

Plant-species richness in corridor intersections: is intersection shape influential?

Samuel K. Riffell^{1*} and Kevin J. Gutzwiller^{1,2**}

¹Department of Environmental Studies and ²Department of Biology, Baylor University, Waco, TX 76798, USA

Keywords: agricultural landscapes, conservation biology, corridors, fencerows, intersection shape, networks, nodes, plant dispersal, plant-species richness, restoration ecology

Abstract

Corridor intersections constitute nodes that can be more mesic than the intersecting corridors themselves. Such microclimatic conditions may lead to an “intersection effect,” in which plant richness is higher in the intersection than in the corridors. We hypothesized that an additional factor contributing to intersection effects is the movement of plants along corridors into intersections by way of bird- and mammal-dispersed seeds. If this hypothesis is correct, one would expect intersection-shape effects, defined herein as differences in intersection richness associated with the number of possible avenues for plant influx into the intersection. Specifically, richness in intersections should be lowest for L-shape intersections (two avenues), higher for T-shape intersections (three avenues), and highest for X-shape intersections (four avenues). We used data from fencerow networks to test this hypothesis about corridor intersections. During October 1992 and March 1993, we determined woody- and herbaceous-plant richness for 25 intersections and their associated fencerows in central Texas, USA. We compared two measures of intersection richness among the three intersection shapes: richness of plants dispersed primarily by birds and mammals (vertebrate-dispersed plant richness), and richness of plants dispersed primarily by wind, ants or other means (non-vertebrate dispersed plant richness). Vertebrate-dispersed plant richness differed significantly among intersection shapes, but no differences in non-vertebrate dispersed plant richness were evident, which is what one would expect if the number of avenues for vertebrate vectors into an intersection was an important factor influencing intersection richness. The intersection-shape effects we found were not attributable to fencerow features (amount of woody cover, width, presence of breaks) or intersection characteristics (amount of woody cover, size, distance to nearest connected intersection or patch). Our results from fencerow networks support the hypothesis that intersection effects on plant richness are influenced by intersection shape via the number of intersecting corridors. Understanding patterns and processes that occur in networks is important for conservation biologists because intersections in networks have the potential to function as refugia for plant species that require conditions more mesic than those of the surrounding matrix. Networks also may be valuable as *in situ* sources of seed for managers attempting to restore plant communities in the matrix.

1. Introduction

Corridors are believed to promote the flow of energy, genes, plants and animals among landscape elements. Accordingly, they have been recommended for maintaining diversity within fragmented land-

scapes (Noss and Harris 1986; Noss 1987), although negative effects of corridors have also been identified (see Simberloff and Cox 1987; Simberloff *et al.* 1992). Networks of intersecting corridors can amplify movement between landscape elements, enhance the accessibility of these

*Present address: Department of Zoology, Michigan State University, East Lansing, MI 48824, USA. ** To whom all correspondence should be sent.

elements (Lowe and Moryadas 1975:75), and supply many sources for species inputs (Benninger-Truax *et al.* 1992). Networks can be composed of a variety of corridor types, such as trails, fencerows, hedgerows, shelterbelts and riparian areas. In and near hedgerow intersections, the ecological conditions of hedgerows are often modified, producing an “intersection effect,” which has been described as higher plant richness in a hedgerow intersection than in the associated intersecting hedgerows (Forman and Godron 1986: 178–181). Forman and Godron (1986: 178–179) hypothesized that intersection effects arise because intersections are more mesic than hedgerows and, consequently, more interior species of plants can persist in intersections than in hedgerows. But intersection richness also may be influenced by the movement of plant species along corridors into the intersection. To the extent that corridors function as conduits to intersections, habitat conditions in narrow corridors – trails, fencerows and hedgerows, for example – may prevent some species from ever reaching corridor intersections. For example, exotic plant species appear more able than some native species to persist in (hence move along) trail corridors (see Benninger-Truax *et al.* 1992), and arid fencerow habitats probably prevent some forest plants from moving independently through fencerow networks (Fritz and Merriam 1993; Fritz and Merriam 1994).

Although microclimate and other corridor conditions may limit some plant species’ movements into intersections, seed vectors might ameliorate such constraints. Mammals (Willson 1993) and birds (Willson 1986), for example, are capable of transporting seeds substantial distances from their source. Seed-dispersing mammals, such as striped skunks (*Mephitis mephitis*; Verts 1967), white-footed mice (*Peromyscus leucopus*; Merriam and Lanoue 1990) and eastern chipmunks (*Tamias striatus*; Wegner and Merriam 1979; Henderson *et al.* 1985; Bennett *et al.* 1994), often use fencerows as travel routes. Birds also use fencerows extensively as movement corridors (Wegner and Merriam 1979); blue jay (*Cyanocitta cristata*) movements in fencerows constitute a primary mechanism by which beech (*Fagus grandifolia*) seeds are dispersed to new areas (Johnson and Adkisson 1985). Because seed-dispersing vectors are often abundant in fencerows, it is conceivable that

fencerows could function as movement corridors for plant species when habitat conditions are inadequate for unaided movement (Fritz and Merriam 1993). Thus, in addition to microclimatic conditions, seeds deposited at intersections (by mammals and birds traveling through corridor networks) may contribute to intersection effects on plant richness.

Our *a priori* hypothesis was that the intersection effect on plant richness arises, in part, because intersecting corridors provide multiple avenues for plant movement into the intersection. The underlying ecological assumptions for this hypothesis, supported by the literature referenced above and field observations (S.K. Riffell, unpublished data) within the networks we studied, are that: seeds are available in or near corridors; seeds are transported substantial distances (tens to hundreds of m) by birds and mammals within corridor networks; seed-dispersing birds and mammals regularly move within corridor networks; and seed deposition specifically at intersections is less likely to occur from vectors that do not regularly travel along intersecting corridors (*e.g.*, ants, wind, and other abiotic vectors) than from vectors that do consistently travel along such corridors. If our hypothesis is true, one should observe intersection-shape effects, defined herein as differences in intersection richness that are associated with the number of intersecting corridors. Specifically, animal-dispersed plant richness should be lowest in L-shape intersections with two avenues for influx, higher in T-shape intersections with three avenues for influx, and highest for X-shape intersections, which could receive inputs from four corridors. An intersection-shape effect would not be expected for plants that are not dispersed by birds or mammals.

Data from fencerow networks were used to test for intersection-shape effects. We tested the hypothesis that the intersection effect on plant-species richness would increase with the number of intersecting fencerows for species dispersed primarily by birds and mammals (vertebrate-dispersed plant richness). We also tested the hypothesis that there would not be an intersection-shape effect on plant-species richness for species that were dispersed by ants, wind or other abiotic vectors (non-vertebrate dispersed plant richness).

2. Methods

2.1. Study area

We sampled 25 intersections and associated fencerows in McLennan County (31°N, 97°W), which lies in the Blackland Prairie region of central Texas, USA (Hatch *et al.* 1990). Fencerow networks were prominent in the surrounding agricultural landscape, in which row-crop fields and livestock pastures were interspersed with woodland patches. Fencerows originated from seeds deposited by wind, birds and other vectors along unplowed borders and fencelines of agricultural fields. Regular spacing of large trees in parts of a few fencerows suggested some trees were planted; fencerows did not appear to be derived from forest remnants. We identified intersections for sampling from aerial photographs. Because our hypotheses related to animal movement through fencerow intersections, we sampled only those intersections connected by a fencerow to at least one other intersection or woodland patch. Sampled intersections also were free of the effects of intense vegetative disturbance, such as grazing or removal of understory vegetation.

2.2. Vegetation sampling

2.2.1. Plant richness

We centered one 10 m × 15 m sample plot in each of the intersections in such a way that the sides of the plot were perpendicular to the associated intersecting fencerows (Fig. 1). Identical 10 m × 15 m plots also were placed in each of the associated intersecting fencerows. Intersection effects can extend 30 m beyond the intersection (Forman and Godron 1986: 180), so sampling plots in fencerows were placed 100 m from intersections (Fig. 1), minimizing the chance that fencerow-plot data would be influenced by intersection effects. Because there can be a positive relationship between plant richness and length of a sample plot (Helliwell 1975), all fencerow plots were positioned so that 10 m of fencerow length were sampled in each plot. Woody-plant cover and richness

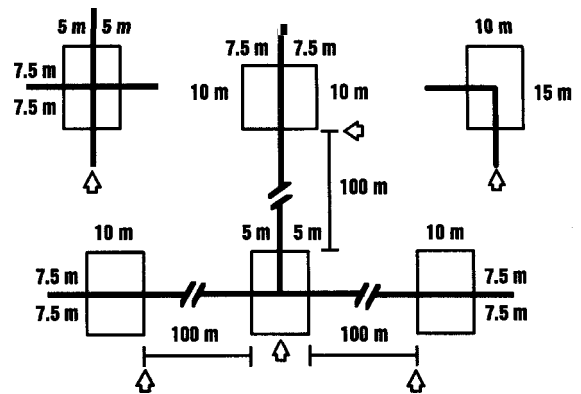


Fig. 1. Orientation of intersection and fencerow sampling plots for each intersection shape. Arrows indicate positions of line-intercept transects.

were measured during a 10-day period before leaf fall in October 1992; all other variables (fencerow and intersection characteristics, see below) and herbaceous-plant richness were measured during a 10-day period in March 1993. During each of these two sampling periods, fencerow plots were sampled on the same day as was the corresponding intersection plot, and the order in which intersections were sampled was randomized to prevent bias in estimates of plant richness due to seasonal changes in species' detectabilities. For woody and herbaceous plants separately, richness was estimated in each plot by direct counts; each count for each plot and plant type lasted 20 min and involved two passes through the plot. Common and scientific names are from Hatch *et al.* (1990).

2.2.2. Fencerow characteristics

Because features of the fencerows may have influenced plant richness in the intersections, we estimated three variables for the fencerows associated with each intersection: percent woody cover, width, and number of intersecting fencerows with a break. Woody cover in the understory of each intersecting fencerow had the potential to affect vertebrate use and movement along fencerows. We therefore estimated woody cover with a line-intercept transect (Mueller-Dombois and Ellenberg 1974: 90) positioned perpendicularly across each intersecting fencerow at 100 m from the associated intersection (Fig. 1); the length of each fencerow transect was

equal to the width of the fencerow at that 100-m point. We did not use a standard transect length for all fencerows because percent cover would have been biased downward for fencerows that were not as wide as the fixed transect length. Percent woody cover was calculated as the percentage of the total length of the transect intercepted by woody vegetation (tree, shrub, vine, or other growth form) < 2 m in height.

Relations between species richness and area exist in a number of systems (see Forman and Godron 1986: 66, and references therein), so we suspected the area (hence width) of intersecting fencerows might influence species richness in the intersections. We measured the width of each intersecting fencerow at the same 100-m point where we placed the transect to estimate woody cover for each fencerow, and we used the mean width of intersecting fencerows in analyses.

We also recorded the number of intersecting fencerows with a break because such breaks can act as barriers to vertebrate movements (*e.g.*, Bennett *et al.* 1994). Eastern chipmunks (*e.g.*, Henson *et al.* 1985) and birds (*e.g.*, Merriam and Saunders 1993), however, often cross breaks in the woody structure of a fencerow if some grass or forb structure is present. Therefore, we defined a break as a segment of an intersecting fencerow within which both woody and herbaceous vegetation were < 20 cm in height. The breaks in the fencerows we studied were approximately 3–10 m long.

2.2.3. Intersection characteristics

Because characteristics of the intersections also may have affected both plant establishment and the dispersal potential of animals, we measured three variables for each intersection: percent woody cover, area, and distance to the nearest connected intersection or patch. Percent woody cover in the understory of each intersection was estimated with a 15-m line-intercept transect that bisected the 10 m \times 15 m plot used for richness sampling (Fig. 1). Percent woody cover of the intersection was calculated as the percentage of the total transect length (15 m) intercepted by woody vegetation < 2 m in height. We calculated intersection area from field measurements of the dimensions of each intersec-

tion patch. Distance to the nearest connected intersection or patch was determined from aerial photographs by measuring the distance from the center of each intersection to the nearest edge of the nearest connected intersection or patch.

2.3. Richness variables

For each intersection and fencerow sampling plot we recorded: vertebrate-dispersed richness – the number of plant species (excluding grasses) dispersed primarily by birds and mammals; and non-vertebrate dispersed richness – the number of plant species (excluding grasses) dispersed primarily by ants, wind or other abiotic vectors. Vertebrate-dispersed richness was determined from a set of species (Appendix A) that were present in the intersections and fencerows we studied and that are known to be dispersed by birds, mammals, or both (Willson 1986, 1993; F.R. Gehlbach and W.C. Holmes, personal communication). We determined non-vertebrate dispersed richness from a set of species (Appendix A) encountered in the intersections and fencerows that are dispersed primarily by means other than bird or mammal vectors (see Mahler 1988).

For each richness variable, we derived a percent richness value by first dividing the value of a particular richness variable for an intersection by the mean of that same variable for the associated intersecting fencerows, and then multiplying by 100%. These percentage data, not the original richness counts, were used in all statistical tests involving the two richness variables. We interpreted a percent richness value as the intersection richness in proportion to the mean richness of the associated intersecting fencerows. A value $> 100\%$ denoted higher plant richness in the intersection than in the intersecting fencerows; a value $< 100\%$ indicated lower plant richness in the intersection than in the intersecting fencerows.

The means of richness variables for intersecting fencerows could have been influenced substantially by either large or small individual fencerow values. Such outliers could have, in turn, biased the percent richness values we calculated, leading to underestimates or overestimates of intersection-shape effects. But we examined the values used to

calculate the means of variables for intersecting fencerows for T- and X-shape intersections, and the means were centered within the range of individual values. And for L-shape intersections, the mean was representative of data from the two fencerows because both individual values from the fencerows were typically quite close or identical to one another. Our data for percent richness thus reflected biological patterns and were not artifacts stemming from outliers.

2.4. Statistical analyses

2.4.1. Fencerow and intersection characteristics

To maintain statistical power, we used an a priori $\alpha = 0.10$ for all statistical analyses. Because characteristics of the fencerows and intersections could have been confounded with intersection shape, we tested the null hypothesis that the means of these characteristics did not differ among intersection shapes. The alternative hypothesis was that these means differed among shapes. We tested these hypotheses for each characteristic using a priori, two-tailed, Student-*t* tests (Ott 1993: 266) and BMDP 3D software (Dixon 1992) for the three pairwise combinations of intersection shape (X vs. L, X vs. T, T vs. L). If variances of the groups were not equal for one or more of the three comparisons for a characteristic, we interpreted Welch's *t* (Ott 1993: 269) for that variable. When the normality assumptions of these parametric *t* tests were not clearly met for one or more of the comparisons for a characteristic, we interpreted instead the results of the nonparametric alternative, the Mann-Whitney test (Zar 1984: 139). Assumptions of the Mann-Whitney test were met for all comparisons. We also used Proc Reg (SAS Institute, Inc. 1989) to determine with regression whether each characteristic was significantly associated with either of the two plant-richness variables. The assumptions of regression (Ott 1993: 692) were satisfied in all cases.

2.4.2. Intersection-shape effects

For each richness variable, we tested the null hypothesis that mean percent richness did not increase

as the number of intersecting fencerows increased. Our alternative hypothesis for each variable was that mean percent richness was lowest in L-shape intersections, higher in T-shape intersections, and highest in X-shape intersections. We tested these hypotheses with a priori, one-tailed, Student-*t* tests (Ott 1993: 266) and SAS software (SAS Institute, Inc. 1989) for the three pairwise combinations of intersection shapes (X vs. L, X vs. T, T vs. L). The assumptions of the *t* test were satisfied for all comparisons.

2.4.3. Significance levels for pairwise comparisons

For each fencerow and intersection characteristic, and for each richness variable, a set of three simultaneous hypotheses (one hypothesis for each pairwise comparison) was tested. We considered each set to be a "family" (*sensu* Miller 1981: 34) of hypotheses because the hypotheses in a set involved the same variable and thus were related to one another. When a family of hypotheses is tested, the α level for each individual hypothesis must be adjusted to ensure that the family-wide α is equal to the preset α . This is the standard Bonferroni method, and it reduces the probability that spurious results will be considered significant. The standard Bonferroni adjustment, however, leads to reduced power when more than one of a group of null hypotheses is actually false (Rice 1989). To avoid this problem, we interpreted the significance levels of our tests using the sequential Bonferroni technique (Holm 1979). Using this method, we first ranked the *P* values for a family of hypotheses from smallest to largest. If the smallest *P* value was $\leq \alpha / k$ comparisons (in our study $0.10/3 = 0.033$), then that *P* was considered statistically significant at the family-wide α of 0.10. If the smallest *P* was considered significant, then the next smallest *P* only had to be $\leq \alpha / (k - 1)$ to be declared significant. If the second smallest *P* was significant, then the third smallest *P* only had to be $\leq \alpha / (k - 2)$ to be judged significant. If a *P* did not meet the criterion for significance, neither that nor any larger *P* within that family of hypotheses was declared significant.

Table 1. Summary statistics for richness variables.

Richness variable	Intersections			Intersecting fencerows		
	\bar{X}	SE	Range	\bar{X}	SE	Range
<i>L-shape Intersections (n = 10)</i>						
Vertebrate-dispersed richness	5.9	0.80	2–10	5.5	0.59	1–10
Non-vertebrate dispersed richness	7.3	0.60	5–10	6.9	0.35	3–10
Total richness	13.2	1.17	10–20	12.4	0.76	6–19
<i>T-shape Intersections (n = 10)</i>						
Vertebrate-dispersed richness	5.7	0.63	3–10	4.9	0.29	3–9
Non-vertebrate dispersed richness	7.2	0.63	5–11	6.8	0.33	3–11
Total richness	12.9	0.87	10–18	11.7	0.37	7–16
<i>X-shape Intersections (n = 5)</i>						
Vertebrate-dispersed richness	6.6	0.98	3–9	4.0	0.39	2–8
Non-vertebrate dispersed richness	8.2	0.58	7–10	7.3	0.48	3–10
Total richness	14.8	1.07	11–17	11.3	0.72	6–18

2.4.4. Data transformations

Before we conducted pairwise comparisons of mean percent woody cover of intersecting fencerows and mean percent woody cover of the intersection, these data were arcsine transformed (Zar 1984: 239). The richness variables also were percentage data, but these data could not be arcsine transformed because many of the percentages were greater than 100%. The reason for the arcsine transformation, however, is to meet an assumption of the *t* test (*i.e.*, that both groups are normally distributed), and this assumption was clearly satisfied without transforming the data for the comparisons involving richness variables. We conducted statistical tests on transformed data when necessary, but the means, SEs and ranges presented in tables and figures are for untransformed data.

3. Results

3.1. Floristic composition of fencerow networks

In the networks we studied, typical fencerows had irregular, broken canopies dominated by sugar hackberry (*Celtis laevigata*) and Osage orange (*Maclura pomifera*). They contained a sub-canopy

layer of vines (*e.g.*, saw greenbriar [*Smilax bona-nox*], Japanese honeysuckle [*Lonicera japonica*], poison oak [*Toxicodendron radicans*]), shrubs (*e.g.*, possum-haw [*Zlex decidua*], waxleaf ligustrum [*Ligustrum quihoui*], Chinese privet [*L. sinense*]), and small trees (*e.g.*, gum bumelia [*Bumelia lanuginosa*], sugar hackberry, honey mesquite [*Prosopis glandulosa*], Texas sophora [*Sophora affinis*]). The total number of plant species in intersection plots ranged from 10–20; the total number of species in fencerow plots ranged from 6 to 19 (Table 1). A total of 24 vertebrate-dispersed species (all woody species) and 26 non-vertebrate dispersed species (3 woody and 23 herbaceous species) were detected in the intersections and fencerows (Appendix A).

3.2. Fencerow characteristics

Mean percent woody cover of the intersecting fencerows, mean width of intersecting fencerows, and mean number of intersecting fencerows with a break did not differ significantly among intersection shapes (Tables 2 and 3). Regression analyses indicated there were no relations between either of the richness variables and: mean percent woody cover of the intersecting fencerows ($t = 0.62 - 1.54$, $df = 23$, $P = 0.140 - 0.540$); mean width of intersecting fencerows ($t = -0.03 - 0.35$, $df = 23$,

Table 2. Summary statistics for fencerow and intersection characteristics.

Characteristic	\bar{X}	SE	Range
<i>L-shape Intersections (n = 10)</i>			
<i>Fencerows</i>			
Mean percent woody cover of intersecting fencerows	36.5	5.0	12.2–54.5
Mean width of intersecting fencerows (m)	11.8	1.3	7.7–20.4
Number of intersecting fencerows with a break	0.1	0.1	0–1
<i>Intersections</i>			
Percent woody cover of intersection	23.0	4.2	4.0–40.0
Intersection area (m ²)	248.5	32.7	140–473
Distance to nearest connected intersection or patch (m)	162.5	26.3	118.9–396.2
<i>T-shape Intersections (n = 10)</i>			
<i>Fencerows</i>			
Mean percent woody cover of intersecting fencerows	47.5	5.7	23.0–69.0
Mean width of intersecting fencerows (m)	13.3	0.9	8.6–17.8
Number of intersecting fencerows with a break	0.5	0.2	0–1
<i>Intersections</i>			
Percent woody cover of intersection	26.6	2.9	15.0–42.0
Intersection area (m ²)	521.0	94.9	247–1189
Distance to nearest connected intersection or patch (m)	214.8	22.2	128.8–317.0
<i>X-shape Intersections (n = 5)</i>			
<i>Fencerows</i>			
Mean percent woody cover of intersecting fencerows	28.7	7.4	12.8–48.1
Mean width of intersecting fencerows (m)	11.6	2.2	6.4–18.2
Number of intersecting fencerows with a break	0.8	0.2	0–1
<i>Intersections</i>			
Percent woody cover of intersection	27.7	6.9	8.5–45.0
Intersection area (m ²)	898.2	254.9	283–1538
Distance to nearest connected intersection or patch (m)	478.3	150.3	168.4–1030.2

$P = 0.732 - 0.975$); or number of intersecting fencerows with a break ($t = 0.71 - 0.88$, $df = 23$, $P = 0.387 - 0.483$). Thus, fencerow characteristics were neither confounded with intersection shape nor associated with richness variables.

3.3. Intersection characteristics

Mean percent woody cover of intersections did not differ among intersection shapes (Tables 2 and 3), and regression indicated percent woody cover was not related to either of the richness variables ($t = -0.76 - 0.07$, $df = 23$, $P = 0.455 - 0.946$). Mean intersection area, and mean distance to nearest connected intersection or patch, differed significantly among intersection shapes (Tables 2 and 3), but regression analyses indicated that neither intersection area ($t = -0.25 - 1.42$, $df = 23$, $P = 0.170 - 0.804$) nor distance to nearest connected intersection or patch ($t = 0.49 - 0.91$, $df = 22$, $P = 0.374 - 0.632$) was significantly related to variation in the richness variables. For the regression analyses involving distance to nearest connected intersection or patch, one extreme distance (> 4 SDs from the mean) was not used in the analyses because it would have disproportionately affected the regression fits and led to misleading interpretations (see Neter and Wasserman 1974: 107).

3.4. Intersection-shape effects on plant richness

We detected intersection-shape effects on vertebrate-dispersed richness (Table 4). Mean percent richness was higher in X-shape intersections than in both L- and T-shape intersections, and the general trend was one of increasing intersection effect (relative richness) as the number of intersecting fencerows increased (Fig. 2). Although no significant intersection-shape effects were evident for non-vertebrate dispersed richness (Table 4), mean percent richness was highest for X-shape intersections and lower for L- and T-shape intersections (Fig. 3).

Table 3. Results of parametric and nonparametric tests for between-shape differences in fencerow and intersection characteristics.

Characteristics and comparisons	Two-group <i>t</i> tests			Mann-Whitney tests	
	<i>t</i>	df	<i>P</i>	<i>U'</i>	<i>P</i>
<i>Fencerow characteristics</i>					
Mean percent woody cover of intersecting fencerows					
X vs. L	-0.90	13	0.386	-	-
X vs. T	-1.95	13	0.073	-	-
T vs. L	1.44	18	0.166	-	-
Mean width of intersecting fencerows (m) ¹					
X vs. L	-0.11	6	0.916	-	-
X vs. T	-0.72	5	0.504	-	-
T vs. L	0.92	16	0.369	-	-
Number of intersecting fencerows with a break					
X vs. L	-	-	-	42.5	0.043
X vs. T	-	-	-	32.5	0.500
T vs. L	-	-	-	70.0	0.160
<i>Intersection characteristics</i>					
Percent woody cover of intersection					
X vs. L	0.62	13	0.543	-	-
X vs. T	0.18	13	0.858	-	-
T vs. L	0.71	18	0.486	-	-
Intersection area (m ²)					
X vs. L	-	-	-	45.0	0.015 *
X vs. T	-	-	-	35.0	0.333
T vs. L	-	-	-	86.0	0.007 *
Distance to nearest connected intersection or patch (m)					
X vs. L	-	-	-	48.0	0.004 *
X vs. T	-	-	-	41.0	0.067
T vs. L	-	-	-	72.5	0.110

¹ Welsh's *t* was used for this family of comparisons because the variances of the groups were not equal.

* Comparison significant at the family-wide $\alpha = 0.10$ after the sequential Bonferroni adjustment.

4. Discussion

Fencerow characteristics had the potential to affect plant richness in the fencerows and, therefore, the intersections. The amount of woody cover in fencerows can influence plant establishment (Rosenberg *et al.* 1983), bird richness (Best 1983; Shalaway 1985), and the extent to which birds

(Wegner and Merriam 1979) and mammals (Bennett *et al.* 1994) use fencerows as movement corridors. Corridor width can influence the richness and abundance of birds (Shalaway 1985), mammal richness (Yahner 1983), and a fencerow's potential to function as an animal corridor (Bennett *et al.* 1994), primarily because wider corridors provide a larger amount and variety of habitat and resources.

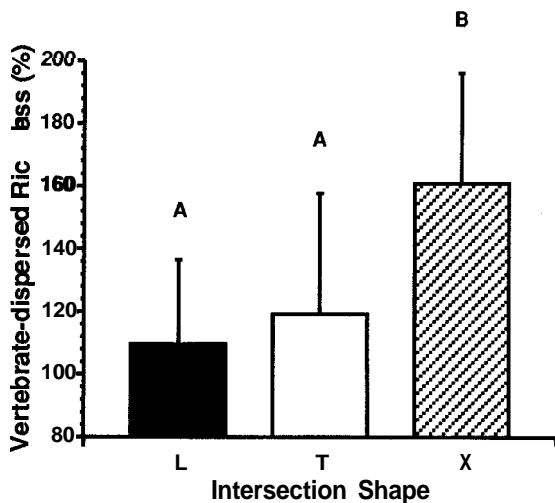


Fig. 2. Mean percent vertebrate-dispersed richness (+ 1 SE) for each intersection shape. Percent vertebrate-dispersed richness is vertebrate-dispersed richness of each intersection divided by the mean vertebrate-dispersed richness of associated intersecting fencerows. Bars with letters in common indicate mean percentages were not significantly different at a family-wide $\alpha = 0.10$.

Table 4. Results of two-group *t* tests for intersection-shape effects on plant richness variables.

Richness variables and comparisons	<i>t</i>	df	<i>P</i>
Vertebrate-dispersed richness			
X vs. L	3.15	13	0.004 *
X vs. T	2.03	13	0.032 *
T vs. L	0.64	18	0.264
Non-vertebrate dispersed richness			
X vs. L	0.63	13	0.270
X vs. T	0.37	13	0.358
T vs. L	0.13	18	0.450

* Comparison significant at the family-wide $\alpha = 0.10$ after the sequential Bonferroni adjustment.

Wide corridors also can influence plant establishment by providing more mesic conditions (Forman and Godron 1986: 390). Our method of dividing intersection values of richness by the mean of the same variable for the intersecting fencerows enabled us to control for variation in intersection richness that might have been related to these fencerow characteristics. In addition, this approach

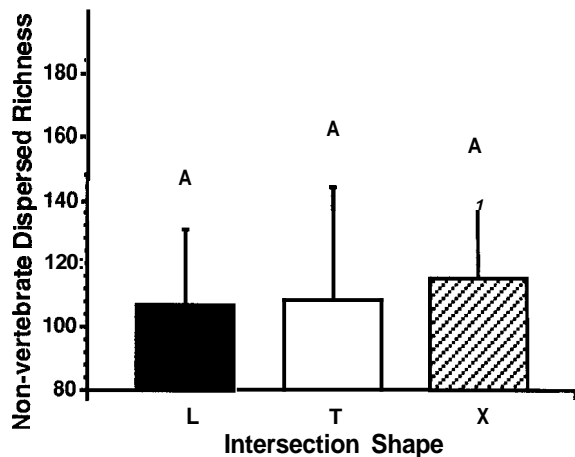


Fig. 3. Mean percent non-vertebrate dispersed richness (+ 1 SE) for each intersection shape. Percent non-vertebrate dispersed richness is non-vertebrate dispersed richness of each intersection divided by the mean non-vertebrate dispersed richness of associated intersecting fencerows. Bars with letters in common indicate mean percentages were not significantly different at a family-wide $\alpha = 0.10$.

controlled for variation in intersection richness that may have been related to fencerow characteristics we did not measure. For instance, hedgerow age (Willmot 1980), hedgerow origin (Forman and Baudry 1984), the structural complexity of fencerows and shelterbelts (Shalaway 1985; Merriam and Lanoue 1990; Schroeder *et al.* 1992), and soil seed banks also can influence plant richness or animal use. Regression analyses indicated that none of the fencerow characteristics were related to the richness variables, implying that this control technique was effective and that we therefore obtained a clear assessment of the effect of intersection shape on plant richness.

Differences in intersection area among intersection shapes (Table 3) were probably just a physical result of the number of intersecting fencerows comprising L, T and X intersections. One could argue, however, that vertebrate-dispersed richness may have been higher in intersections with more avenues for influx simply because such intersections happened to be larger and therefore more structurally diverse (*cf.* Gutzwiller and Anderson 1987), which could have attracted a greater variety of birds and mammals, and hence plant seeds. That

is, the number of avenues of influx *per se* may not have been influential. Or, perhaps larger intersections had more species because these intersections were remnants of interior forest that still supported interior species as well as edge species that colonized sites following forest fragmentation. Both explanations are inconsistent with our data. Neither of the richness variables was correlated with area of the intersection (or, presumably, structural correlates of area), whereas vertebrate-dispersed richness was significantly associated with the number of possible avenues for plant influx. In addition, none of the plant species we encountered in intersections or fencerows requires mesic interior conditions (W.C. Holmes, personal communication), and the fencerows and intersections originated from seeds deposited along unplowed fencelines.

Distance to nearest connected intersection or patch differed among intersections shapes in such a way that this distance would have been expected to obscure rather than generate the hypothesized intersection-shape effects (Table 2). Significantly greater intersection effects were observed in the X-shape intersections (Fig. 2). Yet, X-shape intersections were located much farther from the nearest connected intersection or patch than were either T- or L-shape intersections (Table 2). Thus, plant richness in X-shape intersections was probably influenced less by connected vegetation than was plant richness in the other intersections that were more closely connected to potential plant sources. Bird and small-mammal abundance in shelterbelts can be high when the amount of contiguous wooded habitat also is high (Yahner 1983). Therefore, intersections located close to other intersections or wooded patches (potential sources of seed-dispersing vertebrates) might be expected to have higher plant richness than intersections that are farther away. In the networks we studied, however, this spatial pattern was not evident. Overall, the intersection-shape effects we detected were attributable to the number of intersecting fencerows, not to the structural or spatial characteristics of fencerows and intersections we measured.

Our analyses of two different measures of plant richness enabled us to compare results for different groups of species. Intersection-shape effects were evident for vertebrate-dispersed richness, but not for non-vertebrate dispersed richness. If intersec-

tions functioned fortuitously as crossroad areas for seed-dispersing birds and mammals moving along different fencerows, one would expect the number of intersecting fencerows to influence vertebrate-dispersed richness at intersections. In contrast, one would expect intersection-shape effects to have been less influential, or not important at all, for plant species that were primarily wind- or ant-dispersed. These latter vectors would be less likely to deposit seeds specifically at or near intersections, whereas birds and mammals that regularly use fencerow networks for feeding and resting move directionally along fencerows and frequently encounter intersections, where they could deposit seeds. Indeed, based on more than 200 hrs of observations in the networks we studied (S.K. Riffell, unpublished data), seed-dispersing birds and mammals regularly moved through intersections and along and within fencerows, using the adjacent agricultural matrix minimally if at all. Furthermore, from fall 1992 through spring 1993 and from fall 1993 through spring 1994, birds and mammals were observed feeding on fruits and nuts of vertebrate-dispersed plants present within the fencerows. Our results involving vertebrate-dispersed plant richness are consistent with reports (*e.g.*, Constant *et al.* 1976 cited in Forman and Godron 1986: 178; Lack 1988) of higher avian richness and abundance in intersections than in associated corridors.

Within the agricultural systems we studied, fencerow intersections were distinct concentrations, or nodes (*sensu* Noss and Harris 1986), of high plant richness relative to surrounding landscape elements. For this reason alone, intersections should be protected from degradation and destruction. Moreover, as concentrations of plant richness, intersections could function as *in situ* sources of plants for restoring and maintaining plant communities in agricultural landscapes. Available sources of seeds (McClanahan 1986), the dispersal and germination of seeds (Robinson *et al.* 1992; Robinson and Handel 1993; Chambers and MacMahon 1994), and the vegetative structure that initially develops after germination (McDonnell and Stiles 1983; McDonnell 1986) are all important in promoting and accelerating succession in disturbed open areas (McClanahan and Wolfe 1993).

Although fencerow networks would help main-

tain plant diversity in agricultural landscapes, network protection and management are not necessary to preserve the particular species we encountered because they are common and invasive. Our results concerning intersection shape may, however, be quite important for managing corridor networks that harbor rare and uncommon vertebrate-dispersed species. Additional work is needed to determine whether the patterns we observed are exhibited in other networks and by other taxa. If intersection-shape effects are widespread, knowledge about the patterns and processes involved could be used by landscape ecologists, conservation biologists, restorationists, and land-use planners to maintain or restore plant diversity.

Acknowledgments

We thank R. Fritz, F.R. Gehlbach, W.C. Holmes, and S.M. Pearson for valuable reviews of the manuscript; W.C. Holmes for help with identifying plants; H.A. Marcum for assistance with figure construction; H. Hohn, J. Pratt and F. Rascoe for permitting access to study sites; R. Schwank and the U.S. Soil Conservation Service for help with aerial photographs; C. McKnight and the Baylor University Geology Department for computer time and technical support; and A. Riffell for logistical support.

References

- Bennett, A.F., Henein, K. and Merriam, G. 1994. Corridor use and the elements of corridor quality: chipmunks and fencerows in a farmland mosaic. *Biol. Conserv.* 68: 155–165.
- Benninger-Truax, M., Vankat, J.L. and Schaefer, R.L. 1992. Trail corridors as habitat and conduits for movement of plant species in Rocky Mountain National Park, Colorado, USA. *Landsc. Ecol.* 6: 269–278.
- Best, L.B. 1983. Bird use of fencerows: implications of contemporary fencerow management practices. *Wildl. Soc. Bull.* 11: 343–347.
- Chambers, J.C. and MacMahon, J.A. 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. *Annu. Rev. Ecol. Syst.* 25: 263–292.
- Constant, P.M., Eybert, C. and Mahed, R. 1976. Avifaune reproductrice du bocage de l'Ouest. *In* Les bocages: histoire, ecologie, economie. pp. 327–332. Institut National de la Recherche Agronomique, Centre National de la Recherche Scientifique, Université de Rennes, Rennes, France.
- Dixon, W.J. (Chief Ed.). 1992. BMDP statistical software manual, Vol. 1. University of California Press, Berkeley, California.
- Forman, R.T.T. and Baudry, J. 1984. Hedgerows and hedgerow networks in landscape ecology. *Environ. Manage.* 8: 495–510.
- Forman, R.T.T. and Godron, M. 1986. *Landscape ecology*. John Wiley and Sons, New York, New York.
- Fritz, R. and Merriam, G. 1993. Fencerow habitats for plants moving between farmland forests. *Biol. Conserv.* 64: 141–148.
- Fritz, R. and Memam, G. 1994. Fencerow and forest edge vegetation structure in eastern Ontario farmland. *Ecoscience* 1: 160–172.
- Gutwiller, K.J. and Anderson, S.H. 1987. Multiscale associations between cavity-nesting birds and features of Wyoming streamside woodlands. *Condor* 89: 534–548.
- Hatch, S.L., Gandhi, K.N. and Brown, L.E. 1990. Checklist of the vascular plants of Texas. Texas Agricultural Experiment Station, College Station, Texas.
- Helliwell, D.R. 1975. The distribution of woodland plant species in some Shropshire hedgerows. *Biol. Conserv.* 7: 61–72.
- Henderson, M.T., Merriam, G. and Wegner, J. 1985. Patchy environments and species survival: chipmunks in an agricultural mosaic. *Biol. Conserv.* 31: 95–105.
- Holm, S. 1979. A simple sequentially rejective multiple test procedure. *Scand. J. Statistics* 6: 65–70.
- Johnson, W.C. and Adkisson, C.S. 1985. Dispersal of beech nuts by blue jays in fragmented landscapes. *Amer. Midl. Nat.* 113: 319–324.
- Lack, P.C. 1988. Hedge intersections and breeding bird distribution in farmland. *Bird Study* 35: 133–136.
- Lowe, J.C. and Moryadas, S. 1975. *The geography of movement*. Houghton Mifflin Company, Boston, Massachusetts.
- Mahler, W.F. 1988. *Shinner's manual of the north central Texas flora*. Botanical Research Institute of Texas, Inc., Fort Worth, Texas.
- McClanahan, T.R. 1986. The effect of a seed source on primary succession in a forest ecosystem. *Vegetatio* 65: 175–178.
- McClanahan, T.R. and Wolfe, R.W. 1993. Accelerating forest succession in a fragmented landscape: the role of birds and perches. *Conserv. Biol.* 7: 279–288.
- McDonnell, M.J. 1986. Old field vegetation height and the dispersal pattern of bird-disseminated woody plants. *Bull. Torrey Bot. Club* 113: 6–11.
- McDonnell, M.J. and Stiles, E.W. 1983. The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. *Oecologia* 56: 109–116.
- Merriam, G. and Lanoue, A. 1990. Corridor use by small mammals: field measurement for three experimental types of *Peromyscus leucopus*. *Landsc. Ecol.* 4: 123–131.
- Merriam, G. and Saunders, D.A. 1993. Corridors in restoration of fragmented landscapes. *In* Nature conservation 3: the reconstruction of fragmented ecosystems. pp. 71–88. Edited by D.A. Saunders, R.J. Hobbs and P.R. Ehrlich. Surrey Beatty and Sons, Chipping Norton, New South Wales.
- Miller, R.G., Jr. 1981. Simultaneous statistical inference, 2nd

- ed. Springer-Verlag, New York, New York.
- Mueller-Dombois, D. and Ellenberg, H. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York, New York.
- Neter, J. and Wasserman, W. 1974. Applied linear statistical models. Richard D. Irwin, Inc., Homewood, Illinois.
- Noss, R.F. 1987. Corridors in real landscapes: a reply to Simberloff and Cox. *Conserv. Biol.* 1: 159–164.
- Noss, R.F. and Harris, L.D. 1986. Nodes, networks, and MUMS: preserving diversity at all scales. *Environ. Manage.* 10: 299–309.
- Ott, R.L. 1993. An introduction to statistical methods and data analysis, 4th ed. Wadsworth Publishing Company, Belmont, California.
- Rice, W.R. 1989. Analyzing tables of statistical tests. *Evolution* 43: 223–225.
- Robinson, G.R. and Handel, S.N. 1993. Forest restoration on a closed landfill: rapid addition of new species by bird dispersal. *Conserv. Biol.* 7: 271–278.
- Robinson, G.R., Handel, S.N. and Schmalhofer, V.R. 1992. Survival, reproduction, and recruitment of woody plants after 14 years on a reforested landfill. *Environ. Manage.* 16: 265–271.
- Rosenberg, N.J., Blad, B.L. and Verma, S.B. 1983. Microclimate: the biological environment, 2nd ed. John Wiley and Sons, New York, New York.
- SAS Institute, Inc. 1989. SAS/STAT User's Guide, Version 6, 4th ed., Volume 2. SAS Institute, Inc., Cary, North Carolina.
- Schroeder, R.L., Cable, T.T. and Haire, S.L. 1992. Wildlife species richness in shelterbelts: test of a habitat model. *Wildl. Soc. Bull.* 20: 264–273.
- Shalaway, S.D. 1985. Fencerow management for nesting birds in Michigan. *Wildl. Soc. Bull.* 13: 302–306.
- Simberloff, D. and Cox, J. 1987. Consequences and costs of conservation corridors. *Conserv. Biol.* 1: 63–71.
- Simberloff, D., Farr, J.A., Cox, J. and Mehlman, D.W. 1992. Movement corridors: conservation bargains or poor investments? *Conserv. Biol.* 6: 493–504.
- Verts, B.J. 1967. The biology of the striped skunk. University of Illinois Press, Urbana, Illinois.
- Wegner, J.F. and Merriam, G. 1979. Movements by birds and small mammals between a wood and adjoining farmland habitats. *J. Applied Ecol.* 16: 349–357.
- Willmot, A. 1980. The woody species of hedges with special reference to age in Church Broughton Parish, Derbyshire. *J. Ecol.* 68: 269–285.
- Willson, M.F. 1986. Avian frugivory and seed dispersal in eastern North America. *Current Ornithology* 3: 223–279.
- Willson, M.F. 1993. Mammals as seed-dispersal mutualists in North America. *Oikos* 67: 159–176.
- Yahner, R.H. 1983. Small mammals in farmstead shelterbelts: habitat correlates of seasonal abundance and community structure. *J. Wildl. Manage.* 47: 74–84.
- Zar, J.H. 1984. Biostatistical analysis, 2nd ed. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

Appendix A. Plant species encountered in fencerow networks.¹

Common name	Scientific name
<i>Trees</i>	
Eastern red cedar (B, M)	<i>Juniperus virginiana</i>
Pecan (B, M)	<i>Carya illinoensis</i>
Blackjack oak (B, M)	<i>Quercus marilandica</i>
Post oak (B, M)	<i>Quercus stellata</i>
Sugar hackberry (B, M)	<i>Celtis laevigata</i>
Cedar elm (B, M)	<i>Ulmus crassifolia</i>
Red mulberry (B, M)	<i>Morus rubra</i>
Osage orange (B, M)	<i>Maclura pomifera</i>
Chickasaw plum (B, M)	<i>Prunus angustifolia</i>
Honey mesquite (M)	<i>Prosopis glandulosa</i>
Texas sophera	<i>Sophora affinis</i>
Hercules club (B)	<i>Zanthoxylum clava-herculis</i>
Chinaberry (B, M)	<i>Melia azedarach</i>
Smooth sumac (B, M)	<i>Rhus glabra</i>
Roughleaf dogwood (B, M)	<i>Cornus drummondii</i>
Gum bumelia (B, M)	<i>Bumelia lanuginosa</i>
<i>Shrubs</i>	
Possum-haw (B, M)	<i>Ilex decidua</i>
Waxleaf ligustrum (B, M)	<i>Ligustrum quihoui</i>
Chinese privet (B, M)	<i>Ligustrum sinense</i>
West Indian lantana	<i>Lantana camara</i>
<i>Vines</i>	
Saw greenbriar (B, M)	<i>Smilax bona-nox</i>
Dewberry (B, M)	<i>Rubus</i> sp.
Poison oak (B, M)	<i>Toxicodendron radicans</i>
Grape (B, M)	<i>Vitis</i> sp.
Japanese honeysuckle (B, M)	<i>Lonicera japonica</i>
<i>Other woody species</i>	
Yucca	<i>Yucca</i> sp.
Pricklypear (B, M)	<i>Opuntia</i> sp.
<i>Herbs</i>	
Crow-poison	<i>Nothoscordum bivalve</i>
Carolina anemone	<i>Anemone caroliniana</i>
Scrambled eggs	<i>Corydalis micrantha</i>
Mustard	<i>Brassica</i> sp.
Wedgeleaf draba	<i>Draba cuneifolia</i>
Tansymustard	<i>Descurainia pinnata</i>
Spreading erysimum	<i>Erysimum repandum</i>
Texas bluebonnet	<i>Lupinus texensis</i>
Vetch	<i>Vicia sativa</i>
Carolina geranium	<i>Geranium carolinianum</i>
Violet woodsorrel	<i>Oxalis violacea</i>
Hammenvort	<i>Parietaria pensylvanica</i>
Downy evening primrose	<i>Oenothera laciniata</i>
Prairie parsley	<i>Polytaenia nuttallii</i>
No common name	<i>Buglossoides arvensis</i>
Henbit deadnettle	<i>Lamium amplexicaule</i>
Mealycup sage	<i>Salvia farinacea</i>
Bedstraw	<i>Galium</i> sp.
Ragweed	<i>Ambrosia</i> sp.
False ragweed	<i>Parthenium hysterophorus</i>
Blessed milk thistle	<i>Silybum marianum</i>
Goldenrod	<i>Solidago</i> sp.
Common dandelion	<i>Taraxacum officinale</i>

¹ Letters in parentheses next to common names of vertebrate-dispersed species indicate known dispersal vectors; B = birds, M = mammals (Willson 1986, 1993; F.R. Gehlbach and W.C. Holmes, personal communication).