelated or correlated fashion, respectively. This result holds for communities with species that show linear or non-linear density dependence. Previous work on linear systems has only considered species that show stable equilibrium type species-level dynamics (in the absence of species interactions). Under this assumption, the conclusion is that only positive or neutral diversity–stability patterns are possible when species respond to environmental fluctuations in a less than perfectly correlated way (Ives *et al.* 1999; Ives & Hughes 2002). Our work and earlier approaches have assumed deterministically feasible, locally stable communities being perturbed by temporally uncorrelated (white) environmental variation.

Fowler (2009) considered a model where species could differ in their intrinsic growth rates, and modified Ives & Hughes (2002) methods in a similar system to the communities we study here, replacing the single r -value used by Ives & Hughes (2002) with the mean of possible r_i values across the community. Although this simple modification was found to capture many features of the simulation results in Fowler (2009), neither those simulations, nor the modified algebraic results demonstrated the negative diversity–stability relationship we highlight here (Fig. 3a). The increase in mean r_i

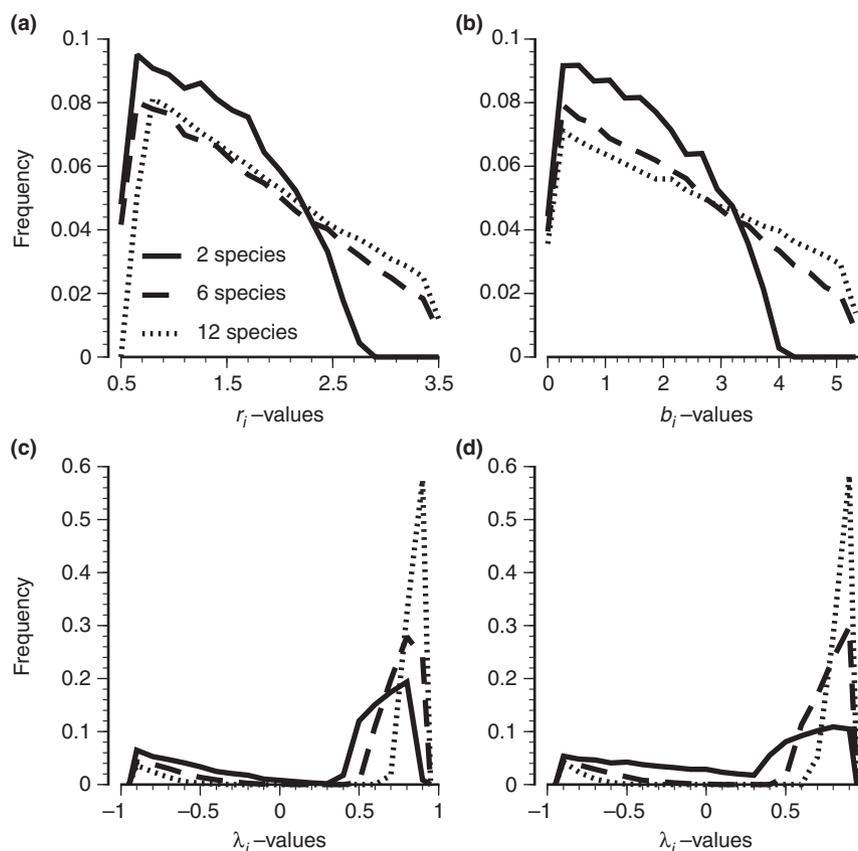


Figure 5 Increasing diversity changes the composition of species in the community. The frequency distributions of (a) intrinsic growth rates (r_i), (b) the shape of density dependence (b_i); and (c, d) eigenvalues (λ_i) based on linear (a, c) and non-linear density dependence (b, d), changes with community size (solid lines = 2 species, dashed lines = 6 species, dotted lines = 12 species). Larger communities tend to contain species with higher intrinsic growth rates or more concave density dependence (stronger competition with increasing density) and more positive eigenvalues. Results based on 10 000 replicate communities for each community size.

(or b_i) values that occurs with increasing diversity in our communities does not provide an intuitive explanation for our results either: replacing r with a mean value which increases with community size, $r(m)$, still does not generate negative diversity–stability patterns with Ives & Hughes’ (2002) approach, but does suggest an interesting feature to look for in natural systems. Similar selection effects during community assembly have been found in related models, for between-species interaction values, α_{ij} (Fowler 2010). These were associated with variation in another stability property: secondary extinction risk following a primary extinction event. Such trait/parameter selection effects during ecosystem assembly therefore appear to have important consequences for a range of community stability properties (reviewed by Ives & Carpenter 2007).

Loreau & de Mazancourt (2008) examined variability in communities composed of species with deterministically unstable dynamics ($r_i > 2$), but did not consider differences amongst community members (all $r_i = r$) as we did ($r_i \neq r_j$). These therefore did not represent locally stable communities when $r > 2$. Loreau & de Mazancourt (2008) also derived an alternative measure of community synchrony, which is a useful summary of dynamics under some circumstances, e.g., avoiding problems of interpretation when taking the mean of strong positive and negative correlation values. However, their measure does not give the same detailed information as considering all correlations between species pairs (Fig. 6) and does not give further insight to our results.

Our results appear to contradict a popular heuristic for interpreting diversity–stability patterns, based on the idea that adding species changes the relative importance of SS and SE interactions, which can in turn be expected to change the direction of diversity–stability patterns (Ives *et al.* 2000; Ives & Carpenter 2007). With unscaled environmental variation ($\sigma_{\varepsilon(t)} = \gamma$), adding species maintains the importance of SE interactions at the species level, while increasing the importance of SE at the community level. Here, species-level variability declines with increasing diversity (Fig. 4). Increasing diversity is also expected to increase the importance of SS interactions in all cases we considered, as competition increases through increasing the number of α values and reduced K_i values.

If adding species increases the importance of SS interactions, increasing diversity is expected to destabilise biomass fluctuations. We only found this result under uncorrelated environments. Likewise, when the variance of the environment declines with community size ($\Sigma \sigma_{\varepsilon} = \gamma$), we found only positive diversity–stability relationships. This is a case where SE interactions are less important and SS interactions relatively more important with increasing diversity, giving a set of results contrary to previous predictions. In this context, the Jacobian matrix (eqns S4 and S5) is considered to summarise all SS interactions. For example, as diversity increases in the Ricker-based model (eqn 1), the off- (main-) diagonal elements of the Jacobian tend to increase to approach zero (approach one) through reductions in N_i^* and K_i values. However, Jacobian ele-

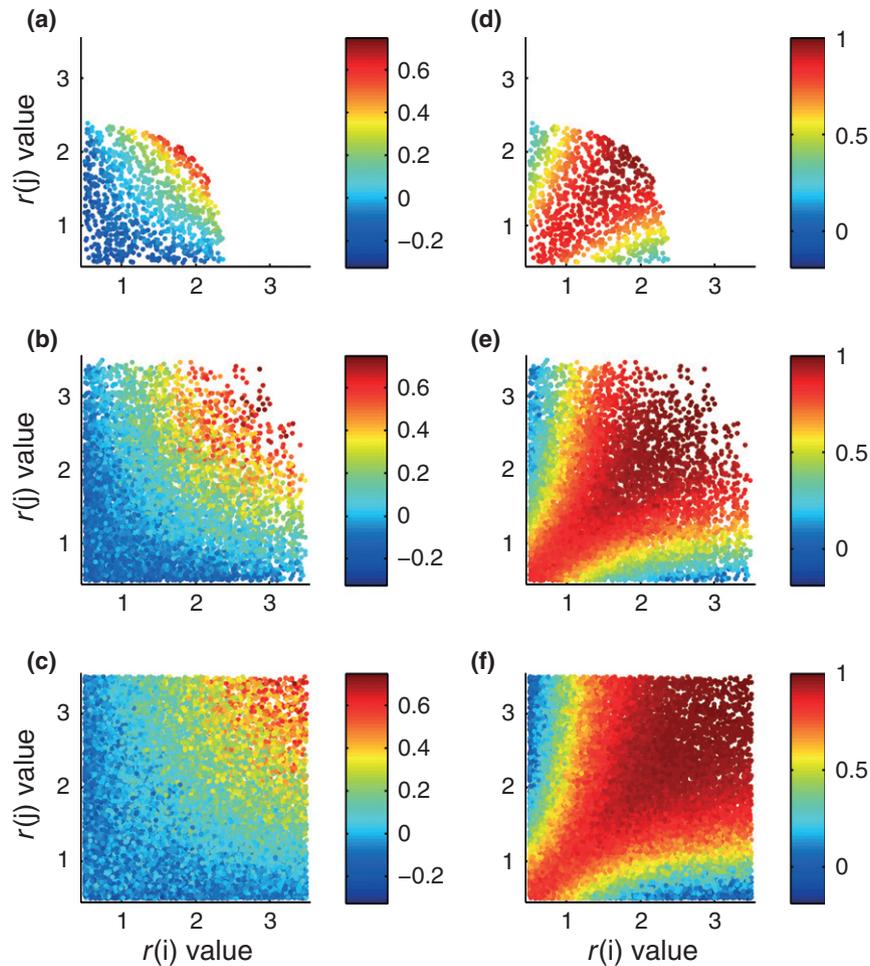


Figure 6 Patterns of between-species synchrony under uncorrelated (a–c; $\rho = 0$) or correlated (d–f; $\rho = 0.9$) environmental fluctuations in communities with linear density dependence differ in their responses to increasing diversity (a, d = 2 species; b, e = 6 species; c, f = 12 species). Under uncorrelated environments, the synchrony patterns between species pairs with given r_i and r_j values changes with community size: synchronised fluctuations only occur for combinations of the highest r_i values present in the community (which varies with community size). Under correlated environments ($\rho = 0.9$), species with similar dynamics always show relatively synchronised population fluctuations and species with different dynamics (e.g., low vs. high r_i values) tend to show uncorrelated fluctuations.

ments also tend to decrease as the average r_i values increase with diversity. These opposing effects of diversity complicate the previous simplified (heuristic) approaches to understanding the relative importance of SS and SE interactions (Ives *et al.* 2000), and underpin the alternative diversity–biomass stability patterns we illustrate here.

More complex, e.g., trophically or niche structured, models have been able to demonstrate negative diversity–stability patterns, in some cases being sensitive to the colour of environmental variation (Ives *et al.* 2000; Thébault & Loreau 2005; Brose *et al.* 2006; Gonzalez & de Feo 2007; Ruokolainen *et al.* 2009b). These studies highlight the importance of considering other species differences in such models, beyond simple difference in their response (correlations) to environmental fluctuations. Our work emphasises that including differences in species intrinsic growth rates or different forms of density dependence within a guild or functional group has important qualitative effects on diversity–stability patterns, even in very simple community models.

Both trophic and mutualistic interactions are important in structuring ecosystems (Thébault & Fontaine 2010). Single trophic level (within guild) models remain useful tools to gain insight into com-

munity stability. Ruscoe *et al.* (2011) recently demonstrated the importance of within-guild competition in structuring a simple ecosystem including invasive species. Other examples of natural communities where competition is thought to play a major role in structuring the community were recently summarised in Fowler (2010). The system we examined is often incorporated as the basal (primary producer) layer of a trophic food web, an approach that commonly assumes stable species-level dynamics. Preliminary investigation of such a system incorporating the same range of intrinsic dynamics we considered here, under correlated environmental fluctuations, indicates that diversity–stability patterns vary with trophic level. The basal level shows a negative diversity–stability relationship, while consumer levels show positive relationships. These results echo other recent work showing that biomass stability patterns can vary with the trophic level of the functional groups considered (Jiang & Pu 2009).

The colour (temporal correlation) of environmental variability also affects the size of species- and community-level fluctuations (reviewed by Ruokolainen *et al.* 2009a), but varying the colour of environmental fluctuations did not change any of our results quali-

tatively. Coloured environments can have important effects on biomass stability patterns in more complex community models (e.g., Gonzalez & de Feo 2007; Ruokolainen *et al.* 2009b), suggesting that including variation in other species traits can generate qualitatively different results.

Recent studies have also highlighted the difficulties and some potential solutions for separating the mechanisms behind biomass stability patterns from laboratory and field data (Petchey *et al.* 2002; Romanuk & Kolasa 2004; Ranta *et al.* 2008a,b; Gonzalez & Loreau 2009; Isbell *et al.* 2009; Leary & Petchey 2009; Romanuk *et al.* 2009; Roscher *et al.* 2011). Valone & Barber (2008) examined between-species correlations in natural assemblages, suggesting that these distribution patterns may not be well represented by field (agricultural) experiments, which tend to show a stabilising effect of diversity on biomass variability (Campbell *et al.* 2011). Examples of negative diversity–stability patterns have also recently been recorded in the field (Valdivia & Molis 2009; Haddad *et al.* 2011; Sasaki & Lauenroth 2011).

Analytical approaches can be extremely useful for identifying ecological relationships under certain simplifying assumptions. The nature of the diversity–stability question does not necessarily lend itself well to such simplifying assumptions. Increasing species richness also increases the complexity and diversity of traits present in a community, complicating analytical treatments, e.g., finding simple algebraic forms for eigenvalues that can inform how changing parameters will affect local stability (Ives *et al.* 1999; Fowler 2009). Previous work has highlighted some problems predicting correlation patterns with the analytical approach we examined here (Greenman & Benton 2005; Ruokolainen & Fowler 2008). It is therefore interesting that Greenman & Benton's (2005) methods do an excellent job of predicting total biomass stability under the range of simulated conditions we considered. The analytical methods are not considered to hold well close to the instability boundaries ($|\lambda_1| \rightarrow 1$). Greenman & Benton (2005) give alternative formulae for such cases, relying on an assumption of perfect symmetry or asymmetry among population fluctuations – an assumption that was not met in our communities (e.g., Figs. 2 and 6).

Theoretical and empirical insights have produced great synergies to improve our understanding of the mechanisms that drive community diversity–biomass stability patterns. Our approach has highlighted a new area that deserves more consideration: the complex interaction of different intrinsic population dynamics with environmental covariance structures. Further work is required to uncover and unravel the range of mechanisms that drive diversity–stability relationships in both model and natural ecological systems.

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AUTHORSHIP

MSF developed and analysed models and wrote the manuscript; JL, VK and LR contributed to discussions and model analyses and wrote the manuscript; ER initiated the project and developed models.

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