Patch dynamics in a landscape modified by ecosystem engineers

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Ecosystem engineers, organisms that modify the environment, have the potential to dramatically alter ecosystem structure and function at large spatial scales. The degree to which ecosystem engineering produces large-scale effects is, in part, dependent on the dynamics of the patches that engineers create. Here we develop a set of models that links the population dynamics of ecosystem engineers to the dynamics of the patches that they create. We show that the relative abundance of different patch types in an engineered landscape is dependent upon the production of successful colonists from engineered patches and the rate at which critical resources are depleted by engineers and then renewed. We also consider the effects of immigration from either outside the system or from engineers that are present in non-engineered patches, and the effects of engineers that can recolonize patches before they are fully recovered on the steady state distribution of different patch types. We use data collected on the population dynamics of a model engineer, the beaver, to estimate the per-patch production rate of new colonists, the decay rate of engineered patches, and the recovery rate of abandoned patches. We use these estimated parameters as a baseline to determine the effects of varying parameters on the distribution of different patch types. We suggest a number of hypotheses that derive from model predictions and that could serve as tests of the model.

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Jones et al. (1994) define organisms that modify, maintain, or create habitats as ecosystem engineers. Although the mechanisms by which ecosystem engineers alter habitats are diverse (Jones et al. 1994, 1997, Crooks 2002), by recognizing common features in the effects of ecosystem engineers on the environment, the concept has produced a number of general predictions. One such prediction is that at a scale that encompasses both patches affected by an ecosystem engineer and patches of unmodified habitat, ecosystem engineering will result in an increase in species richness (Jones et al. 1997).

Several empirical studies have suggested that the presence of engineered habitat increases landscape-level species richness (Collins and Uno 1983, Guo 1996,

Wright et al. 2002). However, the magnitude of the engineering effect on richness at the landscape scale will depend on the proportion of engineered and unmodified habitat in the landscape. If the total area of engineered habitat in the landscape is too low to support the full complement of species capable of persisting in engineered habitat due to species-area relationships, species richness is likely to be low relative to landscapes with a mix of engineered and unmodified habitat. Likewise, if the landscape is dominated by engineered habitat, species richness in unmodified habitats will decline leading to lower species richness at the landscape scale. Thus understanding the controls on the relative abundance of different patch types in an engineered landscape

is critical for predicting the effect of engineers on species richness at the landscape scale.

Gurney and Lawton (1996) developed a model of the population dynamics of ecosystem engineers that linked the production and decay of engineered habitats to the population dynamics of engineers. Specifically, the model focused on allogenic engineers that must modify their habitat to survive, (e.g. beaver damming streams and pocket gophers digging burrows) as opposed to those where the engineering activity has no effect on the engineers performance (e.g. hippopotamus forming trails and buffalo creating wallows). Allogenic engineers are those engineers that modify the environment by transforming living or non-living materials from one physical state to another primarily by mechanical means (Jones et al. 1994), and as a result create patches that can persist even if the organism that created them is no longer present. Gurney and Lawton (1996) focused primarily on the conditions for stability of populations of engineers. However, their model also predicted steady state values for the proportion of engineered and unmodified habitats.

Here, we modify Gurney and Lawton's original (1996) model and analyze how the model's parameters affect the steady state abundance of different habitat types. We also use data collected on the population dynamics of a particularly well-studied ecosystem engineer, the beaver, to estimate values for several of the model's parameters. Using these estimated parameter values, we explore the effects of varying parameters on the relative abundance of different habitat types.

Models

Simple patch dynamic model

In the simplest version of the model, patches within a landscape can be found in one of three potential states: potential, active, and degraded. Patches in the potential state are transformed into active patches via the process of colonization of the patch by dispersing ecosystem engineers arriving from active patches. Patches are transformed from the active state to the degraded state when the patch is abandoned, and patches change from degraded to potential through a process of recovery (Fig. 1A, Table 1). If we denote the proportion of patches in the potential, active, and degraded states at time t by P, A, and D respectively, then we know that

$$1 = P + A + D \qquad (1)$$

We assume that a unit of active habitat has a constant probability per unit time of decaying into the degraded state (δ) and that a unit of degraded habitat has a constant probability per unit time of recovering to the potential state (ρ). We further assume that each active patch generates a constant number of individuals per
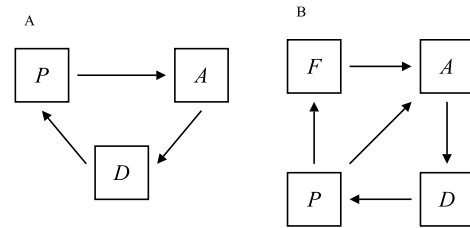

Fig. 1. A) Structure of the simple (3-patch) model and B) complex (4-patch) model of the dynamics of patches in an engineered system. Patches that are actively occupied by engineers are designated A, and decay into degraded patches (D) following abandonment. Degraded patches recover into potentially habitable patches (P) which are then recolonized to form active patches. In the 4-patch model, if potential patches are not recolonized, they progress to the fully recovered (F) state.

Table 1. Description of the parameters in simple (3-patch) and complex (4-patch) models of the dynamics of patches in an engineered system.

Parameter	Description
n	Per-patch production rate of new colonists
δ	Decay rate of patches from active (A) to degraded (D) state
ρ	Recovery rate of patches from degraded (D) to potential (P) state
i	Immigration rate
r	Recovery rate of patches from potential (P) state to fully recovered (F) state
ζ	Discrimination of colonists against potential (P) relative to fully recovered (F) patches

unit time that succeed in converting a potential patch into an active patch (n). Recalling that Eq. 1 allows us to calculate P_t given A_t and D_t, we can describe the dynamics of this system by two differential equations:

$$\frac{dA}{dt} = nA(1 - A - D) - \delta A \qquad (2a)$$

$$\frac{dD}{dt} = \delta A - \rho D \qquad (2b)$$

This system has two biologically relevant steady states. One, which we call the zero-engineer state has A* (the proportion of the landscape in the active state at equilibrium) = D* = 0 and P* = 1. The other, which we call the finite engineer state, has

$$A^* = \frac{1 - \delta/n}{1 + \delta/\rho} \qquad D^* = \frac{\delta A}{\rho} \qquad (3)$$

For this steady state to be biologically meaningful, it must have A* > 0 and D* > 0, which in turn requires n > δ > 0. This implies that for the engineer to persist, the number of new patches created per unit time must exceed the patch degradation rate.

Simple patch dynamic model with immigration

In the initial formulation of the model, the rate of transformation of all P patches to A patches is dependent on the abundance of A patches in the landscape. This is the case when dispersing engineers can only arise from engineered patches within the system. However, it is conceivable that there are patches in the landscape that can support engineers without habitat modification and thus persist indefinitely. For example, beaver live primarily in ponds that they create by damming streams (converting a patch from P to A). These active colonies produce new colonists that disperse and create new active patches. However, beaver can also live in natural lakes and ponds, producing a source of colonists that is independent of the number of beaver-created ponds in the landscape. To address a situation where there is a source of colonists independent of the stock of engineered patches, we modify the original model to include an additional constant inflow of immigrants at rate i, thus yielding:

$$\frac{dA}{dt} = (nA + i)(1 - A - D) - \delta A \qquad (4a)$$

$$\frac{dD}{dt} = \delta A - \rho D \qquad (4b)$$

This system has only one biologically meaningful steady state, at which A* is a solution of

$$(n[1 + \delta/\rho])A^{*2} + (i[1 + \delta/\rho] + \delta - n)A^* - 1 = 0 \qquad (5)$$

If all parameters (including i) are assumed to take positive values, this equation must have exactly one finite positive solution. Thus, when immigration is added to the model, the system always has a single finite-engineer steady state but no longer has a zero-engineer steady state.

Partial patch recovery

We now recognize an additional patch state to reflect an additional stage of recovery from the effects of ecosystem engineering (Fig. 1B). This can occur when ecosystem engineers create patches where recovery rates of the necessary resource are not equal throughout the patch. For example, beaver can recolonize a meadow site that has undergone sufficient forest regeneration around the edge of the former pond prior to any woody regeneration within the former pond site itself. In this system, patches in the P state represent a recolonisable but not fully recovered state, and patches can additionally exist in the fully recovered state. Hence, if we denote the proportion of fully recovered patches in the landscape by F, then

$$1 = F + A + D + P \qquad (6)$$

We again assume that a unit of active habitat has a constant probability per unit time of decaying into the degraded state (δ), that a unit of degraded habitat has a constant probability per unit time of recovering to the potential state (ρ), and that each active patch generates a constant number of individuals per unit time that succeed in converting a potential patch into an active patch (n). The rate at which A is generated is no longer strictly dependent on P, but on the sum of $(F + \zeta P)$ where ζ represent the degree of discrimination against previously modified patches. At this point we assume that production of colonists from active patches is independent of patch history. We also assume that patches in the P state recover at a constant rate per unit time to the F state (r). Remembering Eq. 6 allows us to calculate any given state variable if we know the other three, so we can represent the dynamics of our extended system by:

$$\frac{dA}{dt} = nA(F + \zeta) - \delta A \qquad (7a)$$

$$\frac{dD}{dt} = \delta A - \rho D \qquad (7b)$$

$$\frac{dP}{dt} = \rho D - rP - nA\zeta P \qquad (7c)$$

The system has two steady states – the zero engineer state where A* = D* = P* = 0 and F* = 1, and a finite-engineer steady state, at which A* is the solution of

$$(n\zeta[1 + \delta/\rho])A^{*2} + (r[1 + \delta/\rho] + \delta[1 - \zeta] - n\zeta[1 - \delta/n])A^* - r(1 - \delta/n) = 0 \qquad (8)$$

Thus, as long as the patch specific colonization rate is greater than the degradation rate ($n > \delta$) there must be at least one non-zero positive (real) solution for A*.

Beaver as a model system

Beaver are a particularly well-studied example of ecosystem engineers. Beaver have been documented to affect riparian trees (Barnes and Dibble 1986, Nummi 1989, Johnston and Naiman 1990b), biogeochemistry of streamwater (Naiman et al. 1986, Margolis et al. 2001) and soil (Johnston et al. 1995), fish populations (Hanson and Campbell 1963, Snodgrass and Meffe 1998), diversity of aquatic invertebrates (McDowell and Naiman 1986), birds (Grover and Baldassarre 1995, Nummi and Poysa 1997), and herbaceous plants (Wright et al. 2002), and succession (McMaster and McMaster 2000). All riparian effects of beaver are the result of their ecosystem engineering activities, with the possible exception of changes in the composition of riparian trees, due in part to herbivory. Specifically, these effects are caused by a beaver dam transforming a free-running stream into a pond that floods the adjacent riparian zone, or by the

draining of a pond and exposure of accumulated sediments following abandonment of a site and subsequent dam failure.

In the model, beaver ponds with a resident colony are considered as active patches (A). Typically, only the oldest pair of beaver in a colony will reproduce, producing on average 3 or 4 young annually (Jenkins and Busher 1979). Colonies typically consist of an adult pair, yearlings, and kits, with an average size of 5.85 ± 0.61 (SE) individuals (Svendsen 1980). Young beaver disperse at about 2 or 3 years of age (Jenkins and Busher 1979, Svendsen 1980), although if food supplies are plentiful or local population densities are high, as many as 50% of two-year old beaver can remain at their natal colony (van Deelen and Pletscher 1996). Dispersal distances tend to be less than 16 km (Beer 1955, Leege 1968), but distances of up to 110 km have been reported (Hibbard 1958). Mortality during dispersal tends to be high relative to non-dispersing beaver, with mortality rates of 40% being reported for the 1.5–2.5 year class of beaver in Newfoundland (Payne 1984). Birth rates per colony, site fidelity and mortality during dispersal are important factors in determining the model parameter n, or the per patch production rate of successful colonists. Although these factors are likely to vary across the range of beaver, if one assumes the figures reported above are standard for beaver across their range, one can estimate a value for n of 0.7 successful immigrants per year.

It is also possible that the creation of active patches may be affected by the presence of colonies of beaver that occur in sites that do not require habitat modification. Beaver are known to build lodges on naturally occurring lakes and ponds as well as in the banks of larger rivers without performing any significant engineering. In landscapes where such patches are present, the number of successful colonists that are produced by these non-engineered sites (i) will influence the rate at which new active patches are formed. Although it is possible that the number of colonists coming from non-engineered patches is not constant and might depend on the number of engineered patches in a landscape, to simplify analysis of the model, we have assumed a constant rate of immigration.

Over time, active colonies deplete the food resources adjacent to the pond, ponds fill with sediment, and resident beaver die eventually leading to abandonment. The rate at which this occurs (δ) will be a function of colony size, beaver activity, the composition and abundance of riparian zone trees or other food resources, and sediment loads of dammed streams. Knudson (1962) reported that beaver ponds may remain active for as long as 8–10 years, while in Algonquin Provincial Park, Canada, sites were occupied for an average of 5.8 ± 0.46 (SE) years over a ten year period (Fryxell 2001). Once ponds are abandoned, they develop into wetlands with variable hydrologic regimes and vegetation compo-

sition (Remillard et al. 1987, Johnston and Naiman 1990c, McMaster and McMaster 2000, Wright et al. 2002). The sites remain in this state (equivalent to degraded, D, patches) until the vegetation in the area adjacent to the former pond site has recovered to a degree sufficient to support a new beaver colony. The rate at which this transformation from D patches to P patches occurs (ρ) depends on the successional dynamics of the forests surrounding pond sites.

In most areas, once beaver have colonized a site, the site enters into a pattern of cyclic abandonment and recolonization. It is relatively rare for a site that has been colonized by beaver to revert back to a forested riparian zone (equivalent to the F state in the more complex patch dynamic model, Ives 1942, Remillard et al. 1987, Johnston and Naiman 1990a, Pastor et al. 1993, Terwilliger and Pastor 1999), thus the parameter r is likely to be extremely low in most ecosystems affected by beaver. The degree to which beaver prefer or avoid sites that have been previously colonized relative to forested riparian zone (ζ) will again depend on the successional dynamics of the riparian zone vegetation. In many areas, recently abandoned sites are dominated by species of *Salix*, *Populus* and *Alnus*, preferred food species of beaver (Jenkins and Busher 1979). The situation where herbivores, such as beaver, create environments favorable for the growth of early-successional species, which are often preferred by beaver, has been termed the retarded succession hypothesis (Pastor and Naiman 1992). However, it is also possible for beaver foraging to facilitate the dominance of conifers and other late-successional species that are typically avoided as food sources, (the accelerated succession hypothesis, Fryxell 2001). Furthermore, it has been shown that browsing by beaver can increase rates of phenolic glycoside production in *Populus fremontii* (Martinsen et al. 1998). If such chemical defenses against mammalian herbivory persist or browsing by beaver leads to dominance of non-preferred species, sites that have been previously occupied by beaver might be avoided.

Beaver activity on the Huntington Wildlife Forest (HWF) has been surveyed annually since 1979. The HWF is a 6000-hectare preserve located in the central Adirondack Mountains, NY (latitude 44°00′N, longitude 74°13′W). The topography is mountainous with elevations ranging from 457 m to 823 m. Vegetation consists of mixed northern hardwood and coniferous forest. As part of the Adirondack Long Term Monitoring Project (ALTEMP), all active beaver sites on HWF have been identified and mapped every fall since 1979. Although the number of colonies has fluctuated over time (Fig. 2), the number of beaver colonies has remained relatively constant, particularly since 1990. Although there is some variability in the numbers of individuals per colony, colony counts can provide a useful estimate of population sizes for beaver (Bergerud
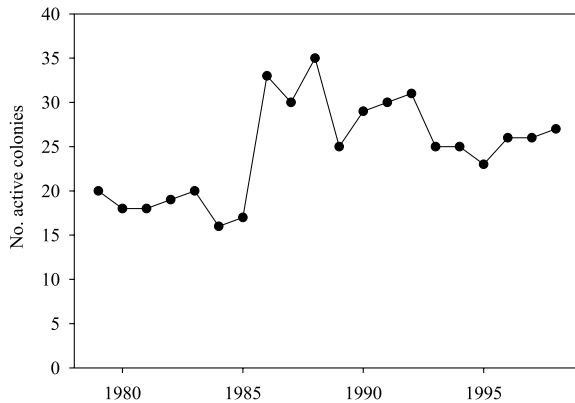
Fig. 2. Number of active beaver colonies on the Huntington Wildlife Forest (HWF) recorded during annual censuses from the period 1979–1998.

and Miller 1977). Assuming that beaver populations are close to steady state in the central Adirondacks, data from these surveys can be used to estimate several of the parameters of the model.

We estimated δ, the rate of decay from A (active) to D (degraded) patches, by calculating the mean period of time that ponds remained active, considering only ponds that were colonized after 1979 and abandoned prior to 1999. If one assumes that δ is distributed exponentially, then the rate of decay is the inverse of the mean age of the patch. For the period from 1979–1999, the mean time of occupation for beaver ponds on HWF was 4.8 years ± 0.34 (SE) yielding an estimate of $\delta = 0.21$.

The production rate of successful colonists per patch (n) is slightly more difficult to estimate. Since beaver colonies occur on natural lakes in HWF, dispersal of individuals from patches not created by beaver almost certainly occurs. However, dividing the number of newly active sites in a year by the number of active colonies in the previous year produces an upper bound for the estimate of n (essentially ignoring the effects of non-engineering colonies). For the period from 1980–1999, this technique yields an average estimate of $n = 0.39 \pm 0.03$, lower than the value of 0.7 predicted from the literature.

The data from the annual beaver census are insufficient for estimating the other parameters of the simple patch dynamic model. Estimating the rate of recovery from degraded (D) to potential (P) patches, ρ, requires measuring recovery in the forests adjacent to pond sites as well as determining the minimum requirements for colonization by beaver. However, the mean time period that ponds were abandoned was 4.79 ± 0.35 years, suggesting a minimum value of $\rho = 0.21$. Estimating immigration from non-engineering patches (i) would require tracking dispersing individuals from such patches and determining successful colonization rates. Estimating the additional parameters of the more complex patch model is also somewhat challenging.

The rate of recovery from previously used sites to forested riparian zone is difficult to estimate, but can be safely assumed to be extremely low given the rarity with which such transitions have been observed (Remillard et al. 1987, Pastor et al. 1993). We can estimate beaver relative preference for virgin or fully recovered versus previously modified patches (ζ) using data from the annual beaver surveys. The ratio of the proportion of previously used available patches that are colonized to the proportion of virgin habitat colonized in a given year is an index of habitat preference. Values greater than 1 indicate a preference for previously used habitat while values less than 1 indicate preference for virgin habitat. If one assumes that all possible patches on HWF have been colonized by the latest year of the beaver survey (1999), one can calculate a lower limit for ζ. Ignoring years in which no beaver colonized previously virgin habitat, the mean value of ζ between 1981 and 1998 is 1.21, indicating a slight preference by beaver for previously engineered habitat. There is a significant trend for this estimate of ζ to decrease over time ($F_{1,12} = 21.32$, $r^2 = 0.66$, $p = 0.0007$, Fig. 3), with preference for previously modified habitats switching to preference for virgin habitat around 1986.

We solved the system of differential equations to determine the steady state values of the proportions of the different habitat types while varying one parameter and holding all other parameters in the model constant. In solutions in which they were held constant we used the values of δ (0.21), n (0.39), and ζ (1.21) estimated from annual beaver surveys. We held ρ constant at 0.25 (yielding a mean recovery time from degraded into potential patches of 4 years), r at 0.01 (yielding a mean recovery time from potential into fully recovered patches of 100 years), and i at 0.1.
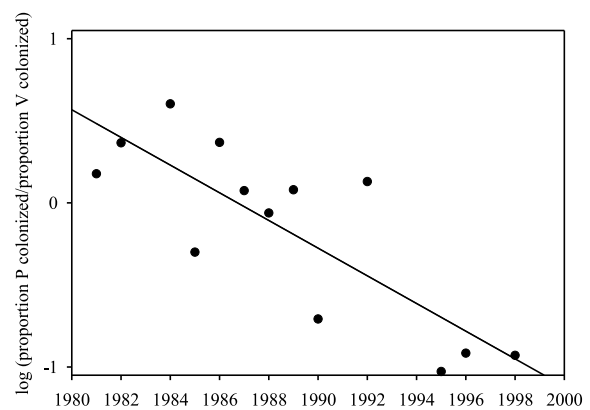

Fig. 3. Log of preference index for fully recovered (F) versus previously modified sites (P) for use as sites for colonization derived from HWF beaver censuses between 1980 and 1998. Untransformed values greater than one indicate a preference for previously occupied habitat. The equation for the best fit regression is log (y) = 167.44 − 0.08x.

Results

Simple model

As δ, the decay rate of patches from the active to degraded state, increases, the proportion of the landscape in the P* (potential) state increases in a near linear fashion until δ = n, the per-patch production rate of new colonists, at which point P* reaches a maximum at 1 (Fig. 4A). At low values of δ, most of the landscape is in the A (active) state, but the proportion of A* decreases steadily as δ increases, reaching 0 when δ = n. The proportion of D* (degraded) patches in the landscape shows a unimodal relationship as δ increases, representing a trade-off between low production of degraded patches at low δ, and a low supply of active patches at high δ.

Varying ρ, the recovery rate of degraded patches into potential patches, while keeping the values of the other parameters constant has no effect on the steady state value of P* (Fig. 4B), as potential patches are rapidly transformed to active patches. As ρ increases, D* decreases and A* increases, with dominance between the two patch types switching when ρ = δ, representing the point at which old patches decay more rapidly than new patches are created.

At levels of n < δ, the landscape is at the zero-engineer steady state with P* = 1, and A* = D* = 0 (Fig. 4C). As n increases above this point, P* decreases steadily while A* and D* increase. If δ < ρ, A* will increase more rapidly than D* and reach a higher value as n increases while if δ > ρ, D* will increase more rapidly.

Simple model with immigration

Adding immigration changes the dynamics of the system quite considerably. Fig. 5A illustrates that increasing δ again causes A* to decrease steadily although, with immigration, a value of 0 is no longer possible. The most striking difference is that even with small amounts of immigration, P* increases much more slowly with δ and at a rate that is far from linear (compared to Fig. 4A). Also, D* only decreases slightly at high values of δ rather than peaking at low values of δ and then decreasing.

With immigration, P* is no longer independent of ρ, but decreases to values near 0 at low values of ρ (Fig. 5B). However, adding immigration does not affect the basic relationship between ρ and A* or D*. At low values of n, immigration prevents the system from becoming fixed at P* = 1 and A* = D* = 0 (Fig. 5C). Apart from that, the relationship between the steady state values of the state variables and different values of n are similar with and without immigration (Fig. 4C, 5C), although the responses are dampened with immigration.
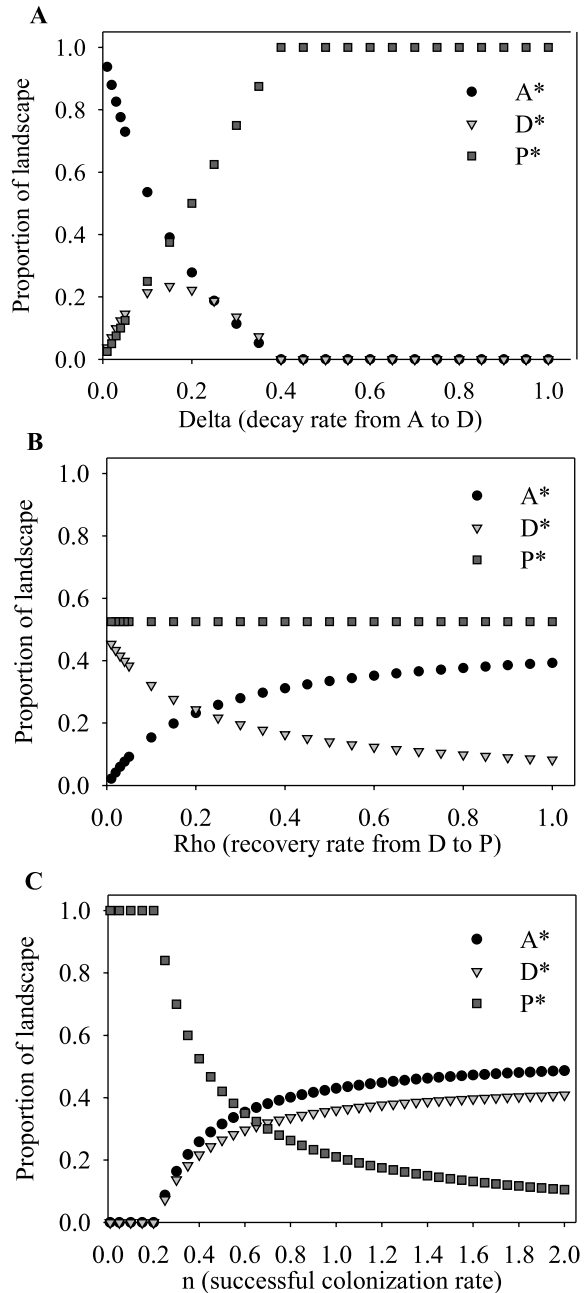

Fig. 4. Dynamics of steady state values for state variables of the simple (3-patch) model without immigration in response to changes in the model parameters. In simulations where they were held constant, δ = 0.21 (A), ρ = 0.25 (B), and n = 0.39 (C).

Although adding immigration to the model alters the relationships between the other parameters and the state variables, varying the immigration rate itself has a relatively small effect on A* and D* (Fig. 5D). At very low levels of i, P* increases while A* and D* decrease.

Figure 6A shows that at low values of δ, adding immigration has little effect on the steady state values of
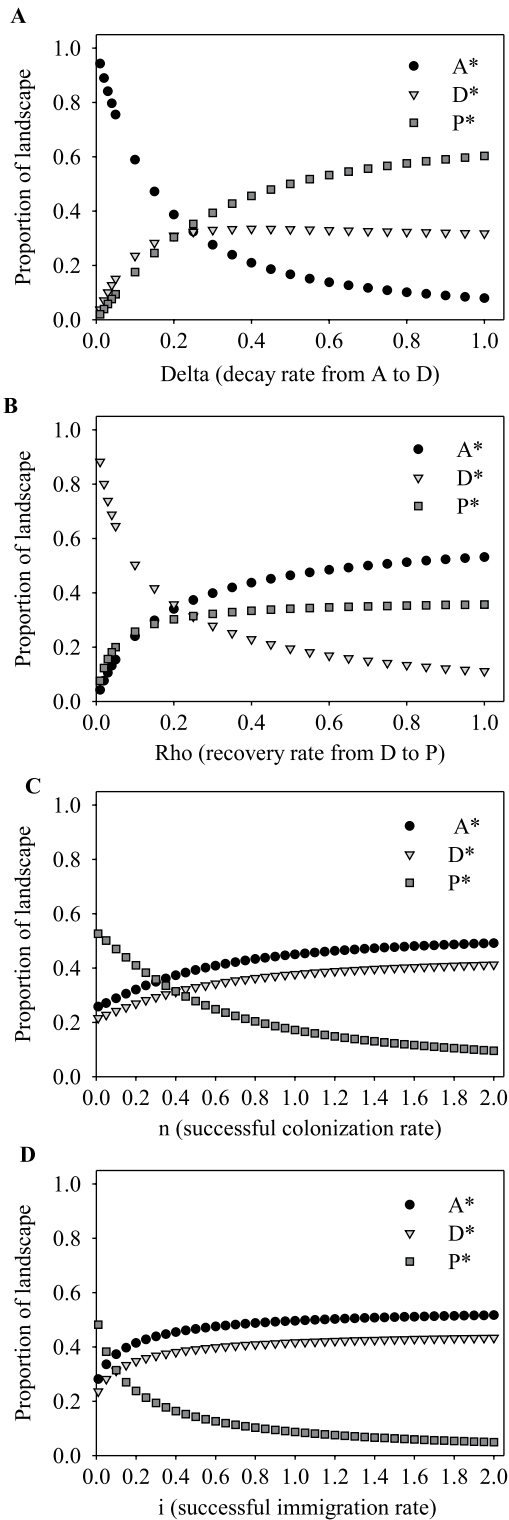
Fig. 5. Dynamics of steady state values for state variables of the simple (3-patch) model with immigration in response to changes in the model parameters. In simulations where they were held constant, $\delta = 0.21$ (A), $\rho = 0.25$ (B), $n = 0.39$ (C), and $i = 0.1$ (D).
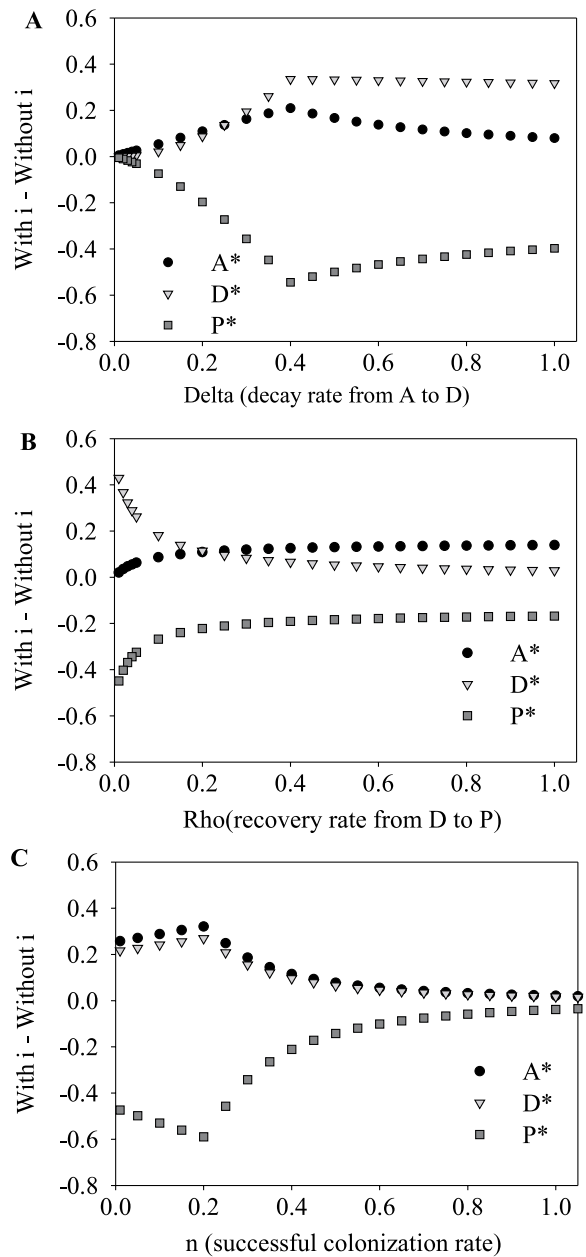

Fig. 6. Difference between the steady state values for state variables with ($i = 0.1$) and without immigration. In simulations where they were held constant, $\delta = 0.21$ (A), $\rho = 0.25$ (B), and $n = 0.39$ (C).

any of the state variables. At high values of δ, the major effect of adding immigration is to increase the proportion of D* while decreasing the proportion of P*. Immigration causes the relative abundance of A* and D* to increase and P* to decrease until $\delta = n$. At values of $\delta > n$, the differences between the values of the state variables with and without immigration begin to decrease. Adding immigration only causes small changes in the effect of ρ, on the steady state values of the state

variables, and this effect is largest at low values of ρ (Fig. 6B). Adding immigration also affects the relationship between n and the steady state values of the state variables at low values of the parameter, but the magnitude of the effect is much larger (Fig. 6C). The differences between the steady state values of the state variables in the model with and without immigration begin to decrease at n > δ. For all values of all three parameters, the effect of adding immigration (at i = 0.1) is to reduce the proportion of P* while increasing the proportion of A* and D*.

Partial recovery model

Adding a fourth patch type to the model causes several important changes to the behavior of the model. Increasing δ causes A* to decrease steadily and F* to increase steadily while D* and P* reach a maximum at intermediate values of δ (Fig. 7A). Not surprisingly, increasing ρ causes D* to decrease (Fig. 7B). Interestingly, varying ρ only results in a slight increase in P* except at low values of ρ presumably because patches in the P state are quickly transformed into A accounting for the increase in A* as ρ increases. Increasing ρ has a negative effect on F*, particularly at low values of ρ. At values of n > δ, F* and P* steadily decrease as n increases while A* and D* increase (Fig. 7C). Increasing r has a negligible effect on A* and D*, and serves primarily to increase F* while decreasing P* (Fig. 7D).

Varying ζ, the degree of discrimination against partially recovered patches relative to fully recovered patches, causes the most interesting changes in the steady state values of the state variables. Increasing ζ, or causing the engineer to prefer sites in the partially recovered state to fully recovered patches, causes both A* and D* to increase (Fig. 7E), presumably since it essentially increases the number of patches that are available to colonization. Interestingly, increasing ζ causes F* to decrease. This is because, as the willingness of engineers to colonize partially recovered patches increases, partially recovered patches tend to be colonized and converted to active patches before they can fully recover. P* shows a unimodal relationship with ζ, with a maximum at intermediate values of ζ. This relationship represents a balance between the direct increase in the rate at which P is converted into A and the indirect effect of increasing A on the production of P (via an increase in D) as ζ increases. At both higher values of δ and lower values of n, the peak in P*, occurs at lower values of ζ.

Although this model is significantly less analytically tractable than the simpler models, under certain conditions, the system behaves essentially like the simple system discussed above. Specifically, as r approaches 1, particularly at values of ζ close to (or greater than) 1, the
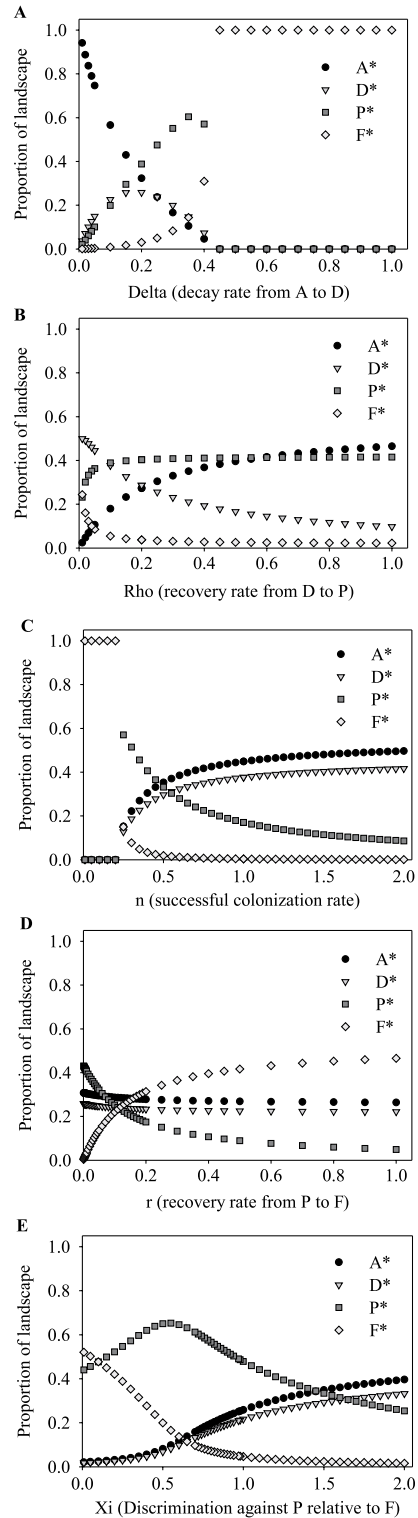

Fig. 7. Dynamics of steady state values for state variables of the complex (4-patch) model in response to changes in the model parameters. In simulations where they were held constant, δ = 0.21 (A), ρ = 0.25 (B), n = 0.39 (C), r = 0.01 (D), and ζ = 1.21 (E).
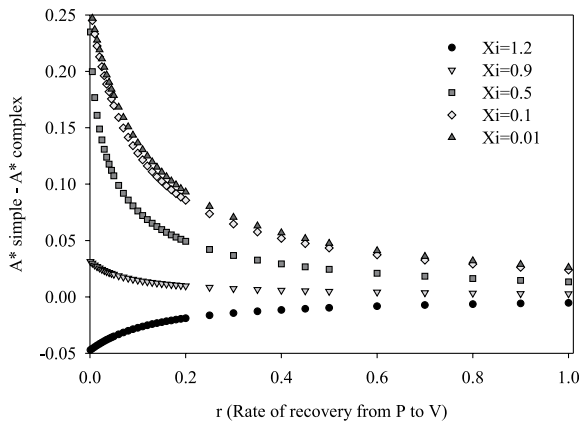
Fig. 8. Effect of varying the rate of recovery from partially recovered patches (P) to fully recovered patches (F) and level of preferences for previously used versus fully recovered habitat (ζ) on the difference between the simple (3-patch) model and complex (4-patch) model in the steady state proportion of active patches (A). Values of ζ greater than one indicate a preference for previously used habitat. In all simulations, $\delta = 0.21$, $\rho = 0.25$ and $n = 0.39$.

values of the state variable at steady state approach those of the simple model with the same parameters (Fig. 8).

Discussion

Model predictions

The three versions of the model presented here produce quantitatively different predictions about the proportion of engineered landscapes in different habitat types as the parameters are varied. However, all three models agree on several important qualitative predictions about engineered landscapes (Table 2). Landscapes will tend to have large proportions of active patches (A) when ecosystem engineers are efficient in their resource use, producing many new colonists while only gradually degrading the resources of the patch, and when resource renewal occurs rapidly after engineers abandon a site. Engineers that create landscapes dominated by abandoned (D) patches would produce large numbers of colonizers by rapidly depleting the resource levels of a patch, and leaving abandoned patches that recover very slowly. In most respects, the proportion of potential sites in the simple model (P) reacts to changes in the parameters in a manner similar to the proportion of

fully recovered sites (F) in the more complex model. Ecosystem engineers that create patches that produce few new colonizers and are abandoned quickly, yet recover rapidly should create landscapes dominated by these fully recovered patch types. In landscapes best described by the partial recovery model, partially recovered patches (P) will be most abundant when abandoned patches rapidly recover to a state sufficient to allow recolonization, but only slowly regenerate to the fully recovered state.

In many cases, sites currently used by ecosystem engineers, and those recently abandoned are easily distinguished from patches that have not been modified by engineers. For example, pocket gophers form distinct mounds of loose soil in many prairie ecosystems (Huntly and Inouye 1988), grizzly bears create extensive patches of tilled soil in alpine meadows while foraging for lily bulbs (Tardiff and Stanford 1998), tilefish and grouper excavate marine sediments (Coleman and Williams 2002), and leaves occupied by shelter-building Gelechiid caterpillars are strikingly tied together, Lill and Marquis 2003. Because these states are readily identifiable, it should be feasible to compare the relative abundance of different patch types in landscapes where the same engineer operates, but where values of the parameters are likely to be different (e.g. predation risk is higher thus lowering the number of successful colonizers, or productivity is higher, thereby speeding up recovery from abandoned sites). Such an analysis would serve as a critical test of whether these models successfully capture the relationship between the population dynamics of an ecosystem engineer and the dynamics of the patches it creates.

Differences between models

Adding a fourth patch type to represent habitat that is partially recovered, yet still capable of being engineered does not alter the fundamental patch dynamics of the model. In both the original and partial recovery versions of the model, the proportion of the landscape that will be in the active and degraded states at steady state reacts similarly to changes in the parameters δ, ρ, and n. Furthermore, the steady state proportion of potential patches (P) in the simple model behaves similarly to the steady state proportion of fully recovered patches (F) in the complex model with respect to changes in δ and n

Table 2. Summary of the parameter combinations that lead to high relative abundance of each of the patch types in the three models.

Patch type	3-Patch model without immigration	3-Patch model with immigration	4-Patch model
A	↑ ρ, n; ↓ δ	↑ ρ, n; ↓ δ	↑ ρ, n; ↓ δ
D	↑ n; ↓ ρ; intermediate δ	↑ δ, n; ↓ ρ	↑ n; ↓ ρ; intermediate δ
P	↑ δ; ↓ n	↑ δ, ρ; ↓ n, i	↑ ρ; ↓ n, r; intermediate δ, ζ
F	N.A.	N.A.	↑ δ, r; ↓ ρ, n, ζ

(and to a lesser degree, to changes in ρ). Given the added difficulty of determining analytical solutions to the more complex model and estimating an additional parameter, the benefits of the four-patch model seem limited. Only in systems where there are important differences between partially recovered and fully recovered patches, e.g. between the vegetation of beaver meadows and riparian zone forest (Terwilliger and Pastor 1999, Wright et al. 2002), would it be worthwhile to model the patch dynamics of the system using the four-patch model.

Immigration, either from outside the boundaries of the system, or from patches within the system where engineers can reproduce without having to modify habitat has the potential to alter the dynamics of the system. With even small amounts of immigration, the zero engineer steady state is no longer possible. The effects of immigration will be highest when engineers reside in a patch for a short time (i.e. high δ), produce few successful colonizers (i.e. low n), and where degraded patches recover rapidly (i.e. low ρ).

Model parameters

While the relative abundance of different patch types in a landscape can be relatively easy to determine, estimating the parameters of the model is somewhat more challenging. Although we were able to estimate some of the model parameters indirectly using data on beaver populations and patch transitions in the central Adirondacks, we are unaware of any data set that would allow independent estimation of all of the model's parameters. Future studies of the effects of ecosystem engineers on patch dynamics would benefit by structuring their questions in a manner that would allow investigators to estimate the parameters of these models.

Of all the parameters, δ, or the rate at which active sites are abandoned, is likely to be the easiest to estimate. Careful long-term monitoring of patch use by engineers will yield average lifetimes of engineered patches, which can be converted into probabilities of patch decay. In general, organisms that exhaust patch resources gradually relative to the rate of resource renewal, e.g. mound-building desert shrubs (Shachak et al. 1998), should tend to create patches with lower values of δ than organisms that are short-lived, e.g. leaf-tying caterpillars (Lill and Marquis 2003), or that use the resources in engineered patches much more rapidly than they are replenished.

Estimating the number of successful colonists produced per engineered patch (n) is a bit more challenging. It can be inferred by dividing the number of newly formed patches by the number of active patches at the previous time step. However, independent measurement of n requires determining two variables: the number of dispersers produced per engineered patch, and rate at which dispersers successfully establish new patches. The

first variable will be a function of birth rates and the probability of individuals to leave their natal patch. The second variable is a function of mortality rate during dispersal and the probability that dispersing individuals will establish new colonies. In general, ecosystem engineers with high fertility, low natal site fidelity, and low mortality during dispersal should have high values of n.

The rate at which abandoned patches recover into potential patches (ρ) is probably the most difficult to estimate independently. This is because the resources necessary for an engineer to recolonize a patch are likely to accumulate steadily over time. Determining when the necessary resources reach the critical level that separates degraded patches from potential patches requires a thorough knowledge of the requirements of the ecosystem engineer. Furthermore, the level to which critical resources are depleted in recently abandoned patches is likely to vary, thus the time needed for a degraded patch to recover will vary, even if recovery rates are constant across the landscape. In general, engineers with low resource requirements and systems with high resource supply rates should have high values of ρ.

In systems where dispersing engineers are produced in patches that have not been modified by the ecosystem engineer, one must differentiate between the proportion of successful colonists that are produced in non-engineered patches (i) and the proportion of colonists that are produced in engineered patches (n). If birth rates are the same in the two patch types and individuals from engineered and non-engineered patches have identical probabilities of successfully producing new patches, the relative importance of n and i in controlling the proportion of active patches will depend on the relative abundance of active engineered and active non-engineered patches in the landscape. If however, birth rates or successful dispersal rates differ between engineered and non-engineered patches, estimating i will require accurate measurements of birth rates in and successful dispersal from non-engineered sites that contain engineers.

Estimating the rate at which partially recovered patches recover fully (r) (i.e. from P to F) has similar challenges to estimating recovery rates from degraded patches to potential patches (i.e. ρ). Tracking patches over time allows estimates of the amount of time required from abandonment to full recovery (assuming one can set the criteria that determine full recovery). However, such an analysis cannot determine how much of the recovery time is spent in the degraded state versus the potential state. Independent estimation of r would again require detailed understanding of the criteria used by engineers when selecting sites, and may require measurements difficult to obtain using typical methods of surveying habitat such as the nutritional quality of different plants species (Martinsen et al. 1998). Despite these difficulties in estimating r, we hypothesize that

systems where engineers perform qualitative transformation of the physical state of the patches they modify, e.g. beaver transforming terrestrial patches into aquatic patches, are likely to have much lower values for r than systems where the engineers only perform quantitative transformations of habitats, e.g. shrub mounds increasing water infiltration rates in desert soils (Shachak et al. 1998).

In systems where engineers can recolonize patches before they have fully recovered, one must also determine the degree to which engineers prefer or avoid partially recovered patches relative to fully recovered patches (ζ). As illustrated above with data from annual beaver surveys, if one can determine the total number of patches available in a landscape, this metric is not difficult to estimate. It requires calculating the degree to which new patches are formed in each of the two habitat types (partially and fully recovered) relative to their availability. In general, most systems are likely to have values of ζ less than one, indicating that engineers prefer fully recovered to partially recovered patches. However, as suggested by the data from the annual beaver surveys, it is possible for positive feedbacks to occur whereby conditions in abandoned sites are favorable for the establishment of species that are preferred to those found in fully recovered sites.

Implications for beaver

Over the past 20 years, beaver populations on HWF have remained relatively constant. The large jump in observed colonies between 1985 and 1986 is due, at least in part, to an increase in the area covered during annual beaver surveys (C. Demers, pers. com.). Since 1989, the number of active colonies on HWF has fluctuated relatively little among years. These data are consistent with the assumption that the beaver populations and the patch dynamics of beaver-modified habitats are at steady state.

Since we were unable to independently estimate all of the model's parameters, we could not directly test the model's predictions as to the relative abundance of different patch types in the landscape. Nevertheless, analyzing the model's behavior using parameters estimated from the annual beaver surveys reveals some interesting features of the system. Our estimate of the number of successful colonists produced per engineered patch (n) is doubtless an overestimate. The calculation of n ignored the role of colonists that originated from non-engineered patches (e.g. natural lakes). Even with the overestimate, our estimate of n (0.39) is close to our estimated value of the decay rate of active patches ($\delta = 0.21$). In both versions of the model without an immigration term, engineers cannot persist in a system where the decay rate, δ, is greater than the patch creation rate, n. Thus, immigration, either from outside the

system or from non-engineered patches, is likely to be important in maintaining beaver populations in the central Adirondacks. The habitat within the HWF is essentially identical to the surrounding area, so there is no reason to expect that HWF is receiving significantly more dispersing beaver than it is losing through emigration. This points to the central importance of colonies of lake-dwelling beaver in maintaining the patch dynamics of beaver-modified habitats.

If the estimates of the model parameters are correct, it would suggest that the relative abundance of different habitat types should be most sensitive to changes in the decay rate of active patches (δ), and the successful colonization rate (n). While decay rates depend primarily on the rate at which beaver use up resources in a site and are unlikely to vary significantly over time, successful colonization rates could vary significantly depending on predation rates during dispersal. Wolf reintroduction to the Adirondacks or increasing populations of coyotes could potentially increase predation during dispersal, thereby lowering n. Based on our parameter estimates, such changes in n would lead to large decreases in the proportion of active ponds and young meadows with concomitant increases in old meadows with well-developed surrounding forests. Older meadows tend to be much drier than new meadows and as a result, contain a quite different community of wetland plants (Wright et al. 2003). Thus, changes in n due to increased mortality during dispersal could have strong effects on diversity at the landscape-scale.

The decline in beaver preference for previously used sites (ζ) over time is somewhat counterintuitive. If there is variability in site quality, and beaver first select optimal sites (Howard and Larson 1985), one might assume that beaver would prefer to re-use high quality sites rather than colonize poorer quality sites, leading to higher values of ζ. The relationship is in part due to the assumption that all possible sites had been colonized by the time of the last survey. However, if we assume that only half of the available sites had been colonized in 1999, the decline over time, while weaker, still remains significant ($F_{1,11} = 25.14$, $r^2 = 0.68$, $p = 0.0004$). It may be that patches that are repeatedly used begin to decline in quality over time, particularly if repeated browsing by beaver leads to dominance by non-preferred species such as conifers or other late-successional species. There is some evidence of such an accelerated succession dynamic caused by beaver in Algonquin Provincial Park (Fryxell 2001), thus it is certainly possible that this is occurring in the Adirondacks as well. If so, this would cause beaver to increasingly avoid previously used patches over time, leading to the observed lower values of ζ. The model predicts that decreases in ζ should lead to decreased proportions of active ponds and new meadows and increased proportions of old meadows, mirroring the effects of lower n.

Conclusions

The set of models developed here helps link the population dynamics of ecosystem engineers to the dynamics of the patches that they create. By predicting the relative abundance of engineered and unengineered patches in a landscape, it has the potential to serve as an important tool in determining the effects of ecosystem engineers on ecosystem structure and function at the landscape scale. Application of the model to a population of beaver in the central Adirondack Mountains suggests that because successful colonization rates are low and site abandonment rates are high, the population persistence may depend on dispersers from beaver colonies in unmodified patches such as natural lakes. Although we are not aware of any data set that would allow for complete parameterization of the model, analysis of the model suggests a number of possible tests of its structure and assumptions. The model makes numerous testable predictions about how the distribution of patch types in a landscape should change in response to changes in the population dynamics of engineers or the recovery rate of patches after they have been abandoned. Furthermore, by combining this model with an understanding of how ecosystem engineering affects diversity at the landscape scale, we now have the tools to relate the population dynamics of an organism to patterns of landscape-level diversity.

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