

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.

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Literature cited

- Anderson, D. R., and K. P. Burnham. 1976. Population ecology of the mallard VI. The effect of exploitation on survival. U.S. Fish and Wildlife Service, Resource Publication 128.
- Boulinier, T., J. D. Nichols, J. E. Hines, J. R. Sauer, C. H. Flather, and K. H. Pollock. 1998*a*. Higher temporal variability of forest breeding bird communities in fragmented landscapes. *Proceedings of the National Academy of Sciences (USA)* **95**:7497–7501.
- Boulinier, T., J. D. Nichols, J. E. Hines, J. R. Sauer, C. H. Flather, and K. H. Pollock. 2001. Forest fragmentation and bird community dynamics: inference at regional scales. *Ecology* **82**:1159–1169.
- Boulinier, T., J. D. Nichols, J. R. Sauer, J. E. Hines, and K. H. Pollock. 1998*b*. Estimating species richness: the importance of heterogeneity in species detectability. *Ecology* **79**:1018–1028.
- Brown, J. H., S. K. M. Ernest, J. M. Parody, and J. P. Haskell. 2001. Regulation of diversity: maintenance of species richness in changing environments. *Oecologia* **126**:321–332.
- Bunge, J., and M. Fitzpatrick. 1993. Estimating the number of species: a review. *Journal of the American Statistical Association* **88**:364–373.
- Cam, E., J. D. Nichols, J. R. Sauer, J. E. Hines, and C. H. Flather. 2000. Relative species richness and community completeness: avian communities and urbanization in the mid-Atlantic states. *Ecological Applications* **10**:1196–1210.
- den Boer, P. J. 1968. Spreading of risk and stabilization of animal numbers. *Acta Biotheoretica* **18**:165–194.
- Dorazio, R. M., and J. A. Royle. 2005. Estimating size and composition of biological communities by modeling the occurrence of species. *Journal of the American Statistical Association* **100**:389–398.
- Goheen, J. R., E. P. White, S. K. M. Ernest, and J. H. Brown. 2005. Intra-guild compensation regulates species richness in desert rodents. *Ecology* **86**:567–573.
- Gotelli, N. J., and G. R. Graves. 1996. *Null models in ecology*. Smithsonian Institution Press, Washington, D.C., USA.
- MacArthur, R. A., and E. O. Wilson. 1963. An equilibrium theory of insular biogeography. *Evolution* **17**:373–387.
- MacArthur, R. A., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization and local extinction probabilities when a species is not detected with certainty. *Ecology* **84**:2200–2207.
- Nichols, J. D., T. Boulinier, J. E. Hines, K. H. Pollock, and J. R. Sauer. 1998. Estimating rates of local extinction, colonization and turnover in animal communities. *Ecological Applications* **8**:1213–1225.
- Nichols, J. D., M. J. Conroy, D. R. Anderson, and K. P. Burnham. 1984. Compensatory mortality in waterfowl populations: a review of the evidence and implications for research and management. *Transactions of the North American Wildlife and Natural Resources Conference* **49**:535–554.
- Nicholson, A. J. 1933. The balance of animal populations. *Journal of Animal Ecology* **2**(Supplement):132–178.
- Nicholson, A. J. 1955. An outline of the dynamics of animal populations. *Australian Journal of Zoology* **2**:9–65.
- Reddingius, J. 1971. Gambling for existence. *Acta Biotheoretica* **20**:1–208.
- Reddingius, J., and P. J. den Boer. 1970. Simulation experiments illustrating stabilization of animal numbers by spreading of risk. *Oecologia* **5**:240–284.
- Ricklefs, R. E. 2004. A comprehensive framework for global patterns of biodiversity. *Ecology Letters* **7**:1–15.
- Ricklefs, R. E., and D. Schluter, editors. 1993. *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago, Illinois, USA.
- Simberloff, D. S. 1969. Experimental zoogeography of islands: a model for insular colonization. *Ecology* **50**:296–314.
- Simberloff, D. 1983. When is an island community at equilibrium? *Science* **220**:1275–1277.
- Williamson, G. B. 1978. A comment on equilibrium turnover rates for islands. *American Naturalist* **112**:241–243.
- Wilson, E. O. 1969. The species equilibrium model. Pages 38–47 in G. M. Woodwell and H. H. Smith, editors. *Diversity and stability in ecological systems*. Brookhaven National Laboratory, Upton, New York, USA.

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INTRA-GUILD COMPENSATION REGULATES SPECIES RICHNESS IN DESERT RODENTS: REPLY

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Null models have had a long and contentious history in community ecology (Connor and Simberloff 1979, Harvey et al. 1983, Gotelli and Graves 1996, Graves and Rahbek 2005). Much of this debate has arisen because multiple strategies for null models can be used to address a particular question of interest, and the present exchange is no exception. To assess constancy in species richness through time in a desert rodent community, Nichols et al. (2006) have proposed a Markov Chain model as an alternative to the random-walk model we

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developed (Goheen et al. 2005). While both null models simulate stochastic local extinction and colonization of species from a regional pool, our objectives differ substantially from those of Nichols et al. in ways that influence the choice of models and interpretation of results.

It is critical to reiterate the questions motivating our original analyses in Goheen et al. (2005). First and foremost, we were interested in determining whether local richness is, in fact, regulated through time; i.e., Is an equilibrium for species richness maintained at our study site near Portal, Arizona? Second, once such an equilibrium has been demonstrated, how strong are the forces that restore the equilibrium when richness is displaced from the long-term average? Finally, what are the processes generating the restoring force? We used our null model to test the first two questions, and then we drew upon independent information from 30 years of research at our site, combined with the results of our null model, to infer the mechanism. As such, the content of the comment by Nichols et al. stems from a misunderstanding of the pattern that our null model was designed to evaluate. Given the confusion on this issue, we appreciate the opportunity to clarify the rationale behind our study and the basis for our conclusions.

Differences between the two null models

Our main goal was to test for the presence of an equilibrium in local species richness. In an equilibrium community, dynamics of species richness should exhibit more constrained variance about the long-term mean than expected under a random walk. Consequently, we tested for an equilibrium by (1) demonstrating no trend in the time series, which also has been shown in three previous publications (Brown et al. 2001, Ernest and Brown 2001, White et al. 2004); and (2) incorporating observed community-wide rates of colonization and extinction into a null model that simulates a random-walk process to determine if the observed variance in species richness is significantly less than expected by chance (Goheen et al. 2005). Having demonstrated the presence of an equilibrium, the next step was to quantify the magnitude of the restoring force. We did this using the tunable parameter c (see also Kelt et al. 1995). This parameter quantifies the tendency for richness to return toward the long-term mean at time $t+1$, given that it deviates from the long-term mean at time t . By comparing the variability produced by random-walk simulations under different values of c to the observed variability in species richness, we are able to quantify the strength of regulation of local richness. The value of c implies nothing about the particular process or combination of processes that generate the restoring force. Thus our null model performs as intended: it tests for an equilibrium in species richness and quantifies the magnitude of the force maintaining this equilibrium.

By itself, our null model *does not test* the underlying mechanism responsible for restoring the local equilibrium. We combined independent information from previous studies at Portal (see the second paragraph of the *Discussion* in Goheen et al. 2005) with the fact that the restoring force appeared to act primarily within the granivore guild (Goheen et al. 2005) to infer that local interspecific competition and niche complementarity among species in the regional pool are primarily responsible for the compensatory colonization and extinction events that maintain the species equilibrium (“[this] support[s] the hypothesis that compensation occurs largely within guilds, so that competition for resources plays a significant role in regulating species richness through time;” Goheen et al. 2005:570, emphasis added). We tried to make this point transparent in our original paper, but we have expanded upon it in the final section of this response.

Alternatively, the null model of Nichols et al. was constructed to discern whether an observed equilibrium arises purely from the independent stochastic colonizations and extinctions of individual species. As such, it does not test for the presence of a community equilibrium per se, nor does it quantify the magnitude of the force maintaining the equilibrium. Nichols et al. used their Markov model to address whether an alternative mechanism (stochastic species-level colonization and extinction events) could account for the observed equilibrium in species richness. Thus our model establishes the presence of an equilibrium, while theirs attempts to determine the processes that generate the equilibrium. Therefore, our model and the model of Nichols et al. are not competing alternatives, but rather ask different and complementary questions.

In particular, two uses of terminology require further attention. First, we used constant community-wide *rates* of colonization and extinction rather than the constant per-species *probabilities* used by Nichols et al. Williamson (1978) noted a similar distinction when commenting on Diamond’s (1969) interpretation of relative turnover of island birds (J. Nichols, *personal communication*). We acknowledge a confusing, but not inaccurate, use of the term “probability” in Goheen et al. (2005) that probably contributed to this misunderstanding. Second, we used “compensation” to reflect one or more processes responsible for maintaining species richness about some equilibrium (i.e., processes that change the net community rates of colonization and extinction) as opposed to processes responsible for changing the per-species probabilities. We believe the primary processes underlying this type of compensation are interspecific competition and niche complementarity (see *Interspecific competition does drive colonization—extinction dynamics at Portal*). However, the more passive changes in these rates suggested by Nichols et al. probably also contribute to the stabilization of richness to some degree. As our use of the term com-

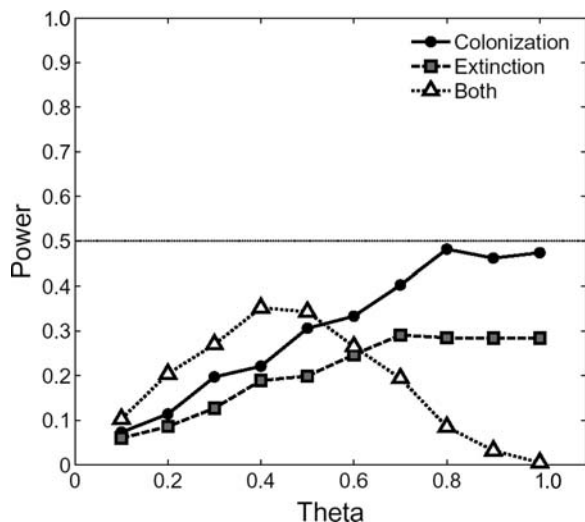


FIG. 1. Results of power analyses for the Markov model of Nichols et al. (2006). Here, the parameter θ indexes the probability that richness returns toward the long-term mean, given that it deviates from the long-term mean at a previous time step. Different symbols represent θ applied to only the probability of colonization, only the probability of extinction, or both probabilities of colonization and extinction simultaneously. Note that for all three scenarios, power (i.e., $1 - \beta$) is low and never rises above 0.5.

pensation has the potential to cause confusion, we have focused in this article on using the term “equilibrium.”

Cautionary notes on the null model of Nichols et al.

The goal of Nichols et al. is an important one: to determine whether processes other than stochastic species-level colonization and extinction (i.e., the processes proposed in island biogeography theory) are necessary to maintain an equilibrium in species richness. Given their goal, it was appropriate for them to use constant, per-species probabilities instead of constant community colonization and extinction rates. However, we see two reasons for caution in interpreting results from null models of the type used by Nichols et al.

First, the tests employed in conjunction with some null models are prone to high Type II error (i.e., failure to detect the influence of nonrandom processes when they are present; Toft and Shea 1983, Kelt et al. 1995, Gotelli 2000). Previously, this has been shown to cause problems in the interpretation of this type of Markov Chain model for equilibria (Boecklen and Nocolad 1991). To reemphasize this limitation, we used Monte Carlo methods to evaluate the Markov model of Nichols et al. (following Kelt et al. 1995) in the presence of nonrandom colonization, nonrandom extinction, and both nonrandom colonization and extinction (Fig. 1; see Appendix A for detailed methodology). While power increases with the strength of either nonrandom colonization or extinction, it fails to reach acceptable

levels. In addition, when both nonrandom colonization and extinction occur simultaneously, the power of the Nichols et al. null model decreases when nonrandomness increases.

Second, Nichols et al. constructed their null model assuming that probabilities of colonization and extinction do not differ among species. Although others have used this same assumption (e.g., MacArthur and Wilson 1967, Boulinier et al. 2001), it is well documented that species differ in their likelihood of colonization and extinction in ways that influence the form of the colonization and extinction curves that generate the observed equilibrium (MacArthur 1972). Therefore, an alternative form of the Nichols et al. null model might be $S_{t+1} = S_t + \sum_{i=1}^P \lambda_i (1 - I(i)) - \sum_{i=1}^P \epsilon_i I(i)$, where λ_i and ϵ_i are the individual species probabilities of colonization and extinction, P is the total number of species in the pool, S_t is the number of species present in the community at time t , and $I(i)$ is a characteristic (or indicator) function that is equal to 1 if the species is present in the community and zero if the species is absent (e.g., Rosenzweig 1995). This introduces the bowing in the colonization and extinction curves of island biogeography (MacArthur 1972, Rosenzweig 1995). We initially considered using a model of this form to supplement our random-walk analysis (i.e., to explicitly test what we had inferred from independent evidence). However, we felt that (1) the low power for this type of analysis would be even more problematic than that discussed for the Nichols et al. approach, and (2) the potential for “smuggling” important biology into this null model was too great given the fact that observed colonization and extinction rates are influenced directly by interspecific competition, thus introducing a deterministic component into this stochastic framework (Valone and Brown 1995; see also MacArthur and Wilson 1967, Simberloff 1969, MacArthur 1972, Rosenzweig 1995). Despite these species differences in likelihood of colonization and extinction, the alternative model we present here would likely yield results similar to those of the original null model used by Nichols et al. (J. Nichols, *personal communication*).

Our concerns highlight the difficulty in drawing inferences from this sort of Markov model; however, we do not mean to imply that research objectives should be dictated by the feasibility of null models themselves. In general, it is difficult to separate the importance of deterministic (i.e., niche-based) from stochastic (i.e., neutral) processes in community assembly and, by itself, neither our null model nor that of Nichols et al. successfully accomplishes this task. Whether local equilibria arise because of neutral processes or are due to some other mechanism is an interesting and challenging question, and one that will benefit from a suite of complementary methods and analyses. Thus we

strongly advocate for the combination of null models and independent evidence whenever possible.

*Interspecific competition does drive colonization—
extinction dynamics at Portal*

Supporting evidence from 30 years of research on this desert rodent community led us to conclude that the observed equilibrium was due in large part to the effect of interspecific competition on colonization and extinction. First, long-term experimental evidence demonstrates that species composition of the local community alters the rates of colonization and extinction of other species in the pool. Valone and Brown (1995) showed that most small granivore species exhibited higher colonization rates, lower extinction rates, or both on plots where *Dipodomys* spp. had been excluded. While Valone and Brown (1995) made no claims as to the effects of richness per se upon local extinction and colonization, they did demonstrate that some granivore species affect the colonization success and extinction rates of other granivore species, highlighting the importance of competition in influencing local community assembly.

Second, long-term observational evidence at the site suggests that interspecific competition is a strong structuring force in our community. This can be seen in the dynamics of species composition and other community-level properties. Long-term increases in winter precipitation have resulted in directional change in the species composition of the rodent community at our site (Brown et al. 1997, Thibault et al. 2004), with species that were historically common declining and/or going extinct and species that were historically rare colonizing and/or increasing. Despite this significant change in species composition, species richness has remained remarkably constant. This is expected from nonrandom compensation among competing species, wherein niche differences lead to particular combinations of species that are favored under different environmental conditions (e.g., Ernest and Brown 2001, Chase and Leibold 2003). Null models that assume that species have equivalent and unchanging probabilities of colonization and extinction cannot generate the observed directional change in species composition through time, because the likelihood that a given species in the regional pool will be present in the local community is equal for all time steps in the simulation. In addition, many of the community-level properties exhibit temporal dynamics consistent with resource limitation at the site (Ernest and Brown 2001, White et al. 2004), supporting the idea that competition within guilds is an important process in this community.

Finally, despite our reservations regarding its power and underlying assumptions, we implemented the Markov process model proposed by Nichols et al. to test for changes in per-species probabilities of coloniza-

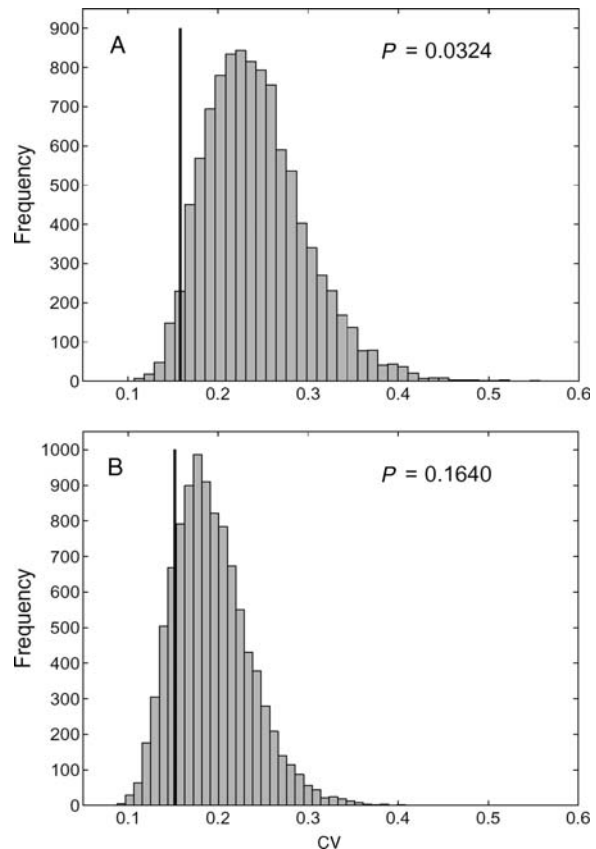


FIG. 2. Histograms of coefficients of variation (cv) in species richness from the Markov process model of Nichols et al. (2006), as applied to (A) only the granivorous rodents at Portal, and (B) the entire rodent community at Portal. Vertical black lines represent the observed cv for each group, which is less than expected for the granivore guild.

tion and extinction. While the simulated variation for the whole community (granivores, herbivores, and insectivores combined) did not differ from that generated by their Markov model, the dynamics of species richness of the granivore guild were significantly less variable than expected (Fig. 2). Although lack of statistical significance is difficult to interpret given the low power and the assumptions of the null model of Nichols et al., the significant difference obtained for the granivores strongly supports the interpretation in our original paper, which was based in part on the fact that the community equilibrium seemed to be generated by an equilibrium in the granivore guild (Goheen et al. 2005).

Clearly, the dynamics of species richness at our site cannot be explained solely by the null model of Nichols et al. Given this and the results mentioned in the previous paragraphs, our conclusion is only strengthened: the local equilibrium is maintained primarily through interspecific competition and niche complementarity within the granivore guild.

Summary

We have shown (1) that colonization–extinction dynamics at Portal maintain a strong local equilibrium in species richness, and (2) that the processes generating this equilibrium operate most strongly within the granivore guild, where strong interspecific competition has been documented independently by manipulative experiments. So, we are confident that interspecific competition and niche complementarity are the primary processes that maintain species richness at our site within narrow limits over time.

We appreciate the thought-provoking exchange with J. Nichols and colleagues. Debates about the applications of null models are common, in part because investigators disagree about which ecological elements to include. In this case, the disagreement about which null model to use stems from the fact that we use our null to address a different question (Is there an equilibrium?) than that addressed by Nichols et al. (What causes that equilibrium?). Both of these questions are important, and amiable discussions such as this one will hopefully lead to progress in our understanding of how local and regional processes combine to generate observed patterns of species richness.

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Literature cited

- Boecklen, W. J., and J. Nosedal. 1991. Are species trajectories bounded or not? *Journal of Biogeography* **18**:647–652.
- Boulinier, T., J. D. Nichols, J. E. Hines, J. R. Sauer, C. H. Flather, and K. H. Pollock. 2001. Forest fragmentation and bird community dynamics: inference at regional scales. *Ecology* **82**:1159–1169.
- Brown, J. H., S. K. M. Ernest, J. M. Parody, and J. P. Haskell. 2001. Regulation of diversity: maintenance of species richness in changing environments. *Oecologia* **126**:321–332.
- Brown, J. H., T. J. Valone, and C. G. Curtin. 1997. Reorganization of an arid ecosystem in response to recent climate change. *Proceedings of the National Academy of Sciences (USA)* **94**:9729–9733.
- Chase, J. M., and M. A. Leibold. 2003. *Ecological niches*. University of Chicago Press, Chicago, Illinois, USA.
- Connor, E. F., and D. Simberloff. 1979. The assembly of species communities: chance or competition? *Ecology* **60**:1132–1140.
- Diamond, J. M. 1969. Avifaunal equilibria and species turnover rates on the Channel Islands of California. *Proceedings of the National Academy of Sciences (USA)* **64**:57–63.
- Ernest, S. K. M., and J. H. Brown. 2001. Homeostasis and compensation: the role of species and resources in ecosystem stability. *Ecology* **82**:2118–2132.
- Goheen, J. R., E. P. White, S. K. M. Ernest, and J. H. Brown. 2005. Intra-guild compensation regulates species richness in desert rodents. *Ecology* **86**:567–573.
- Gotelli, N. J. 2000. Null model analysis of species co-occurrence patterns. *Ecology* **81**:2606–2621.
- Gotelli, N. J., and G. R. Graves. 1996. *Null models in ecology*. Smithsonian Institution Press, Washington D.C., USA.
- Graves, G. R., and C. Rahbek. 2005. Source pool geometry and the assembly of continental avifaunas. *Proceedings of the National Academy of Sciences (USA)* **102**:7871–7876.
- Harvey, P. H., R. K. Colwell, J. W. Silvertown, and R. M. May. 1983. Null models in ecology. *Annual Review of Ecology and Systematics* **14**:189–211.
- Kelt, D. A., M. L. Taper, and P. L. Meserve. 1995. Assessing the impact of competition on community assembly: a case study using small mammals. *Ecology* **76**:1283–1296.
- MacArthur, R. H. 1972. *Geographical ecology*. Princeton University Press, Princeton, New Jersey, USA.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Nichols, J. D., J. E. Hines, J. R. Sauer, T. Boulinier, and E. Cam. 2006. Intra-guild compensation regulates species richness in desert rodents: comment. *Ecology* **87**:2118–2121.
- Rosenzweig, M. L. 1995. *Species diversity in space and time*. Cambridge University Press, Cambridge, UK.
- Simberloff, D. S. 1969. Experimental zoogeography of islands: a model for insular colonization. *Ecology* **50**:296–314.
- Thibault, K. M., E. P. White, and S. K. M. Ernest. 2004. Temporal dynamics in the structure and composition of a desert rodent community. *Ecology* **85**:2649–2655.
- Toft, C. A., and P. J. Shea. 1983. Detecting community-wide patterns: estimating power strengthens statistical inference. *American Naturalist* **122**:618–625.
- Valone, T. J., and J. H. Brown. 1995. Effects of competition, colonization, and extinction on rodent species diversity. *Science* **276**:880–883.
- White, E. P., S. K. M. Ernest, and K. M. Thibault. 2004. Trade-offs in community properties through time in a desert rodent community. *American Naturalist* **164**:670–676.
- Williamson, G. B. 1978. A comment on equilibrium turnover rates for islands. *American Naturalist* **112**:241–243.

APPENDIX A

Evaluation of the statistical power of the null model of Nichols et al. (*Ecological Archives* E087-131-A1).