Society for Conservation Biology

Fencerows, Edges, and Implications of Changing Connectivity Illustrated by Two Contiguous Ohio Landscapes

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Abstract: *We evaluated the amounts and implications of changes in habitat connectivity on rural landscapes by modeling the colonization success and subsequent habitat colonization of a model edge organism within real landscapes. We first inventoried the changes in the fencerow and forest-edge network of two contiguous Ohio (U.S.A.) landscapes, an agriculturally dominated till plain and a more diverse and dynamic moraine landscape, from 1940 to 1988. On the moraine the number of fencerows changed little from 1940 to 1971. The number increased by 86 during 1971–1988 as marginal farms were subdivided. The total length of fencerows on the moraine increased 2.5-fold over 48 years. On the till plain the number and total length of fencerows remained relatively constant through the study period. The sum of fencerows and forest edges was used as a measure of total ecotonal edge. On the moraine total edge increased through the study period, whereas on the till plain it decreased. We selected two levels of landscape connectivity, low and high, to model animal habitat colonization success. As connectivity increased the earliest successful colonists preempted an increasingly large proportion of the total suitable habitat, and the probability of successful colonization by later-arriving individuals decreased. The changes in connectivity that resulted from changes in both the fencerow network and the proportion of forested land have resulted in contiguous landscapes that present very different colonization potentials to organisms with long-distance dispersal capability. Given the current uncertainty of the effects of corridors on species-preservation efforts, we suggest that further modeling of this type prior to field testing will add useful insights, especially if conducted using specific species and landscape types.*

Las cercas, los bordes y las connotaciones de los cambios en la conectividad ilustrados por dos paisajes contiguos de Ohio

Resumen: *Evaluamos la cantidad y las connotaciones de los cambios en la conectividad del hábitat, en paisajes rurales modelando el éxito en la colonización y la subsecuente colonización del hábitat en un organismo de los bordes modelo dentro de paisajes reales. En primer lugar, inventariamos los cambios en las cercas y el sistema de bordes del bosque de dos paisajes contiguos de Ohio, una planicie de tillita dominada por agricultura y un paisaje morenico más diverso y dinámico, durante 1940-1988. En la morena el número de cercas cambió poco entre 1940-1971. El número se incrementó en 86 durante 1971-1988, a medida que las granjas marginales fueron subdivididas. La extensión total de las cercas en la morena se multiplicó 2.5 veces durante un período de 48 años. En la planicie de tillita el número y la extensión total de las cercas permaneció relativamente constante a través del período de estudio. La suma de las cercas y el borde del bosque fue utilizado como medida del borde total del ecotono. En la morena el borde total se incrementó durante el período de estudio, mientras que en la planicie de tillita decreció. Seleccionamos dos niveles de conectividad del paisaje, bajo y alto, para modelar el suceso de la colonizacion del hábitat animal. En la medida en que la*

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conectividad se incrementó, los colonizadores tempranos más exitosos se apropiaron de una gran proporción del hábitat total disponible y la probabilidad del éxito en la colonización de los individuos que fueron llegando más tarde decreció. Los cambios en conectividad que resultaron de los cambios en el conjunto de las cercas y la proporción de la tierra forestada, ha resultado en paisajes contiguous que presentan potenciales de colonización muy diferentes para los organismos con una capacidad de dispersión a gran distancia. Dada la incertidumbre actual sobre los efectos de los corredores sobre los esfuerzos de preservación de las especies, sugerimos que la intesificación en este tipo de modelado antes de ser probando en el campo puede adicionar información útil, especialmente si se conduce utilizando especies y tipos de paisajes específicos.

Introduction

In recent years the emerging principles of landscape ecology have been increasingly applied to conservation planning and initiatives. Of these principles, the concept of landscape connectivity has shown perhaps the greatest utility in conservation biology. Connectivity, as defined by Merriam (1984), is the product of those landscape properties that facilitate the movement of organisms among pathches in a landscape, as well as the colonization patterns and population dynamics of species within the connecting corridors. Under this definition, changes in the amount of forest or field edge (through changes in forest-patch size, number, and/or shape) and changes in the length, number, and dispersion of fencerows can all lead to changes in connectivity within a landscape. With increased human intervention on landscape structure, including that related to habitat fragmentation and changes in habitat edge, it is necessary that the impact of such changes both on landscape connectivity and on those organisms dependent on connecting corridors and edges be examined in a quantitative manner.

Fencerows and edges bounded by forest on one side and agricultural field on the other are important landscape features for both plants and animals. Edges and fencerows are common roosting sites for birds and often have high nest density (Robbins 1979). Many bird and mammal species depend on fencerows for foraging and shelter (Constant et al. 1976a, 1976b). Such habitat provides sites for forest-edge plants (Pollard et al. 1974) that have difficulty persisting either under the intact forest canopy or in the face of competition from farming practices or from perennials in pastures and old fields. Finally, edges and fencerows may be important corridors for dispersal of both plants and animals (Bennett 1990; Merriam & Lanoue 1990).

As farming practices have changed, with road-to-road cultivation and with growing dependence on fewer crops and varieties, the frequency of hedgerows has decreased in many areas (Leonard & Cobham 1977; Burel & Baudry 1990a). In areas where the overall intensity of agriculture has decreased, smaller forest patches now coalesce into larger tracts, with a concomitant decrease in the amount of edge per unit forest area (Nilon 1986).

Such changes in land use have the potential to greatly reduce the amount of forest edge and hedgerow in a landscape and to result in decreased habitat (beta) diversity. These changes in connectivity have important implications for the movement of individual animals and animal gene flow (Bennett 1990) and for the probability of success of chance colonizations by propagules of wind- or bird-dispersed plant species (McDonnell & Stiles 1983).

We present an analysis of 41 years of change in forest areas, forest edges, and fencerows in two contrasting Ohio landscapes: an agriculturally dominated till plain with strong landscape inertia and a more diverse moraine area with a somewhat more dynamic landscape. We than used the analytical capabilities of a geographic information system (GIS) to test a model designed to simulate the effects of such changes in landscape connectivity on the colonization success and dynamics of an organism dependent on edge for successful colonization and subsequent population growth.

Methods

The study area covered approximately 242 km^2 in central Ohio and was nearly evenly divided into a relatively flat, agriculturally dominated till plain in the southern half and an undulating, more diverse and complex glacial moraine in the northern half (Simpson et al. 1994). Land-use mosaics for these two landscapes were interpreted from aerial photographs taken in 1940, 1957, 1971, and 1988. We mapped all fencerows from aerial photographs directly onto mylar overlays and then created individual, digital fencerow and forest-edge coverages in a vector-based GIS. We defined edges as all polygon boundaries that had taller vegetation on one side (upland closed canopy forest, riparian woodland) and low vegetation on the other (agriculture, early successional fields, pastures, stream corridors). Because each edge was digitized with a specific identification code corresponding to the land-use classifications of the polygons it separated, edges could be analyzed independently or pooled with fencerows for further analysis. We selected and reexamined specific fencerows if they appeared to lie across polygon boundaries or in water bodies. Finally, we used GIS to calculate the number and

lengths of all fencerows and forest edges as measures of landscape connectivity. We defined "total edge" as the sum of all fencerows plus ecotones that separated forest and areas of shorter vegetation (fields, pastures, early successional fields). A complete description of the methods for ARC/INFO GIS database development and analysis is given by Simpson et al. (1994).

To evaluate the functional importance of changes in connectivity over time in these two landscape segments, we designed a "virtual organism" that was capable of colonizing either fencerows or forested land. We modeled how the number of successful colonizations and the potential area occupied by populations of virtual animals (for example, hypothetical small mammals) changed with the number of colonization events in each of the eight landscape-by-year combinations we generated (2 landscape × 4 time periods). For this simulation, we "dropped" these virtual animals at random points in the digital GIS landscape and allowed them to move within and among only those landscape elements that were considered suitable for movement, nesting, foraging, and other aspects of population support. Such landscape elements included woodlands (forest or riparian woodlands), woodland edges, and the vegetated fencerows. For area calculations, the vegetated fencerows were assumed to have a width of 2 m; the habitat occupied by the virtual animals included both forest area and fencerow area.

Beyond the requirements that the virtual organisms were limited in their movement and settlement to suitable habitat elements, we developed specific decision rules governing their behavior. When the virtual organisms had successfully colonized ("occupied") all the continuous or connected woodland and fencerows, members of that population could then cross a maximum of 40 m of matrix (hereafter "snap distance") and continue colonizing woodlands and/or fencerows falling within that distance. Movement and settlement could continue unchecked as long as there was suitable, connected edge/hedge habitat or where the edge/hedge habitat was within the 40-m snap distance of another suitable habitat element. Although the 40-m distance was chosen arbitrarily, increasing or decreasing it changed only the absolute results of the modeling, not the general trends. Inherent within this rule is that population spread, as a function of natality, mortality, and dispersal, is allowed to continue until suitable, connected habitat is used up. Our guiding hypothesis was that increasing landscape connectivity, primarily through increases in the fencerow network, would result in predictable changes in the relationships between the number of colonization attempts, the average edge length and area of colonized home ranges and the proportion of suitable habitat occupied.

There was no minimum length or area rule within our decision rules because such a rule would have had to be

set arbitrarily. Our use of a generic, virtual animal was meant to allow the development of a general model from which extensions to more species-specific models could later be made. Such an extension to real species would require empirically based minimum-area rules.

To remain within the capabilities of the GIS software, we imposed two further restrictions on the model system. First, any individual model organism initially dropped onto a point not within 40 m of a woodland patch of fencerow was assumed to have died. This rule accounted for mortality of organisms through predation or through an inability to find suitable habitat. Second, once a given area of woodland or fencerow was colonized, it could not be occupied by a subsequent colonist. Thus, we modeled this virtual organism as one in which space preemption determined subsequent coloni-
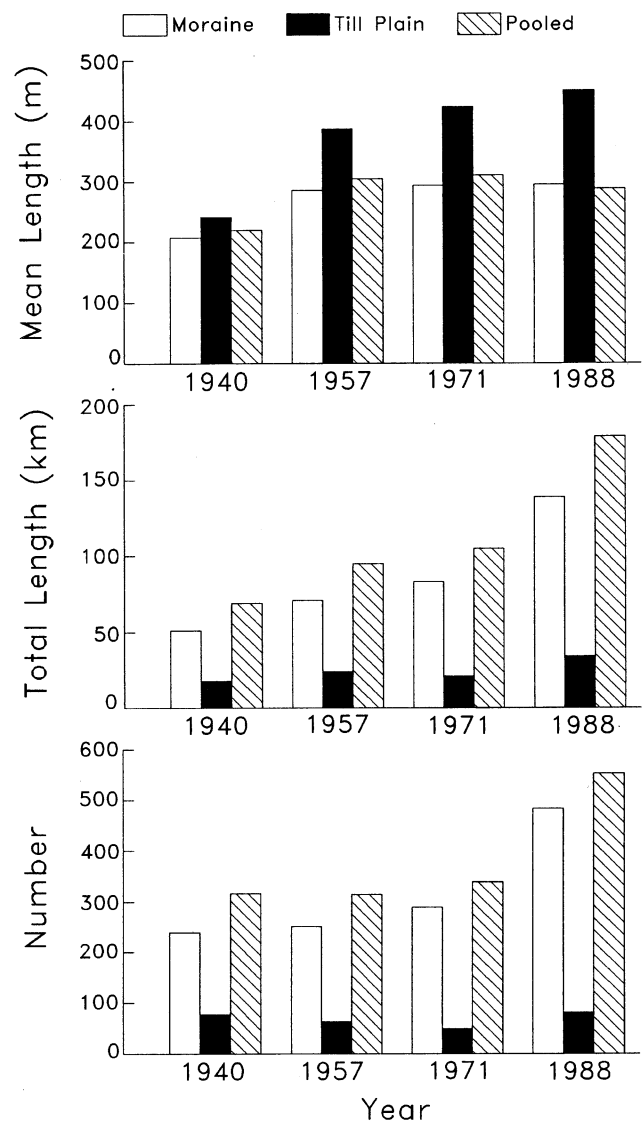

Figure 1. Number, total length, and mean length of fencerows in two contiguous Ohio landscapes (moraine and till plain) at four points in time.

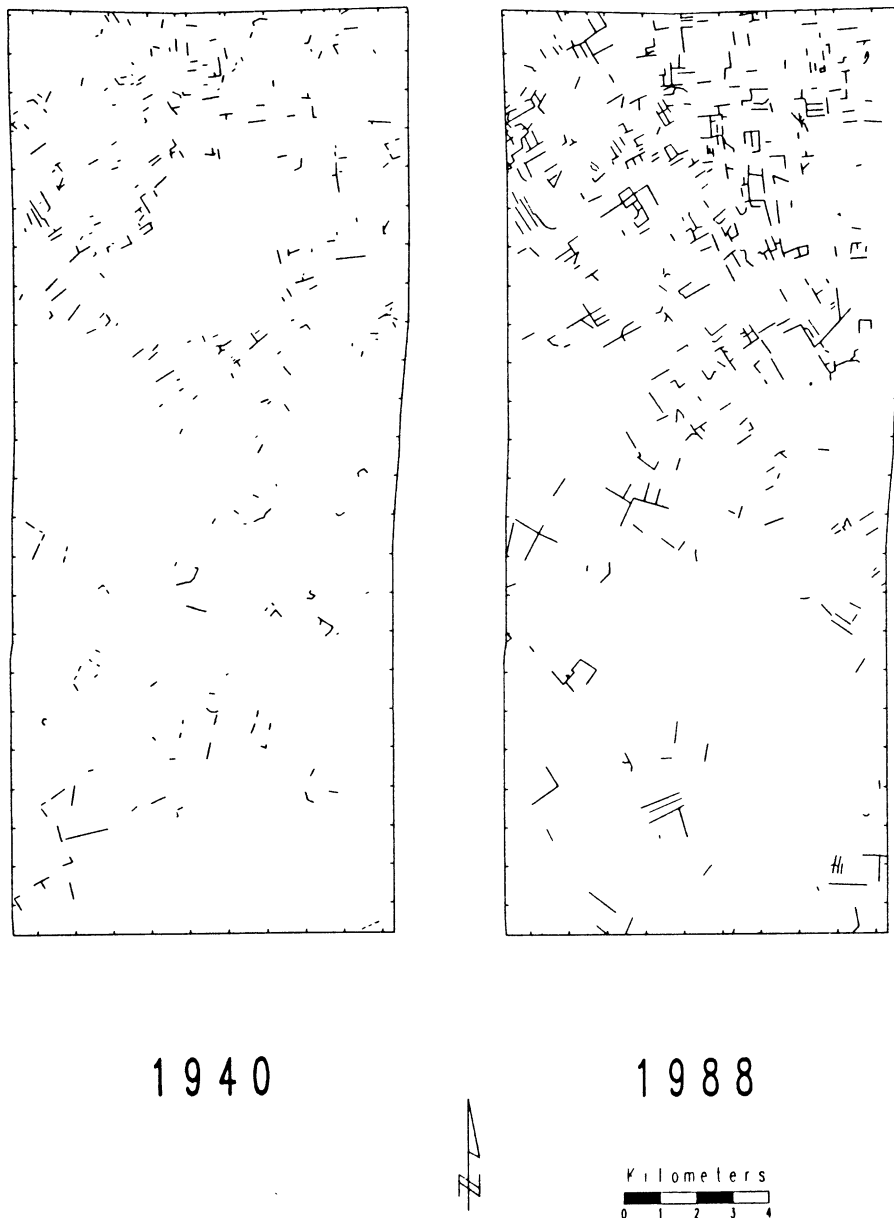1 9 4 0   1 9 8 8

Kilometers
0 1 2 3 4

Figure 2. Fencerow positions and lengths in the study area between 1940 and 1988.

zation probabilities, a common approach to competition/coexistence models for sessile organisms. We made runs with 10, 40, 70, and 100 drops in each landscape and then calculated the total length and area of hedgrow and forest edge colonized by the offspring of each successful organism.

Results

Landscape Connectivity

The total number of fencerows within our full study area remained constant from 1940 to 1971 and then increased 86% by 1988 (Fig. 1). Fencerows were much less dense on the till plain than on the moraine (Fig. 2),

and their numbers remained essentially constant over the 48-year study period (Fig. 1). Conversely, the number of fencerows on the moraine increased significantly with time (number on moraine = 0.16 [year] -26.71; $r^2 = 0.77$), as did their density (approximately five fencerows per year). Total fencerow length increased significantly on both the till plain (1.9 times) and the moraine (2.7 times), but the till plain fencerows still made up a relatively small proportion of the total for the study area. Average fencerow length for both landscapes increased from 1940 to 1957, then leveled off, with average fencerow length on the till plain remaining consistently greater than that on the moraine.

The total number of fencerows and forest edges (hereafter "edges") decreased from 1940 to 1971 and then increased again to 1988 (Fig. 3). Edge numbers decreased
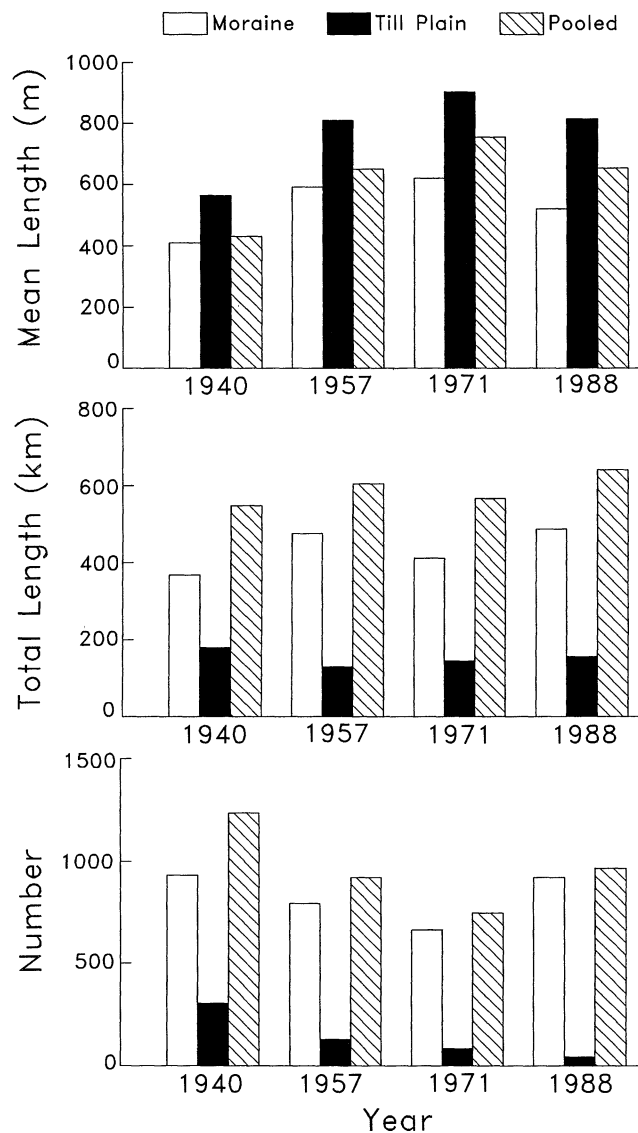
Figure 3. Number, total length, and mean length of total ecotonal edge (fencerows plus forest edges) in two contigous Ohio landscapes (moraine and till plain) at four points in time.

steadily on the till plain (Fig. 4), while on the moraine they decreased from 1940 to 1971 and then increased again to 1988 (Figs. 3 & 4). The total length of edge increased slowly over the 48-year period, both overall and on the moraine (Fig. 3). Total edge length of the till plain decreased slightly over the 48-year period. Average edge length over the entire study area and in the two separate landscape segments increased from 1940 to 1971 and then decreased to 1988. Average edge lengths on the till plain consistently exceeded those on the moraine by 32–57%, with the difference increasing through time.

The contribution of fencerows to total edge length increased with time, both overall and in each of the separate landscapes (Fig. 5) By 1988, 22–29% of the edge was made up of fencerow. In contrast to other regions

in which changes in land use and agricultural practices have reduced fencerow and forest-edge length (Nilon 1986; Burel & Baudry 1990*a*, 1990*b*), we found that total edge length, fencerow length and frequency, and the contribution of fencerows to a growing edge total all increased in the moraine and in the total study area. Though density and total length have not increased to the same degree on the till plain, average length has increased. Thus, temporal changes in both fencerows and forest edges in these landscapes have tended to increase the potential for connectivity over the 48-year study period.

Connectivity Components

On the moraine, total forest cover increased 37% during 1940–1988 (Simpson et al. 1994). The number of forest patches changed little during this time, whereas the mean forest patch size increased from 10.1 to 13.1 ha (Simpson et al. 1994) Concurrent with this increase in forest area were increases in the number and length of fencerows and in total forest edge. Thus, there was a general increase in all connectivity components on the moraine during the study period.

In contrast, there was no significant change in the total area, patch number, or patch size of the forested area on the till plain during 1940–1988 (Simpson et al. 1994). At any time during that period, there was less than 20% as much forested land on the till plain as on the moraine (Simpson et al. 1994). There was only a small increase in connectivity during 1940–1988 on the till plain, and virtually all of that was due to an increase in mean fencerow length. This pattern of dynamism on the moraine and strong inertia on the till plain was consistent with that for other changes in land cover and landscape structure described by Simpson et al. (1994).

Model Behavior

The connectivity of a landscape for a given species is a function of the proportion of the landscape occupied by suitable habitat patches, the dispersion of those patches, and the nature of the elements that separate or connect those patches. In a landscape with either a high proportion of both suitable habitat or viable connecting corridors, the first populations that develop from successful colonists would preempt the majority of the suitable habitat. As a result, man area occupied per successful colonization (hereafter "mean area") or mean occupied edge length would decrease rapidly as the number of colonization attempts increased. This sharply exponential relationship between mean area and number of colonization attempts should quickly level off (Fig. 6a), and the percentage of suitable habitat occupied should quickly become asymptotic (Fig. 6b). One consequence of colonization in such a highly connected landscape is
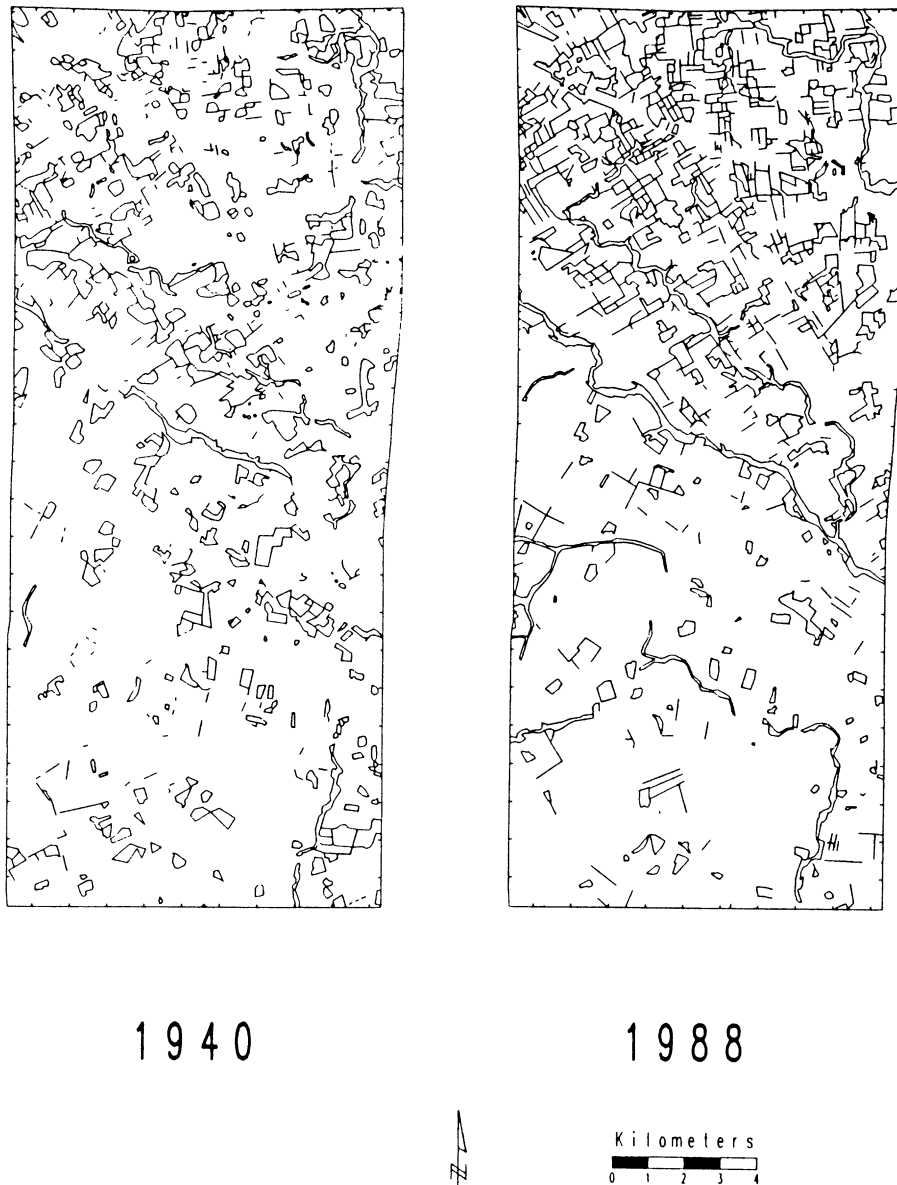
1940   **1988**

Figure 4. Total edge (fencerows and forest edges) in the study area between 1940 and 1988.

that the number of unsuccessful colonizations would increase with the number of attempts.

Modest increases or decreases in the number of suitable habitat patches and/or corridors will likely have little effect on the relationship between mean area and frequency of colonization attempts. Changes in hedgerow networks could be expected to influence mean edge length, whereas changes in habitat patch density would affect mean area.

In a landscape with low densities of both suitable habitat patches and connecting fencerows or corridors, such as our till-plain landscape, the slopes of the relationships between mean area or edge and colonization attempts should be shallow and might even fit a linear model better than an exponential model (Fig. 6a). The percentage of suitable habitat occupied should increase linearly with the number of colonization attempts be-

cause each successful colonization would essentially be an independent event (Fig. 6b). In such a case modest increases or decreases in the density of habitat patches or fencerows would be expected to affect similarly modest changes in slope and intercept. Overall, the proportion of successful colonizations in the poorly- connected landscape should be lower than in the two cases described above.

To anticipate the behavior of our random colonization model, we made two simplifying assumptions: the suitable habitat patches were uniform in size, and both habitat patches and fencerows were randomly distributed. Although these assumptions clearly do not fit our landscape, we believed that if the output of the model using the actual landscape configuration fit our prediction based on these simplifying assumptions, the model would have to be considered fairly robust.
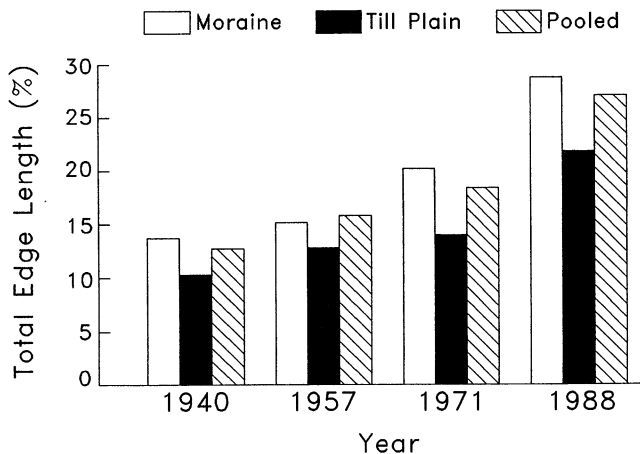
Figure 5. Fencerows as a percentage of total ecotonal edge (fencerows and forest edges) in two contiguous Ohio landscapes (moraine and till plain) at four points in time.

Over all years and runs, 89.7% of the colonization attempts on the moraine were successful, and there was no significant relationship between percentage success and the number of attempted colonizations (Fig. 7). These results suggested that the moraine habitat was not saturated with animals, even at the highest colonization density (100 colonization attempts), and that the probability of a successful colonization was still a function of the proportion of the landscape with suitable habitat patches, even after 100 colonization attempts.

On the till plain in contrast, there was a strong negative relationship between percentage success and the number of colonization attempts in all four years. The proportion of successful colonists decreased from 100% at the lowest colonization density (10 animals/run) to 73.5% at the highest density (100 animals/run). We found these results counterintuitive. Given the low proportion of suitable habitat and the low connectivity of the till plain, we would have expected the percentage of successful colonizations to be lower at any given density than on the moraine and for the percentage of successes to decrease more gradually as low-probability successes accumulated.

On the moraine, the relationships between mean area and the number of colonization attempts fit first-order negative exponential functions in all four test years (Fig. 8), with the coefficient of determination (r^2) ranging from 0.825 to 0.927. The y-intercept for the relationship between area and colonization attempts increased with time, such that the 1988 intercept was 161% greater than that for 1940. In addition, the slopes of the best-fit functions for 1957, 1971, and 1988 for the relationship between mean area and colonization attempts was 34.0% steeper (more negative) than was the 1940 function. These changes in the shape of the functions correlated with major changes in the moraine landscape be-
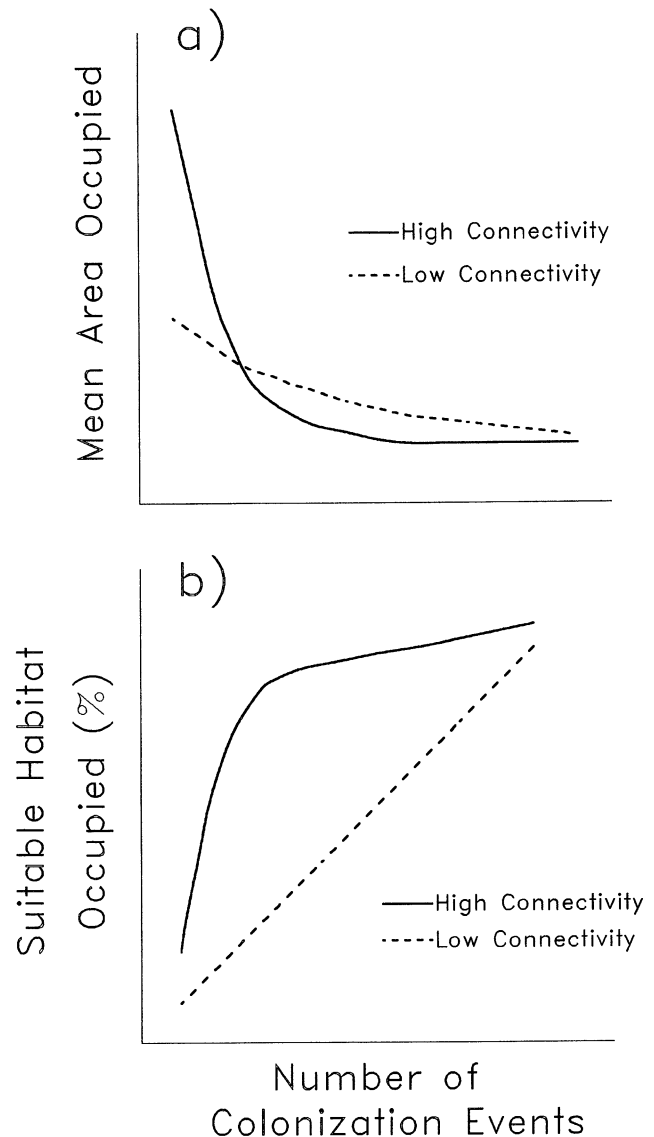

Figure 6. Predicted model behavior of the relationship between mean area occupied (a) and percentage of suitable habitat occupied (b) as a function of the number of colonization events in relation to landscape connectivity.

tween 1940 and 1957. During this time, mean fencerow length increased, total edge (forest edges and fencerows) increased, and the number and total area of forested patches increased (Simpson et al. 1994). The rates of change for these important landscape attributes were significantly less from 1957 through 1988. Thus, the behavior of the model for the moraine fit reasonably well with our predictions: a general, negative exponential relationship of mean area versus number of colonization attempts and increases in both y-intercept and slope steepness resulting from increases in connectivity.

The percentage of suitable mean area occupied increased linearly with the number of colonization events
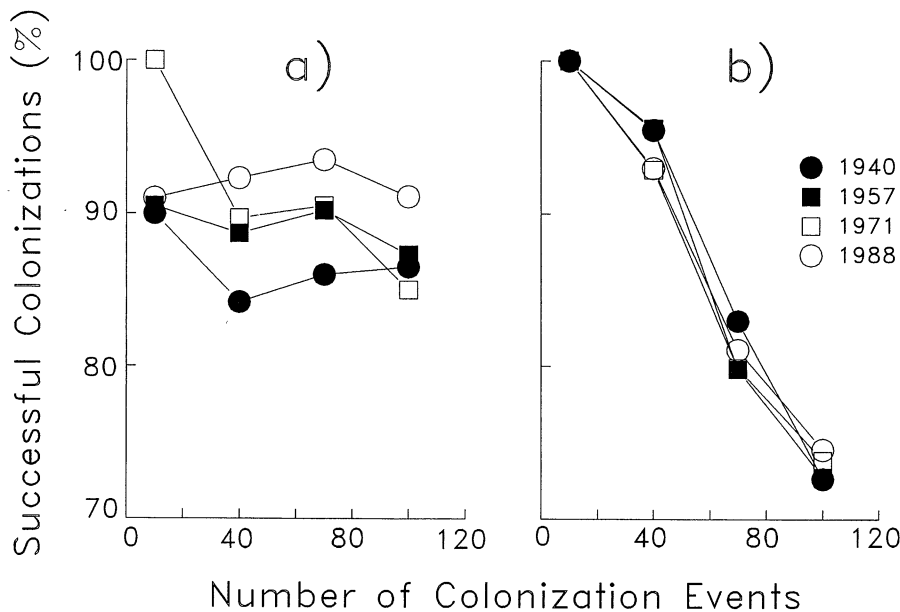
Figure 7. *Percentage of successful colonization events as a function of landscape for moraine (a) and till plain (b), and the number of colonization attempts.*

Discussion

in 1940, but it fit an asymptotic, logistic function better from 1957 to 1988 (Fig. 8). As connectivity increased on the moraine over time, the individual home ranges became so large that the landscape began to become saturated somewhere between 10 and 40 colonization attempts.

For the till plain, the relationships between mean area occupied and number of colonizations fit only exponential functions well (Fig. 8). The change in y-intercept from 1940 to 1957 was positive, with a decrease from 1957 to 1971 and from 1971 to 1988. This paralleled the pattern of change in fencerow density and length on the till plain: a moderate increase during 1940–1957 followed by a slow, steady decline through 1988. The slopes of the relationships also became more negative with time, such that the mean of the slopes for mean length and area for 1957–1988 were 69.1 and 21.5% greater, respectively, than were the 1940 slopes. This change paralleled the rate of loss of forested land on the till plain: faster between 1940 and 1957 than later in the study period (Boerner et al., in press).

There was no consistent temporal pattern of change in the relationships between the percentage of suitable area occupied and the number of colonization events (Fig. 8). In all cases, linear and exponential functions fit the relationships equally well. Overall, the percentage of suitable area colonized on the till plain was 10–20% lower than on the moraine.

The model results for the till plain were also consistent with our predictions. Though the rates of change were considerably smaller than those on the moraine, the overall shape of the functions and the patterns of change in relation to changes in connectivity and suitable habitat density did follow predictions.

The density, length, and pattern of temporal change in fencerows differed dramatically between our two landscapes. On the more complex and diverse moraine landscape, the number and total length of fencerows increased 2–3 times during our 1940–1988 study period. Most of this increase occurred during 1971–1988, a period during which many of the small, integrated farms that dominated the moraine were sold to "gentlemen farmers." The result of this change in land tenure was often the subdividing of the farms into distinct patches of different land uses, often including fencerows or with fencerows separating them (Simpson et al. 1994). In contrast, the density of fencerows on the till plain remained relatively constant over the same period, and the total length of fencerow grew very slowly. Although the mean fencerow length on the till plain was 50% greater than that on the moraine, the total length and number of fencerows on the till plain were less than one-quarter of those on the moraine.

These increases in total fencerow length (on both landscapes) and number (on the moraine) contrast with reports of progressive decreases in fencerows over the last 40 years in the United Kingdom (Leonard & Cobham 1977) and France (Burel & Baudry 1990a). These differences may be related in part to differences in the agricultural support of Europe and the United States (Burel & Baudry 1990a; Simpson et al. 1994) and to differences in the inherent agricultural capability of the soil. Burel and Baudry (1990b) described a relationship between soil capability and the appearance and disappearance of fencerows in France. On sites with highly productive soils, fencerows were being cleared and planted with
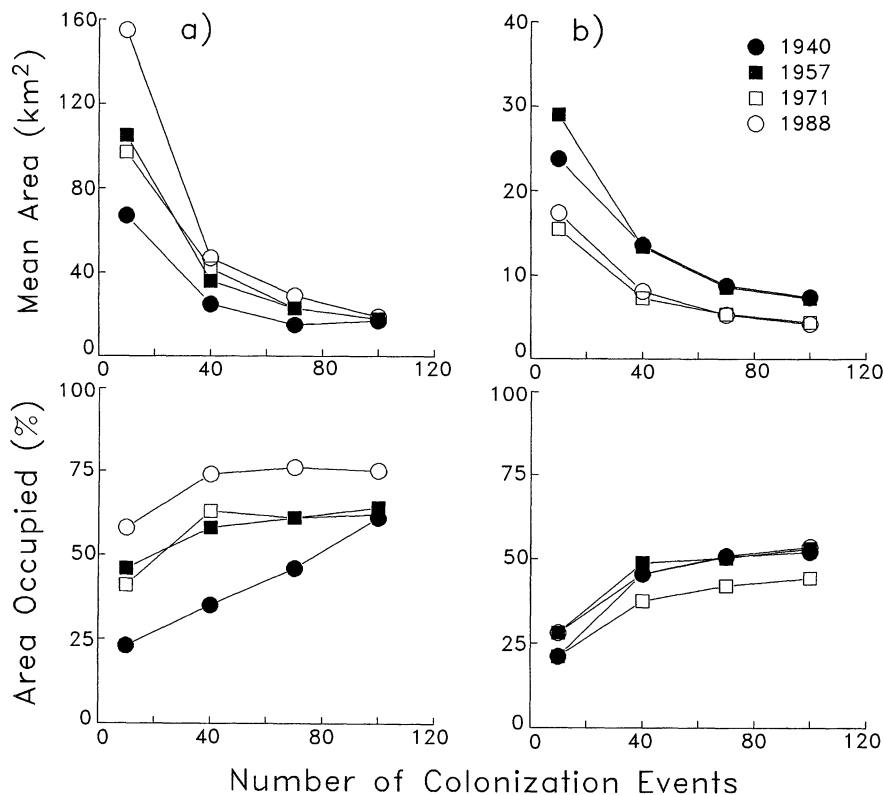
Figure 8. Actual model of the relationship between mean area (area and perimeter) and percentage of suitable habitat occupied (area and perimeter) on the moraine (a) and till plain (b) landscapes as a function of the number of colonization events and time.

crops, whereas on marginal or poor soils abandonment led to an increase in fencerows. There is some parallel here with Ohio landscapes because we observed a much greater rate of appearance of fencerows on the less-fertile moraine than on the till plain.

From 1940 to 1988, total edge length increased slowly on the moraine and decreased slowly on the till plain. These changes were functions both of changes in fencerow numbers and lengths and of changes in the number and size of forested patches (Simpson et al. 1994). On both landscapes, the proportion of total edge contributed by fencerows increased almost two-fold over 48 years. Thus, the importance of fencerows to edge-dwelling organisms and to landscape connectivity grew through the study period.

On both landscapes, as connectivity increased with time, the ability of the offspring of the earliest successful colonists to preempt most of the suitable habitat increased, and the rate at which these relationships changed was greater for the more dynamic, more connected moraine landscape than for the less dynamic, less connected till plain. Fahrig and Merriam (1985) also modeled changes in connectivity and found that increasing connectivity reduces the frequency of local extinctions and facilitates recolonization after local extinction. Our data support both of these notions. Our model data also suggest, however, that the increase in the probability of successful recolonization that results from increased connectivity may not be entirely positive. In a highly connected landscape, suitable habitat will be

quickly saturated with the offspring of the earliest successful colonists. This, in turn, could result in a lower genetic diversity across the landscape because fewer independent, successful colonization attempts are possible. On the more highly connected moraine, the result might be a relatively small number of populations of limited genetic diversity. On the till plain, where founder effects might be expected to be more important, we would anticipate a larger number of isolated populations with a greater probability of local extinction, but also with the potential for greater across-landscape genetic diversity than might be the case on the moraine.

Our model clearly simplifies these relationships. For example, we chose to consider all fencerows as a single, functional class of landscape features. But factors such as origin, width, height, and species composition can affect the suitability of fencerows for various animals (Forman & Godron 1986). Also, we have considered only a single spatial scale, when, clearly, each potential colonizing organism will respond at a scale unique to the behavior and biology of that species (Gardner et al. 1991). Despite these simplifications, we have demonstrated that changes in fencerow network characteristics in a pair of actual rural landscapes do have the potential to influence the species composition and genetic diversity of organisms that might colonize these changing landscapes over time.

The current controversy over the utility of corridors in species preservation efforts is likely to continue. Experimental manipulation of landscape edges will become in-

creasingly important in determining when and under what conditions landscape corridors increase species richness. Such experiments are time-intensive, however, and require careful control of the landscape variables and the species examined. We suggest that modeling such landscapes with a GIS prior to field experimentation will strengthen the initial hypothesis formulation and may suggest needed modifications of field experiments. Because of the ease with which species and landscape variables can be manipulated, the coupling of GIS modeling with field experimentation may prove a useful means of determining how effective corridors are for conservation.

Acknowledgments

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