

Linking populations to landscapes: richness scenarios resulting from changes in the dynamics of an ecosystem engineer

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Abstract. Predicting the effects of the loss of individual species on diversity represents one of the primary challenges facing community ecology. One pathway by which organisms of one species affect the distribution of species is ecosystem engineering. Changes in the dynamics of ecosystem engineers that lead to changes in the distribution of the patches of altered habitat are likely to lead to changes in diversity. I link data on the distribution of plant species found in the riparian zone of the Adirondacks (New York, USA) in patches modified by beaver and in unmodified forest patches to a model connecting the dynamics of ecosystem engineers to the dynamics of the patches that they create. These analyses demonstrate that changes in key parameters of the model, such as decreases in beaver colonization rates and rate of patch abandonment, lead to changes in species richness of up to 45% at the landscape scale, and that these changes are likely to occur over long time scales. This general approach of linking the population dynamics or behavior of a single species to changes in species richness at the landscape scale provides a means for both testing the importance of ecosystem engineering in different systems and developing scenarios to predict how changes in the dynamics of a single species are likely to affect species richness.

Key words: *beaver; beaver meadows cf. riparian zone; Castor canadensis; ecosystem engineer; population dynamics; riparian zone of the Adirondacks, New York, USA; species richness; succession.*

INTRODUCTION

Predicting the effects of the loss of individual species on the diversity of communities has proven remarkably challenging (Menge et al. 1994, Wootton 1994, Power et al. 1996). Species interact with each other through numerous complex pathways, the outcomes of which are often highly contingent (McGill et al. 2006). However, in light of increasing rates of extinction, the task of determining how diversity is likely to respond to changes in the abundance of species and other drivers of global change has become ever more pressing (Sala et al. 2000). One potential solution to this problem is to take a more mechanistic approach and try to understand the dominant pathways by which species affect the distribution and abundance of other species.

One key pathway by which one organism can affect others is the creation, destruction, or modification of habitat—ecosystem engineering (Jones et al. 1994, 1997). While several recent studies have documented large landscape-scale effects of ecosystem engineers on diversity (Wright et al. 2002, Lill and Marquis 2003, Castilla et al. 2004, Crain and Bertness 2005, Badano et al. 2006), it is important to note that these effects are likely to be dynamic over time and space. One of the critical factors regulating the magnitude of the effect of

ecosystem engineers on richness that has yet to be considered is the relative proportion of the landscape that is in different patch types, i.e., patches that have been modified by ecosystem engineers and patches that have not been affected by the ecosystem engineer of interest. As long as at least one of the species in the regional species pool is dependent on one of the patch types, landscape-scale richness will be diminished in landscapes where there are no patches modified by engineers (excluding “engineer specialists”) and in landscapes where there are no unmodified patches (excluding “unmodified specialists”), relative to landscapes that have a mixture of both patch types. Between these two endpoints, ecological theory predicts that diversity should be maximized at intermediate levels of “disturbance,” in this case habitat modification by ecosystem engineers (Connell 1978, Petraitis et al. 1989). However, studies based on the intermediate-disturbance hypothesis have yet to predict exactly how “intermediate” a disturbance should be to maximize diversity. Indeed, the shape of the curve relating the relative cover of different patch types to diversity at the landscape scale is likely to be variable and to depend on factors such as the degree of overlap in composition between the patch types and the rate at which species accumulate with area in the different patch types. The question becomes even more complicated if there is the potential for the composition of patches to change over time through succession.

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One of the most important controls on the relative proportion of engineered and unmodified patches in the landscape is likely to be the population dynamics and behavior of the ecosystem engineer. The creation and maintenance of patches is typically a function of population size and behavior governing preferences for where new patches are created and when old patches are abandoned. Variation in these parameters has been shown to result in differences in the distribution of patch types in a model relating the dynamics of ecosystem engineers to the dynamics of the patches that they create (Wright et al. 2004). The links between engineer dynamics and patch dynamics and between patch dynamics and diversity at the landscape scale, should allow us to develop scenarios to predict how changes in the dynamics of a single species will result in changes to diversity at the landscape scale.

Beaver (*Castor canadensis*) represent an ideal ecosystem engineer for developing such scenarios. They are a particularly well-studied example of ecosystem engineers that transform free-flowing streams into impounded ponds. In large areas of their range, these ponds then transform into wetlands through the processes of dam decay and site abandonment (Naiman et al. 1988). In many areas of their range, the wetland habitat created by beaver form large, discrete, and readily recognized patches (Johnston and Naiman 1990*a, b*), often termed "beaver meadows," that have distinctive patterns of light, water, and nutrient availability (Johnston et al. 1995). As a result, beaver meadows harbor assemblages of wetland plants that differ from those found in areas of riparian zones unaffected by beaver (Wright et al. 2002; R. A. Bartel, N. M. Haddad, and J. P. Wright, *unpublished manuscript*).

Given the differences in composition between beaver meadows and riparian zones, it seems likely that varying the relative abundance of beaver meadows should have significant effects on the number of species found in the landscape. Additionally, previous studies have shown significant changes in composition within beaver meadows over time due to successional processes (Remillard et al. 1987, Pastor et al. 1993, McMaster and McMaster 2001, Wright et al. 2003), suggesting that varying the age distribution of beaver-modified patches in the landscape may have additional impacts on diversity at the landscape scale. There have been dramatic historic fluctuations in beaver populations in much of the continental United States, including large areas of extirpation due to hunting (Muller-Schwarze and Sun 2003). These changes had obvious impacts on the population dynamics of beaver and almost certainly altered the distribution of patch types in the landscape. However, it is uncertain whether these extirpations lasted for a long-enough time, ranging from over 200 years in Massachusetts to approximately 50 years in the Adirondacks (Muller-Schwarze and Sun 2003), to lead to the loss of beaver-meadow specialists.

The engineering activities of beaver fit well with a general model constructed to link the dynamics of ecosystem engineers to the dynamics of the patches that they create (Gurney and Lawton 1996, Wright et al. 2004). Due to their importance, both as an economic resource and as a pest, there has been considerable research on the population dynamics and behavior of beaver (Jenkins and Busher 1979, Muller-Schwarze and Sun 2003). As a result, the combination of data from the literature with data derived from long-term data sets provided independent, well-bounded estimates of the general model's parameters for the same landscape for which data on the effects of beaver on plant composition were available (Wright et al. 2002, 2004).

In general, while we know that beaver alter plant community composition and that beaver population dynamics affect the distribution of patches in the landscape, predicting to what degree and over what time scales changes in beaver population dynamics are likely to affect species richness is less straightforward. The combination of a parameterized model linking engineer dynamics to patch dynamics and an empirical data set on the distribution of species in engineered and unmodified patches provides an important opportunity to test the general approach of linking the dynamics of ecosystem engineers to diversity at the landscape scale outlined above. In particular I wished to address three questions: (1) Do changes in the relative proportion of engineered and unmodified habitat lead to significant changes in the predicted number of riparian plant species in the landscape? (2) Can changes in the dynamics of an ecosystem engineer cause substantial-enough changes in distribution of patch types to lead to changes in species richness? and (3) Over what time scales are predicted changes in diversity likely to occur? While the first question is a relatively straightforward extension of previous work (Wright et al. 2002, 2004), it allows for a baseline against which to compare the magnitude of the effects of changes in population dynamics and the importance of temporal dynamics addressed in questions (2) and (3). Addressing these questions will allow me to generate specific scenarios to determine how changes in parameters reflecting specific aspects of the dynamics of beaver (e.g., birth rates, death rates, and patch selection behavior) are likely to affect diversity at broad scales.

METHODS

Study site

The data used in the simulations described below were collected at the Huntington Wildlife Forest (HWF), a 6142-ha forest reserve located in the central Adirondack region of New York, USA (latitude 44°00' N, longitude 74°13' W, elevation 457–823 m). In this area, abandoned beaver ponds develop into open meadows dominated by the grass *Calamagrostis canadensis* and several species of sedge (*Carex* spp.), with occasional stands of speckled alder, *Alnus incana*. Visual analysis of historical aerial

photographs taken at roughly 10-year intervals between 1942 and 2002 indicated that in this region beaver activity is the only large-scale form of disturbance in the riparian zone. Furthermore, aerial-photograph analysis suggests that all large, open-canopy wetland areas in the landscape are associated with active or abandoned beaver dams.

Linking patch dynamics to landscape-scale richness

To determine the effects of varying the relative proportion of beaver-modified and forested patches in the riparian zone on species richness at the landscape scale I used empirical data in Monte Carlo simulations. I first collected data on plant assemblages associated with beaver-modified wetlands and forested riparian zone areas in the HWF. I selected sites from the different habitat types in multiple watersheds. All beaver-modified sites ($n = 14$) showed evidence of past modification by beaver, either by the presence of a beaver impoundment in aerial photographs or the visible presence of a collapsed dam in the field. Beaver-modified sites were only selected if historical photographs demonstrated that they had been forested at one point over the period from 1942 to 2002. To account for previously detected temporal effects on meadow composition (Wright et al. 2003) and to match the model structure (see *Linking beaver dynamics...*, below), sites were classified as young (<5 years) or old (>5 years). This age cut-off reflects the average amount of time (4.76 years) it takes for a meadow to transition from the degraded state (D), i.e., "young" meadow sites that are newly abandoned and not suitable for recolonization) to a potentially colonizable state of older meadows (P) at $p = 0.21$ as was used in all simulations (see *Linking beaver dynamics...*, below). To test whether these two age classes of meadows differed in composition, I performed an ordination using nonmetric multidimensional scaling (McCune and Mefford 1999). Undisturbed riparian forest sites ($n = 4$) that showed no evidence of beaver modification at any point during the 60-year period covered by aerial photographs were selected to match sites that had been modified by beaver in terms of gradient, elevation, and surrounding forest type.

I sampled the herbaceous plant community in 0.5×1.0 m plots and identified all vascular plants present in each plot. In meadow habitats, plots were laid out every 5 m along a series of five parallel transects with 10 plots per transect and 10 m between transects, resulting in a maximum of 50 plots per site. Plots falling outside the boundary of the meadow were not included in the analysis resulting in 276 plots from six sites classified as young and 330 plots from eight sites classified as old. The number of plots at each forested site was limited by the length of the stream reach, with two sites containing 12 plots, one site with 36 plots, and one site with 60 plots, for a total of 120 plots. Forested plots were located randomly within 1 m of the edge of the stream. Species-accumulation curves for all three habitat types

reached a plateau after 50 plots, indicating that our sampling effort fully captured the richness and composition of both habitats. For further details on sampling and effects of beaver modification on community composition see Wright et al. (2002, 2003).

I used the data from the community sampling in Monte Carlo simulations of landscapes containing different proportions of the three habitats. I randomly selected plots from each habitat type to generate simulated landscapes of 120 total plots with all possible combinations of proportions of the three habitat types ranging from 0% to 100% in 10-percentile increments (e.g., to simulate a landscape containing 20% young beaver-modified, 30% old beaver-modified and 50% forested riparian zone, I randomly selected 24 plots collected in young beaver meadows, 36 plots from old beaver meadows and 60 plots in forested riparian zones). I replicated this process 100 times at each level of relative abundance. I calculated the Chao 2 species-richness estimator using the formulas provided by Colwell (2006) for each simulated landscape as an estimate of the total number of species present in the landscape, and calculated the mean and 95% confidence intervals of estimated richness across the 100 simulations (see Appendix B for calculation of species-richness estimator).

Linking beaver dynamics to patch dynamics

I used a previously developed model (Wright et al. 2004) to characterize the transitions between different patch types in a landscape modified by ecosystem engineers (see Appendix A for model details). The model is a non-spatial series of linked differential equations that explores the dynamics of multiple patch types. It was developed to be general enough in its structure to apply to any ecosystem engineer for which the creation of patches is necessary for reproduction. In the case of beaver, these patch types are: Active ponds (A), newly abandoned ponds (D), abandoned ponds that potentially could be recolonized (P), and unmodified/fully recovered patches (F). In addition, in this landscape there is an additional patch type (U) that represents the constant proportion of the riparian zone that is incapable of being modified by beaver due to geomorphological constraints (Howard and Larson 1985). Active ponds tend to have minimal non-aquatic vegetation associated with them, so I was interested in the relative proportion of meadow patches ($D + P$) and unmodified patches ($F + U$).

Using a combination of long-term data on patch occupancy at HWF and estimates from the literature, I was able to parameterize the model (see Wright et al. [2004] for details). While I was unable to fully validate the model due to constraints on what types of data had previously been collected, the estimate of the relative proportion of active ponds (A) to meadows ($D + P$) derived from the model using estimated parameters is

within 5% of the proportion derived from visual analysis of aerial photographs ($[D + P]/A = 2.17$ from model and 2.07 from photographs) suggesting that parameter estimates lead to reasonable outcomes.

To understand the effects of variation in the population dynamics and behavior of beaver on the relative abundance of different patch types, I identified three key parameters of interest from the model: n , the per-patch production rate of successful colonists, δ the decay rate of patches from active to degraded, and ζ , the degree to which colonists preferentially colonize or discriminate against partially recovered patches (P) relative to fully recovered patches (F). The parameter n integrates birth rates of beaver, rates of site fidelity, and mortality during dispersal, all critical aspects controlling the population dynamics of beaver. In sum, high values of n reflect systems where active ponds create many successful colonists. The parameter δ could reflect environmental factors such as the rate at which ponds fill up with sediment, or the quality of forage around active ponds. However, it will also be affected by the mortality rate of adult beaver, another key variable affecting the population dynamics of beaver, with high mortality rates leading to high values of δ . The parameter ζ reflects an important aspect of beaver behavior, namely their willingness to recolonize previously used patches. I was particularly interested in investigating the effects of varying ζ on the relative abundance of different patch types because evidence suggests that it has been decreasing over the past 30 years, i.e., currently beaver prefer to colonize previously uncolonized patches, whereas in 1981 beaver preferred to recolonize previously used sites (Wright et al. 2004).

I conducted a series of analyses to determine the effects of changing each of the target parameters on the equilibrium proportions of all habitat types while holding all other parameters constant. As in Wright et al. (2004), in simulations in which the parameters were held constant, I used parameter values of $\delta = 0.2$, $n = 0.4$, $\zeta = 1.2$, ρ (the rate at which abandoned patches recover to a sufficient degree to be recolonized) = 0.21, and r (the rate at which patches that could potentially be colonized fully recover back to forest) = 0.01.

These calculations provided estimates of the equilibrium proportions of *potentially modifiable* habitat in the landscape under different scenarios. However, as mentioned above, a constant fraction of the actual landscape is never used by beaver (i.e., in patch type U). Using high-resolution aerial-photograph layers in a GIS, I was able to calculate the current area of active ponds (patch type A) and beaver meadows (patch types $D + P$) within the boundaries of HWF. I estimated the total area of unmodified riparian zone by multiplying the total length of unmodified stream by an average riparian zone width of 3 m, estimated from digital elevation models. To estimate the area of this unmodified riparian zone that

was potentially usable by beaver (i.e., the area of patch type F), I solved the equation

$$F_{\text{map}} = (F_{\text{mod}}/A_{\text{mod}}) \times A_{\text{map}}$$

where F_{mod} and A_{mod} are the equilibrium proportions estimated from the model using standard parameter values and A_{map} is the area of active ponds identified using GIS. By subtracting this value of F from the total area of unmodified riparian zone, I calculated an area of patch type U of 14 ha. I added this derived estimate of patch type F to the observed areas of patch types A , P , and D to calculate a total area of potentially modifiable riparian zone of 203 ha. Using these values, I calculated the total area of forested riparian zone ($203 \times F_{\text{eq}} + 14$ [where eq = equilibrium]), young beaver meadow ($203 \times D_{\text{eq}}$) and old beaver meadow ($203 \times P_{\text{eq}}$) for every parameter combination. Given the uncertainties involved in these calculations and the inability to independently validate the model's parameter estimates, estimates of the absolute size of the effects of changes in beaver population dynamics and behavior on species richness should be interpreted with caution. However, the relative effects of variation in the different parameters should be largely unaffected by these uncertainties.

The above analyses provide estimates for the expected relative proportion for each habitat type at equilibrium under different scenarios. However, they do not provide information on the dynamics of the system as it shifts from one equilibrium to another. To explore these temporal dynamics, I developed two scenarios affecting n that were meant to simulate a pulse disturbance (n immediately changes from 0.2 to 0 at the start of the simulation) or a press disturbance (n decreases by 1% each year of the simulation). These two scenarios are intended to bracket the historical effects of beaver hunting that, in many areas of North America, significantly reduced beaver populations over a number of years. I made the assumption that change in the proportions of patch types occurs at an annual increment and calculated the annual change in cover of each of the patch types using Eq. 7a-c in Wright et al. (2004) using the appropriate values of n and the previous year's cover of each patch type. Using the methods described above, I then determined the proportion of each habitat in the landscape for the first 500 years of both simulations.

Linking population dynamics to species richness at the landscape scale

For each of the landscapes predicted by the parameter combinations and time steps described above, I performed 500 Monte Carlo simulations with the appropriate relative proportions of the three patch types. For each simulated landscape, I calculated the Chao2 estimate of species richness and then calculated the mean and 95% confidence intervals for the predicted number of species across the 500 simulations.

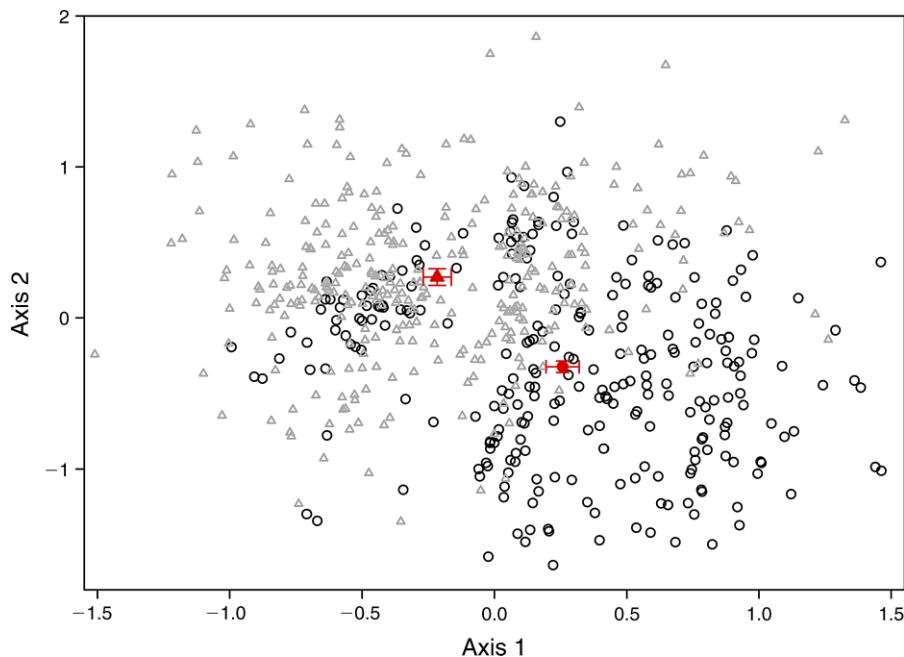


FIG. 1. Nonmetric multidimensional scaling (NMS) ordination of vegetation plots from young (circles; <5 yr old) and old (triangles; >5 yr old) beaver meadows showing significant differences along both axes in the means (red symbols \pm 95% confidence interval) for the two groups. Axis 1 ($R^2 = 0.148$) and Axis 2 ($R^2 = 0.403$) collectively explain 55.1% of the variance in the original distance matrix, and both show significantly less stress ($P = 0.02$ for both axes) than randomized runs.

RESULTS

Linking patch dynamics to species richness at the landscape scale

Although there was overlap in the composition of meadow sites <5 years old and >5 years old, these two habitat types differed significantly in their composition (Fig. 1). Maximum landscape-scale richness was estimated using Monte Carlo simulations in a landscape containing 40% young meadows, 30% old meadows, and 30% forest, although there is a fairly broad range over which the number of species in the landscape is relatively insensitive to the relative proportions of beaver-modified and forested patches (Fig. 2A). There is evidence of a hump-shaped curve as the proportion of forest in the landscapes moves from low to high, particularly when the proportion of young meadow in the landscape is low. This results in a strongly significant hump-shaped relationship between the fraction of forest in the landscape and predicted richness (Fig. 2B; $P < 0.001$, $df = 63$, adjusted $R^2 = 0.9979$).

There are only minor changes in richness when the amount of forest in the landscape is held constant and the relative abundance of young and old meadow varies, suggesting that the differences in composition between these two habitat types are less significant than the differences between beaver-modified habitats and forested habitats. In general, the largest changes in richness occur when transitioning from 10% to 0% forest. There are also rapid declines in richness when the landscape

shifts from 10% to 0% young meadow, but only when the fraction of old meadow in the landscape is low. Likewise, rapid declines when moving from 10% to 0% old meadow only occurred when the fraction of young meadow in the landscape is low. Together these data suggest that variation in the proportion of forest is the strongest driver of richness in this landscape while variation in the age distribution of beaver meadows is a weaker forcing variable.

Linking beaver dynamics to landscape richness

Given the landscape configuration of the Huntington Wildlife Forest (HWF; Adirondacks, New York, USA) and the baseline set of parameters, I estimate that young beaver meadows currently occupy 34% of the landscape available for riparian zone plants, old beaver meadows occupy 53%, and forest covers the remaining 13% of the landscape. Increasing the parameter n , the rate at which new colonists are produced from existing patches, above the currently estimated value of n (0.4) appears to have little effect on the percentage of the landscape that would be covered by forest at steady state with a shift towards a younger age distribution of meadows (Fig. 3). However, the model indicates that declines from the current of value of n are likely to lead to rapid increases in the percentage of forest in the landscape until the point where n is equal to δ , the rate at which active patches are abandoned, at which point, beaver cannot be sustained in the system (Wright et al. 2004). The changes in the distribution in patch types resulting from

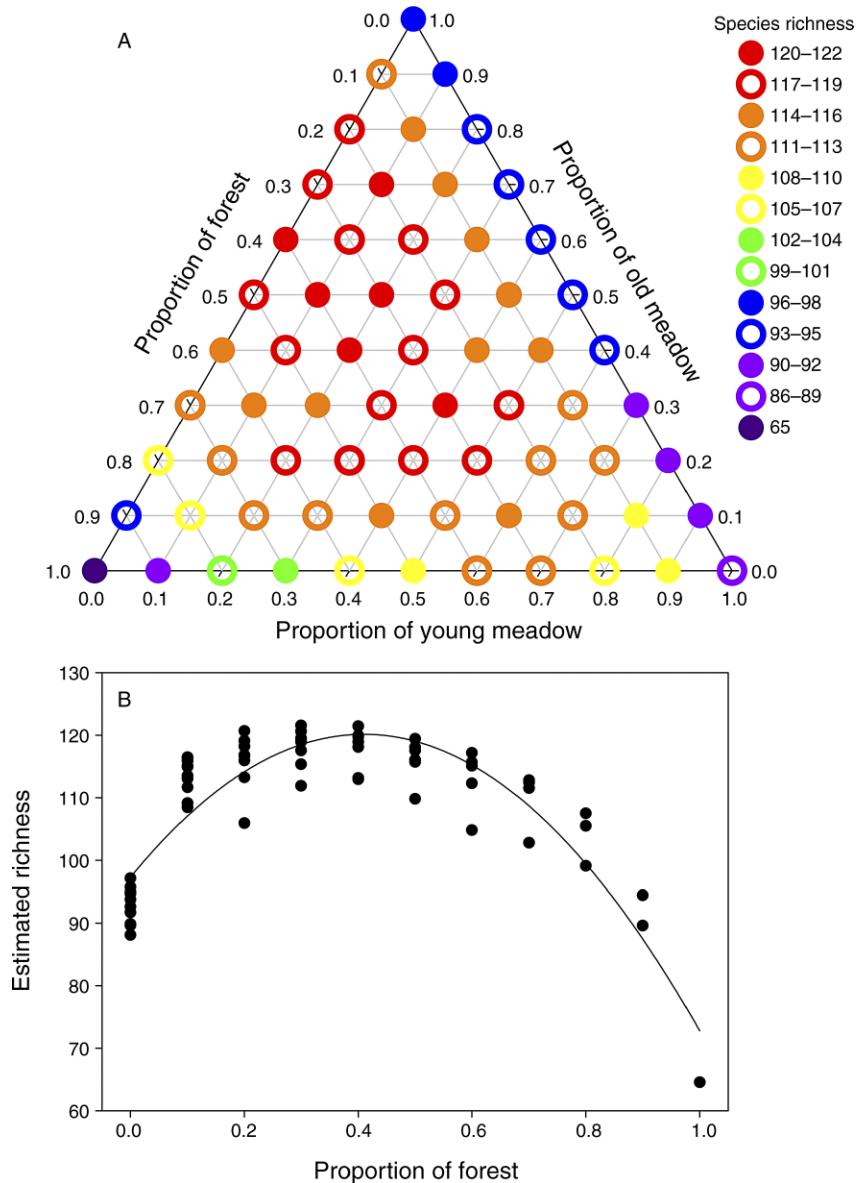


FIG. 2. (A) Estimated richness of simulated landscapes containing varying proportions of young meadow, old meadow, and forest. Across all combinations of habitat proportions, the average 95% confidence interval was 2.48. Warmer colors represent higher estimated richness, and points that are different by more than two intervals can be interpreted as being significantly different. (B) Relationship between proportion forest and estimated richness. Data points within a level of forest cover represent the mean estimated richness of 100 runs at varying relative cover of old and young meadow. The curved line represents the results from a second-order polynomial regression fitted using least-squares regression. The equation of the best-fit line is $y = 97.3 + 111.6x - 136.0x^2$.

increasing n from the currently estimated value of 0.4 are not predicted to lead to significant changes in species richness at the landscape scale. Decreasing n from current values is predicted to lead first to a small, but significant increase in richness, followed by a reduction in richness by 44% when beaver are removed from the landscape.

Variation in δ , the rate at which active patches are abandoned, has little effect on the steady state proportion of forest in the landscape over a range of values

from ~ 0.1 to 0.25, encompassing the current value of 0.2 (Fig. 4), with a shift towards increasing cover of older meadows at higher values of δ . Values of δ outside this range, however, will lead to rapid increases in the percent forest present in the landscape. As δ approaches both 0 and the value of n (in these simulations, 0.4), the system approaches a state where no beaver meadows are present. Correspondingly, there are no predicted changes in richness at values of δ between 0.1 and 0.25 compared to the current landscape. More extreme values

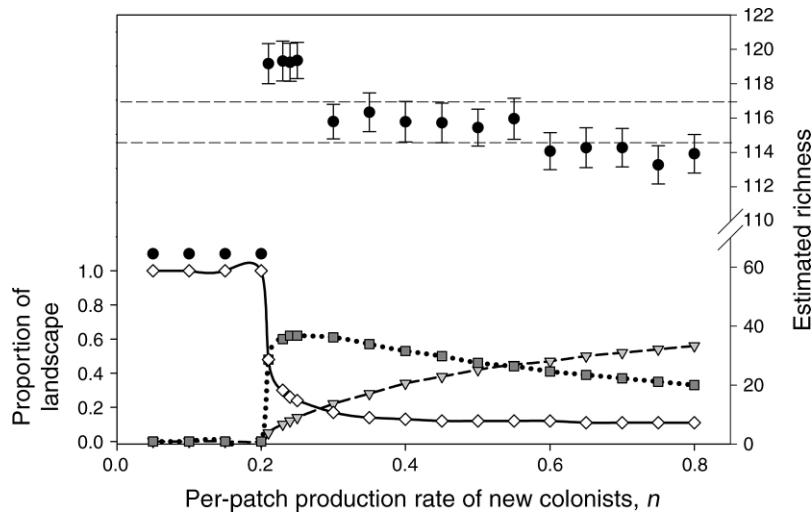


FIG. 3. Variation in the proportion of the landscape in young meadow (triangles and dashed line), old meadows (squares and dotted line), and forest (diamonds and solid line) at equilibrium resulting from variation in the parameter n , the per-patch production rate of new colonists, is shown on the left-hand axis and the bottom left. Estimates of richness (mean of 500 runs \pm 95% confidence interval [CI]) are from simulated landscapes with the corresponding relative proportions of the three habitat types and are shown by the solid circles, using the right-hand axis at the top right of the panel. The dashed horizontal lines depict the 95% CI around the mean estimate of richness given the current configuration of the landscape.

of δ that still allow for persistence of beaver are predicted to lead to small, but significant increases in riparian zone plant richness, with richness crashing when δ reaches values that preclude the persistence of beaver-meadow habitats.

Increasing the parameter ζ , the degree to which beaver prefer to colonize forest patches over partially recovered meadow patches, reflects an increasing preference of beaver to recolonize previously used sites. Values of ζ

over 1.2, the estimate obtained from long-term data, lead to little change in the steady-state proportion of forest in the landscape, and a shift towards a younger age distribution of meadows (Fig. 5). As ζ decreases below 1, indicating a switch from a preference for meadow patches to a preference for forest patches, the proportion of forest in the landscape increases. This counterintuitive result is due to declines in the number of beaver that can be sustained when beaver have strong

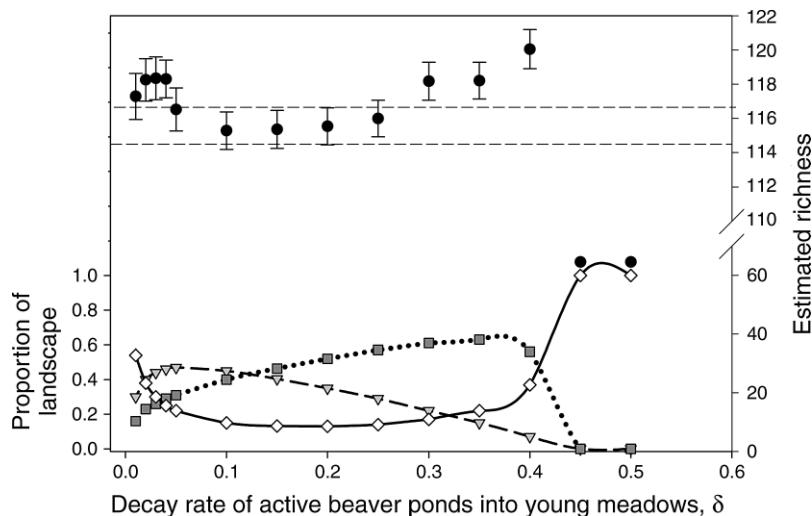


FIG. 4. Variation in the proportion of the landscape in young meadow (triangles and dashed line), old meadows (squares and dotted line), and forest (diamonds and solid line) at equilibrium resulting from variation in the parameter δ , the decay rate of active ponds into young meadows, is shown on the left-hand axis and the bottom left. Estimates of richness (mean of 500 runs \pm 95% CI) are from simulated landscapes with the corresponding relative proportions of the three habitat types and are shown by the solid circles, using the right-hand axis at the top right of the panel. The dashed horizontal lines depict the 95% CI around the mean estimate of richness given the current configuration of the landscape.

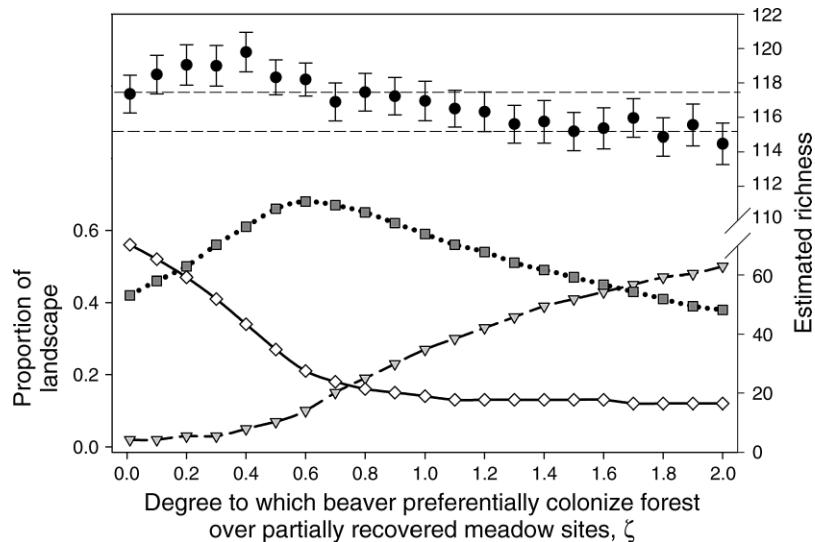


FIG. 5. Variation in the proportion of the landscape in young meadow (triangles and dashed line), old meadows (squares and dotted line), and forest (diamonds and solid line) at equilibrium resulting from variation in the parameter ζ , the degree to which colonists discriminate against partially recovered patches relative to fully recovered patches, is shown on the left-hand axis and the bottom left. Estimates of richness (mean of 500 runs \pm 95% CI) are from simulated landscapes with the corresponding relative proportions of the three habitat types and are shown by the black circles, using the right-hand axis at the top right of the panel. Horizontal lines depict the 95% CI around the mean estimate of richness given the current configuration of the landscape.

preferences for forested patches leading to landscapes with few active ponds, leading to low production of meadows (for further discussion see Wright et al. [2004]). These changes in ζ are only predicted to significantly alter richness from current estimates of richness at values between 0.1 and 0.5.

Temporal dynamics of changes in beaver dynamics

I investigated two scenarios of reduction in n : an immediate extinction causing n to decrease from 0.2 to 0, and a gradual decrease in population size with n decreasing by 1% each year of the simulation. The temporal dynamics resulting from these scenarios were qualitatively similar, resulting in an immediate decline in young meadows, a peak in cover of old meadows in intermediate years, followed by a rise in forest cover (Fig. 6). In the pulse-extinction scenario, I estimate that it would take more than 125 years before richness would decline significantly below current levels. In the press population-decline scenario, it would take closer to 200 years for richness to decline significantly.

DISCUSSION

Due to the large differences in composition between beaver meadows and areas of the riparian zone unaffected by beaver (Wright et al. 2002), changes in the relative cover of beaver meadows in the landscape are predicted to lead to substantial changes in the expected number of species in the landscape. Furthermore, the steady-state distribution of patch types in the landscape appears to be sensitive to certain changes in parameters reflecting patch creation (n), patch aban-

donment (δ) and the degree to which colonists prefer different patch types (ζ). These parameters describing patch dynamics can be related to birth and colonization rates (n), death rates (δ), and foraging behavior (ζ) of the engineer. Together, these two lines of evidence imply that changes in the population or behavioral dynamics of ecosystem engineers have the potential to alter species richness at large spatial scales in landscapes such as the Huntington Wildfile Forest (HWF; in the Adirondacks, New York, USA), although these changes are likely to take place on the scale of decades to centuries.

In this data set the relationship between forest abundance and species richness is a unimodal relationship with maximum species richness predicted at forest cover of $\sim 40\%$. The underlying mechanisms are likely to be the same ones postulated for the intermediate-disturbance hypothesis when applied at the scale of landscapes (Connell 1978, Petraitis et al. 1989), namely, that a mix of patch types allows for co-occurrence of specialists on both patch types in the landscape. However, it is important to note that there is no a priori expectation that the relationship should be either symmetrical or centered around 50%. In this case, it is, but that is because both beaver meadows and forested riparian-zone habitats have similar levels of richness, there is relatively low overlap between the species pools of the two habitats, and species accumulate at similar rates with increasing area reflecting similar relative abundance distributions in the two habitat types (Wright et al. 2002). One would expect situations where these three factors vary to show different relationships

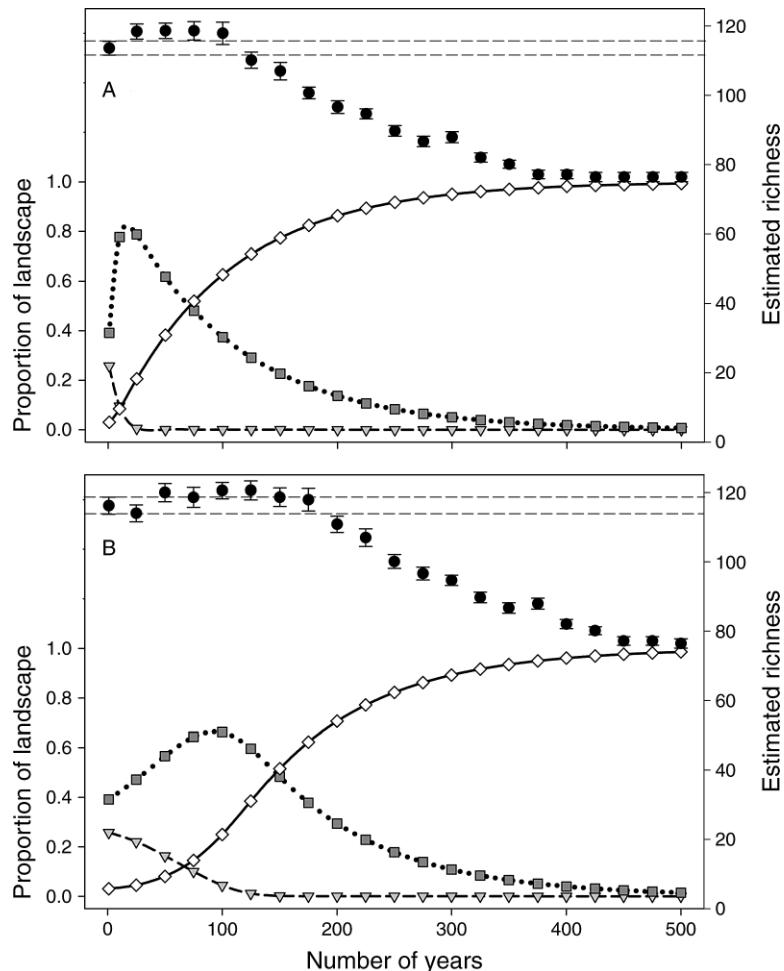


FIG. 6. Variation in the proportion of the landscape in young meadow (triangles and dashed line), old meadows (squares and dotted line), and forest (diamonds and solid line) over time resulting from (A) a decrease of n (the per-patch production rate of new colonists) from 0.2 to 0 in Year 1, or (B) a decrease in the value of n by 1% each year. Estimates of richness (mean of 500 runs \pm 95% CI) from simulated landscapes with the corresponding relative proportions of the three habitat types are shown by the solid circles, using the right-hand axis at the top right of the panel. Horizontal lines depict the 95% CI around the mean estimate of richness given the current configuration of the landscape.

between the proportion of engineered habitat in the landscape and the expected number of species. For example, in situations where habitat type contains only a subset of the species found in the other patch type, as is the case with patches of crusted soil vs. relatively high-moisture, high-nutrient environments under shrubs in the Negev Desert (Wright et al. 2006), one would predict the maximum diversity to shift towards landscapes with increased cover of the more diverse patch type. Future studies using the general approach developed here to linking the population dynamics of ecosystem engineers with species richness at the landscape scale are necessary to determine whether general predictive patterns emerge.

In the case of beaver meadows, successional changes in plant composition are likely to be driven by changes in local hydrology (McMaster and McMaster 2001, Wright et al. 2003). Given that changes in hydrology

occur at different rates in different sites, age is, at best, a rough proxy for the mechanisms driving compositional change. While the effects of varying the relative cover of young and old meadows did not have as strong an effect on richness as varying the relative cover of forest patches, at a constant level of forest cover, richness could vary as much as 14% at different levels of cover by young and old meadows. This suggests that when species composition shifts significantly over time, even relatively unrefined attempts to capture that variability, such as splitting “beaver modified” patches into two groups as was done here, can have important implications for understanding the impacts of ecosystem engineering on community dynamics. Recognizing this variability becomes even more critical when species of conservation interest are associated with particular successional stages following disturbance by an ecosystem engineer (R. A.



PLATE 1. Aerial photograph of Adirondack landscape (USA) showing beaver-modified meadows and ponds set within a matrix of forest. Photo credit: J. Wright.

Bartel, N. M. Haddad, and J. P. Wright, *unpublished manuscript*).

The relative abundance of different patch types in the landscape, and hence landscape diversity, was most sensitive to decreases in the parameter n , the rate at which new colonists are produced. Such a change could result from changes in a number of important components of beaver population dynamics including decreasing birth rates or increased mortality during dispersal (Wright et al. 2004). However, the model also suggests that changes in patch-abandonment rates, δ , and beaver foraging behavior, as reflected by the parameter ζ , have the potential to lead to significant changes in the distribution of patch types and consequently species richness. Thus changes in both the behavior and population dynamics of an ecosystem engineer are predicted to lead to changes in species richness at the landscape scale.

It is important to note that the predictions of species richness in the scenarios involving changes in parameter values are for equilibrium states of the system. Thus, changes in the population dynamics or behavior of beaver may not lead to immediate changes in the distribution of species. This is an important consideration given the history of beaver in the Adirondacks, and, indeed, throughout much of their native range. In the Adirondacks, beaver were extirpated for a period of ~ 40 years. The analysis of the temporal dynamics of patch cover and species richness resulting from two different scenarios for changes in n suggest that even under the most extreme case, it would take at least 125 years for species richness to decline significantly from current levels. This is largely due to the fact that transitions from beaver meadow to forest occur at a very

slow rate in the Adirondacks (Remillard et al. 1987), buffering the system from large changes over relatively long time scales. Given the long lag times in the patch dynamics of this system, it is possible that current estimates of richness are still in recovery from the period of beaver extirpation. However, the time lag operates primarily following declines in beaver populations. Increases in beaver populations lead to rapid reappearance of young meadows.

For simplicity, I have predicted changes in species richness based purely on species–area effects. However, if there are important interactions between patches that affect the persistence of species in the landscape, as is the case in metapopulations, my estimates of species loss as either habitat type declines may, again, be conservative. Tilman et al. (1994) demonstrated that the loss of species in patchy landscapes occurs at a much greater rate in landscapes that have already lost much of their suitable habitat. They also demonstrated that in landscapes where such an “extinction debt” occurs, the loss of habitat leads to greater species loss than would be predicted based on species–area relationships alone. However, in this particular case, dispersal limitation does not seem to limit species richness of beaver-modified habitats (Wright et al. 2003), suggesting that metapopulation dynamics are not likely to be important.

In the case of beaver, the model predicts strong dependencies between population dynamics of an ecosystem engineer and the dynamics of species richness at the landscape scale. While beaver may be unique in their effects on the environment, there are several features of beaver ecosystem engineering that might lead to broader generalizations. First, due to the large

changes in the physical environment created by beaver, there are a significant number of species that specialize on either beaver-modified habitats or unmodified habitats. In general, without the presence of specialists on engineered habitats, there are unlikely to be large effects of ecosystem engineers on richness at the landscape scale (Badano et al. 2006). Second, because this analysis focused on riparian-zone plant richness, active patches (i.e., ponds) were ignored in this analysis. For many engineers, the actively used patches are likely to be the most different in terms of environmental parameters, and presumably species composition. Indeed, if this analysis had focused on the effects of beaver on fish or aquatic insects (Hanson and Campbell 1963, McDowell and Naiman 1986, Snodgrass and Meffe 1998, Rolauffs et al. 2001), the relative proportion of abandoned and degraded patches would have been much less important than the relative abundance of active patches in the landscape. While the same general approach of linking engineer population dynamics to community structure at the landscape scale could be used in these situations, adequate knowledge of the life history of the engineer and responding taxa are clearly necessary. Furthermore, unless the alterations to the physical environment persist long after the engineer abandons a patch, the long-term dynamics of species richness following changes in the population dynamics of the engineer are less likely to exhibit the long lag time observed in these simulations, when active patches are the key patch type. Thus, understanding the persistence of environmental changes created by ecosystem engineers is necessary to predict the long-term effects of changes in the population dynamics of engineers on species richness.

Generality of the approach

The novel approach described here for estimating species richness at the landscape scale under various scenarios of population dynamics and behavior of ecosystem engineers has the potential to be broadly applicable. As described before, the model linking ecosystem-engineer dynamics to the distribution of patch types in the landscape is relevant for any species that must create discrete patches with levels of resources that differ from the surrounding landscape (Wright et al. 2004). While I am unaware of any other system where sufficient data have been collected to parameterize the model, it has the potential to apply to a diverse assemblage of organisms such as burrowing polychaete worms (Gutiérrez and Jones 2006), tussock-forming sedges (Crain and Bertness 2005), kangaroo rats (Guo 1996), and leaf-tying insects (Lill and Marquis 2003). One of the major challenges of research on ecosystem engineering is developing broadly applicable methods that will allow us to determine such questions as How many new engineered patches are produced from single patches? How long are patches active? and What factors affect where new patches are constructed (Wright and

Jones 2006)? Answering such questions would allow us to parameterize the model for additional systems and determine its general utility.

The approach for linking patch dynamics to landscape-scale richness using resampling techniques and species-area relationships should prove to be quite general. In theory, it could be applied to any landscape containing multiple patch types, and only requires sufficient sampling so that the taxa of interest present in each patch type have been well characterized. It makes the assumption that the total area of the landscape is sufficiently large that, when the landscape is composed of only one patch type, all of the species from the regional species pool that can persist in that patch type will be present in the landscape. This assumption is likely to hold in the case illustrated here, as the curve of observed species reached an asymptote after sampling less than 120 m² of cumulative area (Wright et al. 2002). Simulations of landscapes of different areas and habitats with different rates of species accumulation with area would help test the general validity of this assumption.

Together, these two approaches offer a powerful technique for linking the population dynamics or behavior of a single species to changes in species richness at the landscape-scale via the process of ecosystem engineering. It should be stressed that in many situations ecosystem engineering could be a trivial process in structuring the distribution and abundance of species at the scale of landscapes (Wright and Jones 2006). However, this general approach provides a means for both testing the importance of ecosystem engineering and developing scenarios to predict how changes in the dynamics of a single species are likely to affect species richness.

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APPENDIX A

Patch-transition model in a landscape modified by ecosystem engineers (*Ecological Archives* E090-239-A1).

APPENDIX B

Equations for calculating Chao2 species-richness estimators (*Ecological Archives* E090-239-A2).