The spatial extent and relative influence of landscape-level factors on wintering bird populations[1]

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Abstract

The influences of the landscape matrix (complex of habitats surrounding a study plot) and within-patch vegetation were studied in bird communities wintering in the piedmont of Georgia, USA. Variation at the landscape and within-patch levels was controlled to reduce the likelihood of confounding and spurious relationships. The landscape matrix within 500 m of each study plot was quantified from aerial photographs. Statistical models using landscape matrix and within-patch vegetation variables explained 73–84% of variation in bird abundance and diversity among sites with landscape matrix variables accounting for 30–90% of the variation. Variation in bird species richness and diversity was explained solely by landscape variables. Models for individual species such as Carolina Wrens (*Thyrothorus ludovicianus*) and Rufous-sided Towhees (*Pipilo erythrophthalmus*) had $r^2 > 0.80$, with the landscape matrix variables accounting for the majority of this variation. However, other species like Northern Cardinals (*Cardinalis cardinalis*) and White-throated Sparrows (*Zonotrichia albicollis*) were most strongly influenced by within-plot vegetation. The landscape influence extended beyond habitats immediately adjacent to the study plots as indicated by significant variables describing variation in more distant habitat patches. These analyses illustrate a technique for comparing the strength of within-patch versus landscape influences and measuring the spatial extent of the landscape influence in fine-grained landscapes.

1. Introduction

In patchy landscapes, the spatial arrangement of habitats is likely to affect populations found within individual habitat patches. Several avian studies have demonstrated landscape-level effects on breeding birds (*e.g.*, Butcher *et al.* 1981; Freemark and Merriam 1986; Askins and Philbrick 1987; Blake and Karr 1987). However, only a few studies have addressed such effects in wintering birds (*e.g.*, Morgan and Gates 1982; Strong and Bock 1990). For example, Strong and Bock (1990) found that bird communities of riparian woodlands could be affected by the type of adjacent upland vegetation.

They showed that upland vegetation had a greater effect on these communities in winter than in summer.

During winter, vegetation provides food and protective cover required by birds (Pulliam and Mills 1977; Schneider 1984; Lima *et al.* 1987; Watts 1990). The type and structure of vegetation often determines the suitability of a particular habitat patch. Small habitat patches may also be functionally linked to a larger regional landscape. The type, variety, and spatial arrangement of habitats in the landscape could influence the number and diversity of birds wintering in a single patch. The landscape can affect the suitability of a particular patch (Bach 1988) or determine the regional pool of species that could potentially exploit a patch.

Determining the importance of local versus landscape-level effects is an important problem in landscape ecology. However, measuring the relative effect of within-patch versus landscape-level factors is difficult because of the logistical problems of conducting broad-scale experiments and manipulating entire landscapes, although this has been done for insect populations (Bach 1988). Correlations between within-patch and landscape variables can lead to ambiguous results. In this study, I measured the relative influence of within-patch conditions and landscape-level variation on wintering bird populations. Within-patch habitat characteristics were quantified by measuring vegetation. The size and spatial arrangements of the surrounding habitat patches were quantified to characterize the surrounding landscape matrix (sensu Forman and Godron 1986).

In this study, study plots that were similar in vegetation and uniform in shape and size were used to control within-patch variation. By choosing sites in primarily forested landscapes, I confined landscape-level variation within a small range relative to the extent of variation found among landscapes in the piedmont region of the Southeast. By limiting the variation at both levels, I controlled the number of factors potentially affecting the bird community. This control effectively reduced the likelihood of spurious relationships and confounding effects.

The relative influences of within-patch (fine scale) and landscape-level (broad scale) factors were evaluated by comparing their explanatory power as measured by coefficients of determination (r^2, Sokal and Rolhf 1981) in statistical models of bird populations. These models also indicated whether more distant patches affected bird populations found in the study plots. Since landscape matrix variables described spatially explicit information, the specific landscape variables included in the resulting models revealed the spatial extent of the landscape influence.

2. Methods

Bird communities were studied at 16 sites in the piedmont region near Athens, Georgia, U.S.A. These sites were located at least 1 km apart in electrical powerline and natural gas pipeline rights-of-way (ROWs) that were 45 m wide and 300 m long (Fig. 1). These ROWs consisted of old-field vegetation that was maintained by periodic mowing. The habitats on both sides of the ROW were considered the landscape matrix (sensu Forman and Godron 1986). The matrix was principally forest but also included some patches of early successional vegetation. I used eight sites in 1989 and eight different sites in 1990. Sites used in 1989 could not be reused in 1990 because they were mowed between field seasons. In each year, one half of the sites was located in powerlines, and the other half was located in pipelines. In each year, the landscape matrix around four of the sites was principally deciduous forest while the matrix around the remaining four sites was mostly pine and mixed woods.

The birds at each site were censused once a week for 12 weeks, January through March, using a fixed-width transect method (Kendeigh 1944). Only those birds observed within the ROW strip were counted. In order to estimate the average use of the study plot, the mean abundance of each species over the 12 censuses was calculated for each site. Means were also calculated for the three community indices: total bird abundance, species richness, and Shannon diversity (Shannon and Weaver 1948). Further details about the selection of study sites and bird censuses are given in Pearson (1991b).
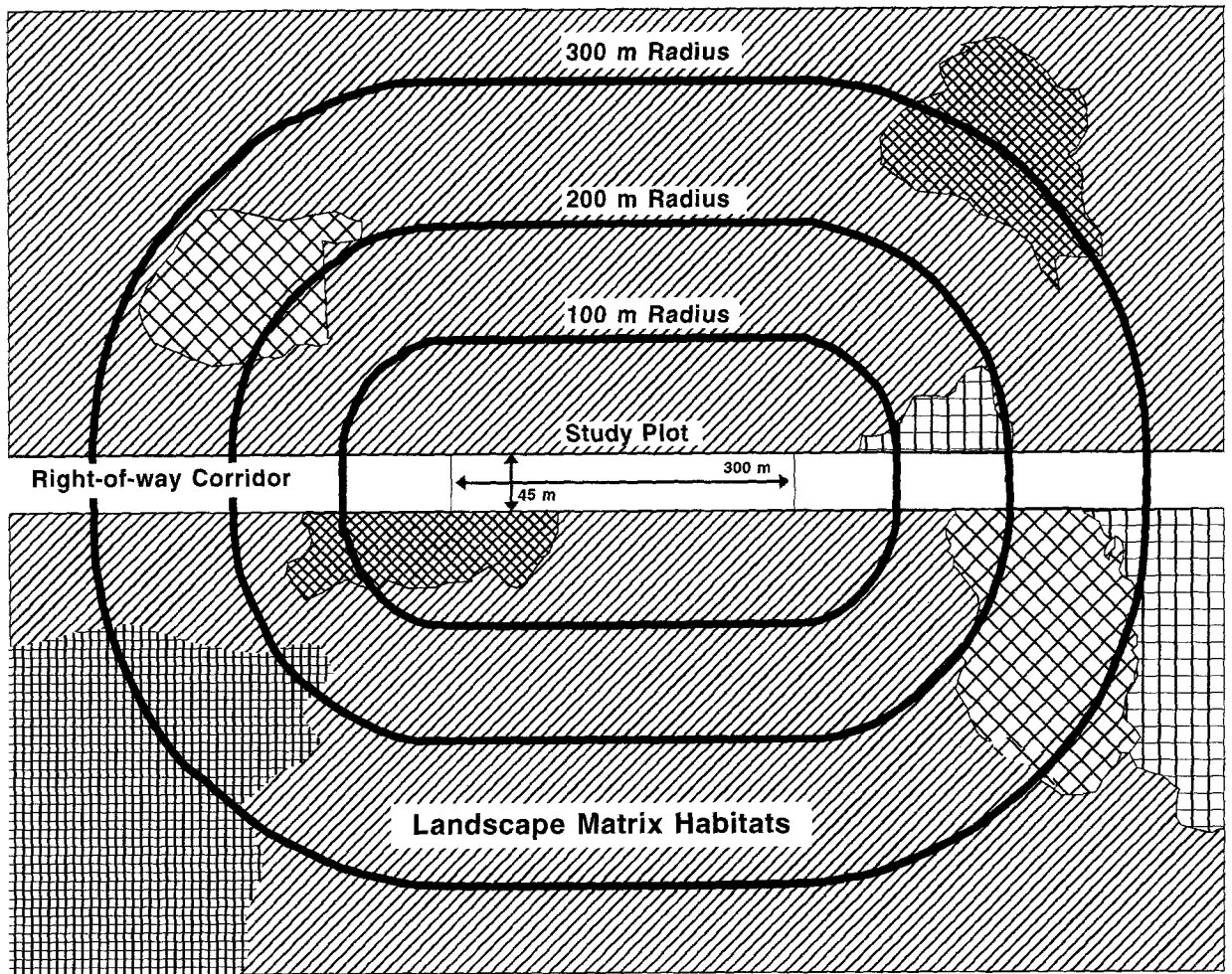
Fig. 1. Schematic diagram of utility right-of-way study plot and surrounding landscape matrix. The number and proportion of area of habitats in each 100 m-radius band were calculated from habitat map of each study site. Though only three are shown here, five 100 m bands were used on the actual maps. Data from each band were considered separately.

Vegetation in each ROW site was measured with a modification of the method of Mills *et al.* (1991). This method provides an index of vegetation volume in vertically stratified layers and records the taxonomic composition and structural physiognomy of the vegetation. Vegetation structure is highly important because most of the bird species studied respond strongly to the presence of protective cover offered by stout or dense vegetation (Lima *et al.* 1987; Watts 1990, 1991; Pearson 1991a).

Vegetation was measured at six groups of 16 points at each site. These 16 points were arranged in two perpendicular lines of 8 points each (*i.e.* a cross). Each cross was randomly positioned within a 50 m subsection of the 300 m long study plot. At each sample point, I held upright a metal pole marked in 10 cm increments to measure the vegetation. In each 10 cm interval along the pole, the taxa of vegetation occupying most of the volume of an imaginary cylinder 10 cm tall with radius of 10 cm circumscribed around the pole was recorded. Measurements were grouped into six vertical layers by combining data from five 10-cm sections into one group. Intervals for the six layers were: 0.1–0.5 m, 0.6–1.0 m, 1.1–1.5 m, 1.6–2.0 m, 2.1–2.5 m, and > 2.5 m. These data consisted of the number of cylinders (range 0–5) in each layer occupied by one of 4 classes of vegetation.

Vegetation taxa were lumped into 4 classes: woody, shrubby, grasses, and forbs (Appendix 1). These classes reflect the vegetative structure and type of protective cover offered by specific plant species. Woody vegetation included tree seedlings, woody shrubs, and vines. Shrubby vegetation included delicate shrubs, bramble-forming plants like *Rubus* spp. and *Rosa multiflora*, and tall stout weeds like *Erigeron canadensis* and *Lespedesa* spp. Members of the Poaceae (Radford *et al.* 1968) comprised the Grass class. The Forb class included more delicate forbs than those in the Shrubby class and shorter, less stout members of the Asteraceae (Radford *et al.* 1968). Plants in the Grass and Forb classes provide most of the winter food eaten by granivorous birds in this study (Pulliam and Enders 1971).

The landscape matrix around each site was quantified from 1988 National High Altitude Photography (NHAP) panchromatic aerial photographs (scale approx. 1:6000). These photographs were obtained from U.S. Agricultural Stabilization and Conservation Service, Salt Lake City, Utah. By visual interpretation, I delineated the boundaries of 10 habitat types (Appendix 2) within 500 m of each study plot on the photographs. The accuracy of habitat identification was verified by ground truthing over 70% of the habitat patches. Polygons describing the outline of each habitat patch were digitized manually by tracing the habitat boundaries. These digitized polygons were used to produce rectified raster grid-cell maps of the landscape matrix surrounding each study plot. These raster maps were generated and analyzed using utilities in Geographic Resource Analysis Support System (GRASS), a geographic information system (GIS) (CERL 1989).

Using the GIS, five concentric bands, each 100 m wide, were demarcated around the ROW study plots on each map (Fig. 1). Within each band, the proportion of area occupied by each of the 10 habitat types was calculated. In addition, I recorded the number of habitats in each band and calculated the Shannon diversity for each band. These data provided measurements of the composition and spatial arrangement of the landscape matrix around each plot. The concentric bands provide a

means of distinguishing between the influence of portions of the matrix close to and more distant to the ROW plot. For example, patches adjacent to the ROW may influence the birds there more strongly than patches 400 m away.

The vegetation and landscape measurements produced two sets of 24 (4 vegetation categories × 6 vertical layers) and 60 (12 habitat variables × 5 concentric bands) variables, respectively, each with its own covariance structure. To avoid the confusion of confounding between variables, this covariance structure was removed with factor analysis. Factor analysis with a principal components solution was used to reduce the number of variables in each data set. The number of factors for each data set was determined by examining the number of principal components having eigenvalues greater than 1.0. The resulting factors and their scores represented interpretable, independent measurements of variation within these data sets that could be used in subsequent statistical analysis (Johnson and Wichern 1988). Landscape and vegetation data were analyzed separately.

Since the numbers of wintering birds differed between years of the study (see Results), I used multiple analysis of variance to test for between-year differences in the vegetation and matrix factors. I also tested for differences in the vegetation between two groups of eight sites. In one group, the matrix was principally pine forest. In the other, it was mostly deciduous forest.

Using the factor scores, statistical models to describe the variation in the bird communities were constructed. The response variables included indices of the whole bird community (total number of birds, species richness, and Shannon diversity), of subgroups within the community (forest, early successional, and generalist species; see Appendix 3), and of individual species for which there were sufficient data. Community subgroups (early successional, forest, and generalist) reflect the type of habitat where individual bird species are most commonly found (Hamel *et al.* 1982). Two species, Carolina Chickadee and Tufted Titmouse (species' scientific names listed in Appendix 3), were combined into one group, parids, to increase sample size and normality of their data. These species are

very similar ecologically and were almost always recorded together. Stepwise multiple regression was used to select and evaluate the explanatory power of specific vegetation and matrix factors for these habitat models. No regression variable was included that had $P > 0.05$ or had $r^2 < 0.10$ unless noted in the results. No more than three variables per model were included. To detect non-linearity between the bird and habitat variables, the residuals from each regression were plotted against the habitat variables included in the model. No non-linear relationships were detected, and a null hypothesis of homoscedasticity among the habitat variables could not be rejected. All analyses were performed using PC-SAS (SAS 1987).

3. Results

3.1. Bird populations

The general trends in the bird populations relative to year of study, ROW type, and dominant habitat in the landscape matrix are presented here. There were more than twice as many individual birds at each site in 1989 as there were in 1990 (means ± SD: 1989, 7.25 ± 5.78; 1990, 2.15 ± 1.27; F = 40.5, P < 0.01). Powerline sites had more individuals (F = 41.1, P < 0.01) and more species (F = 79.8, P < 0.01) than the pipeline sites (Fig. 2). Sites with the landscape matrix dominated by deciduous woods had more individuals (F = 26.2, P < 0.01) and higher species richness (F = 32.0, P < 0.01, Fig. 2) than ROWs surrounded primarily by pine woods. Bird abundances tended to decline toward the end of the winter in both years (mean ± SD number of birds/site/census: first 6 censuses, 5.1 ± 0.18; last 6 censuses 2.6 ± 0.13; t_{10} = 5.26, P < 0.005). However, these within-year trends were removed by averaging over the 12 censuses.

3.2. Factor analysis

The first 5 vegetation and first 12 matrix PCs had eigenvalues > 1 and accounted for 88.1% and 97.3% of the variation of their respective data sets.
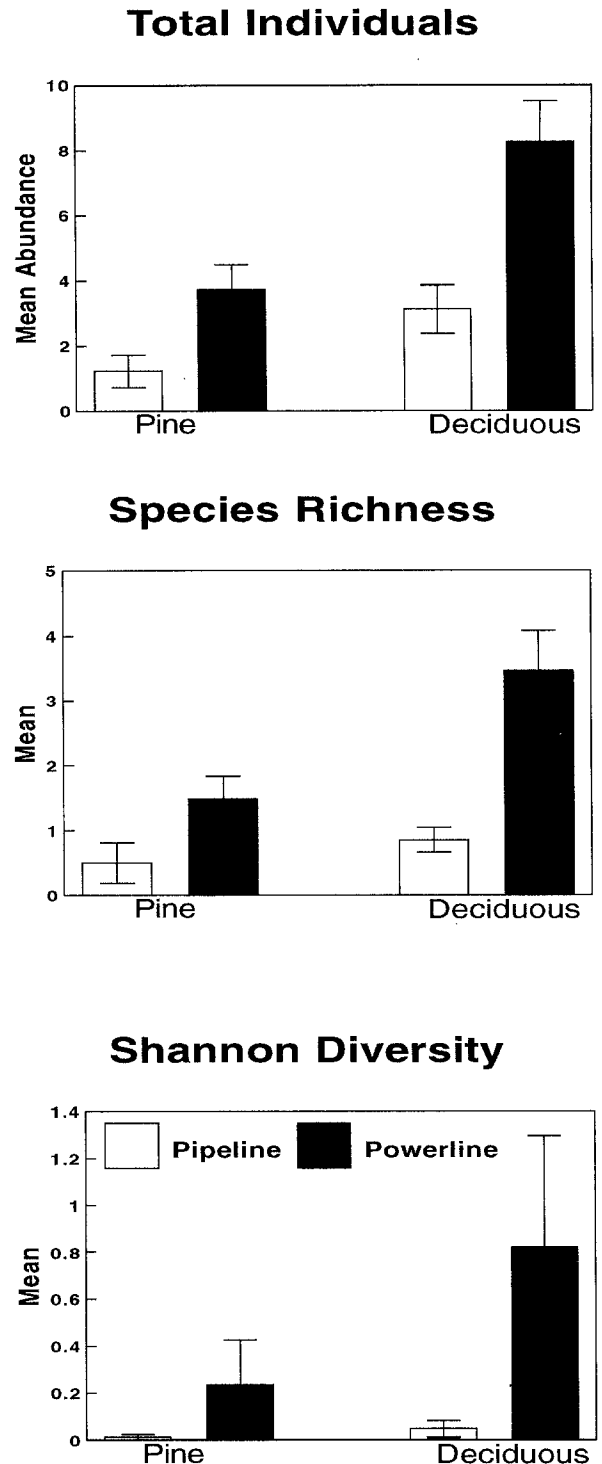

Fig. 2. Community-wide indices of ROW bird communities. Each bar represents mean ± SE of 4 sites in that particular treatment combination.

Table 1. Interpretation of vegetation and matrix factors based on factor loadings. Vegetation factors explain variation in the vertical stratification of four types of vegetation. Matrix factors summarize variation in 12 landscape variables measured in five concentric bands around each ROW plot.

Vegetation factor	Description	Proportion of Total variation
V1	Woody $<$ 1.5m, Forbs $>$ 0.5m	0.264
V2	Woody $>$ 1.5m, Grass $>$ 1.5m, Shrubb $>$ 2.0m	0.261
V3	Shrub	0.239
V4	Grass $<$ 1.5m	0.140
V5	Forb $<$ 0.5m	0.096
Matrix Factor	Description[1]	
M1	Deciduous 100–500, Pine 100–400[2]	0.137
M2	Clearcut 100–300, Scrub 200–500	0.130
M3	Residential/Many trees 100–500, Clearcut 500	0.100
M4	# Habitats 300–500[3], Habitat diversity 400–500	0.096
M5	Scrub 100	0.094
M6	# Habitats 200, Pasture 400–500	0.078
M7	Residential/Few trees 100–400	0.074
M8	Pasture 100–300	0.070
M9	Abandoned Agriculture. 200–300, Row Crops 200	0.066
M10	# Habitats 100, Habitat Diversity 100–200, Mixed Woods 300	0.063
M11	Mixed Woods 400–500	0.049
M12	Abandoned Agriculture 400–500	0.042

[1] Numbers represent 100 m-wide bands. For example, M1 includes variation in proportion of deciduous woods in all five 100 m-wide bands and proportion of pine woods in the first four bands. The first band (100 m) is closest to the ROW plot. See Fig. 1.

[2] Deciduous and pine woods are negatively correlated (see Results). All other habitats within a factor are positively correlated.

[3] Number of habitats recorded in the 300, 400 and 500 m concentric bands. M6 and M10 also follow this format.

Therefore, five vegetation and 12 matrix factors were obtained using factor analysis (Table 1). These factors were interpreted by examining their loadings on the original variables (Table 1, loadings are listed in Pearson 1991b). Vegetation factors V1 and V2 represent woody vegetation less than and greater than 1.5 m tall, respectively. Tall shrubs, forbs, and grasses also contribute to these factors. Factor V3 describes shrubby vegetation in general, and factors V4 and V5 represent shorter grasses and forbs (Table 1).

Some large habitat patches were wider than the 100-m bands and therefore occupied several contiguous, concentric bands. This resulted in correlations between data in adjacent bands. The factor analysis identified this correlation structure and extracted orthogonal, independent factors from the matrix data. Matrix factor M1 included deciduous woods across all five bands and pine woods across the first four (Table 1). This spatial correlation

reflected the fact that deciduous and pine forests tended to occur in large patches around the study sites. The occurrence of pine and deciduous forest were negatively correlated with each other, as reflected in the factor loadings of M1 (listed in Pearson 1991b). Except for M1, all habitat variables included in a single factor were positively correlated. The factor scores (Appendix 4) are scaled measures of frequency of given habitats relative to other sites in the data set. A large negative score indicates a relatively low frequency of habitats characterized by a factor, and a large positive score indicates relatively high frequency of those habitats as compared to other sites. Several landscape factors described habitat diversity close to (M6, M10) and farther away from (M4) the ROW plots. Factors M8, M9, and M12 describe the occurrence of agricultural land in the surrounding landscape. A few variables like the proportion of mixed woods in the first and second 100-m bands did not load

Table 2. Habitat models generated by stepwise regression analysis. Variables beginning with a 'V' denote within-plot vegetation factors. Variables beginning with a 'M' denote landscape matrix factors (see Table 1 for variable definitions). The partial r^2 for each variable is given in parentheses. Variables with higher r^2 are listed first. Unless noted all habitat variables have P < 0.05 (*P ≤ 0.03, **P ≤ 0.02, ***P ≤ 0.01). Model r^2 is coefficient of determination for entire regression equation. Matrix r^2 shows amount of variation explained by only the landscape matrix variables. The intercepts and coefficients for these models are listed in Pearson (1991b).

Bird variables		Habitat variables					Model r^2	Matrix r^2
Total birds	=	V3*** (0.49)	+	M4*** (0.24)			0.73	0.24
Species richness	=	M1*** (0.64)	+	M6 (0.10)			0.74	0.74
Shannon diversity	=	M1*** (0.59)	−	M8** (0.12)	+	M6* (0.11)	0.82	0.82
Forest	=	M1*** (0.57)	+	V1*** (0.17)	+	V3** (0.10)	0.84	0.57
Early successional	=	M4 (P = 0.10) (0.18)					0.18	0.18
Generalist	=	V3*** (0.60)	+	M4* (0.14)			0.73	0.13
Parids	=	M1*** (0.65)	+	V1* (0.11)			0.76	0.65
Carolina Wren	=	M1*** (0.48)	+	V1*** (0.24)	+	V3** (0.11)	0.83	0.48
Field Sparrow	=	M4 (P = 0.053) (0.24)					0.24	0.24
Dark-eyed Junco	=	M4 (P = 0.055) (0.24)					0.24	0.24
Northern Cardinal	=	V3*** (0.52)	+	M1*** (0.19)	+	M2** (0.12)	0.83	0.31
Rufous-sided Towhee	=	M1*** (0.54)	−	V4** (0.18)	+	V3** (0.11)	0.83	0.54
Song Sparrow	=	M1 (P = 0.09) (0.19)					0.19	0.19
White-throated Sparrow	=	V3*** (0.83)					0.83	0

heavily into any of the factors.

There were no between-year differences in the landscape matrix (F = 1.78, P = 0.42) or vegetation (F = 2.00, P = 0.17). None of the landscape and vegetation factor scores was significantly correlated among sites (P > 0.05). The group of sites surrounded principally by deciduous woods had significantly higher positive scores of factor M1 than sites surrounded mainly by pine woods (F = 9.69, P = 0.043). These two groups were not significantly different as measured by the other 11 matrix factors (all P > 0.09). The two types of ROW, powerline and pipeline, were significantly different with respect to their vegetation (F = 6.67, P < 0.01). Powerlines had more short woody vegetation, *i.e.* higher scores of vegetation factor VI. The ROW types did not differ for any of the other vegetation factors. The landscape matrix measurements were not significantly different for the two types of ROW (F = 5.53, P = 0.16).

3.3. Habitat regression models

While the total number of birds was most strongly related to the amount of shrubby vegetation (V3, r^2

= 0.49, Table 2), over 30% of the variation was accounted for by habitat diversity and forest type. Variation in species richness and Shannon diversity was explained solely by landscape matrix variables describing forest type, habitat diversity, and pasture. Forest birds were related to both forest type and ROW (Table 2). Birds of early successional habitats were not significantly correlated to any variable although landscape diversity explained about 18% of their abundance. Habitat generalist birds were modeled by shrubby vegetation and to a lesser degree by landscape diversity.

The landscape matrix explained 0–65% of the variation in abundances of individual species. Matrix factors had a combined r^2 of 48% or higher for Carolina Wren, Rufous-sided Towhee, and the parid species. Forest type (deciduous or pine) was the most important variable in these models followed by short woody vegetation (V1) in the wren and titmice models. Grasses (V4) were important in explaining the abundance of the towhees. Shrubby vegetation was important in models of towhees and wrens, and had the highest r^2 among variables in Northern Cardinal and White-throated Sparrow models. Models for Song Sparrow, Field Sparrow, and Dark-eyed Junco were only marginally significant ($0.10 > P > 0.05$) and included one matrix variable, either forest type (M1) or distal landscape diversity (M4). Song Sparrows and Field Sparrows were the most regular species among the study sites occurring in 90% of the ROW plots. In contrast, Dark-eyed Juncos were found at only 31% of the sites.

Matrix factors M4, M6, M9, M11, and M12 represent variation in the more distal patches (beyond the first 100 m band) of the landscape matrix (Table 1). The inclusion of these factors in habitat models indicates that the landscape influence extended beyond the more proximal matrix patches. At least one of these distal landscape factors was included in two of the community-wide (total number of birds and Shannon diversity) and two of the community subgroup (generalist and early successional) models (Table 2). Other matrix factors (*e.g.*, M2) also included information from distal portions of the matrix. However, this distal variation is not separable from variation in more proximal areas due to the covariance structure of the landscape data. Because the factors M4 and M6 do not include any proximal matrix variation, their significance suggests that the landscape influence extended beyond the habitats immediately adjacent to the ROWs.

4. Discussion

Landscape variables accounted for a large percentage of the explanatory power of the statistical habitat models. Some models, particularly of bird diversity, demonstrate the strong influence that the landscape had on these relatively small strips of old-field habitat. The inclusion of both landscape and within-plot vegetation in these models indicates that variation both within the right-of-way (ROW) and in the surrounding landscape matrix was important to these bird communities. Despite the between year differences in bird abundance, the year variable was not included in any of the habitat models.

4.1. Community-level patterns

Bird species diversity in the ROW can be explained as a function of the landscape. Deciduous woods hold more species than pine forest and, accordingly, ROW sites surrounded by deciduous woods contained more bird species (Quay 1947, Fig. 2). Species diversity was positively related to landscape diversity in the band immediately adjacent to the ROW (M6), a result that agrees with other studies (Freemark and Merriam 1986; Raivio and Haila 1990). Most of the species recorded in the ROWs are rarely observed in pasture habitats (M8) (Quay 1947) which had a negative effect on both models of species diversity (Table 2).

Functionally, the landscape determined the pool of potential species that could exploit the small old-field patches, whereas the vegetative characteristics within the ROWs determined whether a patch was suitable for individual species. For example, birds associated with forest habitats (Appendix 3) are more common in deciduous forest than in pine

forest in the southeastern U.S. (Quay 1947; Hamel *et al.* 1982) as well as in my study area (Pearson 1991b). Accordingly, the forest type (M1, M11) surrounding a patch affected the local abundance of these birds. Woody and shrubby vegetation (V1, V2, V3) provide appropriate foraging substrate for the bark-foraging species of these forest birds. Therefore, the combination of suitable landscape and suitable ROW results in the highest abundance of these forest species. In the four powerline ROWs where the matrix was dominated by deciduous woods, the mean abundance of forest birds was 1.7 individuals/census; however, mean abundances for all other sites were less than 0.4 individuals/census (Fig. 2).

Results pertaining to generalist birds (Appendix 3) can be interpreted in a similar way. Generalist species winter in a variety of habitat types (Hamel *et al.* 1982), so the landscape effect should not be as strong as for more specialized species. The generalists may have responded more strongly to fine-scale features of habitats rather than to gross habitat categories like those obtained from the aerial photographs. The regression model for generalists shows that they were highly correlated with a component of the ROW vegetation (V3, $r^2 = 0.60$) demonstrating this fine-scale discrimination. They were also correlated with landscape diversity (M4) reflecting their ability to use a wide range of habitat types.

Analyses of community-wide indices are more difficult to interpret because they include a composite response of many individual species. However, some species may respond similarly to local and landscape-level habitat characteristics. Over 80% of individuals recorded in the ROW plots belonged to species classified as either early successional or generalist, based on habitats where they are most frequently observed. The abundance of generalists was positively correlated with the total number of individuals (Table 3). Therefore, the model for generalist was statistically related to the total bird abundance model. Not surprisingly, variables describing within-plot vegetation and landscape diversity (V3 and M4) were included in both models. The abundances of some members of the forest (Carolina Wrens, Carolina Chickadee, Tuft-

ed Titmouse) and generalist (Northern Cardinal, Rufous-sided Towhee) subgroups were correlated (all $r > 0.70$, Table 3). Forest type (M1) was included in models for each of these species and for the forest subgroup. Shrubby vegetation (V3) was included in models for these species (except the parid model) and in the generalist model (Table 2). Thus, these species responded in a similar way to the same pair of landscape and within-plot variables.

4.2. Individual species

Statistical models for individual species are best understood from the perspective of each species' natural history and habitat preferences. The abundance of parids in the ROW was positively related to deciduous forest and woody vegetation in the ROW but negatively related to habitat diversity immediately adjacent to the ROW. This latter result may reflect their preference for forested (particularly deciduous forest) habitats. As the habitat diversity increases, the proportion of the landscape in deciduous or mixed woods must decline since habitat types were exclusive.

Northern Cardinal is a generalist species that prefers deciduous forest landscapes (Austin 1968; Hamel *et al.* 1982; Kroodsma 1982) but also responded to local vegetation in this study. This species is capable of feeding on the buds and fruits of shrubs and trees, which were more abundant in deciduous forests. Rufous-sided Towhee is a relatively large, granivorous, cover-dependent species (Lima *et al.* 1987). It responded positively to shrubby vegetation (V3) which provided protective cover and negatively to the grass component (V4) of the ROW vegetation. This negative response to grass may reflect the extreme cover dependence of towhees. Thickets of heavy cover often have little grass underneath the short canopy of brambles or saplings (pers. obs.). The model for White-throated Sparrow, another cover-dependent species (Morgan and Gates 1982; Schneider 1984; Pearson 1991a), included only one variable (V3) describing variation in the amount of shrubby vegetation in the ROW. This model explained 83% of the variation in this species abundance.

Table 3. Pearson correlation coefficients among bird variables. Only correlations with P < 0.01 are listed. Variable abbreviations as in Appendix 4.

	Rich	Diver	Forest	Esucc	General	Titmice	CAWR
Total	0.87	0.80	0.67	–	0.89	0.67	0.64
Rich	1.00	0.97	0.86	–	0.72	0.86	0.84
Diver		1.00	0.88	–	0.67	0.86	0.89
Forest			1.00	–	–	0.92	0.95
Esucc				1.00	–	–	–
General					1.00	–	–
Titmice						1.00	0.88

	FISP	DEJU	NOCA	RSTO	SOSP	WTSP
Total	–	–	0.69	–	0.70	0.80
Rich	–	–	0.72	0.84	–	0.69
Diver	–	–	0.72	0.84	–	0.69
Forest	–	–	0.64	0.78	–	0.63
Esucc	0.89	–	–	–	0.72	–
General	–	–	0.70	0.63	–	0.83
Titmice	0.88	–	–	0.74	0.82	–
CAWR	–	–	–	0.82	–	0.62
FISP	1.00	–	–	–	–	–
DEJU		1.00	–	–	–	–
NOCA			1.00	0.75	–	0.76
RSTO				1.00	–	0.70
SOSP					1.00	–

Models explaining a significant amount of variation could not be constructed for the abundance of Song Sparrows, Field Sparrows and Dark-eyed Juncos. Song Sparrow was the most commonly observed species in the ROW and can be found in most early successional and brushy habitats in the southeastern U.S. piedmont (Quay 1947; Austin 1968). Song Sparrows were not significantly affected by either the landscape or the ROW vegetation, although they tended to be more abundant in deciduous forest landscapes. The abundances of Field Sparrows and Dark-eyed Juncos might have been complicated by their social behavior. During the winter, both species congregate into flocks that wander over areas much larger than the study plots. This behavior leads to high variance in abundance estimates since the number of birds recorded depends on the presence or absence of an entire flock. The abundance estimate at any one site depended on number of times the resident flock was recorded. Many of the other species observed also occur in flocks. However, these flocks tended to be more sedentary and more likely to be found in the same area from census to census (pers. obs.).

4.3. The likelihood and measurement of landscape-level effects

The landscape influence is important in open systems (Wiens 1989) where the dynamics within habitat patches are strongly coupled to other patches (*e.g.* Pulliam and Danielson 1992) and when the ecological neighborhood (Addicott *et al.* 1987) is larger than an individual patch. Mobile organisms may regularly travel between different patches in search of resources. A landscape may support a population or community where individual habitat patches alone cannot. The suitability of different landscapes will depend on the frequency and spatial distribution of critical habitats and resources.

The ecological neighborhood of an individual depends on the distribution of its required resources.

Maximum neighborhood size is determined by maximum distance an individual travels during the study (Addicott *et al.* 1987). The landscape configuration may influence these movement rates (Gardner *et al.* 1989; Wiens and Milne 1989). The minimum neighborhood size contains the minimal amount of resources required. Therefore, neighborhood size should be different in landscapes that vary in the amount and spatial distribution of primary and complementary resources (O'Neill *et al.* 1988; Dunning *et al.* 1991). The neighborhood may also depend on the spatial distribution of other interacting organisms, like competitors or predators, which in turn may be affected by the landscape. Knowledge of species resource requirements and how those resources are distributed in the landscape may allow ecologists to predict when a landscape effect is likely. Simply predicting that landscape is important is not sufficient for understanding its role in population regulation and community composition. Ecologists must also assess its relative importance to animals in specific habitat or patch types.

Measuring the landscape influence presents several experimental design problems. First, proper sample sizes for rigorous testing are difficult to obtain. One site is one sample. When estimating parameters for one site is labor and time intensive, the number of sites is constrained by logistical considerations. In this study, the number of sites was also limited by their availability. Small numbers of sites (small samples) may result in statistical tests of low power. Experiments suffering from pseudoreplication (Hurlbert 1984) provide only equivocal results. Secondly, landscape-level factors must be separable from within-patch factors. When these two sets of factors are confounded, the appropriate statistical tests may be, at best, difficult to perform, and the results may not adequately answer the questions that motivated the experiment. Multivariate data reduction techniques, such as principal components analysis, are useful for removing the covariance structure often characteristic of large observational data sets. Small sample size and confounding of factors affect correlative analysis, including regression, as well as analysis of variance.

In long, narrow plots like ROW corridors, the surrounding matrix is likely to have a strong influence on the dynamics within the plot due to the high edge-to-area ratio. The relative influence of the matrix will depend on the distance that matrix effects extend into a habitat patch and the shape and area of the patch (Wilcove *et al.* 1986). These ROW plots were probably too narrow to have a core area unaffected by the matrix. Due to the proximity to forest edge, forest birds recorded were able to use resources distributed through most, if not all, portions of the ROW plot. Nevertheless, the results show the importance of the within-plot vegetation. The abundance of White-throated Sparrows was not affected by variation in the matrix but strongly dependent on ROW vegetation. ROW vegetation explained at least 50% of the variation in the total number of birds and the abundance of generalists and Northern Cardinals (Table 2). If the ROW corridor had been substantially wider, the within-plot vegetation would have had a stronger influence on the bird community. Portions of the ROW might have been inaccessible to the forest birds due to distance from the edge. Some species, like Savannah Sparrows, typically found in larger patches of old-field habitat would have become more common and accounted for a higher proportion of the community.

4.4. Spatial extent of landscape influence

The landscape had the strongest influence on the diversity of the ROW bird community. It also explained much of the variation in species normally associated with forested habitats. How much of the surrounding landscape contributed this influence? The spatial extent of the landscape influence on a site might be measured by the distance to the most distant habitat patches that influence populations in a given patch. This distance measurement would be useful for designing management and conservation strategies that strive to preserve threatened or rare populations. If this distance were known, a manager would know how much of the landscape matrix to include in management scheme designed to protect populations in a particular patch. Edge effects, a type of landscape influence, have been

measured in large continuous habitat patches such as large tracts of forest (Temple and Cary 1988) by recording gradients in physical properties (temperature, light), nest predation rates, or 'edge' species abundance. However, measuring the spatial extent of the landscape influence in habitat mosaics is very different since gradients like these may not be apparent. The extent of this influence in these mosaics depends on spatial patterns of variation in the landscape and the ecological neighborhood of the study organisms (Addicott *et al.* 1987; Wiens 1989).

If spatial patterns in the landscape are very coarse (*i.e.* large patches) relative to the ecological neighborhood of the study species, then the landscape influence may not extend beyond adjacent patches. Alternatively, if landscape-level variation is fine (*i.e.* small patches), then more distant patches may have an effect. Measuring the extent of the influence may be possible in these fine-grained landscapes. Consider the effect of landscape diversity (number and Shannon diversity of habitats) on the bird community as an illustration. The grain of the landscape was more coarse than the spatial data. Landscape patterns were quantified to grain size of 100 m (the concentric bands, Fig. 1). However, many of the patches occupied more than one band resulting in correlations among some of the 100 m-wide bands (Table 1 and Pearson 1991b). Variation in landscape diversity was correlated among the first and second 100 m bands and among the third through the fifth bands (cf. M4, M6 and M10 in Table 1; Pearson 1991b).

This study provides an example of measuring the extent of influence in landscapes with some fine-grained variation. Matrix factor M4, which describes variation in distal portions of the matrix, was a significant variable in models for total number of birds, number of generalist, and abundance of Field Sparrows and Dark-eyed Juncos. For these bird measurements, there is evidence that the landscape influence extended to at least 300 m from the ROW plot. It may have extended further, but it could not be measured beyond the 300 m band since data from the 400 and 500 m bands were correlated with that band. Landscape diversity in the more proximal bands (100–200 m) described, in part, by M6 was included in the model of bird species diver-sity. For this model, the extent of the landscape effect was not detectable beyond 200 m in this study. It may have been somewhat less than 200 m, but I cannot know because of the covariance structure of the landscape data. These conclusions about the extent of landscape influence apply only to this particular data set, but illustrate how similar models produced from spatial data may be interpreted.

The recognition of landscapes as functional units is an important development in our understanding of ecological processes. In open systems, the landscape setting of individual habitat patches cannot be ignored. Landscape ecology will be important in understanding ecological process, but it will also benefit applied problems in conservation and land management. Beyond the intuitive opinions of natural resource scientists, landscape-level studies will provide the empirical evidence to convince policy makers of the necessity of a broader-scale (in both time and space) perspective for environmental protection and management.

5. Acknowledgements

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Appendix 1. Plant species recorded during vegetation measurement and their assignment to four groups. Names from Radford *et al.* (1968). Group designations: W = woody, S = shrubby, G = grasses, and F = forbs.

Species	Group	Species	Group
Acer spp.	W	*Andropogon* spp.	G
Alnus serrulata	W	*Aristida* spp.	G
Carya spp.	W	*Arundinaria* gigantea	G
Cornus spp.	W	*Bromus* sp.	G
Crategus spp.	W	*Digitaria* spp.	G
Liquidambar styraciflua	W	*Egagrostis* spp.	G
Liriodendron tulipifera	W	*Hordeum pusillum*	G
Oxydendrum arboreum	W	*Leptoloma cognatum*	G
Pinus spp.	W	*Panicum* spp.	G
Platanus occidentalis	W	*Paspalum* spp.	G
Prunus spp.	W	*Festuca* sp.	G
Quercus spp.	W	*Setaria* spp.	G
Robinia pseudo-acacia	W	*Sorghum halepense*	G
Salix spp.	W	*Stipa* sp.	G
Sassafrass alibdum	W	*Tridens flavus*	G
Smilax spp.	W	*Allium* sp.	F
Sumac spp.	W	*Ambrosia artemisiifolia*	F
Ulmus alata	W	*Aster* spp.	F
Vitus sp.	W	*Carduus* spp.	F
Erigeron canadensis	S	*Carex* spp.	F
Eupatoria capillifolium	S	*Cassia obtusifolia*	F
Heterotheca subaxillaris	S	*Chenopodium* sp.	F
Lespedesa sp.	S	*Cyperus* spp.	F
Ligustrum sp.	S	*Dioda* spp.	F
Lonicera japonica	S	*Eupatoria* spp.	F
Phytolacca americana	S	*Helianthus* spp.	F
Pueraria lobata	S	*Hypericum* spp.	F
Rosa multiflora	S	*Opuntia compressa*	F
Rubus spp.	S	*Polystichum acrostichoides*	F
Sambucus canadensis	S	*Verbena urticfolia*	F
Solidago spp.	S		

Appendix 2. Habitats identified by visual interpretation of panchromatic aerial photographs.

Name (abbreviation)	Definition

Clearcut (CC) − Formerly forested areas where all mature trees were removed by logging operations.
Pasture (PA) − Agricultural areas dominated by cool season grasses (primarily *Festuca*) used for grazing.
Row Crops (RC) − Agricultural land that had been actively cultivated with the past 2 years.
Residential Areas / Many Trees (RM) − More than 30% of lawn areas covered tree canopy.
Residential Areas / Few Trees (RF) − Less than 30% of lawn areas covered tree canopy.
Deciduous Woods (DW) − Forest where < 20% of canopy contained coniferous trees.
Pine Woods (PINE) − Forest where > 70% of canopy contained coniferous trees of genus *Pinus*.
Mixed Woods (MW) − Rest where between 20% and 70% of canopy comprised of coniferous trees or principally deciduous forest with coniferous or evergreen understory.
Abandoned Agricultural Land (AAGR) − Agricultural land no longer being cultivated or grazed covered by short or tall weeds and successional grasses such as Andropogon. Furrows from cultivation no longer apparent from ground or on aerial photograph.
Scrub (SCRB) − Formerly open areas presently covered by thickets and brambles.

Appendix 3. Scientific names of birds recorded in ROW study plots. Species grouped according to the habitats where they are most commonly observed. Compilied using data from Hamel *et al.* (1982).

Habitat group/Common name	Scientific name
Forest group	
Carolina Wren	*Thyrothorus ludovicianus*
Winter Wren	*Troglodytes troglodytes*
Tufted Titmouse	*Parus bicolor*
Carolina Chickadee	*Parus carolinensis*
Red-bellied Woodpecker	*Melanerpes carolinus*
Brown-headed Nuthatch	*Sitta pusilla*
Pine Warbler	*Dendroica pinus*
Yellow-rumped Warbler	*Dendroica coronata*
Blue Jay	*Cyanocitta cristata*
Hermit Thrush	*Catharus guttatus*
Fox Sparrow	*Pasarella iliaca*
Early successional group	
Common Yellowthroat	*Geothlypis trichas*
Northern Mockingbird	*Mimis polyglottos*
Field Sparrow	*Spizella pusilla*
Song Sparrow	*Melospiza melodia*
Savannah Sparrow	*Passerculus sandwichensis*
Vesper Sparrow	*Pooecetes gramineus*
Eastern Meadowlark	*Sturnella magna*
Grasshopper Sparrow	*Ammodramus savannarum*
Northern Bobwhite	*Colinus virginianus*
House Wren	*Troglodytes aedon*
General group	
Dark-eyed Junco	*Junco hyemalis*
Eastern Bluebird	*Sialia sialis*
Eastern Phoebe	*Sayornis phoebe*
Swamp Sparrow	*Melospiza georgiana*
Brown Thrasher	*Toxostoma rufum*
White-throated Sparrow	*Zonotrichia albicollis*
Rufous-sided Towhee	*Pipilo erythrophthalmus*
Northern Cardinal	*Cardinalis cardinalis*
Armerican Goldfinch	*Carduelis tristis*

Appendix 4. Data for each study site used in multiple regression models. Total number of individuals (Total) and number of species (Rich) is listed. Species diversity (Diver) was measured by Shannon diversity index. The number of individuals belonging to three groups of species: forest (Forest), generalist (General), and early successional (Esucc) (see Appendix 3), and the abundance of Caroliona Wrens (CAWR), Field Sparrows (FISP), Northern Cardinals (NOCA), Rufous-sided Towhees (RSTO), Song Sparrows (SOSP), White-throated Sparrows (WTSP), Dark-eyed Juncos (DEJU), and Carolina Chickadees and Tufted Titmice (Titmice) are listed. Veg1–5 and Mat1–12 list the factor scores for the vegetation and landscape matrix factors, respectively.

Variable name	Study sites															
	Hwy441	barnett	belmont	botgar	carith	holiday	kraft	manvill	newton	nwinder	river	rocky	russell	tallas	wages	yargo
Year	1989	1989	1989	1989	1989	1990	1990	1990	1989	1990	1989	1989	1990	1990	1990	1990
Total	0.91	19.58	6.91	10.16	2.00	3.58	1.83	4.50	7.41	8.00	5.66	5.33	3.00	1.58	1.42	0.00
Rich	0.83	4.17	2.00	5.75	0.92	1.92	1.08	1.58	1.33	3.33	2.17	1.00	0.58	1.08	0.75	0.00
Diver	0.14	0.97	0.45	1.55	0.11	0.51	0.27	0.36	0.22	0.89	0.63	0.14	0.05	0.25	0.03	0.00
General	0.00	17.08	5.00	6.33	0.33	1.00	0.25	2.50	5.67	1.92	2.75	0.08	2.83	0.75	0.50	0.00
Forest	0.25	1.67	0.25	2.92	0.00	0.58	0.33	0.25	0.08	2.33	0.17	0.00	0.00	0.00	0.08	0.00
Esucc	0.67	0.75	1.67	0.67	1.67	1.92	1.17	1.67	1.33	3.75	2.33	5.25	0.17	0.75	0.83	0.00
CAWR	0.00	0.67	0.25	1.58	0.00	0.42	0.33	0.17	0.00	1.08	0.08	0.00	0.00	0.00	0.00	0.00
FISP	0.17	0.25	1.50	0.17	0.92	0.92	0.67	0.25	0.92	1.17	1.92	3.17	0.17	0.50	0.58	0.00
NOCA	0.00	4.00	0.58	1.58	0.00	0.83	0.00	0.00	0.00	0.33	1.92	0.00	0.00	0.08	0.50	0.00
RSTO	0.00	1.00	0.33	1.50	0.00	0.17	0.08	0.00	0.00	0.33	0.08	0.08	0.00	0.25	0.00	0.00
SOSP	0.50	0.50	0.08	0.50	0.75	1.00	0.50	1.33	0.42	0.50	0.17	2.08	0.00	0.25	0.25	0.00
WTSP	0.00	11.92	3.75	1.67	0.00	0.00	0.00	1.00	0.00	1.17	0.75	0.00	0.00	0.00	0.00	0.00
DEJU	0.00	0.00	0.00	0.92	0.33	0.00	0.00	1.25	5.50	0.00	0.00	0.00	2.83	0.00	0.00	0.00
Titmice	0.00	0.42	0.00	0.67	0.00	0.17	0.00	0.00	0.00	0.50	0.08	0.00	0.00	0.00	0.00	0.00
Veg1	−0.754	−0.753	−0.186	0.589	−0.623	0.473	0.850	0.229	−0.645	3.191	0.021	−0.661	−0.552	−0.594	−0.634	0.048
Veg2	−0.447	−0.222	−0.698	3.502	−0.277	0.369	−0.234	−0.211	−0.032	−0.942	0.015	−0.300	−0.382	−0.252	0.553	−0.442
Veg2	−0.558	3.390	0.892	0.208	−0.609	−0.437	0.041	−0.265	−0.675	0.246	−0.342	−0.664	−0.019	−0.580	−0.074	−0.556
Veg4	0.554	0.175	−1.361	−0.861	−0.076	0.930	0.852	1.033	−0.197	0.003	−0.522	−0.942	−0.249	−0.062	2.346	−1.625
Veg5	2.196	0.613	−1.704	0.445	0.128	−1.421	−0.524	0.112	0.212	0.813	−1.298	0.637	−0.150	−0.854	−0.109	0.905
Mat1	−0.501	1.460	−1.279	2.099	−0.935	0.567	0.114	−0.444	−0.442	0.773	0.507	0.574	−1.044	−0.266	0.391	−1.574
Mat2	−0.072	−0.739	−0.136	−0.147	−0.436	−0.529	−0.381	−0.238	−0.359	−0.558	3.430	0.436	−0.644	−0.328	−0.187	0.887
Mat3	−0.713	−0.214	−0.599	−0.863	−0.520	−0.083	−0.325	−0.081	0.001	−0.062	−0.753	3.455	0.100	0.449	−0.223	0.432
Mat4	0.215	−1.540	0.204	0.627	1.638	−0.318	−1.097	−0.384	1.649	−0.086	0.398	0.626	0.228	−0.052	0.054	−2.163
Mat5	−0.379	−0.535	−0.017	0.226	−0.433	−0.242	−0.937	3.375	−0.603	−0.453	−0.100	−0.030	−0.390	0.000	1.014	−0.495
Mat6	−0.106	0.180	3.299	−0.104	−0.707	0.126	0.425	−0.173	−0.737	−0.005	0.006	0.650	−0.923	−0.397	−0.466	−1.067
Mat7	0.079	−0.701	0.266	1.011	−0.628	−0.870	−0.377	−0.447	−0.379	−0.064	−0.214	−0.399	−0.496	3.347	−0.296	0.167
Mat8	0.008	−1.173	0.238	−0.058	−0.574	−0.635	0.480	−1.115	−0.182	0.443	−0.378	0.033	−0.249	−0.410	3.266	0.304
Mat9	3.038	−0.735	−0.552	0.081	−0.088	1.327	0.041	−0.130	−1.102	−1.055	−0.336	0.491	−0.618	−0.081	−0.034	−0.246
Mat10	−0.658	−0.179	−0.622	−1.864	−0.137	1.119	2.024	0.298	0.542	−0.532	0.685	−0.311	−0.483	1.218	0.386	−1.486
Mat11	1.584	1.249	−0.157	−1.800	−0.577	−1.216	−1.120	0.151	0.502	1.825	0.339	−0.113	−0.487	0.329	0.192	−0.700
Mat12	−0.306	−0.271	0.337	−0.057	−1.212	2.006	−1.391	−0.156	2.069	−0.003	−0.286	−0.440	−1.334	−0.016	0.100	0.958