REPORT

Markov chain models predict the consequences of experimental extinctions

J. Timothy Wootton

Department of Ecology & Evolution, The University of Chicago, Chicago, IL, USA
Correspondence: E-mail: twootton@uchicago.edu

Abstract

Predicting the effects of species extinction is challenging because of ecosystem complexity. Using novel long-term experimental deletions of two mussel species, I found that a multi-species Markov chain model, which was parameterized under non-experimental conditions, accurately predicted the effects of local extinction in an intertidal community. Systematically deleting species from the model predicted declining ecosystem biomass with reduced biodiversity, but relatively constant ecosystem resilience following disturbance. The effects of reduced biodiversity on these variables ranged widely, illustrating the need for species-specific predictions of extinction effects. The results show that Markov chain models can be useful tools for predicting consequences of local species extinction without extensive experimentation.

Keywords

Biodiversity, ecosystem Function, intertidal, *Mytilus*, resilience, species diversity.

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INTRODUCTION

The current rate of species extinction is one of the highest known and is strongly affected by human activity (Pimm *et al*. 1995). Understanding and predicting the consequences of reduced biodiversity in natural ecological communities is essential to establish conservation priorities and inform environmental policy, but the complexity of natural ecosystems makes meeting this challenge difficult. Aside from the loss of a species, an extinction also can indirectly impact other ecosystem components because of the complex web of interactions among species and their physico-chemical environment (e.g. Paine 1966; Estes & Palmasano 1974; Wootton 1992; Menge 1995). Ignoring the indirect effects of species extinction minimizes our perception of the consequences of reducing biodiversity and hinders informed decision-making. Because multiple pathways of interactions occur simultaneously, mathematical models of multi-species systems often are necessary to predict the ecosystem-wide consequences of an extinction event. To make useful predictions, however, model parameters usually must be constrained by empirical information (Yodzis 1988), which can be difficult to obtain, particularly in experimentally intractable systems with relevance to conservation (Bender *et al*. 1984; Paine 1992; Schmitz 1997; Laska & Wootton 1998). Consequently, predictions of extinction made by multi-species models have rarely been tested experimentally in nature (Wootton 1994; Schmitz 1997). Here I report experimental tests of an empirically-accessible theoretical approach to predicting direct and indirect consequences of extinction and discuss the broader predictions of the model in light of these findings.

Markov chain models and their extensions can model multi-species systems (Horn 1975; Caswell 2001) and are less difficult to parameterize empirically without extensive experimentation than are other approaches, such as multi-species differential equations. These models focus on points in space and derive from transition probabilities of points changing from one ecological state to another after a defined interval of time. Ecological states can take many forms, including particular species, size classes of a species, groups of species, and combinations of species and physical characteristics of the environment (Horn 1975; Usher 1979; Lough *et al*. 1987; Saila & Erzini 1987; Pastor *et al*. 1993; Wootton 2001). Because transition probabilities are abstractions of complex nonlinear mechanisms involving interactions among species and their environment, such models have fewer parameters to estimate and are therefore easier to parameterize with field data. Typically multi-species Markov chain models focus on sessile species, although approaches are available to incorporate mobile consumers (e.g. Saila & Erzini 1987). Hence, transitions among sessile species may be mediated by interactions involving mobile species that are not included in the models.

Several studies have developed multi-species Markov chain models and found that they accurately recreate the

structure of the ecosystem that they model (Horn 1975; Usher 1979; Lippe *et al.* 1985; Lough *et al.* 1987; Wootton 2001; Hill *et al.* 2002). To be useful, however, these models must predict ecosystem structure in novel situations, such as those following species extinction. Previously, I showed that a Markov chain model could quantitatively predict the community composition of several novel situations that were independent of the data used to parameterize the model (Wootton 2001), but the species composition in these situations was previously known. No experiments have been implemented specifically to test the predictions of multi-species Markov models in the face of extinction. Here I test predictions of this model for completely novel situations where previous knowledge of their long-term outcome was unknown empirically. I also use the model explore the predicted general consequences of reducing biodiversity on two ecosystem function variables of recent interest: standing biomass (Loreau & Hector 2001; Tilman *et al.* 2001; Pfisterer & Schmid Bernhard 2002) and ecosystem resilience (Loreau & Behera 1999; Pfisterer & Schmid Bernhard 2002).

METHODS

The study took place in a rocky intertidal community, located on Tatoosh Island in Washington State, USA. Because the moderate size and relatively rapid dynamics of organisms in this system make experimentation tractable (Paine 1994), intertidal communities can be particularly powerful testing grounds for theoretical approaches to ecology. Previously, I repeatedly censused in the spring and late summer of 1993–1998 the ecological state of *c.* 1700 fixed points located in unmanipulated areas of the intertidal zone. I used these data to parameterize a multi-species Markov chain model and to generate predictions of the effects of species extinction (Wootton 2001). To evaluate whether the Markov model could correctly predict the consequences of extinction, I implemented local extinction experiments on two common, closely related species, the mussels *Mytilus californianus* Conrad and *M. trossulus* Gould. Although these species are taxonomically and ecologically similar, the model predicted large impacts of eliminating *M. californianus*, the ecological dominant, but small impacts of *M. trossulus* extinction. In each experiment, one mussel species was chronically and selectively removed from experimental plots ranging from 4 years, the maximum predicted time of convergence to the average species composition (Wootton 2001), to 9 years.

As soon as they became large enough to be identified, individual mussels were selectively removed by hand from plots using pocketknives to cut the byssal threads. At the start of the experiment, replicate plots were in different stages of recovery from wave disturbance, which allowed an assessment of convergence from a range of starting

conditions. *M. californianus* was removed from 60 × 60 cm plots. Ten plots were initiated in 1993 and an additional five plots were initiated in 1997 to provide more comprehensive coverage of the study area and to permit precise estimates of transition probabilities for another study. *Mytilus trossulus* was removed from 10 29 × 34 cm plots, seven of which were initially dominated by *M. trossulus* (started in 1998), and three of which began in other starting configurations (started in 1999). All plots were censused annually through June 2002 and data were expressed as average per cent cover of sessile species across all annual censuses.

To test statistically whether the experimental results deviated from model predictions, I evaluated whether the distribution of distances in multivariate space between each replicate and the predictions was significantly larger than that derived from pairs of experimental replicates. I focused on Euclidean distances in multivariate space because this metric is intuitively clear, but to insure that the distance metric I used did not affect my interpretations, I also compared predicted and observed community composition using three alternative distance metrics: Bray–Curtis, proportional dissimilarity, and proportion variance in species abundance explained. In no case did the conclusions using these metrics differ from those of Euclidean distance. Because pairwise comparisons among replicates are not completely independent, I used Monte Carlo methods to assess whether deviations between the model and the experimental plots were statistically significant. To do this, I randomly chose 15 replicate pairs, determined the multivariate distance between them, calculated the average distance between them, and compared that value to the average distance between model predictions and each plot. I repeated the procedure 1000 times and determined the fraction of times the average distance between model predictions and the plots was larger than the average between randomly selected plot pairs.

I also explored the model in more detail than previously reported (Wootton 2001) to determine predicted general effects of reducing biodiversity on two aggregate ecosystem variables: standing biomass and resilience. To do this, I systematically deleted every combination of species or taxon from the model by removing individual transitions involving each deleted species in the underlying data set and recalculating the transition matrix with the remaining transition data. This procedure guaranteed that the columns of the new matrix of transition probabilities sum to 1, a requirement of these models because they keep track of a fixed number of spatial points (Caswell 2001). From the modified models, I calculated the eigenvalues and dominant eigenvector from the model (Caswell 2001), and used these to predict standing crop and resilience. For standing crop, I used the dominant eigenvector (standardized so that its elements summed to 1) from each model variant to predict

the long-term species composition (Caswell 2001; Wootton 2001). I then multiplied the predicted proportional contribution of each species by the mean biomass per unit area of monospecific stands of that species and summed the biomass across all species to obtain a prediction of standing crop. Species-specific biomass was estimated empirically by finding monospecific stands of each sessile species in the middle intertidal zone of the study site at low tide, harvesting all individuals in a defined area of the stand, and deriving shell-free wet weight by weighing the harvested individuals after removing any calcium carbonate skeleton via dissection or combustion in a muffle furnace at 500 °C. For resilience, I calculated for each model the damping ratio, which is defined as

$$\ln(\lambda_1/|\lambda_2|) = \ln(1/|\lambda_2|),$$

where λ_1 and λ_2 are the dominant and subdominant eigenvalues, respectively. This expression is an estimate of the minimum rate of convergence back to steady state conditions following a pulsed perturbation (Caswell 2001). The resulting model predictions were analysed by plotting the number of species present in the model against the dependent variable of interest. I also analysed the output with an ANOVA to estimate relative contributions of specific taxa to the predicted biomass and resilience from this modelling 'experiment'. Because examining interactions among taxa would have required evaluating 4083 terms in the ANOVA, I restricted my analysis to additive effects of taxa, noting how much of the overall variation could be explained by these terms. Note that because the model was not stochastic, all variation in the model output was explained either by additive effects or by interactions among species, and no statistical testing was carried out. Finally, I examined the role that species sampling (Huston 1997) contributed to any observed relationship between biodiversity and ecosystem variables by using ANOVA to extract additive variation explained by particular taxa, and then determining the fraction of the residual variation associated with variation in biodiversity. The fraction of residual variation associated biodiversity indicates compensatory effects among taxa, whereas the fraction removed reflects sampling effects of biodiversity.

RESULTS

The experimental results quantitatively matched predictions of the multi-species Markov model (Fig. 1). When *M. californianus* was removed, other species in the community exhibited large changes in abundance, with articulated coralline algae (*Corallina vancouveriensis* Yendo) and acorn barnacles (*Semibalanus cariosus* Pallas) dominating the community. The model correctly predicted 84.2% of the

variance in mean abundance of taxa, and the Euclidean distance in multivariate space between observed and predicted species composition [0.30 ± 0.12 (SD), $n = 15$] was not larger than the average distance between experimental replicate pairs (0.38 ± 0.18, $n = 105$), indicating that model predictions did not differ significantly from experimental results ($P > 0.95$). In comparison, predictions generated simply by increasing the other taxa in proportion to their abundance in the unmanipulated community (Wootton 2001) did not predict the dominance of *C. vancouveriensis* and correctly predicted only 23.6% of the variance in the mean abundance of taxa in the experimental plots.

When *M. trossulus* was deleted from the system, the community remained dominated by *M. californianus*. The model correctly predicted 94.2% of the variation in mean abundance among taxa, and the Euclidean distance in species composition between experimental results and model predictions (0.28 ± 0.20, $n = 10$) again was not larger than distances between pairs of experimental replicates (0.36 ± 0.30, $n = 45$), demonstrating that the model predictions did not differ significantly from experimental results ($P > 0.75$).

Reducing biodiversity in the model caused a general decline in standing biomass, but the range of values exhibited was wide (Fig. 2a). In the ANOVA of the model output, species diversity overall explained 1.4% of the variation in predicted standing crop, whereas the presence of *M. californianus* alone explained 97% of the variation (Table 1). The total variation contributed by interactions in species presence was slight (1.3%). After factoring out the additive effects of each species on biomass, the amount of variation in standing biomass associated with biodiversity dropped to 0.03% of the total variation, indicating that species sampling contributed 98% of the observed overall relationship between biodiversity and standing biomass.

The model predicted that reducing biodiversity should on average have fairly modest effects on system resilience, except at very low diversity where average resilience increased. Again, the range of effects was fairly wide. In the ANOVA of model output (Table 1), species diversity explained 2.3% of the variance in resilience, whereas several taxa, including *M. californianus* (11.8%), *Balanus glandula* Darwin (4.7%), *Pollicipes polymerus* Sowerby (3.8%), and ephemeral algae (3.1%) predicted more variation by themselves. Interactions among taxa contributed substantially to the predicted variation in resilience (72.6%). After factoring out the additive effects of each species on resilience, the amount of variation in resilience associated with biodiversity dropped to 1.9% of the total variation, hence species sampling contributed only 20% to the effects of biodiversity on resilience.

(a)

(b)
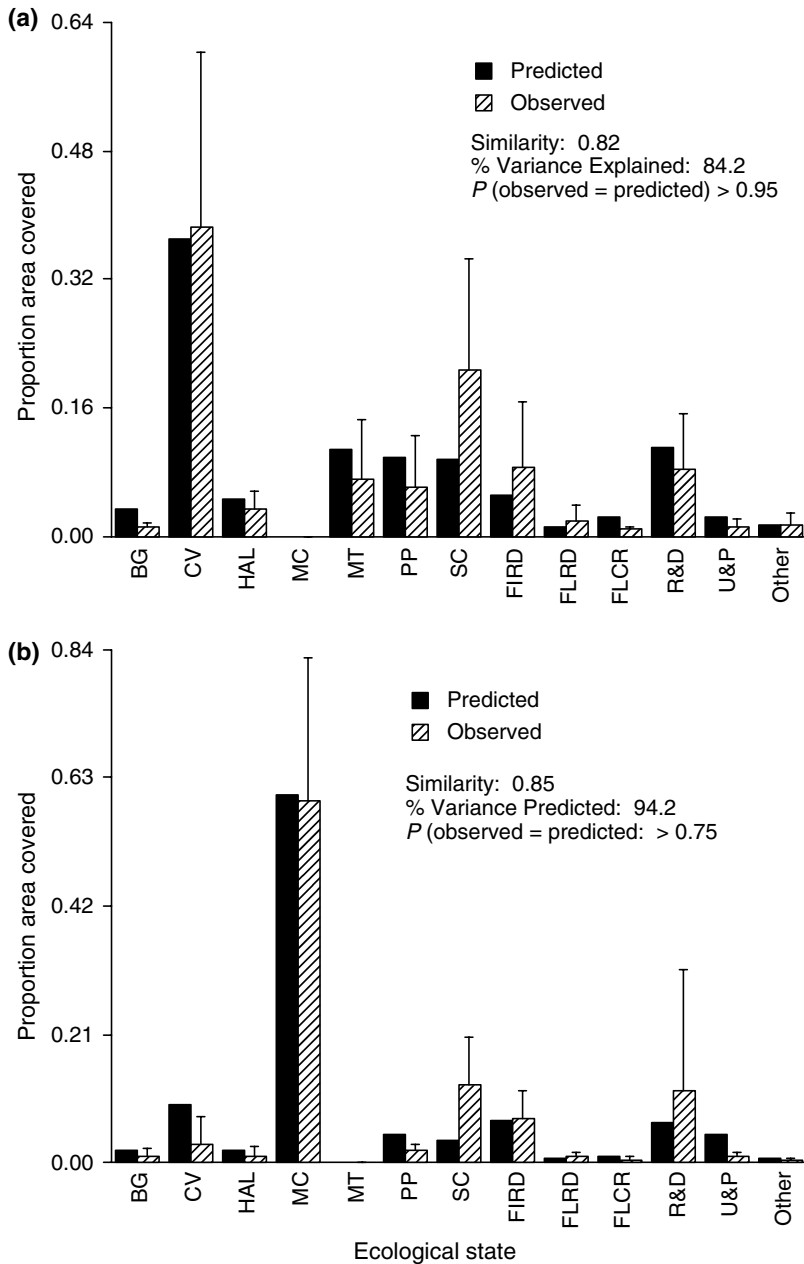
Figure 1 Comparison of experimentally observed (hatched bars) species composition with that predicted by Markov chain models following local extinction of two mussel species. (a) Effects of *Mytilus californianus* removal ($n = 15$), (b) Effects of *Mytilus trossulus* removal ($n = 10$). Error bars ± 1 SD. Taxon codes: BG, *Balanus glandula*; CV, *Corallina vancouveriensis*; HAL, *Halosaccion glandiforme*; MC, *Mytilus californianus*; MT, *Mytilus trossulus*; PP, *Pollicipes polymerus*; SC, *Semibalanus cariosus*; FIRD, filamentous red algae (mostly *Microcladia borealis*, *Polysiphonia* spp., *Callithamnion* spp., *Endocladia muricata*); FLRD, fleshy red algae (mostly *Mastocarpus pappilatus*, *Mazzaella* spp.); FLCR, fleshy crusts (*Mastocarpus pappilatus*, *Ralfsia* spp., *Hildenbrandia* spp.); R&D, rock and diatoms; U&P, ephemeral algae (*Ulva* spp. and *Porphyra* spp.); Other-rare sessile species. Taxonomy follows Kozloff (1996) and Gabrielson *et al.* (2000).

DISCUSSION

Experimental tests

Because of the difficulty of estimating parameters, few multi-species models parameterized with data from natural communities exist, and quantitative experimental tests of such models are extremely rare (Schmitz 1997). Yet such models are essential to providing useful predictions of the consequences of species extinction or other environmental perturbations in complex natural systems. Using a Markov chain community model, I was able to quantitatively predict

the long-term configuration of an intertidal community following two novel experimental extinction events.

The model predicted a large shift in community structure in response to local *M. californianus* extinction from the system, with dominance by coralline algae. Although the prediction that removing *M. californianus* has a large impact is not particularly surprising, given its dominance in the community and its central role in the classic keystone predation scenario advanced by Paine (1966) in lower intertidal habitats, the quantitative result of selectively removing *M. californianus* on the rest of the community

(a)

(b)
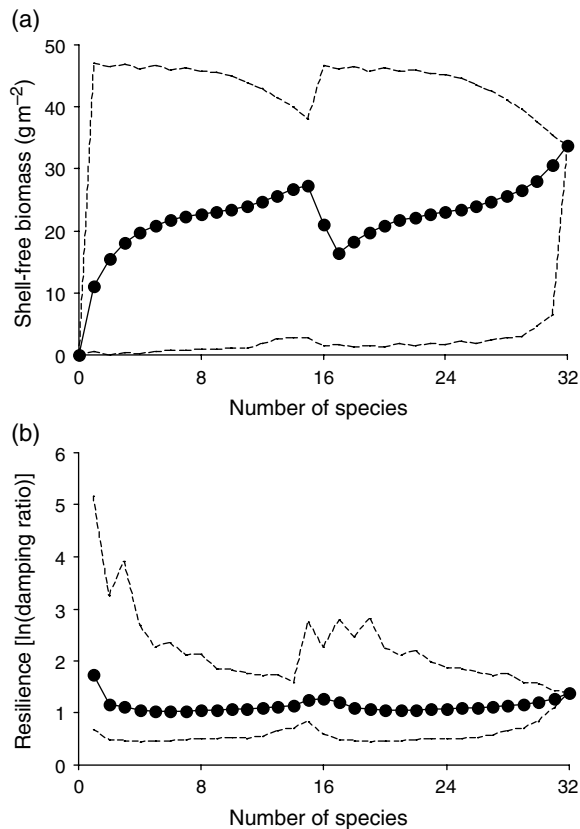
Figure 2 Predicted effects generated by the Markov chain model of all possible combinations of reduced biodiversity on (a) standing crop of all organisms (g m^{-2}) and (b) resilience, the minimum rate of ecosystem recovery following disturbance. Line with points represents average effect, dashed lines show the range of effects. The strong shifts in average patterns seen in the centre of the graphs result because the 15 rarest species are lost as a group in the analysis. Because rare species are predicted, on average, to have small impacts on these variables when other species are present, a similar relationship with the diversity of more common species obtains whether (right part of curve) or not (left part of curve) rare species are present.

was previously unknown. The prediction that coralline algae should dominate is not expected intuitively from several lines of evidence. First, when the seastar *Pisaster ocraceous* Brandt removes *M. californianus* lower on the shore, kelps become the dominant species in the community. Because *Pisaster* consumes organisms other than *M. californianus* and because there is lower desiccation stress in this habitat, however, the failure to obtain kelp dominance is perhaps understandable. Second, during succession following disturbance in the middle intertidal (mussel) zone, two other species, *M. trossulus* and *P. polymerus*, are the sub-dominant species in succession of the community (Paine & Levin 1981), and therefore would be expected to dominate in the absence of *M. californianus*. Consumer suppression of these

two species once they are established (Wootton 1993, 2002) apparently precludes them from maintaining dominance in the long-term when *M. californianus* is absent, and allows the relatively consumer-resistant coralline algae to dominate the community.

The model also predicted that the local extinction of *M. ctrossulus* would have minor effects on community structure. This prediction is also somewhat surprising because previous experiments have demonstrated that *M. trossulus* has clear short-term impacts on the dynamics of the intertidal zone (Navarrete 1996; Noda 1999; Wootton 2002). This circumstance can be explained by the apparent size-dependence of the interaction between *M. californianus* and *M. trossulus*: *M. trossulus* facilitates recruitment and/or survival of *M. californianus* spat (Petersen 1984; Navarrete 1996), whereas it inhibits larger individuals (Noda 1999; Wootton 2002). The divergent effects of two closely-related congeners emphasizes that the functional role of very similar species can be quite different in natural ecosystems, but suggests that relative abundance or biomass in a system may be one useful indicator of species impact, at least for sessile species or species at the base of the food web (Hurlbert 1997, but see Paine 1980; Power *et al.* 1996).

For ethical and logistical reasons, experimental extinctions were necessarily implemented locally rather than globally. Hence, populations of the remaining species might be influenced by the presence of the deleted species in other areas through immigration rates. The effects of the scale of extinction on community composition merits further study. Regardless of the effects of scale, predicting the consequences of local extinction remains important because large changes generated locally will probably produce the strongest feedbacks involving immigration from elsewhere in a metacommunity, and because local species extinction is a conservation concern.

Model predictions: biomass and resilience

Recently there has been great interest in exploring the ecosystem consequences of reduced biodiversity (Loreau *et al.* 2001). These empirical studies have been limited logistically in the range of species combinations manipulated and have been restricted to laboratory or semi-natural conditions. In light of the good match between experimental extinctions and model predictions reported here, and of the model to other novel situations (Wootton 2001), I systematically explored the model to evaluate expected impacts of reduced biodiversity on two aggregate properties of the intertidal system. The model predicted a general decline in standing ecosystem biomass with reduced biodiversity. Similar trends have been reported in several empirical studies in terrestrial systems (Griffiths *et al.* 2000; Spehn *et al.* 2000; Loreau & Hector 2001; Tilman *et al.* 2001; Pfisterer &

	Standing crop			Resilience		
Source	Sum of squares	d.f.	% Variance explained	Sum of squares	d.f.	% Variance explained
Mytilus californianus	1 140 927.02	1	97.21	44.182	1	11.77
Balanus glandula	1168.47	1	0.10	17.473	1	4.65
Corallina vancouveriensis	3620.51	1	0.31	0.060	1	0.02
Hallosaccion glandiforme	444.80	1	0.04	5.703	1	1.52
Mytilus trossulus	867.79	1	0.07	0.372	1	0.10
Pollicipes polymerus	2967.82	1	0.25	18.849	1	3.77
Semibalanus cariosus	405.05	1	0.03	4.038	1	1.08
Filamentous Red Algae	75.24	1	0.01	0.380	1	0.10
Fleshy Red Algae	26.28	1	0.00	0.007	1	0.00
Fleshy Crustose Algae	233.27	1	0.02	0.019	1	0.01
Ulva & Porphyra spp.	7617.04	1	0.65	11.631	1	3.10
Other species	0.89	1	0.00	0.227	1	0.06
Interaction terms	15369.66	4083	1.31	272.524	4082	72.57
Biodiversity (total)	16879.97	32	1.43	8.715	31	2.32
Biodiversity (non-additive)	316.38	32	0.03	6.971	31	1.86
Total variation	1173723.85	4095		375.512	4094	

Table 1 Additive effects of deleting taxa on the variation in shell-free standing crop and resilience (minimum rate of return to equilibrium) of the middle intertidal zone predicted by the Markov chain model, in comparison with the general effects of biodiversity (number of species). No resilience calculation is possible for the case without any species

Schmid Bernhard 2002). Although this trend exists, the results generally indicate that species affect this ecosystem attribute in idiosyncratic ways. First, the amount of predicted variation explained by species richness in general is very small, and the observed range of predictions is quite wide. Furthermore, in comparison with the amount of variation explained by biodiversity, the amount explained by the presence of individual species, particularly the mussel *M. californianus*, is far more substantial. Finally, removing the additive effects of taxa on standing biomass eliminated most of the relationship with biodiversity, indicating that the relationship was largely the result of sampling individual taxa.

The model predicted a weak relationship between biodiversity and resilience, as measured by the rate of return to equilibrium following a perturbation, with a tendency for the least diverse communities to have the highest resilience. This pattern probably arises because interactions among species tend to delay attainment of steady-state conditions (Tilman 1996; Cottingham *et al.* 2001), and may also be linked to predicted declines in standing biomass with reduced biodiversity, which may weaken the strength of species interactions (Loreau & Behera 1999; Pfisterer & Schmid Bernhard 2002). Again, the amount of variation explained by biodiversity was slight, whereas individual species contributed substantially more to variation in resilience, supporting an idiosyncratic perspective for this variable too. In contrast to the predictions for standing biomass, several species made important contributions to variation in resilience, and a majority of the variation was explained by interactive effects of the presence

of multiple species. This difference may be explained because the subdominant eigenvalue underlying the resilience calculation is a complex function of all the transitions among species in the model. In contrast, *M. californianus* both can maintain a substantially higher biomass per unit area than other species by developing a multi-layered bed, and has traits (predator resistance, large size, reattachment ability following disturbance) that maintain its dominance regardless of the number and identity of co-occurring species. Unlike standing biomass, only a small fraction of the relationship between resilience and biodiversity was accounted for by species sampling. Because interactive effects among species accounted for a high fraction of variation in resilience and biodiversity accounted for a very small fraction, idiosyncratic species interactions seem to govern system resilience. Aside from the mechanisms causing the differences in response of ecosystem variables, the analysis reinforces conclusions from a preliminary examination of this model (Wootton 2001) that the importance of particular species varies with the ecosystem metric being examined. It is critical, therefore, that a range of ecosystem functions be evaluated when considering the effects of extinction, and the relative importance of sampling effects and species compensation may change depending on the ecosystem function being examined.

CONCLUSIONS

This study shows that Markov chain models are accessible to empirical parameterization in natural ecosystems and

provides the first experimental demonstration that they can generate useful predictive information about broader consequences of local species extinction in the face of ecological complexity. Therefore, Markov chain models might be profitably applied in other less experimentally tractable systems of conservation interest. Although not extensively mechanistic, these models also point to the most sensitive components of an ecosystem to guide further mechanistic study. Finally, the results of both the experiments and model analysis show that effects of reduced biodiversity are highly species-dependent (Huston 1997; Downing & Leibold 2002). Therefore, predicting the consequences of particular extinctions will likely require the application of empirically parameterized multi-species models to inform environmental decision-making.

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