A Comparison of Landscape Metrics in Relation to Neotropical Migratory Bird Occurrence in the Driftless Area of the Upper Mississippi River Basin

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Abstract

Bird count data for southeastern Minnesota were used to compare landscape metric values associated with the occurrence of species from two functional groups. Four forest interior dependent and four non-interior dependent species were assessed. Species included American redstart, Cerulean warbler, Least flycatcher, Woodthrush, Blue-winged warbler, Indigo bunting, Ruby-throated hummingbird, and Warbling vireo. Landscape metrics included: patch cohesion index, fractal dimension, aggregation index, total edge length, total core area, landscape context, distance to edge, distance to nearest road, distance to stream, and patch area. Landscape metrics were derived for a 3,090ha window (radius = 3,163 meters) around each census point to allow comparison with bird occurrence at a biologically relevant scale. Non-parametric Mann-Whitney comparisons were completed for each metric and pairwise species combination to test the hypothesis that interior specialists occur more frequently at sites in less fragmented, and more densely forested landscapes. Significant relationships between bird occurrence and some landscape metrics were supported by this study. Overall, patch cohesion index, aggregation index, and distance to road provided the most significant ($\alpha_{(1)}$, $p \leq 0.05$) distinctions between rates of occurrence for different species. The results of this study indicate that appropriate landscape metrics can provide biologically relevant information about habitat distribution and the corresponding likelihood of species occurrence. Precise relationships are more difficult to quantify, and further study is needed to illuminate the generalized theory of landscape ecology, proposed by Gardner et al. (1987).

Introduction

Theoretical Foundations

A foundational question of landscape level ecological analysis concerns the response of populations to change in, and spatial variation of relevant landscape characteristics. A variety of factors such as altitude, latitude, moisture gradient, soil type, land cover, etc. are known to influence the distribution and abundance of species. Several characteristics of primary interest are related to habitat extent and configuration. Although these are not the only characteristics relevant to population

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dispersal and survival, they are factors that can be analyzed using existing tools and available landscape-scale data.

Gardner et al. (1987) proposed that since individual species display differential responses to spatial characteristics of habitat, it may be possible to develop a generalized theory of landscape ecology by comparing various landscape metrics to species occurrence. An empirically based spatial distribution model of species abundance at the landscape scale could then be derived. Researchers have performed progressively more complex spatial analyses in an attempt to associate particular species with observed variations in habitat extent, configuration, and landscape structure (Hansen and Urban, 1992; Austen et al., 2001; Lee et al., 2002; Bunn et al., 2000; Flather et al., 1992; Donovan and Flather, 2002; Keitt et al., 1997; Riiters et al., 2002; Riiters and Coulston, 2005; Schumaker, 1996; With and Crist, 1995; He et al., 2000; and Thogmartin et al., 2004). These approaches have explored many (>50) indices of landscape structure, most of which were summarized and assessed by Neel et al. (2004).

Diverse bodies of research show both theoretically and empirically, that structural habitat connectivity is an important factor influencing the utilization of landscapes by wildlife. Variation in structural connectivity has different effects on separate species due to the unique gap-crossing abilities of each (Bélisle and Desrochers, 2002). Since functional landscape connectivity is an emergent property of species-landscape interactions (Taylor et al., 2006), characterising the nature of these interactions and defining mechanisms through which they are mediated is a pivotal concern in the study of this concept.

Habitat fragmentation can be thought of as the lack of connectivity brought about by habitat loss and/or disturbance. Extensive evidence suggests that factors related to habitat fragmentation (Rosenberg et al., 1999) affect neotropical migratory bird populations by reducing nesting and pairing success, and by increasing nest predation and parasitism. A review by Lampila et al. (2005) shows that fragmentation has the greatest effect on Nearctic long-distance migrants that nest on the ground, or in the open, and specialize in mature forest habitat.

There is little disagreement regarding the mechanisms by which fragmentation affects population dynamic. However, some studies examining the breeding success of neo-tropical migratory birds with respect to forest fragmentation have resulted in questions regarding interactions among species specific mechanisms and scales of interaction (Herkert, 1995; Gustafson et al., 2002; Friesen et al., 1998; Knutson et al., 1996; Knutson et al., 2004, Jones et al., 2004; Thogmartin et al., 2004). Most authors have suggested that differences in landscape context (e.g. the large-scale distribution of habitat and the influences of land use in the surrounding matrix) mediate differences in population response.

Behavioral mechanisms through which dispersal effects mediated by the spatial distribution of habitat influence survival and metapopulation dynamics have been demonstrated (Bélisle et al., 2001; Bélisle and Desrochers, 2002). Intensive field work and focal species analysis can clarify relationship between structural and functional connectivity, but results from these studies are not generalizeable. This mechanistic approach must be replicated for each species, or group of closely allied species, to determine relevant scales and limitations of dispersal capabilities.

Studying the interactions of individual ecosystem components with spatially variable habitat characteristics can be illuminating. However, by focusing solely on functional connectivity, we may be overlooking related, but currently unknown, processes. The study of meta-population distribution as it relates to landscape structure, without reference to species specific scales or limitations, may allow the discovery of relevant patterns not apparent from solely mechanistic observations. A measure of landscape structural connectivity that is independent of any single species' home range size or gap-crossing ability will be a critical tool in efforts to quantify the response of populations to variations in that structure.

Significant shortcomings exist in terms of our ability to quantify some habitat characteristics of interest on a landscape-scale (e.g. variations in vertical habitat structure, microsite characteristics, age structure, and sub-canopy composition), and formalize their relationship to landscape metrics and population dynamics. These shortcomings present a serious impediment to understanding relationships between species habitat response and indices of landscape structure.

Landscape Metrics: A partial review

Habitat extent and arrangement are often described using a variety of landscape and patch level indices. Among others, patch area (Curtis, 1956), area/perimeter ratio (Herkert, 1995), core habitat area (Temple, 1986), fractal dimension (Milne, 1992), aggregation index (He et al., 2000), patch cohesion index (Schumaker, 1996), and lacunarity (Gamarra, 2005) have shown promise as metrics describing biologically significant landscape characteristics. Additional factors influencing dispersal, territory selection, and survival include distance to edge (Temple and Cary, 1988), distance from nearest road, distance from agricultural lands, distance to water, moisture index (Thogmartin et al., 2004), aspect, slope, and others.

Milne (1992) highlights the importance of scale, likening the resolution provided by different scales of observation to the different images revealed by light in the visible and x-ray spectra. The explicit spatial context provided by landscape connectivity analysis allows for adjustments in "spectral" resolution through adjustments in the search radius of focal analysis. This approach has been termed "moving window" analysis. Analysis scales should relate to dispersal thresholds of species using the landscape (With and Crist, 1995; Gardner et al., 1987), and/or biologically significant portions of the larger landscape (Knutson 2005, pers. comm.).

The non-linear nature of some indices (Neel et al., 2004) complicates the discovery of potential relationships between landscape metrics and population responses. Metrics that seem to describe meaningful relationships on one landscape may have little or no relationship to changes in ecological function on structurally different landscapes. Therefore, more cumbersome non-parametric analyses are needed to uncover relationships described by such metrics. It is also recommended (Bogaert, 2003) that multiple metrics be examined concurrently to overcome peculiarities of non-linear behavior and limitations imposed by landscape structure.

Collectively, patch cohesion, aggregation index, total core area (>100m from edge), and fractal dimension appear to provide a useful range of response. Although patch cohesion index is relatively unresponsive to changes in percent habitat cover or habitat aggregation when one or both of these factors are high (Neel et al., 2004), it does provide good differentiation at lower values. At low levels of habitat aggregation, patch cohesion appears to be relatively responsive to changes in habitat area below the percolation threshhold (Stauffer and Aharony, 1992) of 59.27% cover. At higher levels of aggregation, the metric is less responsive throughout the range of total habitat cover. Aggregation index, total core area, and standard deviation of the fractal dimension appear to provide different, but relatively consistent responses across most of the real range of percent cover and habitat aggregation.

O'Neill et al. (1988) suggest that the percentage cover needed to ensure a percolating habitat cluster may be either higher or lower in real landscapes. Further, ecologically relevant responses to changes in landscape structure may not follow a linear pattern. Small changes in habitat extent or configuration may have dramatic effects on species dispersal, survival, and population dynamics at critical points along the structural connectivity spectrum (Bunn et al., 2000; Gardner et al., 1987; Keitt et al., 1997; Schumaker, 1996; With and Crist, 1995; Milne et al., 1996; Solé et al., 2004).

Using a Morisita Index (Hurlburt, 1990) of 2.5, With and Crist (1995) derive a 40% threshold below which habitat specialists tend to aggregate in preferred habitat patches. This value corresponds to a scenario in which two individuals, selected at random, would be 2.5 times as likely to have been selected from the same cell than if they had come from a randomly distributed population. In reality, a much lower tendency for individuals to aggregate in prefferred habitat may be ecologically significant. The proposed 40% habitat threshold may, therefore, be too low, and fail to predict meaningful aggregation at a higher threshold. Empirical observation of species response paired with non-parametric analysis of structurally-based landscape indices will be needed to more fully assess their relationship to ecological function.

A useful quality of patch cohesion is that it is independent of species gap-crossing abilities and home-range size, yet captures a biologically relevant aspect of landscape structure not described by other metrics (Schumaker, 1996). Just as importantly, patch cohesion captures multiple structural properties of the landscape on a continuous scale. Patch cohesion may, therefore, provide an index applicable to multiple species dependent on similar habitat, but with varying dispersal scales and abilities. If patch cohesion provides a consistent measure of landscape structure across a realistic range of habitat cover and arrangement, it may prove to be a metric against which partial habitat suitability values for a variety of species can be assigned.

Following the conclusions of Neel et al. (2004), patch cohesion should provide useful information about ecological relationships related to habitat connectivity on less heavily forested portions of the landscape. If the ability of patch cohesion to describe changes in connectivity mediated by interactions between patch area and aggregation does break down, the deficiency will certainly occur in the most heavily forested areas. It is important to note that for landscapes where forest cover exceeds the percolation threshold, habitat connectivity may decrease in importance as a limiting factor for forest interior specialists. Additional metrics may become increasingly important in that context.

Focal species (O'Neill et al., 1988; Bunn et al., 2000; Bélisle et al., 2001; Bélisle and Desrochers, 2002) and functional group analyses (Hansen and Urban, 1992) will remain useful in characterising the mechanisms through which lanscape connectivity affects community dynamics and the distribution and life-cycle of species. Similar assessments will also be pivotal in assigning species of interest to a relevant portion of the habitat connectivity spectrum.

Goals of Study

Divergent claims have been made about the relationship of various indices to habitat characteristics and population interactions. Unfortunately, significant redundancy exists, and little agreement has been reached on which indices provide useful information relating to habitat management concerns (Bogaert, 2003).

A review of the literature on landscape connectivity points to three major issues that future research should address (Goodwin, 2003). These topics include: (1) exploring the relationships among landscape structure, organism movement and behavior, and landscape connectivity, (2) clarifying relationships among the many different structural and functional measures of connectivity, and (3) developing a body of empirical evidence relating structurally-based model predictions to ecological functions on real landscapes.

In an effort to clarify the relationships identified by Gardner et al. (1987), this study uses species occurrence data derived from systematic non-road-based point counts to compare an array of readily obtainable landscape metrics with populations of several neo-tropical migratory birds from two functional groups. The hypothesis that indices related to the extent and distribution of forest habitat will yield significant information about where interior forest dependent and area sensitive bird species are likely to occur compared to generalist and non-interior species is tested. The utility of the patch cohesion index for identifying variations in organismal response to landscape structure is tested empirically in a landscape straddling the theoretical percolation threshold. The non-parametric approach used here may allow us to relate structural characteristics to ecological function of a landscape via a focal species independent index.

Methods

Study Area and Data

The study area includes a portion of the Driftless Area of the Upper Mississippi River Basin (Figure 1) encompassing much of southeastern Minnesota (USA). Forest habitat in the Driftless Area (Figure 2) has been described as highly dissected and has been influenced by increasing levels of human development and agricultural activity over the past century. Soils are erosive, and forests tend to dominate the steep slopes of valleys carved into the carbonate bedrock by coldwater streams.

Data from bird counts conducted by the Natural Resources Research Institute (NRRI) (Hanowski et al., 2003) from 1995 – 2002 were used to compare landscape metrics and bird occurrence. To summarize, standard ten minute, unlimited radius point counts were conducted by trained observers within specific habitat types to allow linking of population trends and bird occurrence to habitat. Counts were conducted during the breeding season from early May through late

Figure 1. Bird census locations in southeastern Minnesota, USA. Land use in the study area is typical of that found throughout the Driftless Area of the Upper Mississippi River Basin.

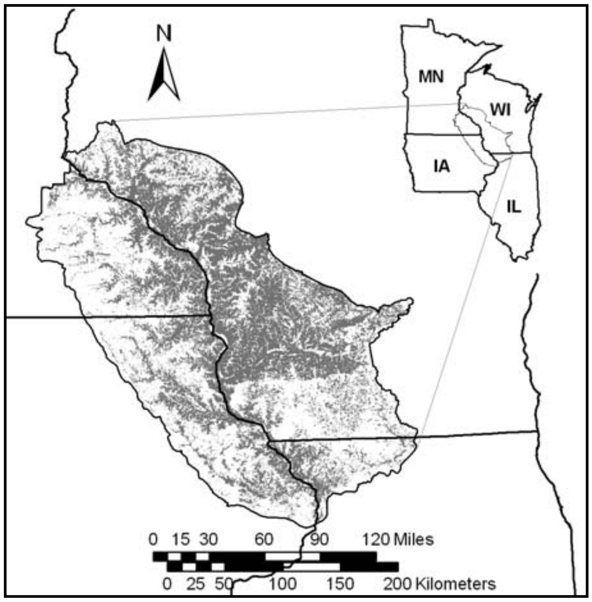


Figure 2. Forest cover in the Driftless Area occurs mostly on the steep unfarmed hillsides of this dissected landscape. 72% of forest cover occurs on slopes greater than 30%.

June of each year. The full dataset contains records for 35,328 individual birds of 102 positively identified species at 214 locations.

Forest cover represented in the 1992 National Land Cover Dataset was used to derive landscape metrics. Road data (2001) were downloaded from http://deli.dnr.state.mn.us/. National Hydrography Dataset (NHD) flowlines (e.g. stream data) were obtained from http://nhd.usgs.gov.

Site metrics assessed include distance to stream, distance to edge, modified distance to edge, distance to road, and patch area. Euclidean distance to stream was calculated based on the NHD streams layer. Distance to edge was defined as the euclidean distance to the nearest non-forested pixel from each location on the landscape. Distance to road was defined as the euclidean distance to the nearest road from each point on the landscape. Modified distance to edge substituted distance to road for distance to edge where distance to road provided a smaller value.

Modified distance to edge was examined because roads are known to influence wildlife behavior, and fragment forest habitat both structurally and functionally. The 30 meter resolution 1992 NLCD dataset does not distinguish most roads through forested areas, so “burning in” a detailed roads dataset (as performed by Riitters and Coulston, 2005) may create a more realistic representation of fragmentation and impediments to dispersal.

Patch area was calculated from forest data with roads burned in, using the four-direction rule. Patch area values corresponding to the nearest patch were manually entered for several points that did not fall on a forested cell. The vast majority of these points occurred in either small openings (a few cells in size) within a forested landscape, or near the edge of a larger forested patch. All other landscape analyses were performed using eight-direction connectivity on the unmodified forest cover dataset.

Neel et al. (2004) question the utility of patch cohesion index in assessing landscape structure at high levels of class aggregation or percent cover. A preliminary assessment of percent forest and spatial autocorrelation of forested cells around groups of census points (radius 3,500 m) was conducted to address this concern.

ArcInfo GRID provides two assessments of spatial autocorrellation; GEARY and MORANS. Neither of these measures is equivalent, or comparable, to the value of aggregation (H, Range: 0 - 1) used to describe random neutral landscapes (Neel et al., 2004). GEARY ranges from 0, strong positive, to +2, strong negative spatial autocorrelation. MORANS ranges from -1 to 1, describing negative and positive spatial autocorrelation, respectively. Nonetheless, these measures do provide an assessment of the tendency for habitat patches to be aggregated on the landscape.

Experimental Design

Life history characteristics for forest dependent neo-tropical migrant species occurring in the NRRI birdcount dataset were summarized in tabular format to allow systematic comparison (Appendix 1). Summaries were based on published species accounts (Niemi and Hanowski, 1992, http://wildspace.ec.gc. ca/, http://www.birds. cornell.edu, http:// nationalzoo.si.edu, and http://www.na.fs. fed.us), and on input from Andy Paulios (2005, pers. comm.). A subset was selected for further analysis (Table 1).

Very common birds occurring at more than 75% of the sites were eliminated, as their distribution would too closely resemble that of the total set of points to provide meaningful comparisons among species (Kelly, 2001). Very rare species occurring at fewer than 10 of the 181 sites (Table 2) were also eliminated, as the resulting set of points could too easily be influenced by chance occurrence and factors outside the analysis (Maraj, 1999; Zar, 1999). Limiting comparisons to species occurring at 10 or more sites also improved the power of the experimental design.

Landscape Context Methodology

Landscape context was developed from landscape scale criteria proposed as a model for Cerulean warbler habitat by Knutson et al. (2001). A GIS model was developed from the description provided by Knutson et al. (2001) through collaboration with regional wildlife biologists, and resource managers versed in the life histories of migratory birds and their habitat needs. Land cover defined as Forest and “Hostile” categories are shown in Table 3.

Table 1. Four area sensitive (Area) or interior forest dependent (Inter) species, and four non-interior species were randomly selected for analysis.

Code	Common Name	Inter	Area
AMRE	American Redstart	Yes	Yes
BWWA	Blue-winged warbler	No	No
CERW	Cerulean warbler	Yes	Yes
INBU	Indigo Bunting	No	No
LEFL	Least Flycatcher	Yes	Yes
RTHU	Ruby-throated Hummingbird	No	No
WAVI	Warbling virio	No	No
WOTH	Wood Thrush	Yes	Yes

Knutson et al. (2001) propose that a 4,000 hectare landscape is relevant to Cerulean warbler nesting success. A slightly smaller 3,090 hectare window is used throughout this study.

Focal analyses were run for each habitat grouping using ArcGIS 9.0. Cover type density grids were then classified to produce data segments (tiers) for each factor (Table 4) and combined to provide 6 landscape context tiers ranging from high to low interior forest habitat potential.

Landscape Indices

Seven analyses of landscape characteristics were conducted. These analyses include percent forest cover, patch cohesion index, fractal dimension, aggregation index, total edge length, total core area, and landscape context as described above.

To gain access to the information associated with various landscape metrics, it was first necessary to extract forest cover data from the relevant landscape around each of the 181 census points in the study area. This process involved the creation of a 3,500m buffer around each point. This buffer was then used to extract the relevant forest cover data. Due to computational requirements, it was necessary to divide this reduced dataset into 5 regions corresponding to groupings of points on the landscape. FRAGSTATS 3.3 (McGarigal et al., 2002) was used to calculate metric values employing a circular search radius of 3,163 meters. The resulting data allowed for comparison of values relevant to landscapes surrounding each census point.

MINITAB 15 statistical software

Table 2. Very common and rare birds eliminated from analysis to increase comparative power.

Very Common Species					Very Rare Species			
Species	# of Sites	% of Sites	Species	# of Sites	% of Sites	Species	# of Sites	% of Sites
BGGN	166	91.209	ALFL	1	0.549	HOWA	1	0.549
EAWP	172	94.505	BAWW	3	1.648	LOWA	3	1.648
GCFL	138	75.824	BBCU	3	1.648	MOWA	9	4.945
OVEN	145	79.67	BDOW	7	3.846	NAWA	1	0.549
REVI	170	93.407	BRCR	1	0.549	NOPA	2	1.099
			BWHA	2	1.099	PROW	3	1.648
			CAWA	5	2.747	RSHA	4	2.198
			CONI	1	0.549	RTHA	8	4.396
			CSWA	7	3.846	SWTH	1	0.549
			GBHE	6	3.297	WPWI	2	1.099

Table 4. Reclassification values used in developing 6 Landscape Tiers from Percent Forest and Percent Hostile data.

Forest Reclass		Hostile Reclass	
% Forest	Value	% Hostile	Value
60.1 - 97	3	0 - 15	3
40.1 - 60	2	15.1 - 33	2
0 - 40	1	33.1 - 60	1
		60.1 - 99	0

was used to subset the grouped species occurrence/landscape metric data and analyze the relationships of metrics to bird occurrence. Single-tailed Mann-Whitney analyses were conducted for each metric/ bird-pair combination. Comparisons for number of years each species was identified at the same point, and the cumulative number of individuals counted for each species at each point were also made.

Hypotheses (Single-tailed)

H_o: $\text{Metric}_{\text{interior bird}} \leq \text{Metric}_{\text{non-interior}}$
H_a: $\text{Metric}_{\text{interior bird}} > \text{Metric}_{\text{non-interior}}$

Table 3. Reclassifications defining Forest and Hostile Landcover. Based on National Landcover Dataset, circa 1992.

Land Cover	Forest	Hostile	% of Total
Open Water	0	0	1.61
Low Intensity Residential	0	1	0.54
High Intensity Residential	0	1	0.27
Commercial/Indust/Transp	0	1	0.84
Bare Rock/Sand/Clay	0	1	0.01
Quarries, Gravel Pits	0	1	0.03
Transitional	0	0	0.04
Deciduous Forest	1	0	22.04
Evergreen Forest	1	0	0.6
Mixed Forest	1	0	1.07
Orchards/Vinyards	0	0	0
Grasslands/Herbaceous	0	1	1.27
Pasture/Hay	0	1	30.05
Row Crops	0	1	39.02
Small Grains	0	1	0.06
Urban Grasses	0	1	0.31
Woody Wetlands	1	0	1.5
Emerg. Herb. Wetlands	0	0	0.72

H_o: $\Sigma(\Delta_{\text{within guild}}) \geq \Sigma(\Delta_{\text{between guilds}})$
H_a: $\Sigma(\Delta_{\text{within guild}}) < \Sigma(\Delta_{\text{between guilds}})$
Where: Δ = Significant metric differences.

Results

Forest cover in the study area ranged from 9.5 to 70.2% ($\mu = 43.05\%$). Spatial autocorrelation indices for the five regions immediately surrounding groups of census points indicate moderate to strong spatial autocorrelation for forest habitat in the study area (Table 5).

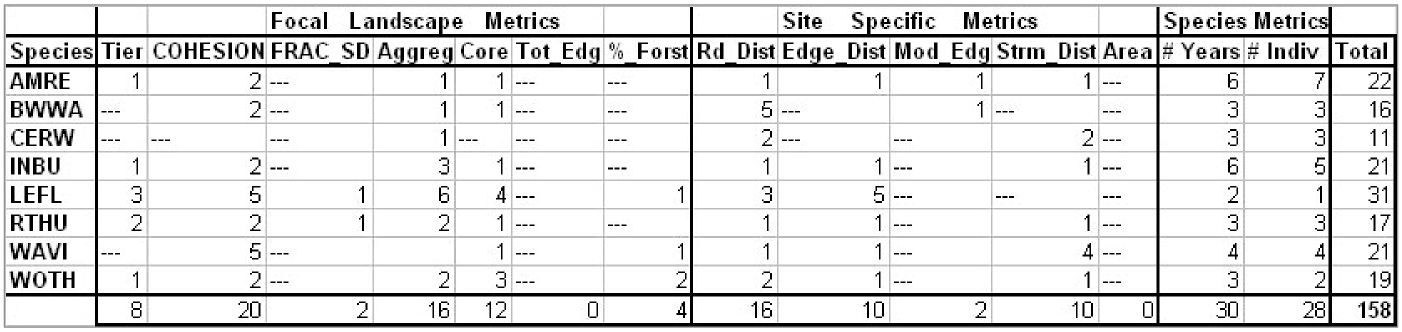
Several significant relationships were revealed between species occurrence and landscape metrics. These results are detailed in Appendix 2 and outlined below.

Noteworthy results (Table 6) are observed for the Blue winged warbler, Least flycatcher, Warbling vireo, and Woodthrush. Occurrences of the Least flychatcher were the most well differentiated overall. Of seven total species-pair comparisons, the Least flycatcher ranked higher in every significant test for patch cohesion (5), aggregation index (6), landscape context (3),

Table 5. Measures of spatial-autocorrelation for forest habitat within 3,500m of census points.

Region	Morans	Geary
0	0.6405	0.356425
1	0.734276	0.262163
2	0.710514	0.286446
3	0.783176	0.209275
4	0.808626	0.188053
Avg	***0.735418***	***0.260472***

Table 6. Number of significant ($p \leq 0.05$) species-metric interactions.



			Focal Landscape Metrics						Site Specific Metrics				Species Metrics		
Species	Tier	COHESION	FRAC_SD	Aggreg	Core	Tot_Edg	%_Forst	Rd_Dist	Edge_Dist	Mod_Edg	Strm_Dist	Area	# Years	# Indiv	Total
AMRE	1	2	---	1	1	---	---	1	1	1	1	---	6	7	22
BWWA	---	2	---	1	1	---	---	5	---	1	---	---	3	3	16
CERW	---	---	---	1	---	---	---	2	---	---	2	---	3	3	11
INBU	1	2	---	3	1	---	---	1	1	---	1	---	6	5	21
LEFL	3	5	1	6	4	---	1	3	5	---	---	---	2	1	31
RTHU	2	2	1	2	1	---	---	1	1	---	1	---	3	3	17
WAVI	---	5	---		1	---	1	1	1	---	4	---	4	4	21
WOTH	1	2	---	2	3	---	2	2	1	---	1	---	3	2	19
	8	20	2	16	12	0	4	16	10	2	10	0	30	28	158

total core habitat (4), and distance to edge (5), but lower in distance to road (3). Blue winged warbler ranked lower in patch cohesion (2) and higher for distance to road (5). Warbling vireo ranked higher in patch cohesion (5) and lower in distance to stream (4). Woodthrush ranked lower in total core forest area (3).

Four of five significant ($p \leq 0.05$), and two borderline significant ($0.10 > p > 0.05$) distinctions explained by distance to stream involved the Warbling vireo. Additionally, two of the significant and three of the borderline significant distinctions provided by this metric involved the Cerulean warbler.

American redstarts had the largest total number of individuals observed (727) of any species included in the study, and were relatively ubiquitous among census points. This observation is evidenced by the close tracking of this species with the overall distribution of metric values (Figures 3 - 6). The next most abundant bird (Indigo bunting) occurred at more sites (130 vs. 116) than the American redstart, but with fewer individuals (367) represented. American redstarts ranked very significantly higher ($p \leq 0.0001$) than Indigo buntings for both number of years counted at the same site and number of individuals counted per site. Only Warbling vireos were not highly significantly differentiated from American redstarts for site recurrence ($p = 0.1364$) and number of individuals ($p = 0.0485$).

Cerulean warblers were not significantly differentiated by most metrics assessed. Only aggregation index (1), distance to road (2), and distance to stream (2) provided significant results. Cerulean warblers ranked lower ($p = 0.0473$) than Least flycatcher for aggregation index, and higher than Least Flycatcher ($p = 0.017$) and Woodthrush ($p = 0.0299$) for distance to road. Cerulean warblers also ranked farther from streams than Warbling vireo ($p = 0.0137$) and American redstarts ($p = 0.0331$). Borderline significant ($p \leq 0.10$) differentiations ranked Ceruleans lower than Least flycatcher and Warbling vireo for patch cohesion, and farther from streams than Blue-winged warbler, Indigo bunting, and Least flycatcher.

Patch cohesion provided the largest number of significant comparisons (10). Aggregation index and distance to road followed with 8 each, then total core area with 6. Probability distribution graphs are shown in Figures 3 through 6. The extreme skew of patch cohesion index (Table 7) and some other metrics may make the mean (Table 8) a poor estimate of central tendency. Reference to median scores (Table 9) may be more meaningful.

Discussion

Results of this study support the conclusion that patch cohesion index provides a biologically relevant assessment of habitat connectivity. Non-parametric methods do

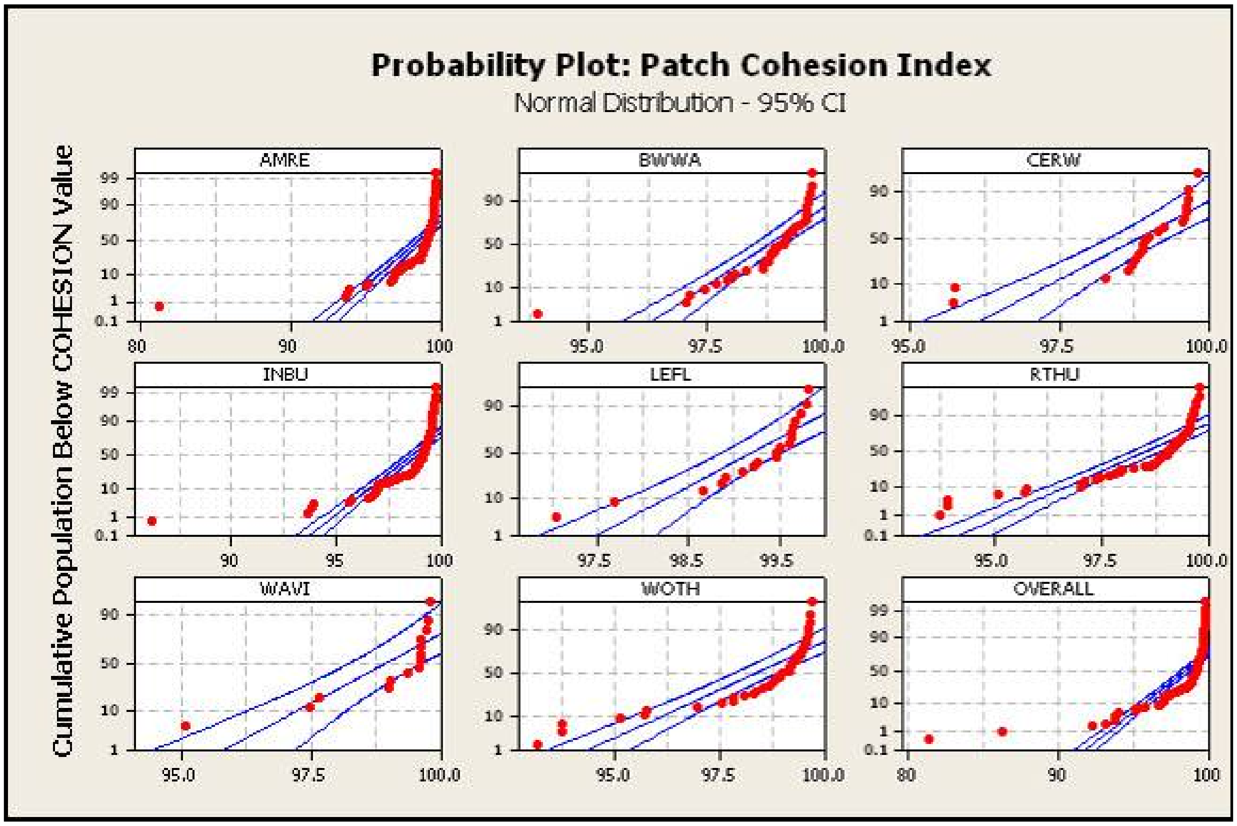


Figure 3. Probability distribution plots of patch cohesion index in 3,090ha landscape.

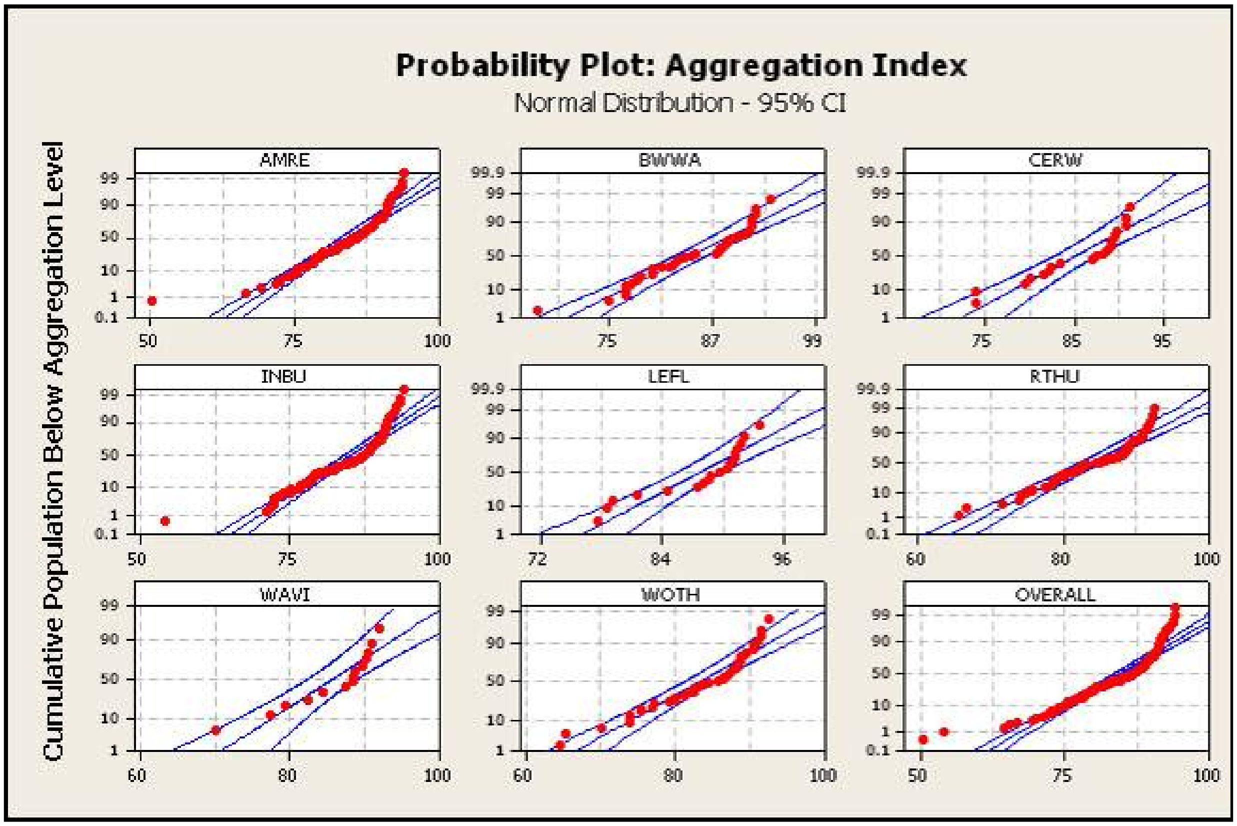


Figure 4. Probability distribution plots of aggregation index in 3,090ha landscape.

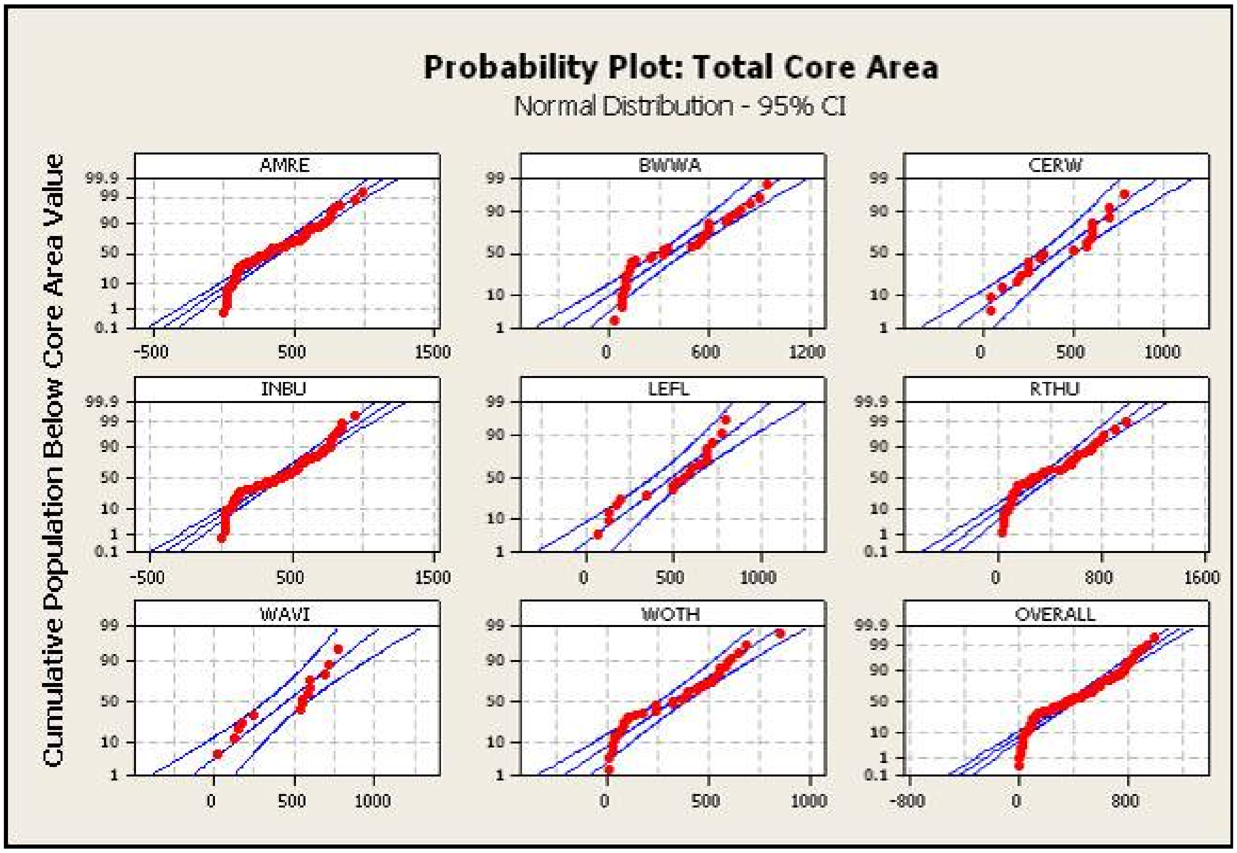


Figure 5. Probability distribution plots of total core area (hectare). Edge depth = 100 meters.

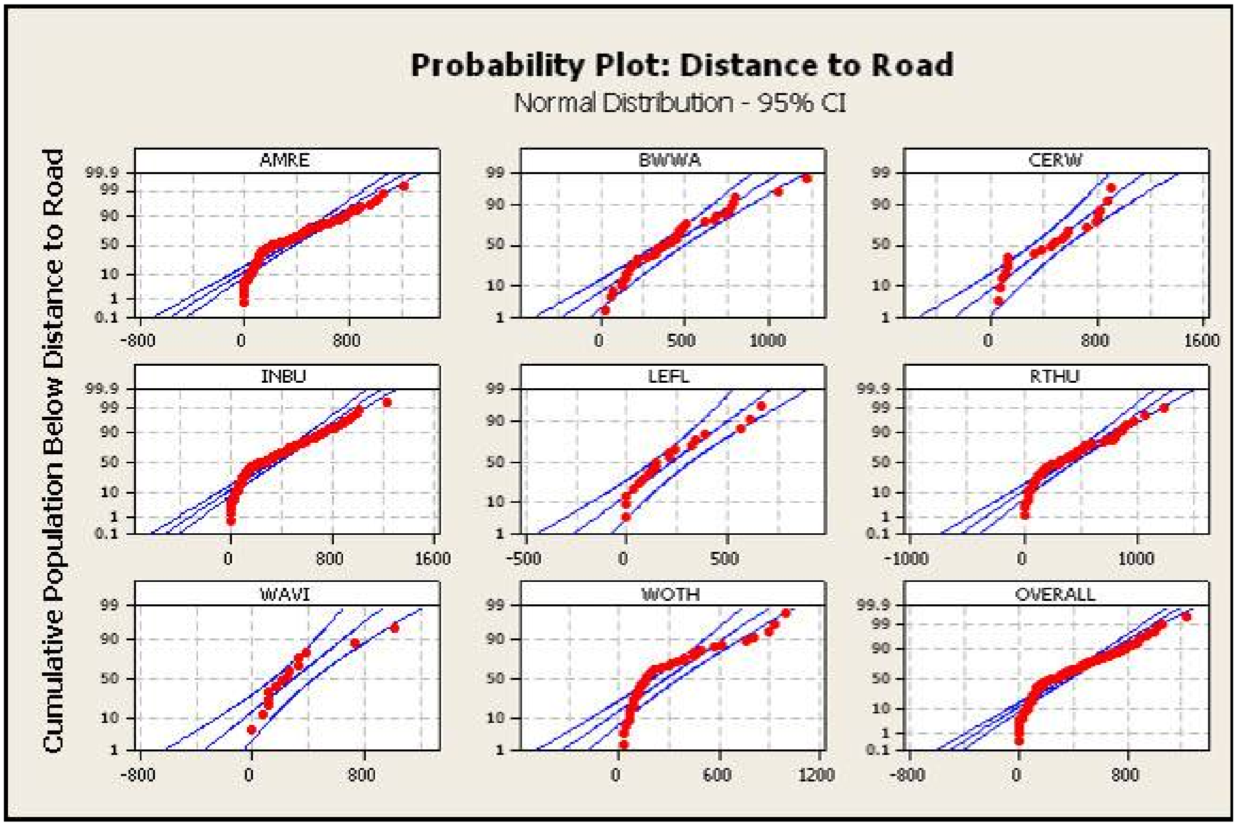
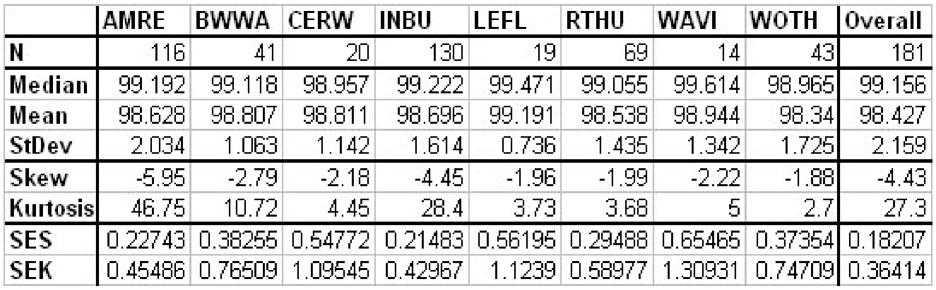


Figure 6. Probability distribution plots of distance to nearest road.

Table 7. All skewness and kurtosis (Fisher) measures for patch cohesion index exceed 1.96 units of standard error. All distributions are significantly skewed and leptokurtic.



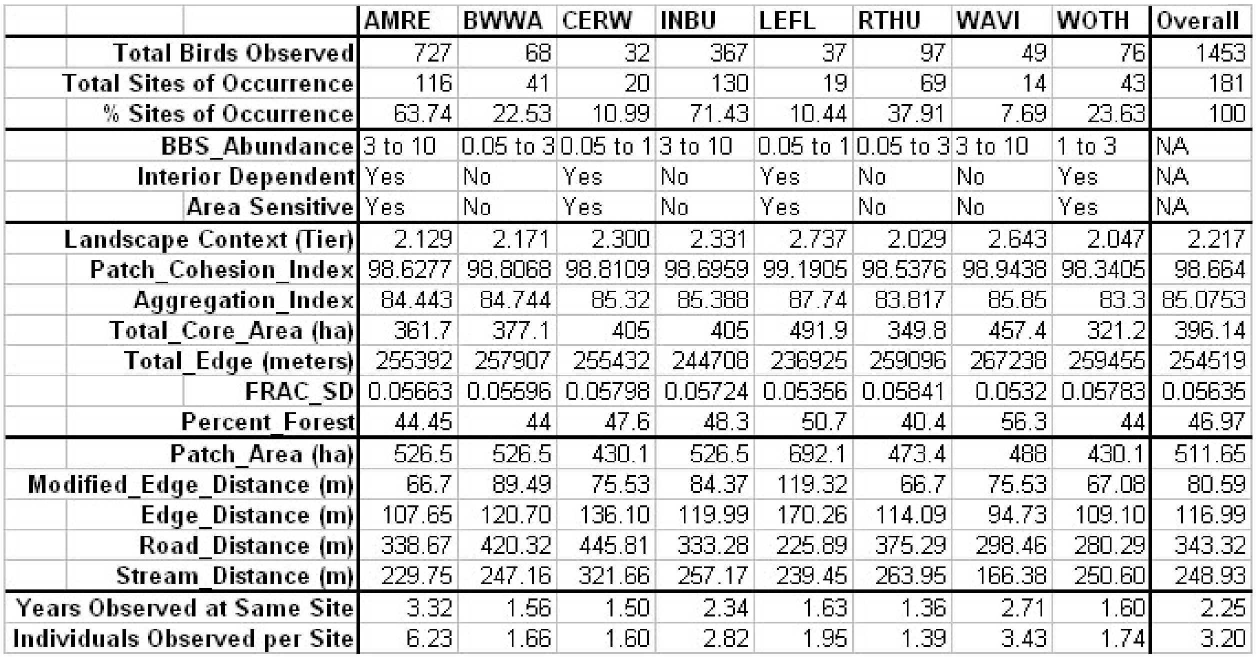
	AMRE	BWWA	CERW	INBU	LEFL	RTHU	WAVI	WOTH	Overall
N	116	41	20	130	19	69	14	43	181
Median	99.192	99.118	98.957	99.222	99.471	99.055	99.614	98.965	99.156
Mean	98.628	98.807	98.811	98.696	99.191	98.538	98.944	98.34	98.427
StDev	2.034	1.063	1.142	1.614	0.736	1.435	1.342	1.725	2.159
Skew	-5.95	-2.79	-2.18	-4.45	-1.96	-1.99	-2.22	-1.88	-4.43
Kurtosis	46.75	10.72	4.45	28.4	3.73	3.68	5	2.7	27.3
SES	0.22743	0.38255	0.54772	0.21483	0.56195	0.29488	0.65465	0.37354	0.18207
SEK	0.45486	0.76509	1.09545	0.42967	1.1239	0.58977	1.30931	0.74709	0.36414

show that a relationship exists, possibly even above the theoretical percolation threshold. However, the extreme negative skew of this metric complicates precise illumination of relationships verified here.

The original hypothesis was that a greater proportion of interior forest dependent and area sensitive birds vs. non-interior forest birds would be associated with sites exhibiting higher values for patch cohesion index. Comparison between guilds does not show a significant difference ($p \geq 0.4353$) between guilds. Analysis of species pairs does, however, uncover some noteworthy relationships.

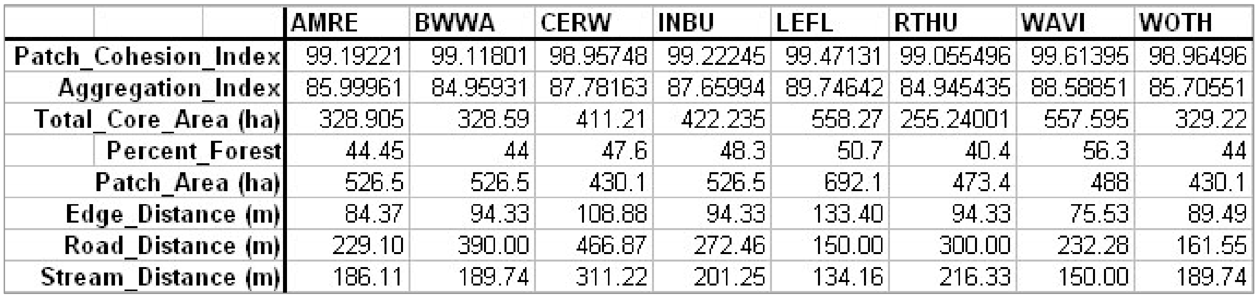
One such relationship involves patch cohesion and the occurrence of Warbling vireo, a species typically not identified as interior forest dependent. Warbling vireo ranked significantly higher for patch cohesion than the American redstart and Woodthrush (area sensitive interior forest species), and higher than all other species included in the non-interior guild. A sixth comparison ranked Warbling vireo marginally significantly higher than the Cerulean warbler. These observations indicate a strong association of Warbling vireo with highly connected woodland landscapes. In the Driftless Area, the riparian corridors that Warbling vireos are typically associated with do tend to provide more highly connected forest habitat than surrounding areas, partially explaining this observation. Inclusion of Warbling vireo in the non-interior forest guild may inappropriately skew results of the interior vs. non-interior guild test.

Table 8. Population means for metrics and key characteristics.



	AMRE	BWWA	CERW	INBU	LEFL	RTHU	WAVI	WOTH	Overall
Total Birds Observed	727	68	32	367	37	97	49	76	1453
Total Sites of Occurrence	116	41	20	130	19	69	14	43	181
% Sites of Occurrence	63.74	22.53	10.99	71.43	10.44	37.91	7.69	23.63	100
BBS_Abundance	3 to 10	0.05 to 3	0.05 to 1	3 to 10	0.05 to 1	0.05 to 3	3 to 10	1 to 3	NA
Interior Dependent	Yes	No	Yes	No	Yes	No	No	Yes	NA
Area Sensitive	Yes	No	Yes	No	Yes	No	No	Yes	NA
Landscape Context (Tier)	2.129	2.171	2.300	2.331	2.737	2.029	2.643	2.047	2.217
Patch_Cohesion_Index	98.6277	98.8068	98.8109	98.6959	99.1905	98.5376	98.9438	98.3405	98.664
Aggregation_Index	84.443	84.744	85.32	85.388	87.74	83.817	85.85	83.3	85.0753
Total_Core_Area (ha)	361.7	377.1	405	405	491.9	349.8	457.4	321.2	396.14
Total_Edge (meters)	255392	257907	255432	244708	236925	259096	267238	259455	254519
FRAC_SD	0.05663	0.05596	0.05798	0.05724	0.05356	0.05841	0.0532	0.05783	0.05635
Percent_Forest	44.45	44	47.6	48.3	50.7	40.4	56.3	44	46.97
Patch_Area (ha)	526.5	526.5	430.1	526.5	692.1	473.4	488	430.1	511.65
Modified_Edge_Distance (m)	66.7	89.49	75.53	84.37	119.32	66.7	75.53	67.08	80.59
Edge_Distance (m)	107.65	120.70	136.10	119.99	170.26	114.09	94.73	109.10	116.99
Road_Distance (m)	338.67	420.32	445.81	333.28	225.89	375.29	298.46	280.29	343.32
Stream_Distance (m)	229.75	247.16	321.66	257.17	239.45	263.95	166.38	250.60	248.93
Years Observed at Same Site	3.32	1.56	1.50	2.34	1.63	1.36	2.71	1.60	2.25
Individuals Observed per Site	6.23	1.66	1.60	2.82	1.95	1.39	3.43	1.74	3.20

Table 9. Population medians for key metrics



	AMRE	BWWA	CERW	INBU	LEFL	RTHU	WAVI	WOTH
Patch_Cohesion_Index	99.19221	99.11801	98.95748	99.22245	99.47131	99.055496	99.61395	98.96496
Aggregation_Index	85.99961	84.95931	87.78163	87.65994	89.74642	84.945435	88.58851	85.70551
Total_Core_Area (ha)	328.905	328.59	411.21	422.235	558.27	255.24001	557.595	329.22
Percent_Forest	44.45	44	47.6	48.3	50.7	40.4	56.3	44
Patch_Area (ha)	526.5	526.5	430.1	526.5	692.1	473.4	488	430.1
Edge_Distance (m)	84.37	94.33	108.88	94.33	133.40	94.33	75.53	89.49
Road_Distance (m)	229.10	390.00	466.87	272.46	150.00	300.00	232.28	161.55
Stream_Distance (m)	186.11	189.74	311.22	201.25	134.16	216.33	150.00	189.74

Observations made here suggest a strong association of Warbling vireo with riparian areas. The consistency with which Warbling vireo and Cerulean warbler were differentiated by distance to stream suggests that this information will be an important factor in models predicting either Cerulean warbler or Warbling vireo occurrence. The connection between moisture gradient/ proximity and potential abundance was also pointed out by Thogmartin et al. (2004), but with a qualitatively different effect for Cerulean warblers. Albeit weaker, the association of Cerulean warblers with elevated distance to stream may relate to a preference for upland habitat on this rugged highly stream dissected landscape. Increased occurrence of mature oaks (preferred nesting trees) on steep slopes and along ridges at maximum distance from streams may also help to account for this observation.

Another unexpected observations concerning the Cerulean warbler involves its relationship to forest abundance and distribution. Despite its documented dependence on intact mature deciduous forests, scores for patch cohesion, aggregation index, total core area, and percent forest were not significantly different than those for the more generalist or early successional dependent species (e.g. Blue-winged warbler, Indigo bunting, or Ruby-throated hummingbird).

Although seemingly contradictory, these observation do make sense in light of the positive association of the Cerulean warbler with interior edges, and preference for canopy openings (Oliarnyk and Robertson, 1996; Hamel, 2000). Hamel proposes that this preference for slightly more open areas within a densely forested matrix (mean canopy closure = 85%) may be related to the relatively weak song of the Cerulean warbler, which is poorly adapted to densely forested habitat. The high distance to road values observed for Ceruleans may also relate to their weak song, as traffic noise may interfere with courting and territorial behaviors. Increased predation resulting from the well defined corridor provide to nest predators by roads may also play a strong role in determining the distribution of Cerulean warblers. Since Cerulean warblers will only attempt a single brood (Oliarnyk and Robertson, 1996), there may be strong selective pressure for them to avoid nesting sites where predation is likely.

It should be noted that several of the less abundant species were more nearly normally distributed around a distinct range metric values (Figures 3 – 6). The more confined shape of these probability distribution graphs indicates that these species may have a narrow range of habitat preference, and tend to occur less frequently at highly altered, low quality sites.

Road distance and patch cohesion appear to be compressed at opposite ends of their respective spectra. This may relate to the fact that patch cohesion is a landscape scale area weighted mean function of the perimeter-area ratio divided by the shape index (SI = perimeter/2(sqrt(π*area))), while distance to road is a site specific characteristic dependent on human activities operating at a very localized scale, but across broad areas. The distinct nature of these two variables combined with the strong differential response shown among species to both, makes them excellent candidates for use in predictive models of species occurrence.

Species with low site re-occurrence can be assumed to either have high mortality, or low site fidelity. Species in this group include Cerulean warbler, Wood-thrush, Least flycatcher, Ruby-throated hummingbird, and Blue-winged warbler. These are also the same species for which the USFWS Breeding Bird Survey (BBS) data show the lowest level of occurrence. Hamel (2000) and Oliarnyk and Robertson (1996) provide convincing evidence of Cerulean warbler nest fidelity. Low re-occurrence may, therefore, indicate high rates of mortality and/or reproductive failure on the study landscape, suggesting that subsidies from the bio-regional metapopulation (Levins, 1969) may be needed for this species to persist in the study area. This conclusion is confounded, however, by the competing observation that Cerulean warblers may tend to roost in locations greater than 1 km apart from day to day (Hamel 2006, unpublished).

Lack of significance for metric comparisons other than site re-occurrence and number of individuals may indicate that American redstarts are not limited by patterns of habitat availability or fragmentation currently observed in the Driftless Area. This species may also be more gregarious than others assessed, and may exhibit significant site fidelity, or fill all available niches on the landscape.

Failure of the modified distance to edge metric, incorporating distance to road as a surrogate edge, to better predict differences in species occurrence indicates that forest edges and roads may have qualitatively different effects on species distribution (discussed above with relation to Cerulean warbler). The effect of roads on species distribution is more powerful than that of simple edge, or of the combined distance to edge/road metric.

One hypothesis concerning the lack of distinction provided by landscape tier with respect to differences in bird species occurrence is that this measure, as developed here, does not provide enough categories among which bird occurrences can be compared. Eight species were compared, while the landscape context measure provided only six categories for use in comparing them. It is suggested that a finer division of this metric may provide more meaningful distinction.

Because the point-count method is not designed for or effective at providing evidence of nesting, the classification of interior forest specialist is not extremely robust (Villard, 1998). Inconsistent relationship found between landscape indices and the occurrence of species from separate functional groups may stem from this uncertainty. Alternatively, either microsite characteristics, or factors operating at scales larger than those assessed here may play stronger roles in the population ecology of some species. It is also important to note that evidence of occurrence, and conclusions drawn from such evidence, do not necessarily equate to reproductive success or population persistence on any particular site or landscape.

Conclusions

The non-parametric approach used here allows differentiation of species specific relationships to various metrics describing landscape structure and habitat distribution. Additional research involving more species, more sample points, and multiple spatial scales (Milne, 1992; Gustafson et al., 2002; Knutson et al., 2004) may help to clarify these relationships. As suggested by Vickers

(2005), parametric ANCOVA comparisons using log-transformation methods may provide an effective size estimate for identified relationships where skewness of the data is not too extreme. Such an approach may provide sufficient power to allow a visualization of the relevant habitat connectivity spectrum associated with individual species or functional groups.

Of the factors assessed, patch cohesion, aggregation index, and distance to road provided the best differentiation of where individual species occured. Landscape context, patch area, and percent forest were poor indicators of differences in species occurrence for most comparisons. Patch cohesion appears to summarize the effects of these variables in a metric more closely linked to the biological/behavioral response of birds to landscape condition.

While a combination of factors may provide even stronger differentiation, patch cohesion provides a useful measure of differences in the response of many species to variations in the extent and arrangement of habitat. Although the exact nature of the relationship between habitat connectivity and species occurrence is difficult to conceptualize and may be challenging to characterize, for many species such a relationship appears to exist.

For landscapes where forest cover exceeds the percolation threshold, habitat connectivity may decrease in importance as a limiting factor. Where total habitat and connectivity are limited, it makes sense that areas with higher connectivity will be favored by forest interior specialists. However, when forest cover and connectivity exceed a critical threshold, other site specific factors may become more important in determining where birds of certain species occur. Such a response is predicted by With and Crist (1995), and may overshadow the effect of landscape structure (at the scale assessed) on Cerulean warblers.

The results of this study corroborate the observations of Schumaker (1996) and Riiters et al. (2002) that habitat area alone is not a sufficient indicator of ecological function. Riiters et al. assessment of forest perforation across large portions of the Unites States suggests that forests are, generally, connected over large regions (e.g. large patches), but fragmentation is so extensive that edge effects dominate many ecological processes. Schumaker found that patch cohesion captured biologically relevant information not apparent from measures of habitat loss alone.

These results seem to indicate that above a minimum threshold (Rosenberg et al., 1999), patch size is not a very good indicator of occurrence probability for area sensitive forest interior species on highly dissected landscapes. Factors related to fragmentation including patch shape, isolation, core area, and location of roads play significant roles in determining where suitable habitat occurs, and may outweigh the patch size effect. Landscape metrics incorporating measures of habitat aggregation, proportion of core area, and connectivity seem to describe real ecological processes underlying site selection and population dynamics.

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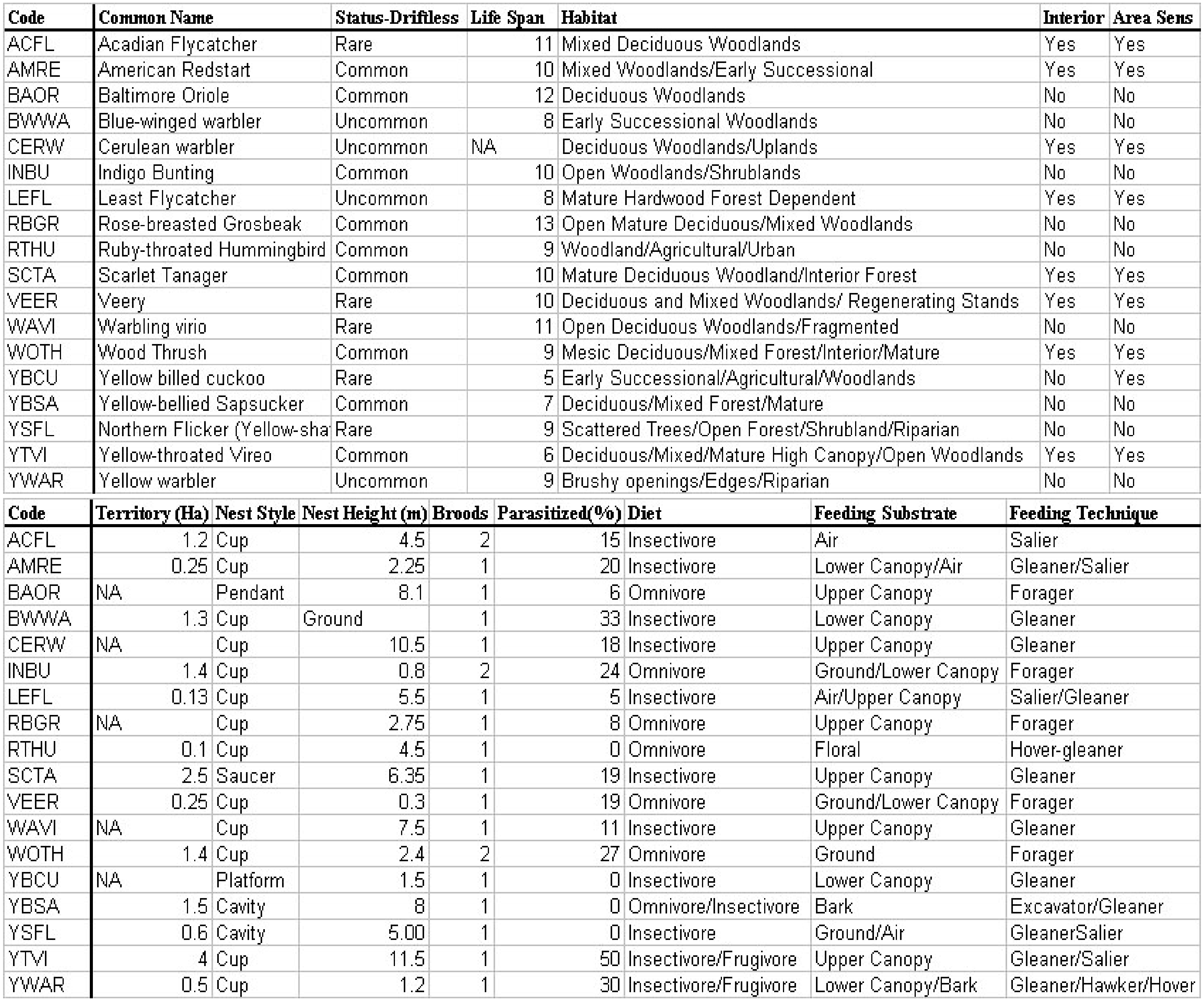
Appendix 1. Summary of life-histories for qualifying neotropical migratory bird species included in the bird count dataset (Hanowski et al., 2003).



Code	Common Name	Status-Driftless	Life Span	Habitat	Interior	Area Sens
ACFL	Acadian Flycatcher	Rare	11	Mixed Deciduous Woodlands	Yes	Yes
AMRE	American Redstart	Common	10	Mixed Woodlands/Early Successional	Yes	Yes
BAOR	Baltimore Oriole	Common	12	Deciduous Woodlands	No	No
BWWA	Blue-winged warbler	Uncommon	8	Early Successional Woodlands	No	No
CERW	Cerulean warbler	Uncommon	NA	Deciduous Woodlands/Uplands	Yes	Yes
INBU	Indigo Bunting	Common	10	Open Woodlands/Shrublands	No	No
LEFL	Least Flycatcher	Uncommon	8	Mature Hardwood Forest Dependent	Yes	Yes
RBGR	Rose-breasted Grosbeak	Common	13	Open Mature Deciduous/Mixed Woodlands	No	No
RTHU	Ruby-throated Hummingbird	Common	9	Woodland/Agricultural/Urban	No	No
SCTA	Scarlet Tanager	Common	10	Mature Deciduous Woodland/Interior Forest	Yes	Yes
VEER	Veery	Rare	10	Deciduous and Mixed Woodlands/ Regenerating Stands	Yes	Yes
WAVI	Warbling virio	Rare	11	Open Deciduous Woodlands/Fragmented	No	No
WOTH	Wood Thrush	Common	9	Mesic Deciduous/Mixed Forest/Interior/Mature	Yes	Yes
YBCU	Yellow billed cuckoo	Rare	5	Early Successional/Agricultural/Woodlands	No	Yes
YBSA	Yellow-bellied Sapsucker	Common	7	Deciduous/Mixed Forest/Mature	No	No
YSFL	Northern Flicker (Yellow-sha	Rare	9	Scattered Trees/Open Forest/Shrubland/Riparian	No	No
YTVI	Yellow-throated Vireo	Common	6	Deciduous/Mixed/Mature High Canopy/Open Woodlands	Yes	Yes
YWAR	Yellow warbler	Uncommon	9	Brushy openings/Edges/Riparian	No	No

Code	Territory (Ha)	Nest Style	Nest Height (m)	Broods	Parasitized(%)	Diet	Feeding Substrate	Feeding Technique
ACFL	1.2	Cup	4.5	2	15	Insectivore	Air	Salier
AMRE	0.25	Cup	2.25	1	20	Insectivore	Lower Canopy/Air	Gleaner/Salier
BAOR	NA	Pendant	8.1	1	6	Omnivore	Upper Canopy	Forager
BWWA	1.3	Cup	Ground	1	33	Insectivore	Lower Canopy	Gleaner
CERW	NA	Cup	10.5	1	18	Insectivore	Upper Canopy	Gleaner
INBU	1.4	Cup	0.8	2	24	Omnivore	Ground/Lower Canopy	Forager
LEFL	0.13	Cup	5.5	1	5	Insectivore	Air/Upper Canopy	Salier/Gleaner
RBGR	NA	Cup	2.75	1	8	Omnivore	Upper Canopy	Forager
RTHU	0.1	Cup	4.5	1	0	Omnivore	Floral	Hover-gleaner
SCTA	2.5	Saucer	6.35	1	19	Insectivore	Upper Canopy	Gleaner
VEER	0.25	Cup	0.3	1	19	Omnivore	Ground/Lower Canopy	Forager
WAVI	NA	Cup	7.5	1	11	Insectivore	Upper Canopy	Gleaner
WOTH	1.4	Cup	2.4	2	27	Omnivore	Ground	Forager
YBCU	NA	Platform	1.5	1	0	Insectivore	Lower Canopy	Gleaner
YBSA	1.5	Cavity	8	1	0	Omnivore/Insectivore	Bark	Excavator/Gleaner
YSFL	0.6	Cavity	5.00	1	0	Insectivore	Ground/Air	GleanerSalier
YTVI	4	Cup	11.5	1	50	Insectivore/Frugivore	Upper Canopy	Gleaner/Salier
YWAR	0.5	Cup	1.2	1	30	Insectivore/Frugivore	Lower Canopy/Bark	Gleaner/Hawker/Hover

Appendix 2. Mann-Whitney Significance ($\alpha \leq 0.05$); single-tailed. Negative p-Values indicate that $\text{Mean}_{N1} < \text{Mean}_{N2}$. Significance scores for metric-species pair combinations with |p-value| greater than 0.20 are omitted to simplify interpretation. Significant comparisons at the $p \leq 0.05$ level are listed in **bold.** Comparisons among functional groups are indicated by I (Interior) and O (Non-interior) in the "Guild" field.

			Focal Landscape Metrics							**Site Specific Metrics**					**Species Metrics**			
Pairing	**N_1**	**N_2**	**Tier**	**COHESION**	**FRAC_SD**	**Aggreg**	**Core**	**Tot_Edg**	**%_For**	**Rd_Dist**	**Edge_Dist**	**Mod_Edg**	**Strm_Dist**	**Area**	**# Years**	**# Indiv**	**# Sig**	**Guild**
AMRE_BWWA	116	41	---	---	---	---	---	---	---	**-0.0217**	-0.1875	**-0.0425**	---	---	**0**	**0**	4	I_O
AMRE_CERW	116	20	---	---	---	---	-0.1915	---	---	-0.0673	---	-0.1221	**-0.0331**	---	**0**	**0**	3	I_I
AMRE_INBU	116	130	-0.0846	---	---	-0.1078	-0.0949	0.0846	-0.1536	---	-0.12	-0.1769	-0.1533	---	**0.0001**	**0**	2	I_O
AMRE_LEFL	116	19	**-0.0326**	**-0.0326**	0.0759	**-0.0144**	**-0.0151**	0.1215	-0.0579	0.0689	**-0.0072**	-0.1017	---	---	**0.0003**	**0.0003**	7	I_I
AMRE_RTHU	116	69	---	0.1152	-0.1363	---	---	---	---	---	---	---	-0.1292	---	**0**	**0**	2	I_O
AMRE_WAVI	116	14	-0.1104	**-0.0366**	0.1691	---	-0.0736	---	-0.054	---	---	---	0.0773	---	0.1364	**0.0485**	2	I_O
AMRE_WOTH	116	43	---	0.0614	---	0.1811	0.1652	---	---	0.1427	---	---	-0.1995	0.1765	**0**	**0**	2	I_I
BWWA_CERW	41	20	---	---	---	---	---	---	---	---	---	---	-0.0834	---	---	---	0	O_I
BWWA_INBU	41	130	---	---	---	---	---	0.1385	---	**0.0183**	---	0.1389	---	---	**-0.003**	**-0.0021**	3	O_O
BWWA_LEFL	41	19	-0.0786	**-0.0258**	0.073	**-0.0484**	**-0.0453**	0.1214	-0.1121	**0.0025**	-0.0551	---	---	---	---	---	4	O_I
BWWA_RTHU	41	69	---	---	---	---	---	---	---	0.141	---	0.1651	---	0.0914	0.0993	0.0976	0	O_O
BWWA_WAVI	41	14	-0.1964	**-0.0347**	0.1575	---	-0.0977	---	-0.0821	**0.0339**	0.1292	0.1646	0.1081	---	**-0.038**	**-0.0464**	4	O_O
BWWA_WOTH	41	43	---	0.176	---	0.1647	0.1135	---	---	**0.002**	---	0.1269	---	0.0652	---	---	1	O_I
CERW_INBU	20	130	---	---	---	---	---	0.1845	---	0.0585	---	---	0.096	---	**-0.006**	**-0.0036**	2	I_O
CERW_LEFL	20	19	-0.1593	-0.0821	---	**-0.0473**	-0.1335	0.1662	---	**0.0147**	-0.1397	---	0.0981	---	---	-0.1162	2	I_I
CERW_RTHU	20	69	---	---	-0.1522	0.1868	0.1409	---	---	0.1727	---	---	0.1271	---	---	---	0	I_O
CERW_WAVI	20	14	---	-0.0782	---	---	---	-0.1071	---	0.1137	0.1469	---	**0.0137**	---	**-0.033**	**-0.0331**	3	I_O
CERW_WOTH	20	43	---	0.1489	---	0.1524	0.0651	---	0.1489	**0.0299**	---	0.178	0.1188	---	---	-0.1489	1	I_I
INBU_LEFL	130	19	-0.1171	**-0.0294**	---	**-0.0494**	-0.0636	---	-0.1508	0.064	**-0.0263**	-0.1966	---	---	**0.0245**	0.071	4	O_I
INBU_RTHU	130	69	**0.0501**	0.1021	-0.1238	**0.0353**	0.0836	-0.0622	0.1928	-0.196	---	---	---	0.1089	**0**	**0**	3	O_O
INBU_WAVI	130	14	---	**-0.0333**	0.148	---	-0.1683	-0.0672	-0.0845	---	0.1137	---	**0.0346**	---	---	---	2	O_O
INBU_WOTH	130	43	0.1027	0.0572	---	**0.0312**	**0.0238**	-0.1138	0.0754	0.1404	---	---	---	0.0827	**0.0025**	**0.0088**	4	O_I
LEFL_RTHU	19	69	**0.0231**	**0.0079**	**-0.0296**	**0.0067**	**0.017**	-0.0793	0.0694	**-0.0317**	**0.0226**	---	-0.1874	0.1367	---	0.0586	7	I_O
LEFL_WAVI	19	14	---	---	---	0.1582	---	-0.0653	---	-0.196	**0.0279**	0.196	---	---	-0.063	-0.1372	1	I_O
LEFL_WOTH	19	43	**0.0318**	**0.0047**	-0.0544	**0.0043**	**0.0034**	-0.1109	**0.0346**	---	**0.0208**	0.1642	-0.168	0.1229	---	---	6	I_I
RTHU_WAVI	69	14	-0.0838	**-0.015**	0.0682	-0.1179	-0.0682	---	-0.0598	---	0.1521	---	**0.035**	---	**-0.008**	**-0.0103**	4	O_O
RTHU_WOTH	69	43	---	---	---	---	---	---	---	0.0528	---	---	---	---	-0.122	-0.0585	0	O_I
WAVI_WOTH	14	43	0.0988	**0.01**	-0.0925	0.0836	**0.0165**	---	**0.0339**	---	---	---	**-0.0407**	---	**0.0383**	0.0715	5	O_I
# Significant @ p<=0.05			**4**	**10**	**1**	**8**	**6**	**0**	**2**	**8**	**5**	**1**	**5**	**0**	**15**	**14**	**79**	
# Significant @ p<=0.10			**8**	**14**	**6**	**9**	**13**	**5**	**9**	**13**	**6**	**1**	**9**	**3**	**17**	**18**	**131**	