

COMMUNITY DISASSEMBLY, BIODIVERSITY LOSS, AND THE EROSION OF AN ECOSYSTEM SERVICE

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Abstract. Distinguishing the mechanisms responsible for the relationship between biodiversity and ecosystem services requires knowledge of (1) the functional roles played by individual species and (2) the sequence with which species are added to or lost from communities in nature (i.e., “community assembly” and “community disassembly,” respectively). Rarely, if ever, are both these issues understood with certainty in any given ecosystem. We used an empirically based simulation model to assess the degree to which the sequence of species loss from vertebrate communities influences risk of human exposure to Lyme disease, as measured by the proportion of ticks infected with the etiological agent. Dramatic differences in the shapes of the curves relating vertebrate biodiversity to disease risk (which we consider an ecosystem service) were observed. Randomized sequences of species loss resulted in a decrease in disease risk with reduced biodiversity, a result that is contradicted by both empirical observations and model results from nonrandomized sequences of species loss (i.e., specific “disassembly rules”). All potentially realistic disassembly rules resulted in increases in disease risk with decreasing biodiversity, although shapes of the curves varied considerably. Our results highlight the importance of both species identity and the order by which species are lost, in understanding the mechanisms by which biodiversity affects ecosystem functioning.

Key words: *biodiversity; blacklegged tick; community assembly; community disassembly; disease ecology; ecosystem function and ecosystem services; functional redundancy; habitat fragmentation; Lyme-disease risk; vertebrate ecology; white-footed mouse.*

INTRODUCTION

The predominant approach to assessing the ecological consequences of biodiversity loss is to assemble experimental communities by drawing species randomly from a species pool and determine how community properties or ecosystem functioning respond to variation in species richness. Such an approach, although rigorous experimentally, leaves open the question of whether enhanced ecosystem functioning in more diverse systems is caused by biodiversity per se or by the chance inclusion of particular species with dominant roles (Loreau et al. 2001). In addition, such studies cannot provide insight into the importance of the sequence of species addition (community assembly) or loss (community disassembly).

Distinguishing the mechanisms by which biodiversity influences a specific ecosystem property or service in natural systems requires knowledge of (1) the functional roles played by individual species, and (2) the sequence with which species are added to or lost from communities in nature. Rarely, if ever, are both these issues understood with certainty in any given ecosystem (Tilman et al. 1997, Knops et al. 1999, Chapin et

al. 2000, Cottingham et al. 2001, Loreau et al. 2001, Schwartz et al. 2000).

Recent empirical and modeling studies have revealed a novel ecosystem property associated with biodiversity—the reduction in transmission of vector-borne disease (Ostfeld and Keesing 2000a, b, Gilbert et al. 2001, Schmidt and Ostfeld 2001). According to this model, termed the “dilution effect,” high species diversity in the community of vertebrate hosts for tick vectors reduces risk of human exposure to tick-borne infections by diluting the impact of highly competent disease reservoirs. The model was developed for the Lyme disease system in eastern North America, in which the tick vector (*Ixodes scapularis*) feeds from a diverse assemblage of mammals, birds, and reptiles, but acquires the etiological agent (*Borrelia burgdorferi*) most efficiently from the white-footed mouse (*Peromyscus leucopus*); however, the dilution effect may also operate in many other vector-borne disease systems (Ostfeld and Keesing 2000b). The model predicts that the presence of alternative (non-mouse) hosts in communities with high species diversity results in fewer tick meals being taken from mice, a lower infection prevalence in the tick population, and perhaps a smaller tick population due to poorer feeding success on non-mouse hosts (Ostfeld et al. 2002). The dilution effect is enhanced when the species added to increasingly diverse communities directly or indirectly reduce population density of white-footed mice, or reduce tick burdens on mice via competition for parasites (Schmidt and Ostfeld 2001).

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We (LoGiudice et al. 2003) recently parameterized a model that accounts for the role of each potentially important vertebrate species in determining the nymphal tick infection prevalence (or NIP), which is an epidemiologically relevant risk factor for Lyme disease (Ostfeld et al. 2002). Lyme disease is transmitted primarily by the nymphal stage of the tick vector (Barbour and Fish 1993), and risk of human exposure is reflected by the proportion of host-seeking nymphs that harbors a *B. burgdorferi* infection. Parameterization of the model required that field estimates be made for each species of vertebrate host regarding: (1) larval tick burden (average number of larvae per host individual); (2) host population density; and (3) reservoir competence (the proportion of larvae that acquire an infection from that species of host). After exhaustively trapping and netting the potentially important mammalian and avian hosts at a local field site in southeastern New York State (USA), we generated an estimate of NIP that was matched closely by empirical data from naturally occurring populations of host-seeking nymphs, indicating that the model and parameter values were representative and accurate (LoGiudice et al. 2003). Our data, therefore, provide reliable estimates for the functional role that each species of host plays in influencing NIP, and they pave the way for understanding mechanistically the role of biodiversity in influencing disease risk.

Little is known about the sequence with which vertebrate species are added to or lost from native ecological communities that vary in diversity. The literature on species assembly rules (e.g., Fox and Brown 1993, Stone et al. 1996) suggests that the order in which species are added to increasingly diverse communities over evolutionary time scales is nonrandom, but this literature is of limited relevance to communities influenced by highly accelerated, anthropogenic alterations of species diversity. Although forest fragmentation is known to reduce species richness of forest vertebrates (Laurance et al. 2000, Crooks 2002, Donovan and Flather 2002), little is known about either the specific sequence of loss, or about the species-specific traits that might influence their likelihood of being lost from a disturbed or fragmented ecosystem. We term the possible relationship between species-specific life-history traits and the probability of local extinction from communities experiencing disturbance or fragmentation, "community disassembly rules." In this paper we use our empirically parameterized model of the individualistic roles of vertebrate hosts in determining NIP to assess, using computer simulations, the impact of a set of plausible community disassembly rules on Lyme disease risk. The primary objective is to evaluate whether different sequences of species loss cause differences in the shape of the relationship between biodiversity and this particular ecosystem function. If so, the importance of the disassembly rules that govern patterns of species loss will be underscored as relevant to the biodiversity–ecosystem function debate, and the

relative importance of species composition vs. species number (e.g., Wardle et al. 1999) highlighted.

THE MODEL

The model is an extension of Giardina et al. (2000), which calculates the predicted nymphal tick infection prevalence (NIP) as the sum across all species of the nymphs infected by each species divided by the total number of nymphs fed by all species. Parameters of the model include: density of host species, N_i ; species-specific body burdens, B_i ; and species-specific reservoir competence, C_i . Therefore, $m_i = N_i B_i$, where m_i is the number of larval meals taken from species i ; $I_i = m_i C_i$, where I_i is the number of nymphs infected from their larval meal on species i ; and the total number of nymphs infected from their larval meal (I_T) is $I_T = \sum m_i C_i$. The number of nymphs not infected in their larval meal, $U_i = m_i (1 - C_i)$ and the total number of nymphs uninfected is $U_T = \sum m_i (1 - C_i)$. Thus, the total nymphal infection prevalence (NIP_T) is $\text{NIP}_T = I_T / (I_T + U_T)$. This allows us to describe the contribution of each species to NIP. Assumptions of this model, and methods for determining parameter values empirically for each species of host, are described in LoGiudice et al. (2003). The model was validated by a close fit between the NIP predicted by the set of species-specific parameter values as determined in a local, relatively intact community consisting of 13 species of mammalian and avian hosts and the NIP determined empirically by assaying field-collected, host-seeking nymphal ticks (LoGiudice et al. 2003). Sensitivity analyses showed that the close fit between predicted and observed NIP was robust (± 1 –3% change) to 20% variation in host population density estimates—the parameter with the largest potential error (LoGiudice et al. 2003).

SIMULATIONS OF COMMUNITY DISASSEMBLY

We used the model to explore the outcomes (values of NIP [nymphal tick infection prevalence]) predicted by disassembling host communities according to specific rules. Initially, we evaluated the hypothesis that NIP increases with decreasing vertebrate diversity when species are removed randomly to deconstruct an initially intact community. Beginning with an intact community of 13 species of mammals and birds known to comprise a nearly complete set of tick hosts at our field site in Dutchess County, New York, USA (Appendix), a specified number of species was drawn in random order for removal to create communities with species richness values of 12, 11, 10 . . . 1 (100 iterations for each community size). We compared this completely random disassembly procedure to model runs in which we assumed that the white-footed mouse is present in all communities, and a third set of runs assuming that mice and white-tailed deer are always present. These latter simulations were intended to more closely reflect the real world. Strong evidence supports the assertion that white-footed mice are ubiquitous

members of vertebrate communities, occurring in both highly fragmented landscapes and pristine, intact communities (Nupp and Swihart 1996, 2000, Krohne and Hoch 1999, Rosenblatt et al. 1999). In addition, because of the importance of white-tailed deer as hosts for adult *Ixodes scapularis* (Barbour and Fish 1993), endemic Lyme disease may require the presence of this host. Thus, the comparison between a completely random removal of species on the one hand, and the assumption that either mice only, or mice plus deer, are always present, allows us to evaluate the consequences of a simple, empirically based rule. In this case, white-footed mice are known to be a high-impact species for Lyme-disease risk, and we can ask how a null model (complete randomness) compares with somewhat more realistic models of community disassembly.

In both cases, we set the population density (N_i) of non-mouse members of the community at either empirically determined values for our site (chipmunks, deer, birds) or a value determined from the literature to represent an average for oak/mixed-hardwood forests of the northeastern United States (see LoGiudice et al. [2003] for details). However, to reflect the dramatic population fluctuations that typify white-footed mice (e.g., Ostfeld et al. 2001) we ran separate simulations at levels of mouse density between 25 and 100 individuals/ha. From the 100 simulations at each combination of species richness and mouse abundance we calculated the mean (± 1 SE) nymphal infection prevalence expected from that level of host community diversity.

We followed simulations of randomized community disassembly with simulations employing strict disassembly rules. We removed species in the orders indicated below until only white-footed mice (set at 25 individuals/ha to reflect long-term averages at local sites; Ostfeld et al. 2001) and white-tailed deer remained. To simulate plausible sequences of species loss from landscapes subjected to forest destruction and fragmentation, we removed species according to the following rules: species are lost (1) in decreasing order of body mass; (2) in decreasing order of home-range size; (3) from highest to lowest trophic level; and (4) in the approximate order described for Midwestern U.S. mammals in forest patches in an agricultural matrix (Rosenblatt et al. 1999, Nupp and Swihart 2000; see Appendix 1 for rankings). Our intention was to also simulate loss in decreasing order of ecological specialization, but data were insufficient for reliable ranking.

We also wished to evaluate the degree to which interactions among the various species in our virtual communities might influence the shape of the relationship between diversity and ecosystem functioning. However, assessing interactions among vertebrate species that might affect their role in feeding and infecting tick populations is not straightforward. As a first attempt at this assessment, we allowed species added to virtual

communities to interact with white-footed mice either by reducing their numbers or by reducing their tick burdens (e.g., by competition for parasites). Data do not exist that would allow us to estimate empirically the net effects of each species added on either population size or tick burdens on white-footed mice. (Moreover, in real communities, the species added could potentially affect both population sizes and tick burdens on all other species present, not only mice.) Given these severe data limitations, we chose to assign species to categories according to the expected intensity of their reduction in mouse numbers and tick burdens on mice. Thus, strong competitors such as sciurid rodents and *Blarina* shrews were each expected to reduce mouse abundance by 1%, generalist predators such as skunks and raccoons by 0.5%, and weak competitors such as birds, *Sorex* shrews, and opossums by 0.1%. Similarly, based on empirical demonstration of strongly reduced average tick burdens on mice with increasing population density of chipmunks (Schmidt et al. 1999), we expected small mammals (shrews, sciurid rodents), which overlap strongly with mice in microhabitat use, to exert the strongest reduction in tick burdens on mice (16%), whereas mesomammals (skunks, raccoons, opossums) would reduce ticks on mice by 5%, and birds by 1%. We emphasize that the assignment of these values represents a crude first attempt to assess the potential for interactions among species, defined relative to a specified ecosystem function, to influence model outcome.

RESULTS

Randomized community disassembly

The relationship between vertebrate diversity and Lyme-disease risk (represented by bacterial infection prevalence in nymphal ticks) differed dramatically between the simulated communities that were disassembled randomly vs. those in which white-footed mice, or mice plus deer, were always present. When all host species, including mice and deer, were removed in random sequence, species richness of hosts had a curvilinear, positive effect on nymphal infection prevalence (NIP), such that species-poor communities had the lowest Lyme-disease risk (Fig. 1). In contrast, when mice were present in all communities, and the removal sequence of non-mouse hosts was randomized, a strong negative relationship was observed between host species richness and NIP (Fig. 1, mouse density set at 25 individuals/ha). Simulations in which mice plus deer were always present were similar to those in which mice were always present; in those two scenarios, population density of mice (25, 50, or 100 individuals/ha) was positively correlated with NIP, as has been observed empirically (Ostfeld et al. 2001). In simulations with completely random removal sequences, the highest NIP typically occurred at intermediate mouse densities, although mouse density had only a modest effect

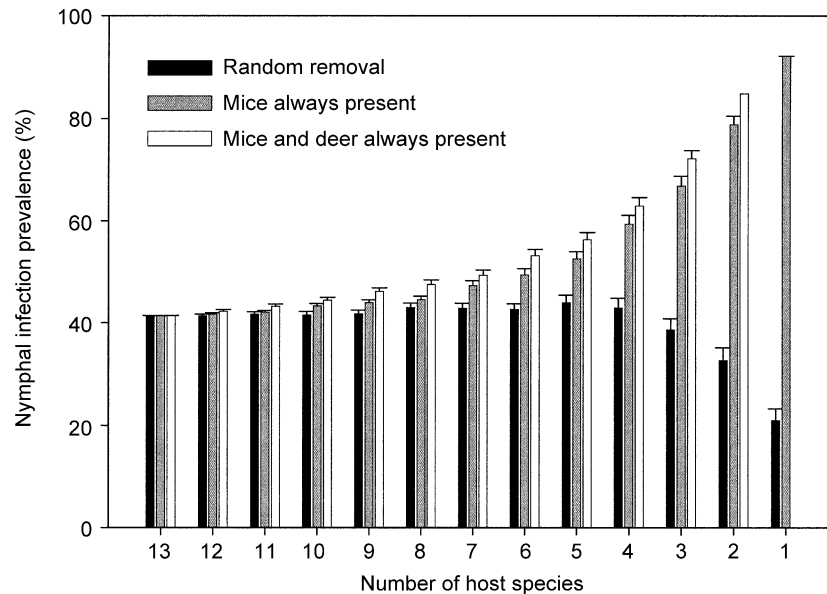


FIG. 1. Results of simulations assessing the effects of reduced species richness on Lyme disease risk, as measured by nymphal tick infection prevalence (NIP). Data are means and 1 SE of 100 replicates. Three types of simulations were run with communities that began as intact assemblages of 13 host species for which we (LoGiudice et al. 2003) empirically determined contributions to NIP: (1) species were removed one by one by a random-selection criterion; (2) white-footed mice were present in all communities, but otherwise removal was in random order; and (3) mice and white-tailed deer were present in all communities, but otherwise removal was in random order.

(data not shown). For all simulations, little change in NIP occurred as species richness declined from 13 to 8 species, after which NIP changed dramatically (Fig. 1).

Community disassembly with rules

The application of different rules by which communities disassemble under habitat destruction or fragmentation caused dramatic variation in the relationship between host species richness and Lyme-disease risk (Fig. 2A). When species were lost in order of largest to smallest home-range size or body mass, the pattern of change in NIP was characterized by a gradual increase as species richness declined from 13 to 4 species, followed by a rapid increase as richness declined from 4 to the final 2 species (mice plus deer). Because home-range size scales strongly to body size, differences between these two models were subtle. In stark contrast, when species were lost in order of highest to lowest trophic level, a *decrease* in NIP was observed in communities as richness declined from 13 to 4 species, followed by a major irruption in NIP as the community lost 2 of its last 4 species. The most gradual pattern of changing NIP with community disassembly was seen for communities losing species in approximately the order observed in forest patches within agricultural matrices observed in Indiana and Illinois (Nupp and Swihart 1996, 2000, Rosenblatt et al. 1999) (Fig. 2A).

Qualitatively similar patterns were observed in model runs in which non-mouse species were assigned interaction coefficients that affected either population

density of mice (via predation or competition) or tick burdens on mice (via competition for generalist parasites) (Fig. 2B). As would be expected from the inclusion of interaction coefficients, NIP was always lower for interaction models than for corresponding runs of non-interaction models. Inclusion of interaction coefficients did not change the shapes of the biodiversity/NIP curves under any of the disassembly rules scenarios.

DISCUSSION

As habitat destruction and fragmentation reduce species diversity in human-impacted communities, ecosystem properties and the services derived from them might be altered. However, change in ecosystem properties might be modest or nonexistent in the face of biodiversity loss if the remaining species compensate for the lost contributions of missing species, or if the species likely to be lost are also likely to have little effect on the ecosystem property of interest. For any given ecosystem property, determining the effects of reduced species diversity requires knowledge of (1) the functional roles played by individual species in governing the property of interest; (2) the degree to which species interactions affect functional roles; and (3) the likelihood of local extinction of individual species.

For the Lyme disease system, we have determined the roles that individual host species play in influencing nymphal infection prevalence (NIP) (LoGiudice et al. 2003), which, due to its association with human disease risk, we consider an important ecosystem function. We

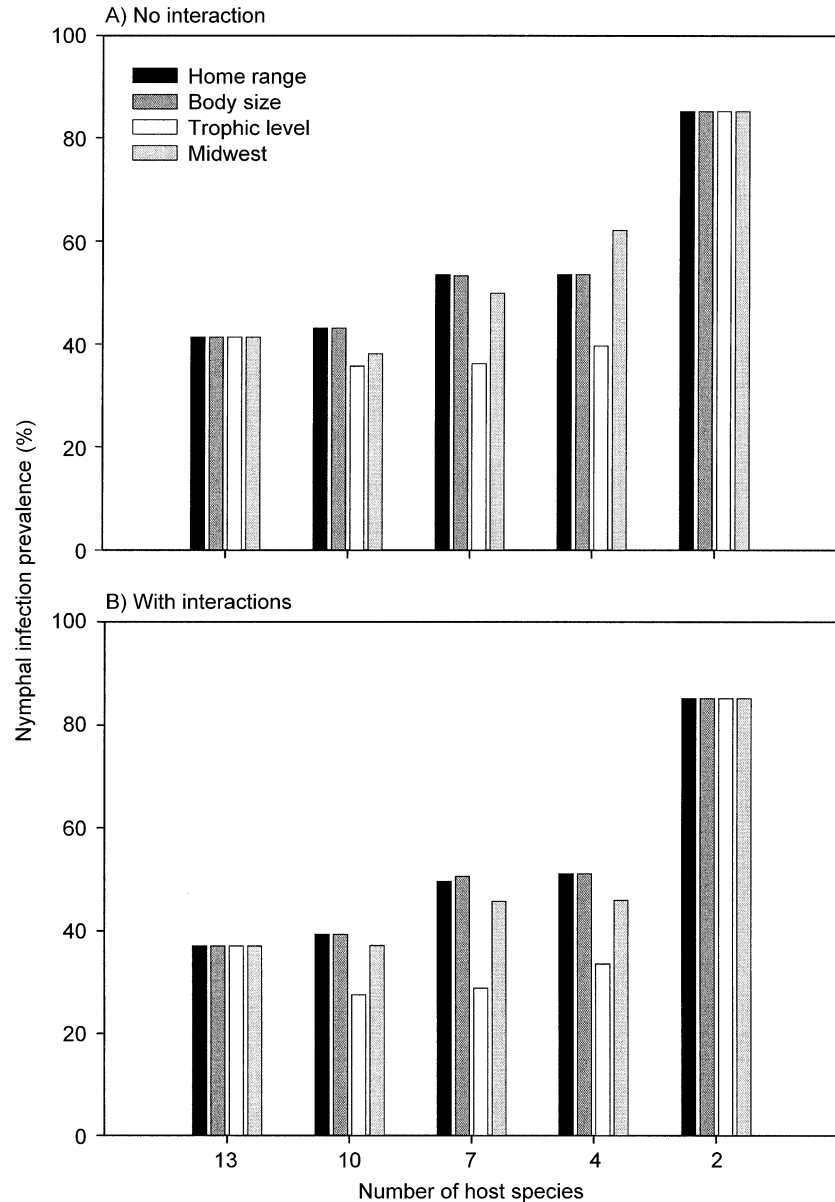


FIG. 2. Results of simulations assessing the effects of reduced species richness on Lyme disease risk, as measured by nymphal tick infection prevalence (NIP). Specific community disassembly rules were applied to reduce richness from communities that began as intact assemblages of 13 host species for which we (LoGiudice et al. 2003) empirically determined contributions to NIP. Species were removed in decreasing order of: (1) body size; (2) home-range size; and (3) trophic level; or (4) according to observations made in fragmented landscapes in the Midwestern United States. In (A) non-mouse species did not affect population density of mice or tick burdens on mice; in (B) interaction coefficients were incorporated (see *Results: Community disassembly with rules*).

do not know, but can estimate, the degree to which host species interact to affect NIP. Our main goal was to ask whether different rules governing the sequence by which species are lost from human-impacted communities (community disassembly rules) result in different shapes of the biodiversity–NIP relationship. In our initial simulations of vertebrate host communities ranging in species richness from 13 to 1 species, we found that removing species randomly from an initially intact

community resulted in no relationship between species richness and NIP until only ~4 species remained, followed by a strong decrease in NIP as richness declined from 4 to 1 species. Under the more realistic scenario of white-footed mice being ubiquitous members of all communities, followed by random draws for species removal, we found a strong, saturating decline in NIP with increasing species richness (cf. Schwartz et al. 2000). Assuming that both mice and deer are always

present gave similar results. This exercise illustrates that the incorporation of even rudimentary knowledge about the sequence by which natural communities are assembled or disassembled can result in profound differences in the postulated relationship between biodiversity and an ecosystem service, such as risk of exposure to an infectious disease.

Our simulation of community disassembly under different plausible sets of rules governing the sequence of species loss demonstrated that these rules might indeed cause dramatic changes in the way NIP declines with the loss of species. When species were removed according to patterns observed in fragmented agricultural landscapes of the Midwestern United States, the resulting increase in NIP was gradual. When species were lost in decreasing order of body size or home-range size, increasing NIP underwent abrupt transitions in the decline from 10 to 7 species and again in the decline from 4 to 2 species. When species were removed in order of highest to lowest trophic level, a counterintuitive decrease in NIP occurred as richness declined from 13 to 4 species, followed by a more than doubling of NIP as the final two species were lost.

Differences in the shape of the biodiversity–NIP curves with different removal sequences resulted from two processes. First, the vertebrate host species differed strongly in their contributions to total NIP. Host species can be arrayed along two axes that determine their impact on NIP. The first axis is the number of ticks fed by the population of any given host species (which is the product of the host population density and average tick burden per individual). This value determines the magnitude of the effect of the loss (or inclusion) of that species. The second axis is the infectivity (or reservoir competence) of that host species for feeding ticks, a value that determines the direction of the effect (higher or lower NIP) when that species is lost or added. Some species feed and infect many ticks (e.g., white-footed mice, eastern chipmunks, and shrews), others feed many ticks but tend not to infect them (“dilution hosts”—e.g., the tree squirrels), and others feed and infect few ticks (e.g., carnivores, birds).

Variation in model outcome arising from different disassembly rules results from changes in the timing of loss of species of high impact, either positive or negative. For example, for the body-size and home-range-size rules, squirrels are lost in the second extinction wave (going from 10 to 7 species) and both shrews were lost in the fourth cut (from 4 to 2 species). These were the transitions associated with the greatest change in NIP. In contrast, for the trophic-level rule, the loss of all shrews in the first cut caused a decrease in NIP, and the persistence of squirrels until the last cut prevented NIP from increasing until the final 2 species were lost. We suggest that such idiosyncratic effects of particular extinction sequences will typify communities in which species differ in the direction and magnitude of effects on ecosystem function.

An additional important mechanism behind the diverse responses to disassembly rules is the contingent nature of species impacts on NIP. The degree to which the loss of any particular species in our system increased or decreased NIP depended on the identities of the other species present. For example, if a moderately reservoir-competent host, such as the chipmunk or *Blarina* shrew, is lost from a low-diversity community with high NIP, the result will be an increase in NIP. But if these same species are lost from a high-diversity community with low NIP, the result will be a strong decrease in NIP.

Our analyses have some important limitations. First, although we found that including interaction terms between white-footed mice and other members of the community had only a minor effect on NIP, we did not assess the impact of allowing all species to interact with one another. Real ecological communities incorporate networks of interactions such that the inclusion or exclusion of one species can, via indirect pathways, cause unexpected changes in abundance of others (Lawton 2000, Pimm 1993). Although a food-web approach to assessing net effects of species loss on abundance and tick burdens of each host species would add realism, the data that would allow parameterization of such a model are lacking. Second, our set of plausible disassembly rules is incomplete, owing to poor information on what factors influence species vulnerability to local extinction. Degree of habitat or trophic specialization, initial population density, sensitivity to human artifacts, or other features could potentially influence the sequence of loss.

Our study has potentially important implications for recent studies that have examined the relationship between biodiversity and other ecosystem properties such as primary production, resistance to invasion, and albedo (Knops et al. 1999, Cottingham et al. 2001, Loreau et al. 2001). The relationships between biodiversity and both NIP and the more traditional ecosystem functions are dependent on the same factors—the interactions among species and their role in governing the functions under investigation. Such relationships are likely to be equally sensitive to the pattern of disassembly or assembly, but studies to date have not examined this possibility.

In conclusion, results of our simulations suggest that, because individual species have effects that are both idiosyncratic and strongly contingent on the identities of the other members of the community, the sequence of species loss (or addition) is crucial to the relationship between biodiversity and ecosystem processes, represented by Lyme-disease risk. Determining the rules that govern the process of species disassembly and assessing the net effects of species losses on the abundance of other species should be included in any deliberations over the role of biodiversity in governing ecosystem properties and functioning and the services we derive from them.

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LITERATURE CITED

- Barbour, A. G., and D. Fish. 1993. The biological and social phenomenon of Lyme disease. *Science* **260**:1610–1616.
- Chapin, F. S., III, E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, S. E. Hobbie, M. C. Mack, and S. Diaz. 2000. Consequences of changing biodiversity. *Nature* **405**:234–242.
- Cottingham, K. L., B. L. Brown, and J. T. Lennon. 2001. Biodiversity may regulate the temporal variability of ecological systems. *Ecology Letters* **4**:72–85.
- Crooks, K. R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation Biology* **16**:488–502.
- Donovan, T. M., and C. H. Flather. 2002. Relationships among North American songbird trends, habitat fragmentation, and landscape occupancy. *Ecological Applications* **12**:364–374.
- Fox, B. J., and J. H. Brown. 1993. Assembly rules for functional groups in North American desert rodent communities. *Oikos* **67**:358–370.
- Giardina, A. R., K. A. Schmidt, E. M. Schaubert, and R. S. Ostfeld. 2000. Modeling the role of songbirds and rodents in the ecology of Lyme disease. *Canadian Journal of Zoology* **78**:2184–2197.
- Gilbert, L., R. Norman, K. Laurenson, H. W. Reid, and P. J. Hudson. 2001. Disease persistence and apparent competition in a three-host community: an empirical and analytical study of large-scale, wild populations. *Journal of Animal Ecology* **70**:1053–1061.
- Knops, J., D. Tilman, N. M. Haddad, S. Naeem, C. E. Mitchell, J. Haarstad, M. E. Ritchie, K. M. Howe, P. B. Reich, E. Siemann, and J. Groth. 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters* **2**:286–293.
- Krohne, D. T., and G. A. Hoch. 1999. Demography of *Peromyscus leucopus* populations on habitat patches: the role of dispersal. *Canadian Journal of Zoology* **77**:1247–1253.
- Laurance, W. F., H. L. Vasconcelos, and T. E. Lovejoy. 2000. Forest loss and fragmentation in the Amazon: implications for wildlife conservation. *Oryx* **34**:39–45.
- Lawton, J. H. 2000. Community ecology in a changing world. Ecology Institute, Oldendorf/Luhe, Germany.
- LoGiudice, K., R. S. Ostfeld, K. A. Schmidt, and F. Keesing. 2003. The ecology of infectious disease: effects of host diversity and community composition on Lyme disease risk. *Proceedings of the National Academy of Sciences (USA)* **100**:567–571.
- Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D. A. Wardle. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* **294**:804–808.
- Nupp, T. E., and R. K. Swihart. 1996. Effect of forest patch area on population attributes of white-footed mice (*Peromyscus leucopus*) in fragmented landscapes. *Canadian Journal of Zoology* **74**:467–472.
- Nupp, T. E., and R. K. Swihart. 2000. Landscape-level correlates of small-mammal assemblages in forest fragments of farmland. *Journal of Mammalogy* **81**:512–526.
- Ostfeld, R. S., and F. Keesing. 2000a. Biodiversity and disease risk: the case of Lyme disease. *Conservation Biology* **14**:722–728.
- Ostfeld, R. S., and F. Keesing. 2000b. The function of biodiversity in the ecology of vector-borne zoonotic diseases. *Canadian Journal of Zoology* **78**:2061–2078.
- Ostfeld, R. S., F. Keesing, E. M. Schaubert, and K. A. Schmidt. 2002. The ecological context of infectious disease: diversity, habitat fragmentation, and Lyme disease risk in North America. Pages 207–219 in: A. Aguirre, R. S. Ostfeld, C. A. House, G. Tabor, and M. Pearl, editors. *Conservation medicine: ecological health in practice*. Oxford University Press, New York, New York, USA.
- Ostfeld, R. S., E. M. Schaubert, C. D. Canham, F. Keesing, C. G. Jones, and J. O. Wolff. 2001. Effects of acorn production and mouse abundance on abundance and *Borrelia burgdorferi* infection prevalence of nymphal *Ixodes scapularis* ticks. *Vector Borne and Zoonotic Diseases* **1**:55–64.
- Pimm, S. L. 1993. The balance of nature? University of Chicago Press, Chicago, Illinois, USA.
- Rosenblatt, D. L., E. J. Heske, S. L. Nelson, D. M. Barber, M. A. Miller, and B. MacAllister. 1999. Forest fragments in east-central Illinois: islands or habitat patches for mammals? *American Midland Naturalist* **141**:115–123.
- Schmidt, K. A., and R. S. Ostfeld. 2001. Biodiversity and the dilution effect in disease ecology. *Ecology* **82**:609–619.
- Schmidt, K. A., R. S. Ostfeld, and E. M. Schaubert. 1999. Infestation of *Peromyscus leucopus* and *Tamias striatus* by *Ixodes scapularis* (Acari: Ixodidae) in relation to the abundance of hosts and parasites. *Journal of Medical Entomology* **36**:749–757.
- Schwartz, M. W., C. A. Brigham, J. D. Hoeksema, K. G. Lyons, M. H. Mills, and P. J. van Mantgem. 2000. Linking biodiversity to ecosystem function: implications for conservation biology. *Oecologia* **122**:297–305.
- Stone, L., R. Dayan, and D. Simberloff. 1996. Community-wide assembly patterns unmasked: the importance of species' differing geographical ranges. *American Naturalist* **148**:997–1015.
- Tilman, D., J. Knops, D. Wedin, P. B. Reich, M. E. Ritchie, and E. Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* **277**:1300–1302.
- Wardle, D. A., K. J. Bonner, G. M. Barker, G. W. Yeates, K. S. Nicholson, R. D. Bardgett, R. N. Watson, and A. Ghani. 1999. Plant removals in perennial grassland: vegetation dynamics, decomposers, soil biodiversity, and ecosystem properties. *Ecological Monographs* **69**:535–568.

APPENDIX

A community-disassembly table for the 13 species of mammals and birds at our field site in Dutchess County, New York, USA, giving parameters used in models relating vertebrate community composition to nymphal tick infection prevalence (NIP), is available in ESA's, Electronic Data Archive, *Ecological Archives* E084-035-A1.