

## *INTRA-GUILD COMPENSATION REGULATES SPECIES RICHNESS IN DESERT RODENTS: COMMENT*

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Goheen et al. (2005) noted that species richness of local communities frequently remains relatively constant despite substantial changes in species composition, and that identification of the processes that produce such constancy represents an important step in understanding community dynamics. Brown et al. (2001) suggested that regulation of species richness within communities should occur if two conditions are met: (1) fluctuations in one or more environmental conditions, despite relatively constant resource availability, and (2) a feedback mechanism between the regional pool and local community, such that the probability of colonization increases when local richness falls below the long-term mean, and the probability of extinction increases when local richness exceeds the long-term mean. Goheen et al. (2005) thus used data from a long-studied desert rodent community to test proposed condition (2) of compensatory changes in probabilities of colonization and extinction.

Goheen et al. (2005) used species richness data from eight plots at 52 sampling periods, each period consisting of six monthly samples. The species pool included 21 species, and mean richness was about 10 species. They developed a simulation approach designed to determine if observed dynamics of species richness differed from those expected based on random colonization and extinction. This approach involved initializing each simulation with the mean number of 10 species. For each subsequent sampling period, they “randomly drew an integer value for the net number of colonizations and extinctions (i.e., the net change in species richness) with

replacement from the observed distribution” (Goheen et al. 2005:569). They noted that this procedure generated a random walk, and they bounded the walk between 0 and 21 species.

In order to investigate the idea of compensatory changes in colonization and extinction, they added to this random walk a compensation parameter,  $c$ . This parameter increased the probability of a net colonization event when time-specific species richness was below the long-term mean and increased the probability of a net extinction event when richness was above the long-term mean. Finally, they viewed the coefficient of variation in species richness ( $cv$ ) as a response variable, and drew inferences about the true value of  $c$  (the actual level of compensation) by matching the median of  $cv$  values simulated with different values of  $c$ , with the observed  $cv$  for the rodent community. Their results led to the conclusions that (1) compensation regulated species richness through time, and (2) the magnitude of the compensatory process was sizeable (Goheen et al. 2005).

In this note, we consider an alternative to the null model used by Goheen et al. (2005). Null models have been the focus of a great deal of controversy in community ecology (Gotelli and Graves 1996), with a key issue being development of a model that is null with respect to a focal process, yet that still includes enough other key processes to provide an otherwise reasonable description for the system of interest. In this particular case, we prefer an alternative to the random selection of species losses and gains in the Goheen et al. (2005) model. We use a Markov model focusing on the dynamics of exchange between local and regional species groups to demonstrate the stabilizing effects of colonization from regional species pools in the absence of compensation.

### *An alternative null model*

In our previous work (e.g., Boulinier et al. 2001:1161), our thinking has been structured by a simple Markov model of community dynamics:

$$S_{t+1} = S_t(1 - \epsilon) + (P - S_t)\gamma \quad (1)$$

where  $S_t$  denotes local species richness at time  $t$ ,  $P$  is the total number of species in the pool (treated as a constant),  $\epsilon$  is the probability of local extinction (probability that a member of  $S_t$  is also a member of  $P - S_{t+1}$ ), and  $\gamma$  is colonization probability (probability that a member of  $[P - S_t]$  is also a member of  $S_{t+1}$ ). Expression (1) simply states that species richness at one time step ( $t + 1$ ) can be viewed as the sum of surviving local species from the previous time step,  $S_t(1 - \epsilon)$ , and colonizing species that were not members of the local community in the previous time step,  $(P - S_t)\gamma$ . Note

Manuscript received 17 June 2005; revised 6 September 2005; accepted 21 September 2005. Corresponding Editor: N. J. Gotelli.

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TABLE 1. Proportion of simulated time steps exhibiting decreases (&lt;0), no change (0), and increases (&gt;0) in species richness.

Pr(extinction)	Change in richness								
	$S_t < 10$			$S_t = 10$			$S_t > 10$		
	<0	0	>0	<0	0	>0	<0	0	>0
$\varepsilon = 0.10$	0.10	0.12	0.19	0.07	0.06	0.07	0.18	0.12	0.10
$\varepsilon = 0.20$	0.10	0.08	0.23	0.07	0.04	0.07	0.23	0.08	0.09
$\varepsilon = 0.30$	0.09	0.07	0.26	0.08	0.04	0.08	0.26	0.06	0.09

*Note:* These proportions are reported separately for the times when richness at the beginning of the step is less than, equal to, and greater than the expected average richness,  $E(S_t) = 10$ . Proportions are computed for local extinction probabilities of  $\varepsilon = 0.10, 0.20$ , and  $0.30$ . In all simulations, the species pool was held constant at  $P = 21$ . For each extinction probability, 10 000 simulations of 50 time steps each were performed.

that the community level vital rates ( $\varepsilon, \gamma$ ) are viewed as constants in this simple model, but if they are treated as random variables with constant expectation, results will be similar. Also note that the regional species pool,  $P$ , is viewed as a constant, whereas the members of the pool available for colonization at any time step,  $(P - S_t)$ , do vary over time. The model in (1) represents a simplification of the Markov model of Simberloff (1983), in which probabilities of extinction and colonization are species-specific (the continuous analog was initially described in the context of island biogeography by MacArthur and Wilson 1963, 1967, Simberloff 1969, and Wilson 1969).

If the local community is at equilibrium (e.g., the dynamic equilibrium of MacArthur and Wilson 1967) such that the expected value of the random variable species richness is a constant,  $E(S_t) = S^*$  for all  $t$ , then on average we expect the number of local extinctions to equal the number of colonizations, i.e.,

$$E(S_t \varepsilon) = E[(P - S_t) \gamma] \quad (2)$$

However, because we view expression (1) as a stochastic process, the equality of expression (2) only applies to expectations and will not be true of the realized process at every time step. Instead, realized richness ( $S_t$ ) will sometimes be below equilibrium richness ( $S^*$ ) and sometimes above it. When fewer species are present in the local community than at equilibrium ( $S_t < S^*$ ), the number of species in the pool that are absent from the community will be greater than at equilibrium ( $P - S_t > P - S^*$ ), so that on average, we expect more colonists than extinctions ( $E[S_t \varepsilon] < E[(P - S_t) \gamma]$ , for  $S_t < S^*$ ). Similarly, when more species are in the local community than at equilibrium, we expect more extinctions than colonists. Thus if the basic model of biogeography expressed in (1) is viewed as an appropriate null model, then even in the absence of compensatory changes in extinction and colonization probabilities, we would expect net gain (colonization) when local richness is below equilibrium value and net loss (extinction) when local richness is above equilibrium.

We illustrate this expectation with a simple set of numerical results. We assumed a species pool of 21 and a

mean local richness of 10, as in the community sampled by Goheen et al. (2005). We arbitrarily used extinction probabilities of  $\varepsilon = 0.10, 0.20$ , and  $0.30$ , and then solved for the corresponding colonization probability that would yield equilibrium,  $\gamma = \varepsilon S^* / (P - S^*) = 10\varepsilon / 11$ . Then for 50 time steps, we simulated dynamics of local species richness using Eq. (1) and treating extinction of each local species as a Bernoulli trial with parameter  $\varepsilon$ , and colonization of each species not in the local community as a Bernoulli trial with parameter  $\gamma$ , using a uniform random number generator. We summarized the number of time steps exhibiting net losses, net gains, and no change, when local species richness at the beginning of the interval was below equilibrium, at equilibrium, and above equilibrium. The 50-step process of Eq. (1) was simulated 10 000 times at each of the three values of extinction probability.

Results of the numerical simulations are presented in Table 1. The proportion of time steps with net increases in local species richness was two to three times larger when local richness was below equilibrium, depending on the magnitude of the extinction probability. Similarly, the proportion of time steps with net decreases in local species richness was two to three times larger when local richness was above equilibrium (Table 1).

#### Discussion

The tendency for local species richness to be stabilized by increased losses when richness is above equilibrium and by increased gains when richness is below equilibrium does not require compensatory changes in probabilities of extinction and colonization. In our simple model, this tendency was a product of the balancing changes in the number of species in the local area and the number of potential colonists. Because the sum of these two species groups is a constant (the number of species in the pool), as one group becomes larger, the other becomes smaller. Thus, application of constant-rate parameters to these groups produces greater or smaller numbers of species extinctions or colonizations, depending on the number of species to which the parameters apply.

The null model of Goheen et al. (2005) involved random selection of species gains and losses from the observed distributions. This random walk was bounded, but otherwise did not include constraints involving the number of species available to either go locally extinct or become local colonists. Absence of this constraint led to a clear difference between null model results and the observed species data, and thus to the conclusion of compensatory changes in probabilities of extinction and colonization. However, imposition of such a constraint in Eq. (1) produced the qualitative stabilizing results without any compensatory changes in underlying probabilities of colonization or extinction.

In a similar exercise, Simberloff (1983) compared observed avian species composition data from three locations with data generated under a null model similar to that of (1) in terms of variances in species numbers, number of runs of species numbers up or down, and numbers of years with no change in species numbers. He concluded that there was no evidence in the data for a regulatory hypothesis involving species interactions.

Correspondence with the authors of the Goheen et al. (2005) paper (J. R. Goheen, J. H. Brown) led to the recognition that our perceived different conclusions about community stability were partly a function of different definitions of key terms. In our modeling and thinking, we define "probability of extinction" as the probability that a member of some group (e.g., the local community) at time  $t$  is not present at some later time (e.g.,  $t + 1$ ). However, when Goheen et al. (2005:567) refer to increases in the probability of extinction, they refer to number of extinctions per unit time (J. Goheen, *personal communication*). Similarly, we view "probability of colonization" as being applied to each species in the species pool that is absent from the local community, whereas Goheen et al. (2005) view this as colonizations per unit time. Thus community stability can arise when probabilities of extinction and colonization (our definitions) remain constant over time or exhibit constant expectation. Our Markov model indeed results in more extinctions than colonizations when local species richness is larger than average and more colonizations than extinctions when local richness is smaller than average, a result consistent with the definitions and conclusions of Goheen et al. (2005). Note that these different ways of defining rates and probabilities of colonization and extinction have led to interpretive problems in the past (Williamson 1978).

Our definition of the term "compensation" also differs from that of Goheen et al. (2005). We think of compensatory changes as occurring in probabilities of extinction or colonization (our model parameters) in response to changes in the proportion of the species pool that is present in the local community. Thus reduced species richness in the local community might result in a

decrease in the probability that a species in that community would subsequently go extinct. Indeed the discussion of possible mechanisms by Goheen et al. (2005) includes niche complementarity and changes in resource abundance, mechanisms consistent with our view of compensation. However, Goheen et al. (2005) also view the more passive changes in net numbers of extinctions and colonizations, such as those of Table 1, as compensation. Once again, the definition of compensation has caused interpretive difficulties in other disciplines, such as in discussions of compensatory mortality of harvested species (e.g., Anderson and Burnham 1976, Nichols et al. 1984). Indeed, our entire argument is reminiscent of historical discussions about population regulation via density-dependent compensatory mechanisms (e.g., Nicholson 1933, 1955) vs. alternatives such as spreading of the risk within heterogeneous populations subjected to a number of different stochastic environmental influences (e.g., den Boer 1968, Reddingius and den Boer 1970, Reddingius 1971).

Our numerical results and those of Goheen et al. (2005) demonstrate that simple models can produce relative stability of local species richness. It is this stability that represents the intersection of our respective model-based lies. In our case, this stability was produced by a null model via the natural stabilizing effects on local species richness of colonization from the regional species pool (also see MacArthur and Wilson 1967, Simberloff 1969, Ricklefs and Schluter 1993, Ricklefs 2004). These stabilizing effects are produced naturally by changes in the numbers of local species and potential colonists; net increases in local richness will typically occur when local richness is below the equilibrium level, and net decreases in local richness will typically occur when local richness is above equilibrium in the absence of compensatory changes in vital rates. Observation of these tendencies thus provides no evidence of compensatory changes in probabilities of extinction and colonization, as we define them.

Although we claim that the results of these two modeling efforts provide no evidence of compensatory changes in community-dynamic parameters, our results do not speak to the issue of whether such changes did or did not occur in the desert rodent community studied by Goheen et al. (2005). The compensatory mechanisms discussed by Goheen et al. (2005) may indeed have operated over the course of their study. Direct estimation of time-specific probabilities of extinction and colonization using methods that deal with imperfect detection (e.g., Nichols et al. 1998, MacKenzie et al. 2003) provide a direct approach to testing hypotheses about mechanisms underlying compensatory changes in community vital rates. These methods provide opportunities to use field data to estimate

species richness, its coefficient of variation, and local rates of colonization and extinction (e.g., see Bunge and Fitzpatrick 1993, Boulinier et al. 1998*a, b*, 2001, Nichols et al. 1998, Cam et al. 2000, Dorazio and Royle 2005) for investigations of more mechanistic hypotheses of community dynamics.

#### *Acknowledgments*

We gratefully acknowledge constructive comments and discussion on an early version of this manuscript by J. H. Brown and J. R. Goheen.

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