

Causes of species diversity differences: a comparative analysis of Markov models

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Abstract

While many dynamic processes have been proposed to produce diversity differences among communities, most empirical investigations focus on static system attributes. An ideal analysis would consider multiple dynamic processes and their impact on many community members, but such analyses can be logistically daunting. I compared Markov chain models of ecological communities to explore general processes leading to diversity differences of sessile species between coral reefs and rocky intertidal mussel beds. As predicted by diversity theory, high diversity coral reefs had lower species replacement probabilities and higher disturbance rates than did lower diversity mussel beds. Intransitivities in species replacements, recruitment limitation and responses to perturbing species from equilibrium (Jacobian elements) did not differ significantly between systems. Tradeoffs between the displacement risk or displacement ability of a species and either disturbance risk or colonising ability were not apparent. Manipulating the coral reef model to eliminate disturbance or intransitivities caused declines in species diversity, whereas removing recruitment limitation or increasing the probability of interspecific replacement did not. Higher overall disturbance levels can explain part of the diversity difference between systems, but much remained unexplained, indicating that details of the pattern and strengths of species interactions were probably extremely important.

Keywords

Biodiversity, coral reef, disturbance, intertidal, mussel bed, transition probability.

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INTRODUCTION

Ecologists have long been fascinated by the causes of the vast differences in species diversity seen in different habitats (Wallace 1876; Fischer 1960; MacArthur 1965, 1972). This interest has spawned numerous hypotheses about the cause of variation in diversity (reviewed in Ricklefs & Schluter 1993; Huston 1994). Pinpointing the mechanisms underlying diversity patterns has been challenging, however, because of the complexity of the systems under study. Ecosystem complexity hampers developing general conclusions of the causes of diversity; detailed experimental studies generally can only tractably evaluate mechanisms of coexistence among a few species (e.g. Werner & Hall 1976; Pacala & Roughgarden 1985; Pfister 1995), and these mechanisms may not characterise the community as a whole or be responsible for the diversity differences observed in different habitats. For example, high water velocity in aquatic habitats may represent a disturbance to some species but not to others.

Furthermore, large-scale analyses generally consider only snapshots of species abundances, and focus on static variables (e.g. latitude or altitude; Fischer 1960; Pianka 1966; MacArthur 1972; Currie & Paquin 1987; Stevens 1989; Roy *et al.* 1994) whereas many hypothesised mechanisms involve dynamic processes such as disturbance (Connell 1978), colonisation rates (MacArthur & Wilson 1967; Roughgarden *et al.* 1988; Tilman 1994), environmental fluctuations (Hutchinson 1961; Chesson & Huntley 1997) and the strengths and nature of species interactions (Paine 1966; May 1973; Buss & Jackson 1979; McCann *et al.* 1998). With the exception of system primary productivity (reviewed in Rosenzweig & Abramsky 1993), general characterisations of the dynamic processes potentially involved in species coexistence are rarely available (but see Simberloff & Wilson 1969). Finally, multiple mechanisms which may affect species diversity are rarely considered simultaneously. Ideally a multispecies, multimechanism dynamic framework would be used both to compare different systems and to evaluate

the consequences to diversity of eliminating any differences in processes between systems, but obtaining the necessary empirical information is logistically daunting. Perhaps the most empirically accessible frameworks meeting these criteria are Markov chain models of communities (Waggoner & Stephens 1970; Horn 1975). Here, I report a comparative analysis of Markov chain models to illustrate one possible approach to explore the relationship between species diversity and multiple dynamic processes.

Marine benthic communities exhibit marked differences in species diversity which have inspired several hypotheses about the mechanisms determining diversity. For example, coral reefs are some of the most diverse ecosystems known (Connell 1978; Ayal & Safriel 1982; Huston 1985; Ormond *et al.* 1997), whereas temperate mussel bed communities have prompted discussion on the implications of species monocultures (Paine 1984). Several factors have been suggested to control diversity in marine benthic communities. Generally, strong interspecific interactions, relative to intraspecific interactions, are predicted to reduce species coexistence (Lotka 1925; May 1973). Furthermore, skewed distributions of interaction strengths among species may facilitate species coexistence (McCann *et al.* 1998). Additionally, biotic or abiotic disturbance has been proposed as an important determinant of diversity by preventing dominant species from monopolizing resources, as long as it is not so intense that it drives species to extinction (Paine 1966; Paine & Vadas 1969; Dayton 1971; Connell 1978; Sousa 1979; Paine & Levin 1981). A tradeoff generally is predicted between displacement ability and disturbance susceptibility of a species for disturbance to facilitate coexistence (Levin & Paine 1974), but this is not necessary in open systems (Wootton 1998). Recruitment limitation has been postulated to reduce the intensity of species interactions (Gaines & Roughgarden 1985; Roughgarden *et al.* 1988; Connolly & Roughgarden 1999), thereby facilitating coexistence, although extremely low recruitment could directly limit the number of species present (Menge & Sutherland 1987). Additionally, recruitment limitation can promote high species coexistence in models with strong asymmetric competition when there is a tradeoff between displacement ability and colonisation ability of a species (Tilman 1994). Furthermore, intransitivities in species dominance patterns, such as competitive reversals or situations where a competitive subordinate of a species can beat the competitive dominant of the same species, have been proposed to lead to species coexistence in marine benthic habitats (Buss & Jackson 1979; Tanner *et al.* 1984, but see Quinn 1982).

Markov chain models are derived from a time series of censuses of multiple fixed points in space, where the

ecological state of each point is characterised at each census. Ecological states might include different species or combinations of species, different size classes or empty space. One can derive from these data transition probabilities that points in one ecological state will either remain in that state or change to another state over the next census interval. Although transition probabilities are not explicit descriptions of different processes, they are likely to reflect different processes. Transitions to empty space reflect disturbance, transitions from empty to occupied space reflect colonisation rates, and transitions from one species to another may reflect species interactions. The correspondence may not be perfect, however, because multiple transitions might occur over shorter time scales than those used to derive transitions or may involve species which were not included in the model. For example, the transition of one species to another over a long time scale might arise from a transition to empty space over a shorter interval, followed by rapid colonisation of space by another species. Recently, detailed Markov models of an Australian coral reef (Tanner *et al.* 1994) and a Washington mussel bed community (Wootton, *in press*) have become available. Here, I illustrate how Markov models might shed light on processes leading to different diversity levels between systems by comparing the mussel bed and coral reef models and asking (1) how their structure differs in relation to differences in species diversity between these two systems and (2) whether eliminating general differences in structure can lead to predicted changes in diversity similar to the observed variation in diversity between systems.

METHODS

Methods of parameterising the coral reef Markov chain models are described in detail by Tanner *et al.* (1994). Briefly, the study took place at Heron Island, Queensland, Australia. Starting in 1962 and continuing through 1989 at approximately two-year intervals, quadrats were placed at fixed points in wave-exposed reef crest, wave-exposed pool and wave-protected reef crest habitats and photographed. The photographs were then analysed in the lab by placing a grid over the quadrat to determine the ecological state (species, bare rock) at each point at each census. The transitions from one ecological state to another in consecutive censuses were then incorporated into three separate models for different habitats, depending on where the data were collected: wave-exposed reef crest ($n = 9522$ transitions), wave-exposed pool ($n = 11\ 233$ transitions) and wave-protected reef crest ($n = 20\ 245$ transitions).

Details of the parameterisation of the mussel bed Markov chain have been described by Wootton (*in press*). This study was carried out in the rocky intertidal zone of

Tatoosh Island, Washington state, located off the north-western tip of the Olympic Peninsula (see Paine & Levin 1981 for details). In this study, quadrats (15 quadrats with 100 points each, one of which was lost after 1 year) and transects (11 transects with 30 points each) were placed at fixed locations and orientations on wave-exposed horizontal rock benches in the spring (late May) and early fall (late August to early September) from 1993 to 1998 and each of the fixed points was censused visually for the ecological state occurring under it. The approximately 17 700 transitions among ecological states between consecutive censuses derived from these data were then pooled and incorporated into a Markov chain with annual transitions generated from the product of two seasonal matrices. Predictions of this model were tested against, and successfully matched, both the natural community on horizontal benches, and communities arising under several novel conditions (experimental bird exclusions, vertical walls) after appropriately manipulating the model (Wootton, in press). Therefore, analysis of these models to understand factors affecting species diversity is reasonable.

The two systems differ markedly in species diversity indices. Species richness at the coral reef site (81 coral and algal species recorded during the Tanner *et al.* 1994 study) was higher than the mussel bed (32 sessile species recorded in the Wootton, in press study). The coral reef also had higher evenness in the abundance of taxa (mussel bed = 0.165; exposed crest coral reef = 0.492, exposed pool coral reef = 0.458). These differences in species diversity index suggested that it was worth comparing the Markov chain models of the two systems to determine whether their structures differed in a manner consistent with several species diversity hypotheses.

The models were compared in several ways to test particular diversity hypotheses using Kolmogorov–Smirnov tests (Sokal & Rohlf 1995) to examine overall differences in distribution. If the distributions differed between habitats, Mann–Whitney *U*-tests were used to evaluate differences in central tendency, and the distributions were examined for skewness and kurtosis (Sokal & Rohlf 1995). Because the models were derived from small-scale quadrats within well-defined habitats, the analysis of diversity in these models is at the local scale (alpha diversity). I only examined the wave-exposed coral reef models, because the intertidal model was derived from wave-exposed sites. Additionally, because of the difference in census intervals between the coral reef and mussel bed study, the annual transition matrix for the mussel bed was multiplied by itself to reflect expected transitions over a two year interval. To aid in the analyses and their presentation, the transition matrices from each study were restructured so that transitions involving empty space were contained in the last row and column (see Table 1),

and taxa were ordered by increasing displacement ability, defined as the average of the transitions from other taxa to the target taxon (see Table 1). I tested different diversity hypotheses as follows.

To test the hypothesis that stronger interspecific interactions among sessile species lead to lower diversity, I compared the distribution of the total probability of displacement by other species across each taxon between the two habitats (Table 1). More intense interspecific interactions should produce higher rates of interspecific displacement, particularly as a result of competitive displacement. I also calculated the net short-term effect of perturbing each taxon away from steady state on the other members of the community. This measure is conceptually equivalent to estimating the elements in the “Jacobian Matrix,” the index of interaction strength originally explored in May’s (1973) analysis of the effects of species diversity on food web stability. I altered the stable stage distribution for the mussel bed or coral reef transition matrices by shifting 1% cover from empty space to a target taxon, and then multiplied the resulting vector by the transition matrix to project the expected change in the cover of each taxon in the following two year interval (see Table 1). This procedure mimics the PULSE experimental protocol suggested by Bender *et al.* (1984) for estimating Jacobian elements. I explored both raw estimates of the Jacobian elements and standardised estimates derived by dividing by the magnitude of the estimated intraspecific elements. The interaction strength hypothesis (May 1973) predicts that the coral reef should have lower interspecific displacement rates and lower magnitude Jacobian elements. The skewed interaction strength hypothesis (McCann *et al.* 1998) predicts that the coral reef should have a greater skew than does the mussel bed.

I explored two aspects of the hypothesis that disturbance affected diversity. First, I examined whether the distribution of probabilities of a taxon being replaced by rock over two years was different between the two habitats (Table 1). Because the coral reef model had fewer ecological states (9) than the mussel bed model (14), transitions would be expected to be higher in the coral reef model due to chance. Therefore, I tested transitions after multiplying those in the coral reef models by 9/14. Because previous coral reef studies emphasised disturbance as a mechanism promoting diversity (Connell 1978; Tanner *et al.* 1994), I expected higher disturbance rates in more species-diverse coral reefs than in mussel beds. I also tested for the tradeoff between disturbance susceptibility and displacement ability hypothesised in several models of disturbance-facilitated diversity. To evaluate this prediction, I plotted the transition probability that a taxon was replaced by bare space after two years against either (1) the displacement ability of a species or (2) the

Table 1 Summary of Markov chain model structure, indices compared between models, and model manipulations used in the paper**General Model Structure**

$\mathbf{X}_{t+1} = \mathbf{P} * \mathbf{X}_t$, where \mathbf{X}_t is a column vector describing the proportion of points in different ecological states (x_j) at a given time t , and \mathbf{P} is a square matrix containing transition probabilities (p_{ij}) in the i -th row and j -th column, defined as the probability of a point in ecological state j at time t being in state i at the next census (time $t + 1$). \mathbf{P} has dimension $S + 1$, where S is the number of taxa in the model. Column and row $S + 1$ contain transition probabilities of points either starting from empty space or ending up as empty space, respectively. Taxa in \mathbf{P} were arranged from lowest to highest displacement ability, defined for taxon i as

$$\left(\sum_{j=1}^S p_{ij} / (S - 1); i \neq j \right). \text{ All } \sum_{i=1}^{S+1} p_{ij} = 1, \text{ and } p_{ij} \geq 0$$

The eigenvector of the dominant eigenvalue of \mathbf{P} gives the predicted equilibrium community composition.

Indices compared between models

Displacement Risk: for taxon j , defined as

$$(1 - p_{jj} - p_{(S+1)j} = \sum_{j=1}^S p_{ij}; i \neq j)$$

Jacobian Elements: predicted change after one census interval of taxon i from steady state (x_i^*) as a result of a small change (Δ) in taxon j ($\partial f_i / \partial x_j$), calculated as:

$$\begin{bmatrix} \partial f_1 / \partial x_j \\ \vdots \\ \partial f_i / \partial x_j \\ \vdots \\ \partial f_j / \partial x_j \\ \vdots \\ \partial f_{S+1} / \partial x_j \end{bmatrix} = \mathbf{P} * \begin{bmatrix} x_1^* \\ \vdots \\ x_i^* \\ \vdots \\ x_j^* + \Delta \\ \vdots \\ x_{S+1}^* - \Delta \end{bmatrix} - \begin{bmatrix} x_1^* \\ \vdots \\ x_i^* \\ \vdots \\ x_j^* + \Delta \\ \vdots \\ x_{S+1}^* - \Delta \end{bmatrix}$$

For interspecific ($i \neq j < S + 1$) elements, $\partial f_i / \partial x_j$ simplifies to $(p_{ij} - p_{(S+1)j})\Delta$.

Disturbance Rate: For taxon j , defined as $p_{(S+1)j}$.

Colonisation/Recruitment Ability: For taxon i , defined as $p_{i(S+1)}$.

Transition Intransitivity: $I = p_{ij} / (p_{ij} + p_{ji}); i < j < S + 1$.

Model manipulations (modified transition probabilities indicated by \mathbf{p}'):

Shannon's Diversity Index calculation: $D = 1 / \sum_{i=1}^S x_i / (1 - x_{S+1})^2$, where x_i is the proportional abundance of ecological state i at steady state.

Increase displacement risk: For each taxon j , $p_{jj}' = 0.2 * p_{jj}$; $p_{ij}' = p_{ij} + p_{ij} * 0.8 / (1 - p_{jj} - p_{(S+1)j})$, where $i \neq j$, and $i, j < S + 1$.

Remove recruitment limitation: $p_{(S+1)(S+1)'} = 0$; $p_{i(S+1)'} = p_{i(S+1)} + p_{(S+1)(S+1)} * p_{i(S+1)} / (1 - p_{(S+1)(S+1)})$; $i < S + 1$.

Eliminate disturbance: row and column $S + 1$ deleted; $p_{ij}' = p_{ij} + p_{ij} * p_{(S+1)j} / (1 - p_{(S+1)j})$.

Remove transition intransitivity: For $i < j < S + 1$, $p_{ij}' = 0$; for $S + 1 > i \geq j$, $p_{ij}' = p_{ij} * (1 + [\sum_{q=1}^{j-1} p_{qj} / \sum_{q=j}^S p_{qj}])$.

displacement risk of a species, defined as the probability of displacement of the target taxon by other taxa (see Table 1). I used Spearman rank correlations (Sokal & Rohlf 1995) to determine whether a significant positive association existed between disturbance rate and displacement ability, and whether a significant negative association existed between disturbance rate and displacement risk. Because columns in the transition matrices must sum to 1, the probability of disturbance and displacement risk by other species might be negatively correlated due to chance. I used Monte Carlo procedures to verify that any negative correlations did not arise by chance, by comparing the relationship between disturbance probability and displacement risk

in 100 matrices with the observed transitions randomly reshuffled within each column.

To examine the hypothesis that recruitment limitation produces diversity differences, I tested whether distributions of transitions from empty space to various taxa (see Table 1) were different in coral reefs than in mussel beds. Again, coral transitions were adjusted by 9/14 to eliminate effects due to different numbers of taxon categories in the different models.

To test the hypothesis that a tradeoff between recruitment probability and the ability to displace other species leads to larger numbers of coexisting species, I plotted the relationship between the probability that a taxon colonised bare rock and either the taxon's

displacement ability or displacement risk (Table 1). Relationships between the variables were tested with Spearman rank correlations. The recruitment–displacement hypothesis predicts a negative relationship between recruitment probability and displacement ability, and a positive relationship between recruitment probability and displacement risk. Furthermore, the coral reef is expected to show stronger relationships than the mussel bed.

I tested the hypothesis that intransitivities, or displacement reversals, promoted species diversity by comparing the asymmetry of transitions from one taxon to another and vice versa (see Table 1). An intransitivity index (I) was calculated for each pair of taxa in a matrix (Table 1). Transitions involving empty space and self–self (p_{ii}) were not included. Because the transition matrix was ordered by increasing displacement ability, I provides a measure of the intransitivity of displacement among taxa. If displacement is perfectly hierarchical, $I = 0$ for all pairs of taxa. If transitions among pairs of taxa are completely symmetrical (all $p_{ij} = p_{ji}$), $I = 0.5$. If $0.5 < I \leq 1$, a transition in the opposite direction of the overall hierarchy of displacement ability is indicated. I compared the distribution of intransitivities among pairs of taxa. The intransitivity hypothesis predicts that the intransitivity index should be higher in the more species diverse coral reef than in the mussel bed.

Comparisons of the structure of the coral reef and mussel bed models only indicate whether particular hypotheses about the causes of diversity differences are plausible. I modified the models to explore whether diversity differences might be explained by the effects of strong species interactions, disturbance, recruitment limitation and the intransitivity of interactions. In each analysis, transitions of interest were adjusted to target values, and the remaining transitions were then changed proportionately so that the sum of each column in the transition matrix was 1. The predicted long-term composition of ecological states was then calculated for the modified model, and the percentage change in taxa diversity, based on Simpson's Diversity Index (Simpson 1949) was determined from the prediction.

I modified the models in the following specific ways (see Table 1). To test the effect of eliminating intransitivities in species replacements, I set all transitions above the diagonal of the transition matrix involving different pairs of taxa (i.e. not involving bare space or self–self transitions) to 0. To test the effect of variation in colonisation ability among taxa, I set the probabilities of colonising bare space equal across all species while leaving unchanged the probability that bare rock remained bare rock. To test the effect of recruitment limitation, I set the probability that bare space remained empty to 0. To test the effect of disturbance, I deleted bare space as a possible

state in the matrix. To test for the effects of high species replacement rates, I reduced the probability that a site occupied by an organism would remain in the same state by 80% and allocated the difference from the original self–self transition proportionally to the transitions from one organism to another. The change in self–self transitions was based on the average percent difference observed between the coral reef and mussel bed models. For the mussel bed models, I evaluated the effect of changing time scales by modifying both the model describing transitions over two years, and the seasonal transition matrices upon which the model was originally based.

RESULTS

Are stronger or less skewed interspecific interactions associated with lower diversity?

Patterns of transitions in the models of coral reefs and mussel beds suggested more intense interspecific interaction in mussel beds, in agreement with theory. The probability of displacement of one taxon by another taxon over a two-year interval in the mussel bed averaged 4.5 times higher than the coral reef, and the distribution of displacement probabilities was significantly different between the two systems (Fig. 1a, Kolmogorov–Smirnov test, $D = 0.923$, $P < 0.0001$; U -test, $P < 0.0001$). The distribution of average displacement risks was highly skewed in the mussel bed (skewness = -3.00 , $P < 0.001$; Sokal & Rohlf 1995), but not in the coral reef (skewness = 0.36 , $P > 0.2$). Mussel beds had many high, but a few very low, displacement risks.

In contrast to probabilities of replacement by other species, estimates of Jacobian elements did not indicate stronger mean interaction strength among sessile organisms in mussel beds nor lower skewness in mussel beds. The distribution of magnitudes of estimated Jacobian elements differed for both raw and standardised values ($D = 0.234$, $P < 0.002$ and $D = 0.313$, $P < 0.0001$, respectively), but mean magnitudes of raw and standardised Jacobian elements were 50% higher in coral reefs (U -tests, both $P < 0.0005$), contrary to the interaction strength hypothesis. The difference in distributions also resulted from the higher skewness in the magnitude of elements from mussel beds (3.746 and 4.138 for raw and standardised values, respectively) than coral reefs (1.893 and 2.711, respectively), with mussel beds having many small and a few large elements.

Does disturbance differ between systems?

Comparisons between habitats of transitions to bare rock indicated that disturbance was substantially higher on

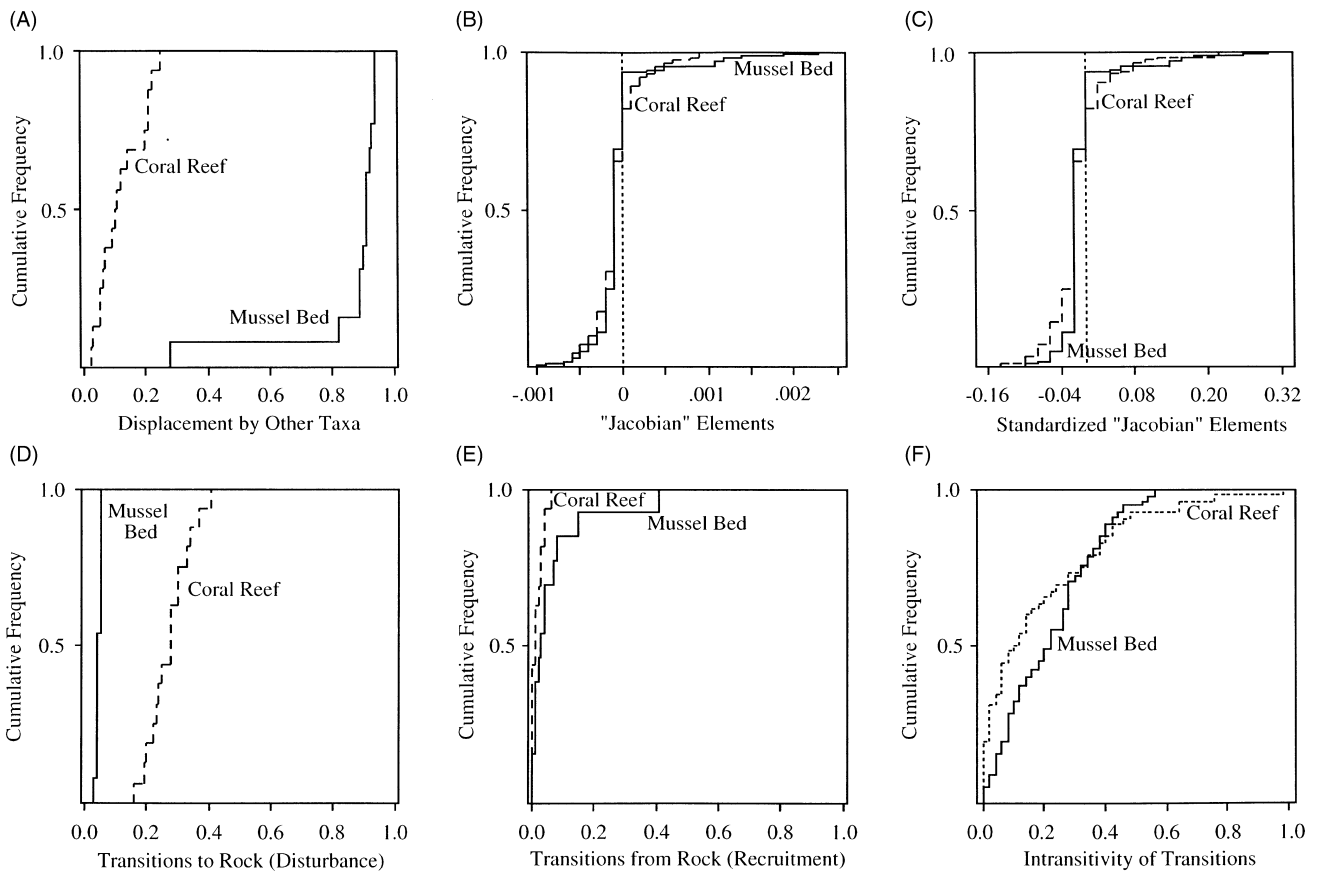


Figure 1 Cumulative frequency distributions of different Markov model parameters or characteristics for a rocky intertidal mussel bed (solid line) and a coral reef (dashed line; exposed crest and pool habitats combined). (A) Probability of a taxon being displaced by another taxon after 2 years. (B) Predicted effect after two years of a 1% increase in a target taxon from steady state conditions on each other taxon ('Jacobian' Elements). (C) Interspecific Jacobian elements standardised by the change in the target taxon following a 1% increase from steady state. (D) Probability of a taxon at a point being replaced by bare space, an index of disturbance. (E) Probability of bare space being colonised by a taxon after two years. (F) Intransitivity in transitions between lower and higher ranked taxa in the hierarchy of average abilities of particular taxa to replace other taxa.

coral reefs than in mussel beds. The probability that a site occupied by an organism became bare rock after two years was 5.8 times higher on coral reefs than in mussel beds (Kolmogorov–Smirnov test, $D = 1$, $P < 0.0001$; U -test, $P < 0.0001$; Fig. 1d). There was no evidence of a positive relationship between displacement ability and disturbance risk in either habitat; the relationships among the variables were negative in both habitats (Fig. 2a, Table 2). Similarly, there was no evidence of a negative tradeoff between interspecific displacement and disturbance risk in either habitat; the relationships among these variables were positive in both habitats (Fig. 2b, Table 2).

Does recruitment limitation differ between systems?

Evidence for differential recruitment between the two habitats was weak. Although the probability of bare rock

being occupied by an organism after 2 years was 3.6 times higher in the mussel bed than on the coral reef, suggesting greater overall recruitment intensity in that habitat, the distribution of recruitment rates did not differ significantly between habitats (Fig. 1e, Kolmogorov–Smirnov test, $D = 0.394$, $P > 0.1$). Contrary to expectations, the relationship between the displacement ability of a taxon and its colonising ability was not negatively related (Fig. 3a, Table 2), nor was the relationship between displacement risk and colonising ability positively related (Fig. 3b, Table 2).

Is greater diversity associated with higher intransitivities?

Patterns of intransitivity in transitions among taxa did not support the hypothesis that intransitivities lead to higher diversity on coral reefs. The distribution of intransitivities

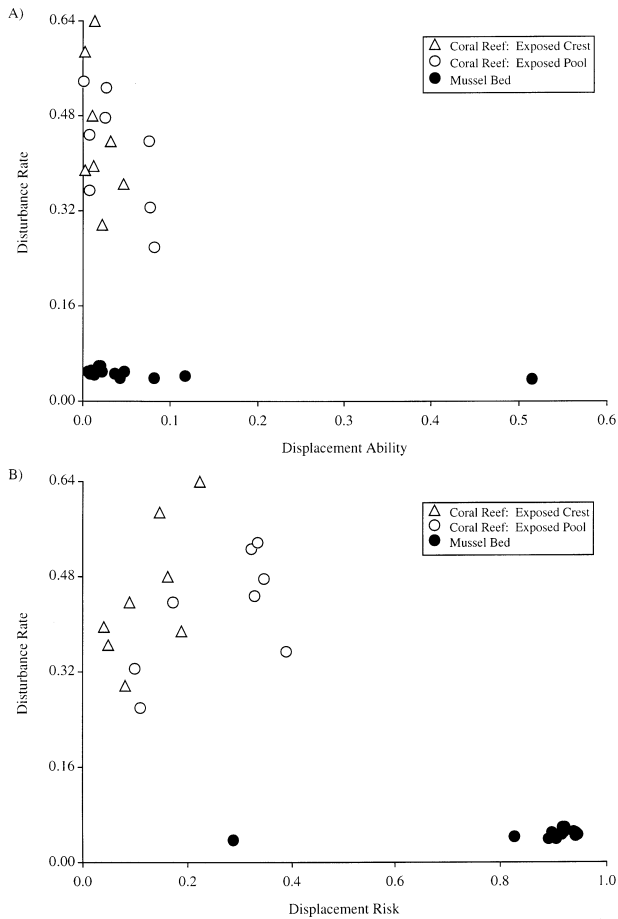


Figure 2 Relationship between disturbance susceptibility of a taxon (probability that a taxon is replaced by bare space after two years) and either (A) its average probability of displacing another taxon (displacement ability) or (B) its probability of being displaced by another taxon (displacement risk). Open symbols: coral reef; solid circles: mussel bed.

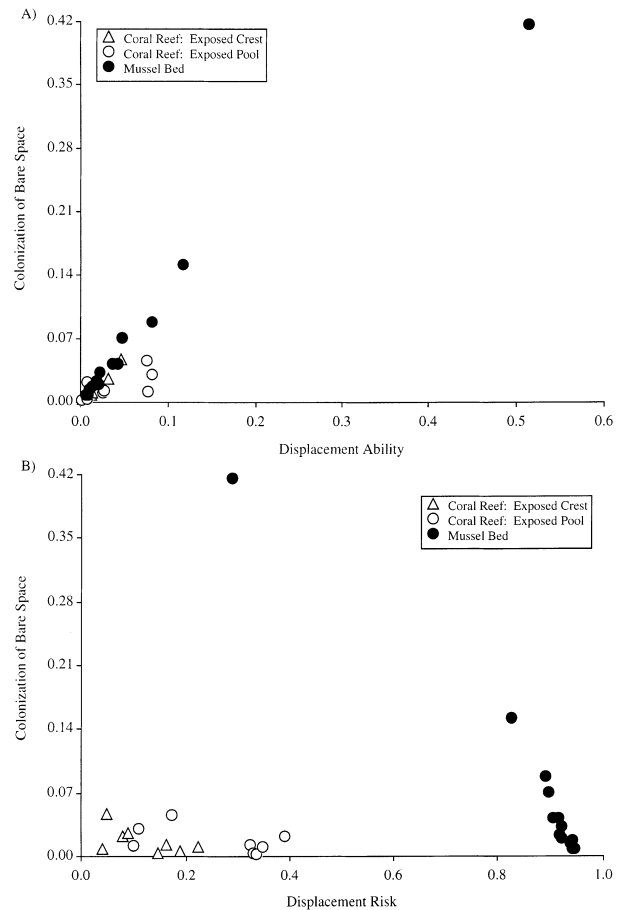


Figure 3 Relationship between colonisation ability of a taxon (probability that a taxon colonises bare space after two years) and either (A) its average probability of displacing another taxon (displacement ability) or (B) its probability of being displaced by another taxon (displacement risk). Open symbols: coral reef; solid circles: mussel bed.

Table 2 Matrix of Spearman rank correlation coefficients between indices of displacement ability or displacement risk and disturbance or colonisation rates. Note that all coefficients are in the opposite direction of those predicted by tradeoff hypotheses (all one-tailed P -values > 0.5). The negative relationship between disturbance rate and displacement risk expected by chance is also not realised

Habitat	Colonisation rate		Disturbance rate	
	Displacement ability	Displacement risk	Displacement ability	Displacement risk
Mussel bed (n = 13)	0.989	-0.978	-0.533	0.478
Coral reef				
Combined (n = 16)	0.929	-0.262	-0.480	0.438
Crest (n = 8)	0.929	-0.381	-0.429	0.595
Pool (n = 8)	0.850	-0.810	-0.695	0.500

differed significantly between coral reefs and mussel beds (Kolmogorov–Smirnov test, $D = 0.256$, $P < 0.04$), but the mean and median intransitivity of transitions among pairs of taxa were 1.1 and 1.8 times higher in mussel beds than in coral reefs, respectively (U -test, $P < 0.04$; Fig. 1f). Aside from having lower average intransitivity, coral reefs exhibited skewed intransitivity (skewness = 1.498, $P < 0.05$), with many very low and a few relatively high values. Two of the six coral reef cases with intransitivity indices > 0.5 were based on 1 and 7 observations, however; thus sampling error could have strongly influenced these estimates.

Effects of model manipulations

Altering models to reflect differences in processes between coral reefs and mussel beds yielded differing effects on diversity (Fig. 4). In general, the directional changes in diversity resulting from different types of model manipulations were concordant between coral reefs and mussel beds, although the magnitudes of the responses varied. Eliminating intransitivities among species reduced diversity in both mussel beds and coral reefs, and did so slightly more strongly in mussel beds (Fig. 4). Excluding variation in colonisation ability had minimal effects on mussel beds, but caused large increases in coral reef diversity. Removing recruitment limitation had no appreciable effect on diversity in either system. Eliminating disturbance lowered diversity in mussel beds slightly, and reduced diversity in coral reefs by up to 28%, with a stronger effect in pools than on the reef crest. Increasing the probability of species replacement caused slight increases in diversity in mussel beds, and strong increases in diversity in coral reefs. For all model variants considered, the results of the mussel bed analysis were insensitive to whether the model was based on seasonal transitions or transitions over a two year period.

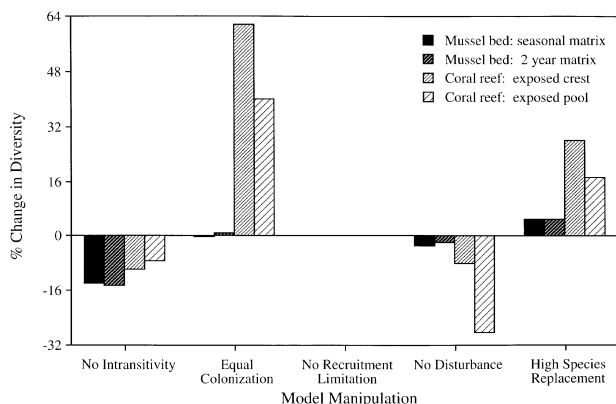


Figure 4 Percentage change in taxon diversity predicted from various manipulations of the coral reef and mussel bed models.

DISCUSSION

Comparisons between the structure of Markov chain models suggested several processes might contribute to diversity differences between mussel beds and coral reefs. Rates of species replacement were substantially higher in the lower diversity mussel bed, consistent with the proposition that high intensities of interactions among species might destabilise communities, leading to lower diversities (May 1973). Conversely, strengths of species interactions measured by estimates of Jacobian elements tended to be higher in the high-diversity coral reef. Rates of disturbance were substantially lower in mussel beds, supporting suggestions that disturbance can enhance diversity on coral reefs (Connell 1978; Tanner *et al.* 1994). Mussel beds also had higher rates of colonisation of bare rock, suggesting that they were less recruitment limited, which might increase intensities of interactions among organisms and higher interspecific displacement rates as a consequence (Underwood & Denley 1984; Menge & Sutherland 1987; Roughgarden *et al.* 1988). The evidence of recruitment limitation was equivocal at best, however, because the observed distributions in colonisation of bare space were not statistically different at the 0.05 level.

In contrast, several hypotheses for explaining diversity differences were not supported by the model comparisons. Although the distribution of interaction strength indices differed between systems, mussel beds had more skewed distributions, contrary to theoretical expectations (McCann *et al.* 1998). There was no evidence that a tradeoff between colonising ability and displacement ability promoted diversity in either habitat (e.g. Levin & Paine 1974; Werner & Platt 1976; Petraitis *et al.* 1989; Tilman 1994; Pfister 1995, 1996; Hubbell *et al.* 1999). In both mussel beds and coral reefs, there was a positive association between the two. There was also no evidence that intransitivities among species promoted higher diversity in coral reefs, as has been suggested by others (Buss & Jackson 1979; Tanner *et al.* 1994). The average intransitivity in transitions among pairs of taxa tended to be lower in mussel beds.

Although model comparisons suggested that several mechanisms might contribute to diversity differences, analysis of manipulated models indicated that not all of the mechanisms were likely to play an important role. Eliminating recruitment limitation had no effect on diversity in either system, raising doubt that it has a major effect on differences between systems. Additionally, increasing the average rates of species replacement actually increased diversity in the models, in opposition to predictions that the intensity of interactions among species tends to reduce diversity. As expected in theory

(Tilman 1994), the positive association between colonisation ability and displacement ability reduced diversity, particularly in coral reef systems. Although removing intransitivity from the models suggested that it could promote species diversity, this mechanism probably did not contribute to differences in diversity between mussel beds and coral reefs both because it had a stronger effect on mussel beds, and because the degree of intransitivity tended to be higher in mussel beds.

Model analysis and manipulations indicated that disturbance could contribute to higher diversity in coral reefs relative to mussel beds. Aside from the observation that the probability of occupied sites becoming bare space was substantially higher in coral reefs than mussel beds, eliminating disturbance from the coral reef models caused declines in diversity in modified models ranging from 8 to 28%. Taken together, these observations support the important role suggested for disturbance for community diversity in general (e.g. Paine & Vadas 1969; Horn 1975; Platt 1975; Sousa 1979). Previous studies of the coral reefs considered here have emphasised an important role for disturbance (Connell 1978; Tanner *et al.* 1994). For example, Tanner *et al.* (1994) found that, for the index of model sensitivity they used, transitions associated with disturbance had some of the largest effects on predicted steady state composition of the system. Although these studies have emphasised an important role for disturbance on diversity, they did not establish that disturbance was higher than in other systems, because of a lack of information, and did not determine whether altering disturbance regimes in theory affected taxa diversity.

Because transition probabilities are abstract indices of disturbance, the precise mechanisms leading to differences in diversity between coral reefs and mussel beds are not clear. Models of both systems were derived from relatively wave-exposed sites, so the effects of wave disturbance on differences in diversity might be minimised. Prior work in the coral reef system has emphasised periodic disturbances imposed by typhoons (Connell 1978; Tanner *et al.* 1994), although previous analysis of the coral reef models found no separation in steady state predictions from matrices derived from years with and without typhoons (Tanner *et al.* 1994). Perhaps the differences between systems are instead a result of chronic effects of biotic disturbance agents, such as parrotfish (Scaridae; Bellwood 1995; Miller & Hay 1998), crown of thorns starfish (*Acanthaster planci* [Linnaeus]; Colgan 1987; Birkeland 1990) or other consumer species. The mussel beds in the middle intertidal zone of Tatoosh Island lack such effective consumers, particularly on the dominant species *Mytilus californianus* (Conrad).

Although between-system patterns suggest an important role of disturbance on diversity, disturbance differences are not the entire explanation. Eliminating disturbance entirely from coral reef models caused only an 8–28% reduction in diversity, but declines in diversity of 60–70% are required to attain the levels seen in the mussel bed community. A substantial amount of the diversity difference between systems remains to be explained. There may be general differences lurking in the empirically based models that I either have not identified or have not been able to adequately evaluate in modified models. Finding such general patterns might lead to new hypotheses of the causes of diversity differences among systems. For example, I noted general differences in the shape of distributions of the intransitivities of transitions among species pairs. Such distribution differences might explain further the differences seen between systems, but they are hard to impose on a modified Markov model. Additionally, differences in species richness may have been shaped in part by historical differences in species origination and extinction rates (e.g. Connor 1986; Kauffman & Fagerstrom 1993). Markov models do not shed insight into such processes unless, perhaps, they are applied to the fossil record. In this study, diversity differences between coral reefs and mussel beds arose in part from differences in the evenness of species abundances, which are likely to arise from ecological rather than historical processes. Environmental fluctuations might also play a role in maintaining diversity. Although not considered in this paper, previous analyses of temporal variation in these models (Tanner *et al.* 1994; 1996; Wootton, in press) found they had minimal effects on model predictions.

Finally, the expectation that general processes can explain diversity levels within a community or major diversity differences among ecosystems may be wishful thinking. Instead, the details of the pathways and strengths of species interactions, and their interplay with the physical environment, may explain the majority of the differences in species diversity among systems. For example, I have evaluated the response of predicted diversity levels to 50% reductions in each transition in these models, but have found no general patterns, aside from the fairly obvious result that increasing the displacement rates of subordinate species and decreasing the displacement rates of dominant species will lead to lower diversity. In any event, results of this study suggest that taking Markov chain models, or other multiprocess, multispecies approaches to exploring species diversity may be a promising and fruitful way to evaluate whether general diversity-controlling mechanisms exist or whether the details of community structure hold the key to understanding diversity.

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REFERENCES

- Ayal, Y. & Safriel, U.N. (1982). Species diversity of the coral reef—a note on the role of predation and of adjacent habitats. *Bull. Mar Science*, 32, 787–790.
- Bellwood, D.R. (1995). Direct estimate of bioerosion by two parrotfish species, *Chlorurus gibbus* and *C. sordidus*, on the Great Barrier Reef. *Australia. Mar Biol. (Berlin)*, 121, 419–429.
- Bender, E.A., Case, T.J. & Gilpin, M.E. (1984). Perturbation experiments in community ecology: theory and practice. *Ecology*, 65, 1–13.
- Birkeland, C. (1990). *Acanthaster Planci: Major Management Problem of Coral Reefs*. CRC Press, Boca Raton, Florida.
- Buss, L.W. & Jackson, J.B.C. (1979). Competitive networks: nontransitive competitive relationships in cryptic coral reef environments. *Am. Naturalist*, 113, 223–234.
- Chesson, P. & Huntley, N. (1997). The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *Am. Naturalist*, 150, 519–553.
- Colgan, M.W. (1987). Coral reef recovery on Guam, Micronesia, after catastrophic predation by *Acanthaster planci*. *Ecology*, 68, 1592–1605.
- Connell, J.H. (1978). Diversity in tropical rainforests and coral reefs. *Science*, 199, 1302–1310.
- Connolly, S.R. & Roughgarden, J. (1999). Theory of marine communities: competition, predation, and recruitment–dependent interaction strength. *Ecol. Monographs*, 69, 277–296.
- Connor, E.F. (1986). The role of Pleistocene forest refugia in the evolution and biogeography of tropical biotas. *Trends Ecol. Evolution*, 1, 165–169.
- Currie, D.J. & Paquin, V. (1987). Large-scale biogeographical patterns of species richness in trees. *Nature*, 329, 326–327.
- Dayton, P.K. (1971). Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monographs*, 41, 351–389.
- Fischer, A.G. (1960). Latitudinal variation in organic diversity. *Evolution*, 14, 64–81.
- Gaines, S.D. & Roughgarden, J. (1985). Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. *Proc. Natl. Acad. Sci. (USA)*, 82, 3707–3711.
- Horn, H.S. (1975). Markovian properties of forest succession. In: *Ecology and Evolution of Communities* (eds Cody, M.L. & Diamond, J.M.), pp. 196–211, Harvard University Press, Cambridge, MA.
- Hubbell, S.P., Foster, R.B., O'Brien, S.T., Harms, K.E., Condit, R., Wechsler, B., De Wright, S.J. & Lao, S.L. (1999). Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science*, 283, 554–557.
- Huston, M.A. (1985). Patterns of species diversity on coral reefs. *Annu. Rev. Ecol. Syst.*, 16, 149–177.
- Huston, M.A. (1994). *Biological Diversity. The Coexistence of Species on Changing Landscapes*. Cambridge University Press, Cambridge, UK.
- Hutchinson, G.E. (1961). The paradox of the plankton. *Am. Naturalist*, 95, 145–159.
- Kauffman, E.G. & Fagerstrom, J.A. (1993). Phanerozoic evolution of reef diversity. In: *Species Diversity in Ecological Communities* (eds Ricklefs, R.E. & Schluter, D.), pp. 315–329, University of Chicago Press, Chicago, IL.
- Levin, S.A. & Paine, R.T. (1974). Disturbance, patch formation, and community structure. *Proc. Natl. Acad. Sci. (USA)*, 71, 2744–2747.
- Lotka, A.J. (1925). *Elements of Physical Biology*. Williams & Wilkins, Baltimore, MD.
- MacArthur, R.H. (1965). Patterns of species diversity. *Biol. Rev.*, 40, 510–533.
- MacArthur, R.H. (1972). *Geographical Ecology*. Harper & Row, New York, NY.
- MacArthur, R.H. & Wilson, E.O. (1967). *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.
- May R.M. (1973). *Stability and complexity in model ecosystems*. Princeton University Press, Princeton, NJ.
- McCann, K., Hastings, A. & Huxel, G. (1998). Weak trophic interactions and the balance of nature. *Nature*, 395, 794–798.
- Menge, B.A. & Sutherland, J.P. (1987). Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Am. Naturalist*, 130, 730–757.
- Miller, M.W. & Hay, M.E. (1998). Effects of fish predation and seaweed competition on the survival and growth of corals. *Oecologia*, 113, 231–238.
- Ormond, R.F.G., Gage, J.D. & Angel, M.V. (1997). *Marine Biodiversity: Patterns and Processes*. Cambridge University Press, Cambridge, UK.
- Pacala, S.W. & Roughgarden, J. (1985). Population experiments with the *Anolis* lizards of St. Maarten St. *Eustatius*. *Ecology*, 66, 129–141.
- Paine, R.T. (1966). Food web complexity and species diversity. *Am. Naturalist*, 100, 65–75.
- Paine, R.T. (1984). Ecological determinism in the competition for space. *Ecology*, 65, 1339–1348.
- Paine, R.T. & Levin, S.A. (1981). Intertidal landscapes: disturbance and the dynamics of pattern. *Ecol. Monographs*, 51, 145–178.
- Paine, R.T. & Vadas, R.L. (1969). The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. *Limnol. Oceanogr.*, 14, 710–719.
- Petriatis P.S., Latham R.E. & Nisenbaum R.A. (1989). The maintenance of species diversity by disturbance. *Q. Rev. Biol.*, 64, 393–418.
- Pfister, C.A. (1995). Estimating competition coefficients from census data: a test with field manipulations of tidepool fishes. *Am. Naturalist*, 146, 271–291.
- Pfister, C.A. (1996). The role and importance of recruitment variability to a guild of tidepool fishes. *Ecology*, 77, 1928–1941.
- Pianka, E.R. (1966). Latitudinal gradients in species diversity: a review of the concepts. *Am. Naturalist*, 100, 33–46.
- Platt W.J. (1975). The colonization and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. *Ecological Monographs*, 45, 285–305.

- Quinn, J.F. (1982). Competitive hierarchies in marine benthic communities. *Oecologia*, 54, 129–135.
- Ricklefs, R.E. & Schluter, D. (1993). *Species Diversity in Ecological Communities*. University of Chicago Press, Chicago, IL.
- Rosenzweig, M.L. & Abramsky, Z. (1993). How are productivity and diversity related? In: *Species Diversity in Ecological Communities* (eds Ricklefs, R.E. & Schluter, D.), pp. 52–65. University of Chicago Press, Chicago, IL.
- Roughgarden, J., Gaines, S. & Possingham, H. (1988). Recruitment dynamics in complex life cycles. *Science*, 241, 1460–1466.
- Roy, K., Jablonski, D. & Valentine, J.W. (1994). Eastern Pacific molluscan provinces and latitudinal diversity gradients: no evidence for 'Rapoport's rule.' *Proc. Natl. Acad. Sciences (USA)*, 91, 8871–8874.
- Simberloff, D.S. & Wilson, E.O. (1969). Experimental zoogeography of islands: the colonization of empty islands. *Ecology*, 50, 278–296.
- Simpson, E.H. (1949). Measurement of diversity. *Nature*, 163, 688.
- Sokal, R.R. & Rohlf, F.J. (1995). *Biometry*. 3rd edn. W. H. Freeman, New York, NY.
- Sousa W.P. (1979). Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology*, 60, 1225–1239.
- Stevens, G.C. (1989). The latitudinal gradient in geographical range: how so many species coexist in the tropics. *Am. Naturalist*, 133, 240–256.
- Tanner, J.E., Hughes, T.P. & Connell, J.H. (1994). Species coexistence, keystone species, and succession: a sensitivity analysis. *Ecology*, 75, 2204–2219.
- Tanner, J.E., Hughes, T.P. & Connell, J.H. (1996). The role of history in community dynamics: a modelling approach. *Ecology*, 77, 108–117.
- Tilman, D. (1994). Competition and biodiversity in spatially structured habitats. *Ecology*, 75, 2–16.
- Underwood, A.J. & Denley, E.J. (1984). Paradigms, explanations, and generalizations in models for the structure of intertidal communities on rocky shores. In: *Ecological Communities: Conceptual Issues and the Evidence* (eds Strong, D.R. Jr, Simberloff, D., Abele, L.G. & Thistle, A.B.), pp. 151–180. Princeton University Press, Princeton, NJ.
- Waggoner, P.E. & Stephens, G.R. (1970). Transition probabilities for a forest. *Nature*, 225, 1160–1161.
- Wallace, A.R. (1876). *The Geographical Distribution of Animals*. Harper, New York, NY, USA.
- Werner, E.E. & Hall, D.J. (1976). Niche shifts in sunfishes: experimental evidence and significance. *Science*, 191, 404–406.
- Werner, P.A. & Platt, W.J. (1976). Ecological relationships of co-occurring goldenrods (*Solidago*: Compositae). *Am. Naturalist*, 110, 959–971.
- Wootton, J.T. (1998). Effects of disturbance on species diversity: a multitrophic perspective. *Am. Naturalist*, 152, 803–825.
- Wootton, J.T. (in press). Prediction in complex communities: analysis of empirically-derived Markov models. *Ecology*.

BIOSKETCH

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