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Corresponding Author: Jessica Diane Davis, M.S.

Corresponding Author's Institution: Iowa State University

First Author: Jessica Diane Davis, M.S.

Order of Authors: Jessica Diane Davis, M.S.; Diane M Debinski, PhD

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LOCAL AND LANDSCAPE EFFECTS ON THE BUTTERFLY COMMUNITY IN FRAGMENTED MIDWEST U.S.A. PRAIRIE HABITATS

Jessica D. DAVIS and Diane M. DEBINSKI

Department of Ecology, Evolution and Organismal Biology, 253 Bessey Hall, Iowa State University, Ames, Iowa 50011 USA; phone: (515) 294-2460; fax: (515) 294-1337; email: Debinski@iastate.edu

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Abstract

The fragmented landscape of the Midwest USA includes prairie remnants embedded in an agricultural matrix, potentially impermeable to dispersing individuals. We examined butterfly responses to local (environmental variables measured within the prairie fragment itself such as vegetative characteristics) and landscape (environmental variables measured up to 2km surrounding the fragment, but not the fragment itself) factors at 20 prairie remnants in Iowa. Our objectives were to: 1) document how the composition and configuration of the landscape affects butterfly community within the fragment, 2) determine whether explanatory power is gained by including both landscape and local variables rather than only local variables, and 3) analyze differences in butterfly community composition between linear and block shaped fragments. Results from partial least squares regression suggest there are effects of the landscape on butterflies at all spatial extents investigated with the 0.5km extent being most highly correlated with butterfly community composition. The local variable that was most highly correlated with butterfly community response was percentage litter, while percentage of roads was the most important variable at all landscape spatial extents. Ordination diagrams clearly separate linear from block sites based on butterfly community composition. Variance partitioning using partial canonical correspondence analysis indicated that landscape variables at all spatial extents add additional explanatory power beyond local variables with little overlap in percentage of variation explained. Our results suggest that butterflies are making decisions based both on the local and landscape environmental factors, thus land surrounding prairie remnants should be included in management decisions.

Keywords: butterflies; conservation; floral resources; habitat fragmentation; partial least squares regression; spatial extent; variance partitioning.

Introduction

Understanding the landscape ecology of fragmented systems is essential to conservation of the flora and fauna in habitat fragments (Fahrig and Merriam 1994). Many landscape scale studies have focused on vertebrates and specifically avian taxa (Mazerolle and Villard 1999), but few have investigated the role of floral resources in the landscape on invertebrates in a highly fragmented landscape. The quality of the matrix surrounding a habitat fragment has impacts on a species' dispersal ability, edge effects, permeability, and isolation (Ricketts 2001). In addition, different species or groups of species perceive the landscape and respond to different landscape features and extents depending on their requirements, sensitivity to disturbance and dispersal abilities (Lord and Norton 1990).

In the Great Plains, the destruction and fragmentation of the tallgrass prairie biome has been particularly severe with over 99% destroyed in most states as a result of conversion to agriculture (Samson and Knopf 1994). Today, all that remains are a few small, protected preserves and numerous smaller, unprotected fragments along railroad right-of-ways and roadsides. Studies indicate that reproduction of butterfly pollinated plant species is often reduced in small populations created by habitat destruction and fragmentation (Hendrix and Kyhl 2000). This leads to the obvious conclusion that butterflies in the Midwest have declined substantially as fragmentation has proceeded.

We are particularly interested in the role tallgrass prairie fragments play in affecting the community composition of butterflies. Prairie fragments often contain high concentrations of floral resources and may be particularly valuable in sustaining butterfly diversity in Iowa where habitat destruction has been so severe. For example, restored roadside prairies in Iowa contained twice as many habitat-sensitive butterflies as did weedy or grassy roadsides (Ries et al. 2001).

Fragments can be categorized into two general shapes. Block-shaped fragments are mainly state prairie preserves which are actively managed with fire. Linear fragments exist along roadsides, railroad rights-of-way, and trails and are generally not actively managed.

From the management perspective, understanding which local and landscape variables affect the butterfly community in fragmented landscapes is critical to sustaining diversity (Saunders et al. 1991). Butterflies forage widely, and studies (Debinski et al. 2001) indicate that the distribution and amounts of adjacent landuse types will likely be important in affecting the butterfly community in fragments. The composition and configuration of landuse types (roads, pasture, agricultural fields, etc.) will likely influence the diversity of butterflies at fragments.

Relatively little is known about the factors that control diversity of butterflies in fragments and the relative roles of local and landscape factors. In such a fragmented landscape the distinction between what we refer to as local and landscape variables is relatively clear. Prairie fragments are isolated and have distinct edges and are often surrounded by a monoculture of an agricultural crop. We refer to any environmental variable measured within the prairie fragment itself as local variables. Local variables including floral abundance (Clausen et al. 2001), width of habitat (Dover 1996; Reeder et al. 2005), shelter (Dover 1996; Dover et al. 1997; Pywell et al. 2004), larval host plant presence (Pywell et al. 2004), habitat quality (Schneider and Fry 2001; Collinge et al. 2003; Jeanneret et al. 2003), and adjacent land use (Sparks and Parish 1995) have been shown to affect butterflies at the extent of the habitat patch itself. We refer to any environmental variable measured in the landscape surrounding the fragment, but not the fragment itself as landscape variables. Landscape variables at larger spatial extents such as connectivity (Haddad 1999b; Haddad and Baum 1999; Sutcliffe et al. 2003), habitat patch size (Dennis and Shreeve 1997; Steffan-Dewenter and Tscharntke 2000; Tscharntke et al. 2002;

Krauss et al. 2003), isolation (Clausen et al. 2001; Sawchik et al. 2003), edge permeability (Haddad 1999a; Ries and Debinski 2001; Schultz and Crone 2001; Merckx et al. 2003), and landscape heterogeneity (Debinski et al. 2001; Ricketts 2001; Schneider and Fry 2001; Sutcliffe et al. 2003) have also been shown to influence butterflies.

The spatial extent at which butterflies actually forage is a logical place to begin analyses of landscape resource abundance and diversity on butterfly community composition. Butterfly dispersal is not random (Conradt et al. 2000; Dover and Fry 2001; Kindlmann et al. 2004; Cant et al. 2005) but rather based on local and landscape variables. Butterflies routinely make dispersal bouts at distances of 1 to 2km (Harrison 1989; Wahlberg et al. 2002; Schneider 2003; Auckland et al. 2004) and daily movements of 200 to 600m (Jones et al. 1980; Auckland et al. 2004); therefore we used landscape spatial extents of 0.5 to 2.0 km in our study.

Different groups of butterflies may be responding to different variables and extents. Mutually exclusive butterfly habitat groups were classified *a priori* based on host plant and nectar resources (Opler and Krizek 1984; Ries et al. 2001; Shepherd 2003; Reeder et al. 2005; Table 3). Disturbance-tolerant (DT) species survive well in agricultural and/or urban areas and occur throughout Iowa. Habitat-sensitive (HS) species are associated with native prairie and require prairie dependent plants for either larval or adult resources.

Objectives

Our first objective was to determine how much explanatory power is gained by including landscape variables in our analyses as compared to using only local variables. We expected the addition of landscape variables to the local model would increase our ability to explain the variability in butterfly community composition between sampling sites. Others have found landscape variables to explain very little of the variation in butterfly species assemblages

(Jeanneret et al. 2003), however we investigated a set of biologically meaningful landscape metrics such as diversity of flowering resources in the landscape.

Our second objective was to document how the composition and configuration of landscape variables affect butterfly community composition at prairie fragments. We anticipated that landscape floral resources would be positively related to community composition. In addition, we wanted to determine whether or not we gain more information by collecting data on landscape floral resources as compared to readily accessible data on landuse types. We examined affects of landscape variables on the butterfly community composition at multiple spatial extents (0.5, 1.0, 1.5 and 2.0km).

Our final objective was to determine whether there are differences in community composition between linear and block sites. We wanted to determine if there are differences in the local and landscape variables between linear and block sites and if so, how the butterfly community is responding to the differences.

Methods

Sampling sites

Sampling sites refers to prairie fragments (block or linear) where butterflies were sampled. In 2003, we sampled the butterfly communities at seven block and ten linear sites. In 2004, we sampled the same 17 sites as 2003, and added three block sites to increase our sample size to 20. All sites were remnant tallgrass prairies located in the northwest quarter of Iowa, far enough from each other so that the 2km buffers did not overlap between two nearby sites. The sample size of block sites was constrained by our *a priori* qualifiers for accepting a site to sample such as a minimum size of 40,000m^2 and a minimal proportion (<30%) of non-native, aggressive plant species at the site. The specific block sites sampled represent a range of sizes

(100,000 – 650,000m^2) and the landscape surrounding them varied considerably in the relative amount of landuse types. At each block and linear site, we established two 100m by 5m transects marked with survey flags. Transect lengths were typical of those used in previous pollinator studies (Ries et al. 2001; Reeder et al. 2005). Transect locations were randomly selected from among areas not dominated by wetland vegetation and at least 50m from each other.

Butterfly sampling

In 2003 and 2004, we surveyed each site once for adult butterflies three times during the growing season (June, July, and August). Butterfly surveys were conducted between 0930 and 1830 hrs when temperatures were between 21^o C and 35^o C, sustained winds were below 16 km/hr and the sun was shining. Butterfly surveys were conducted by walking each 100m transect at a pace of 10 m/min and observing butterflies within 2.5m on either side and in front of the observer (Thomas 1983). During each visit, all butterflies (including skippers) were counted and identified on the wing if possible; otherwise they were netted. The amount of time used to handle individuals, record field notes, etc., was not counted towards sampling effort.

Quantification of local and landscape resources

Floral resources at the local extent were estimated by a direct count of flowering ramets in each 100m transect during all rounds of butterfly sampling. We choose to survey the floral resources rather than host plants because of the direct comparison between adult butterflies and nectar sources. Relative proportions of forbs, native grass, non-native grass, litter, and bare ground were estimated for each transect. Approximations were averaged using values from two observers after a relevé of each transect to avoid observer bias.

In order to identify the spatial extent at which butterflies respond to landscape features, we chose to use spatially nested circular buffers (i.e., larger extents include smaller extents; Figure 1) rather than separate annular rings (i.e., concentric rings, independent ellipses or circles at all extents). The literature is divided as to the preferred approach with examples of both annular rings (Pearson 1993; Graham and Blake 2001) and nested buffers (Bergin et al. 2000; Ribic and Sample 2001). Because spatially nested buffers are not statistically or biological independent, we did not include multiple extents in a given model but rather compared the correlation between butterfly assemblage and each spatial extent.

#Figure 1 approximately here#

We quantified resources in the landscape surrounding each site within a 2km radius centered in the middle of the site. We analyzed landscape data using nested spatial extents of 0.5, 1.0, 1.5 and 2.0km because different butterflies may respond to landscape features at different spatial extents. We used digital color infrared orthophotographs with a resolution of 1m pixels taken in 2002 along with ArcMap 8.3 (Environmental Systems Research Institute 2004) to divide each 2km radius landscape into visually distinct, homogeneous polygons based on differences in landuse types. Grain size was a minimum of 6m by 50m because butterflies are known to have a perception ability of 50 m to a suitable patch (Harrison 1989) and to include linear features in the landscape such as roadsides (Ries et al. 2001) and buffer strips (Reeder et al. 2005) known to influence butterflies. Grain size was constant across extents. The boundaries of the polygons for half of the sites were checked in 2003 and the remaining half in 2004. We used visual inspection by walking, observing from the road with binoculars and driving along polygon boundaries to assess any recent landuse changes and to assign a floral resource index (FRI) value of 0 to 5 to each polygon on the basis of the richness and abundance of all forb species in the polygon (Table 1). The landscape dataset was created in conjunction with another project including other pollinator taxa and therefore includes all forb species rather than only those forbs known to be associated with butterflies. The FRI rankings were based on the types of patches we encountered and may not reflect the variability in diversity and abundance of flowering resources in other landscapes.

#Table 1 approximately here#

Data analysis

From the initial set of biologically meaningful variables, where pairs of independent variables were highly correlated (r>0.7), the variable that was most strongly correlated with other variables was eliminated from analyses. Our reduced set of variables included three local (litter coverage, floral abundance and site size) and four landscape (distance to nearest polygon with FRI≥3, percentage coverage non-linear grassland, percentage coverage road and percentage coverage of polygons with FRI≥3) variables (Table 2). We chose to use metrics that included FRI≥3 because this may be a large enough magnitude to attract butterflies to a polygon in the landscape, although there is little data to support this (but see Kuussaari et al 1996, Luoto et al. 2001). Landscape variables at all extents did not include the area encompassed by the sampling site. Arcsin square-root transformations were applied to percentage variables and log transformations were applied when abundance and environmental data were not normally distributed. Local variables and butterfly response variables were averaged over the two years of sampling. General patterns of differences in local and landscape variables between linear and block sites were analyzed using multivariate analysis of variance (MANOVA).

#Table 2 approximately here#

For a community-based analysis, we used partial least squares (PLS) regression to investigate the correlation between the species abundance matrix and environmental variables at different spatial extents (ter Braak and Verdonschot 1995). We chose this method over other ordination techniques because PLS relaxes restrictions on colliniarity among groups of variables and is more biologically meaningful than using factor analysis separately on the species and environmental matrices (Johansson and Nilsson 2002). PLS explains the maximum covariation between species abundance and environmental variables at each extent. Before performing PLS we standardized each species abundance to a mean of zero and variance of one. We performed PLS for species matrix of all species with total abundance greater than 10, disturbance-tolerant, and habitat-sensitive species. We used XLSTAT-PLS, an add-in created for Microsoft Excel (Addinsoft 2005) to perform the PLS regression.

We used the correlation of the first X to the first Y component at each extent (local, 0.5, 1.0, 1.5, and 2.0 km) from the PLS results to find the extent at which there is the greatest correlation. We also investigated the variable importance projection (VIP) values for each landscape variable at each extent (Johansson and Nilsson 2002). VIP-values quantify the influence of each variable on the ability to explain the variation in the response variables. VIP-values greater than one are considered the most relevant, although this does not indicate the direction of influence (i.e., positive or negative). We used model equations from PLS to examine the ability of environmental variables to explain species abundance. Model equations were created using local variables, landscape variables, and the global model which included all variables from both local and landscape extents

We used partial canonical correspondence analysis (pCCA) in R-project (R Development Core Team 2004) to show the percent of the variation in butterfly community composition that is explained by local variables alone, landscape variables alone, and the overlap of local and landscape variables for each landscape extent (0.5-2.0 km; Borcard et al. 1992). The percent of the variation explained is the ratio of the sum of the constrained eigenvalues to the sum of the unconstrained eigenvalues (total inertia). We first conducted a canonical correspondence analysis (CCA) using local variables. For each landscape extent we then conducted a series of constrained ordinations: one using the local variables as covariables, one using the landscape variables as covariables and one on landscape variables alone to partition the variance.

Results

#Table 3 approximately here#

We identified 27 species of butterflies and 1057 individuals. We eliminated woodland species (*Papilio glaucus* and *Enodia anthedon*) from all analyses to focus our results on grassland butterflies. Landscape variables were not constant in magnitude across spatial extents and differed between linear and block sites (Table 4). ROAD and FRI did not show a consistent pattern across extents whereas MINDIST increased with extent. GRASS decreased with extent for block sites but increased with extent for linear sites. The MANOVA of local variables showed no significant differences between linear and block sites (df=1, Wilk's λ=0.86, p=0.26). MANOVAs of landscape variables showed significant differences between linear and block sites (df=1; Wilk's λ=0.29, 0.37, 0.47, 0.48; p<0.001, 0.003, 0.016, 0.019) at all spatial extents: 0.5, 1.0, 1.5 and 2.0km respectively.

#Table 4 approximately here#

The correlation of the first component of the species matrix to the first component of each environmental matrix from the PLS regression was plotted at all extents (local, 0.5-2.0km; Figure 2). The extent with the highest correlation to the species matrix was 0.5km, with a small range of correlation across extents. VIP-values for local variables indicated that LITTER and FABUND are the most relevant to explain variation in the butterfly community composition. VIP-values for each landscape variable were plotted against all landscape extents (Figure 3). ROAD is an influential variable at all extents. MINDIST is marginally influential at all extents. GRASS becomes more important with increasing extent. FRI is marginally influential at 0.5km with decreasing influence with extent.

#Figure 2 approximately here#

#Figure 3 approximately here#

Ordination diagrams derived from PLS allow us to visualize the influence of the environmental variables on sites, species and site shape. Given the biplot where the local variables were plotted along with the species and site scores we can infer that SIZE is strongly correlated with block sites (Figure 4a) because the SIZE arrow points in the direction of block sites. FABUND and LITTER were not associated with one habitat shape over the other. *Danaus plexippus*, *Papilio polyxenes*, *Speyeria idalia* and *Vanessa cardui* were associated with block sites. *Anatrytone logan*, *Colias eurytheme, Polites mystic*, *Polites peckius* and *Speyeria cybele* were associated with linear sites.

#Figure 4 approximately here#

We also created a biplot with landscape variables at the 0.5km extent (Figure 4b). Ordination diagrams of the 1.0-2.0km extents resembled the 0.5km biplot but were omitted here for simplicity. ROAD was most associated with linear sites while GRASS and MINDIST were most associated with block sites. *Speyeria idalia* and *Ancyloxypha numitor* were associated with block sites. *Anatrytone logan*, *Colias eurytheme, Celastrina neglecta*, *Pholisora catullus*, *Polites mystic*, and *Pieris rapae* were associated with linear sites.

Model equations from PLS were evaluated by examining the R^2 from plotting observed versus predicted abundance for each species (Table 5). The majority of the species responded to LITTER (10 out of 13, 77%) and FABUND (9 out of 13, 69%) positively and SIZE (8 out of 13, 62%) negatively. Individual species showed mixed responses to all landscape variables. FRI (6 out of 10, 60%), ROAD (6 out of 10, 60%), MINDIST (5 out of 10, 50%) and GRASS (6 out of 10, 60%) were positively associated with butterfly abundance. Again, we only report landscape variables at the 0.5km extent for simplicity.

#Table 5 approximately here#

We compared the ability to explain species abundance between local and 0.5km extent variables by sorting the list of species and groups by R^2 for each extent (Table 5). We are able to explain abundance of *Phyciodes tharos* relatively well using local variables (R^2 = 0.30-0.46), but lack explanatory power with landscape variables. Disturbance-tolerant species, *Danaus plexippus*, and *Speyeria idalia* abundance can be explained relatively well at local and landscape extents. *Speyeria cybele* and *Anatrytone logan* abundance can be explained using landscape variables, but not local variables. Habitat-sensitive species abundance cannot be explained using either local or landscape variables.

Landscape variables alone explained between 19.8 and 23.4% of the variation, depending on extent, and local variables alone explained 25.3% of the variation in community composition (Figure 5). The amount of overlap in the proportion of the variance explained by the local and landscape variables ranged between 0.8 and 5.5%, depending on landscape extent, with decreasing shared percentage as landscape extent increased. The overall percentage explained by local and landscape variables ranged from 42 to 46%.

#Figure 5 approximately here#

Discussion

Local versus landscape

Our results show that butterflies are most correlated with landscape variables at the 0.5km extent. Results also indicate that butterflies to some degree are influenced by the landscape up to 2.0km. Roads at all landscape extents influence butterfly community composition in prairie fragments.

Butterfly composition was more correlated with floral resources than with grassland in the landscape at small landscape extents. Although grassland becomes more important with increasing extent, it may be an artifact of increasing variance of the metric with extent. Explanatory models for individual species confirm that floral resources in the landscape are an important indicator for which the majority of species responded positively to and to a stronger degree than the amount of grassland in the landscape (Table 5). Based upon these results, if a land manager is interested in sustaining butterfly communities, creating a grassland conservation buffer which includes a high diversity of forbs will provide the greatest success.

Understanding landscape configuration and composition added considerable ability to explain variation in community composition beyond what the local variables explained. Landscape metrics alone added additional explanation of the variation in butterfly community composition beyond what the local variables explained. The percent variation explained by local variables was comparable to that of landscape variables at all extents. Variance partitioning has been used in multiscale studies and some have found similar results with taxa other than butterflies with respect to the amount of overlap (Titeux et al. 2004), and the total percentage of variation explained by local and landscape variables (Chust et al. 2003; Williams and Wiser 2004). Others have found opposite results with high overlap between local and landscape factors

(Chust et al. 2003; Miller et al. 2004; Williams and Wiser 2004) and with local factors explaining more variance than landscape factors (Miller et al. 2004; Titeux et al. 2004). In a review of all studies that compared local versus landscape effects, Mazerolle and Villard (1999) found that in general, landscape variables explain a small percentage of the variance with respect to local environment. Contrary to these general trends, our results suggest that in the Midwestern prairie ecosystem, landscape variables explain a relatively large percentage of the variance in butterfly community composition.

We know that butterflies are capable of moving within the landscape to high-quality patches, which suggests they are either assessing patches from a distance or moving within the landscape and sampling (Matter and Roland 2002). Our results support the hypothesis that butterflies are making decisions based both on the local and landscape environmental factors. Additionally, our results suggest that the primary sphere of landscape influence for a butterflies in Midwest prairies occurs at a relatively fine scale (0.5km). This is consistent with other studies (Jeanneret et al. 2003; Krauss et al. 2003) that examined extents of 200 and 250m respectively. Other multiscale studies found scales of 5km to be the landscape scale most correlated with butterfly diversity (Bergman et al. 2004). Differences in results could be due to method of analysis, dispersal abilities among the butterflies in different systems and/or landscape composition and configuration. Our results are consistent with an understanding of landscape ecological processes and dispersal patterns in the agriculturally fragmented Midwestern U.S. prairie ecosystem.

Linear versus block habitat

The PLS ordination diagrams (Figure 4) clearly separate linear from block sites based on butterfly community composition. Local biotic variables were not significantly different between linear and block sites, indicating that although the butterfly community differed, this difference was probably not a result of difference in local biotic variables, but rather a difference in site size or shape. The landscapes surrounding linear sites had less grassland and fewer polygons with high floral diversity in closer proximity to the site than block site, whereas linear sites had more roads in the immediate landscape. Thus the habitats are very different between linear and block sites and species are responding to these differences.

Butterfly responses

Species responses to local and landscape variables differ remarkably as did the amount of variation explained at both extents. Habitat-sensitive species as a whole were marginally positively correlated with litter (especially *Anatrytone logan*, *Cercyonis pegala*, and *Speyeria idalia*) whereas disturbance-tolerant species were negatively correlated with litter, with some exceptions (*Polites peckius*). Habitat-sensitive species associated with linear sites such as *A. logan* and *P. mystic* were highly correlated with linear sites suggesting these species may be responding to the increased amount of litter at linear sites. Generally, in order to increase habitat-sensitive butterfly abundance, a manager would want to increase or maintain the amount of litter through a decrease in fire frequency and intensity. Increased litter may be ecologically important because it provides increased moisture and cover for overwintering larvae.

Disturbance-tolerant species were negatively correlated with site size. Disturbance-tolerant species may be responding positively to linear habitats because of the larger edge to area ratio and thus increased disturbance. This result however, may be an effect of site shape on species composition because the linear sites are significantly smaller in size than block sites.

Individual species responses to landscape variables varied and this variation can often be explained by analyzing life histories of each species. Roads are highly and positively correlated with some species such as *Anatrytone logan*, *Celastrina neglecta*, and *Pholisora catullus* which all use weedy plant species (Poaceae, *Melilotus officinalis* and *Chenopodium album* respectively) commonly found in roadside ditches as hostplants. *A. logan* may be responding positively to roads because of the associated increased connectivity grassy roadsides provide. *Speyeria idalia*, a species of special concern in Iowa, is positively correlated with the minimum distance to nearest polygon with high floral resources. In order to increase the abundance of *S. idalia*, patches of habitat should be created with high floral diversity in close proximity to prairie fragments.

Limitations

Similar to previous studies (Luoto et al. 2001), there are some limitations in our ability to explain butterfly assemblages at any extent. The amount of variation explained is relatively low, suggesting that there are additional variables that are influencing community composition. We have no data on host plants which may influence habitat-sensitive species because of their specificity for certain larval hostplants.

One solution to understanding the ways in which adult butterflies use linear and block habitats would be to study differences in behavior (Ouin et al. 2004). This method is still one step away from truly studying the reproductive biology of butterflies and how the local and landscape environment affects source-sink dynamics in linear versus block habitats.

In order to interpret fully the mechanisms behind the correlations of each spatial extent to butterfly abundance patterns, we need to collect data on movement (Mazerolle and Villard 1999). Behavioral data on movement is essential to understanding movement and dispersal at an extent larger than a patch (Lima and Zollner 1996). There are two studies, both of one species of butterfly which documented detection ability of 70 m to unfamiliar habitat and 125 m to familiar habitat (Conradt et al. 2000) and 50m to a suitable patch (Harrison 1989). A tracking study reports a perceptual range of 100-200m for five species of butterflies (Cant et al. 2005). The reason for the lack of data on dispersal and movement is the difficultly associated with tracking individual butterflies. Modeling may be a good alternative to field studies given the constraints of mark recapture studies. Sutcliffe et al. (2003) modeled movement of two common butterflies in a fragmented landscape and found that increasing the amount of linear features in landscapes improved movement by increasing connectivity between suitable habitat patches.

Conservation implications

Responses of species differ drastically for different local and landscape variables. Assuming that the goal of management is to preserve biodiversity with a focus on conserving species sensitive to disturbance, managers should consider the ability of roadsides to provide connectivity. Dispersal rates are lower in highly fragmented landscapes, indicating that connectivity and spatial configuration need to be taken into account (Baguette et al. 2003). Given our findings, we argue that preservation and restoration of prairie fragments on railroad rights-of-way is essential to sustaining butterfly diversity in the tallgrass prairie ecosystem of the Midwestern U.S. including conservation of state threatened species such as *Oarisma powesheik* which was only surveyed at linear sites and may be barely hanging on in isolated fragments.

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Table 1. Floral resource index (FRI) descriptors used to quantify the floral resources in each distinct polygon in the landscape.

Resource Value	Description
0	No forbs (<1/1000 m^2) and low diversity, i.e., 1-2 species (spp).
0.5	Very scanty forbs (>1/1000 m^2 but <1/100 m^2) and low diversity (1-2 spp).
1	Scanty forbs (>1/100 m^2 but <1/m^2) and low diversity (1-2 spp).
2	Either scattered forbs (1/m^2) and low diversity (1-2 spp) or scanty (<1/m^2) forbs but more diverse (>2 spp). Includes alfalfa fields which are very dense stands of a single flowering forb.
3	Either dense forbs (4-6/m^2) and diverse (2-3 spp) or not dense (2-3/m^2) but more diverse (3-5 spp).
4	Either dense forbs (4-6/m^2) and highly diverse (>5 spp) or high density (>6/m^2) and not as diverse (3-5 spp).
5	Exceptionally dense forbs (>6/m^2) and highly diverse (>5 spp).

Table 2. Local and landscape variables and associated descriptions. Each landscape variable was measured at four spatial extents (0.5, 1.0, 1.5 and 2.0km) from the center of each site, but metrics do not include the site itself.

Scale/Variable	Unit	Description	Biological Significance
Local			
LITTER	%	Percent cover of litter	Overwintering habitat for larvae.
FABUND	count	Floral abundance	Food resource for adults.
SIZE	m^2	Site size	Habitat availability.
Landscape			
GRASS	%	Proportion of each buffer that is non-linear grassland	Habitat availability (composition).
ROAD	%	Proportion of each buffer that is road	Measure of connectivity/fragmentation.
FRI	%	Proportion of each buffer with FRI $\geq$ 3	High forb diversity.
MINDIST	m	Distance to nearest polygon with FRI $\geq$ 3 within each buffer	Habitat availability (configuration).

Table 3. Latin and common names for each species including acronyms. Group distinctions are listed for each species as well as total abundance at block and linear sites summed across years.

			Habitat	Abundance	
Latin Name	Common Name	Acronym	Group[a]	Linear	Block
Anatrytone logan	Delaware Skipper	ALOGA	HS	20	2
Ancyloxypha numitor	Least Skipper	ANUMI	DT	2	3
Atalopedes campestris	Sachem Skipper	ACAMP	DT	0	1
Celastrina neglecta	Summer Azure	CNEGL	DT	5	0
Cercyonis pegala	Common Wood Nymph	CPEGA	HS	82	53
Colias eurytheme	Orange Sulfur	CEURY	DT	95	37
Colias philodice	Clouded Sulfur	CPHIL	DT	7	2
Cupido comyntas	Eastern-Tailed Blue	CCOMY	DT	185	72
Danaus plexippus	Monarch	DPLEX	DT	34	67
Euphyes dion	Dion Skipper	EDION	HS	0	1
Eurema lisa	Little Yellow	ELISA	DT	2	0
Lycaena dione	Gray Copper	LDION	HS	1	0

Oarisma poweshiek	Poweshiek Skipper	OPOWE	HS	4	0
Papilio polyxenes	Black Swallowtail	PPOLY	DT	5	9
Pholisora catullus	Common Sootywing	PCATU	DT	7	0
Phyciodes tharos	Pearl Crescent	PTHAR	DT	35	19
Pieris rapae	Cabbage White	PRAPA	DT	10	3
Polites mystic	Long Dash Skipper	PMYST	HS	62	5
Polites peckius	Peck's Skipper	PPECK	DT	12	6
Polites themistocles	Tawny-Edged Skipper	PTHEM	DT	5	1
Pyrgus communis	Checkered Skipper	PCOMM	DT	2	0
Satyrium titus	Coral Hairstreak	STITU	HS	2	0
Satyrodes eurydice	Eyed Brown	SEURY	HS	0	3
Speyeria cybele	Great Spangled Fritillary	SCYBE	HS	18	2
Speyeria idalia	Regal Fritillary	SIDAL	HS	8	99
Vanessa atalanta	Red Admiral	VATAL	DT	13	4
Vanessa cardui	Painted Lady	VCARD	DT	19	33

[a]HS represents butterflies classified as habitat-sensitive whereas DT represents disturbance-tolerant butterflies.

Table 4. Summary statistics for all local and landscape variables for linear and block sites. Local variable statistics are averaged over rounds and years. Landscape extents 1 to 4 correspond to spatial extents of 0.5 to 2.0km.

	Block		Linear	
Variable	Mean	Min-Max	Mean	Min-Max
Local Variables				
LITTER (%)	11.25	2.50-25.00	15.75	7.50-26.25
SIZE (m^2)	339864	114322-665870	29346	7899-76740
FABUND (count)	2640.50	139-6210	2178.50	828-3485
Landscape Variables				
FRI:1 (%)	0.00	0-0	0.00	0-0
FRI:2 (%)	1.33	0-9.82	0.10	0-0.60
FRI:3 (%)	1.27	0-6.98	0.09	0-0.56
FRI:4 (%)	1.02	0-3.82	0.28	0-2.05
ROAD:1 (%)	1.21	0-2.95	2.65	0.99-5.23
ROAD:2 (%)	1.44	0.46-2.96	1.60	0.81-3.30
ROAD:3 (%)	1.28	0.69-2.23	1.37	0.80-2.36
ROAD:4 (%)	1.28	0.74-1.68	1.44	0.97-2.17
MINDIST:1 (m)	203	0-445	73	0-285
MINDIST:2 (m)	262	0-587	173	0-997
MINDIST:3 (m)	525	43-1326	173	0-997
MINDIST:4 (m)	525	43-1326	357	0-1841
GRASS:1 (%)	26.86	0-62.66	2.45	0-6.76

GRASS:2 (%)	19.97	0-59.07	4.86	0-14.05
GRASS:3 (%)	15.80	0.36-53.68	5.17	0.76-11.04
GRASS:4 (%)	14.19	0.33-48.54	6.14	0.62-17.24

Table 5. Local and 0.5km landscape regression coefficients associated with explanatory equations. Response variables included abundance of each species found in more than 20% of all sites and total abundance for each of two groups (habitat-sensitive and disturbance-tolerant). R-square corresponds to the ability to explain abundance given local variables, landscape variables or global model. Species with p>0.05 were omitted and non-significant (NS) model details are removed for simplicity.

	Local Models				Landscape Models					Global model
Species	LITTER	SIZE	FABUND	R^2	FRI	ROAD	MINDIST	GRASS	R^2	R^2
Danaus plexippus	-0.01	0.30	0.49	0.35	0.50	-0.40	-0.19	-0.37	0.39	0.72
Speyeria idalia	0.24	0.56	-0.32	0.45	0.04	-0.32	0.47	-0.20	0.37	0.69
Anatrytone logan	0.36	-0.24	0.06	0.22	-0.19	0.58	-0.34	0.17	0.46	0.57
Speyeria cybele	–	–	–	NS	0.70	0.26	0.00	-0.16	0.54	0.57
Disturbance-tolerant	-0.23	-0.45	0.44	0.46	0.16	0.20	0.11	-0.31	0.22	0.56
Pieris rapae	0.23	-0.33	0.23	0.20	-0.25	0.44	-0.06	0.02	0.26	0.49
Phyciodes tharos	-0.39	-0.41	0.26	0.39	–	–	–	–	NS	0.47
Cercyonis pegala	0.43	0.19	-0.06	0.21	–	–	–	–	NS	0.42
Polites peckius	0.40	-0.13	0.52	0.28	–	–	–	–	NS	0.41

Habitat-sensitive	0.27	0.09	-0.33	0.25	–	–	–	–	NS	0.30
Polites mystic	0.14	-0.29	-0.23	0.22	–	–	–	–	NS	0.27

Figure 1. Schematic drawing of spatially nested landscape extents. The center rectangle represents the sampling site with the center of the site marked with a dot. Buffers at 0.5km increments radiate out from the center of the sampling site.

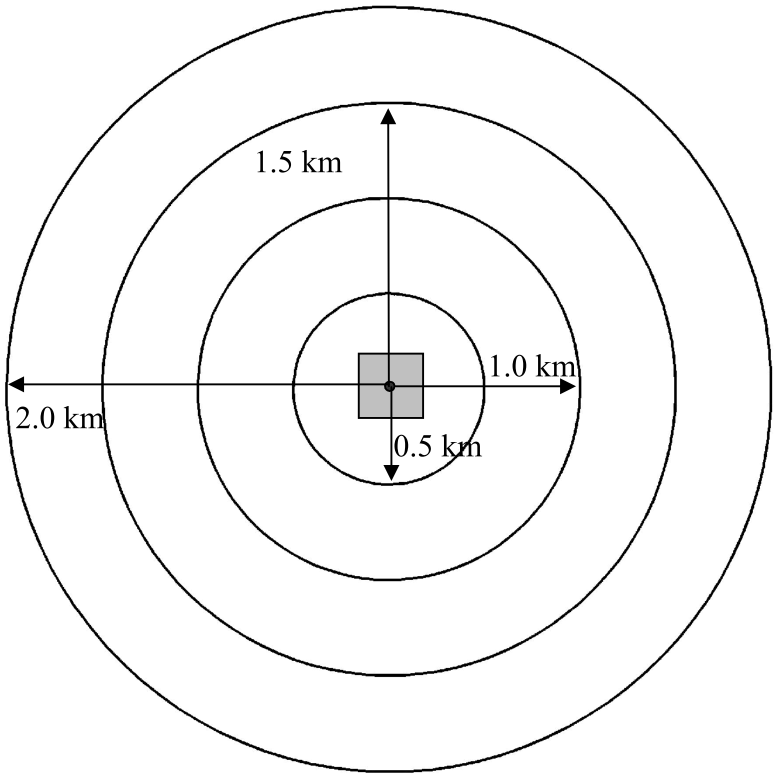
Figure 2. Coefficients are plotted for the correlation between the first PLS component of the species matrix with the first PLS component of the environmental matrix at all extents. All correlations are significant ($p<0.001$).

Figure 3. Variable importance projection (VIP) values from PLS regression are plotted against all landscape extents. Values greater than one are considered high importance. Proportion of road is an important variable at all landscape extents. Proportion of the landscape that is grassland is important at larger extents of 1.5 and 2.0km.

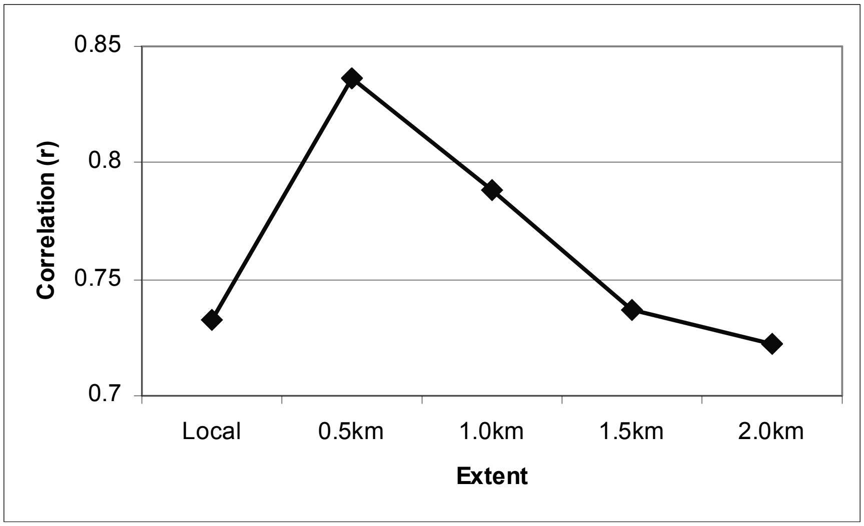
Figure 4. Partial least squares ordination biplot based on a species by site matrix of abundant butterflies (abundance >10) where site scores, species scores and environmental variables are plotted in two dimensions at the a) local and b) 0.5km landscape extents. Dotted ellipses represent groupings of sites by shape. Butterfly species scores are denoted by abbreviations of Latin names (Table 3). The X and Y axes are the first and second components respectively.

Figure 5. Percentage of the variance in the species abundance matrix which is explained by each extent of environmental variables measured from the pCCA. Percent variation explained by local variables alone was 25.3%. Percent variation explained by landscape variables alone was 23.4, 22.9, 19.8 and 21.2% at landscape extents of 0.5, 1.0, 1.5 and 2.0km respectively. Percent variation explained by local plus landscape variables was 5.5, 3.5, 2.0 and 0.8% at landscape extents of 0.5, 1.0, 1.5 and 2.0km respectively.

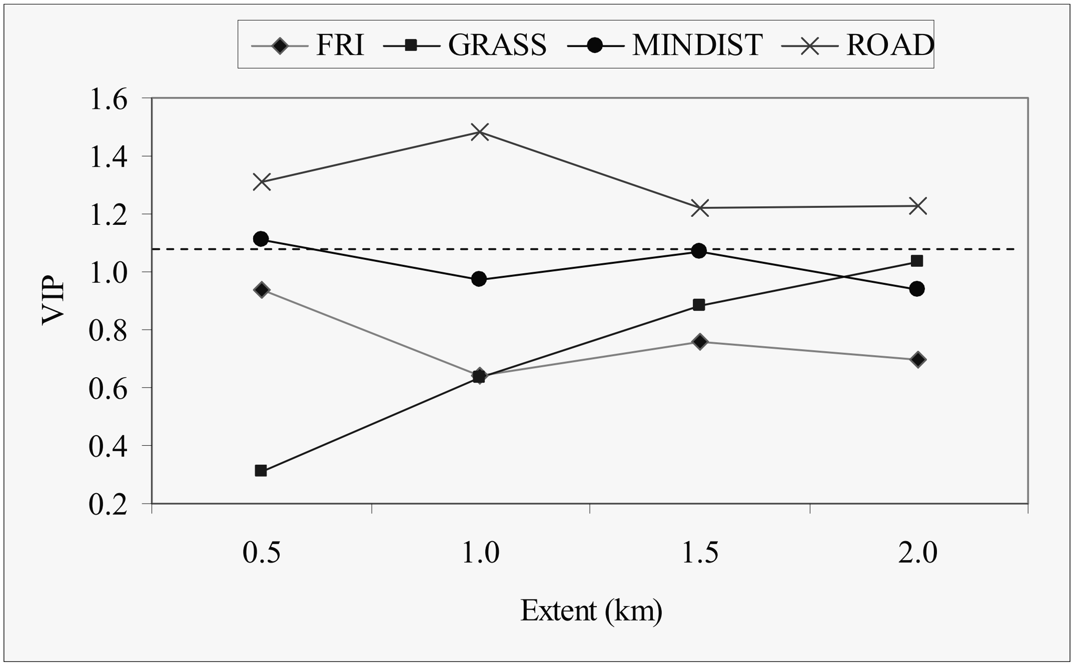
I.



II.



430 III.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MINDIST
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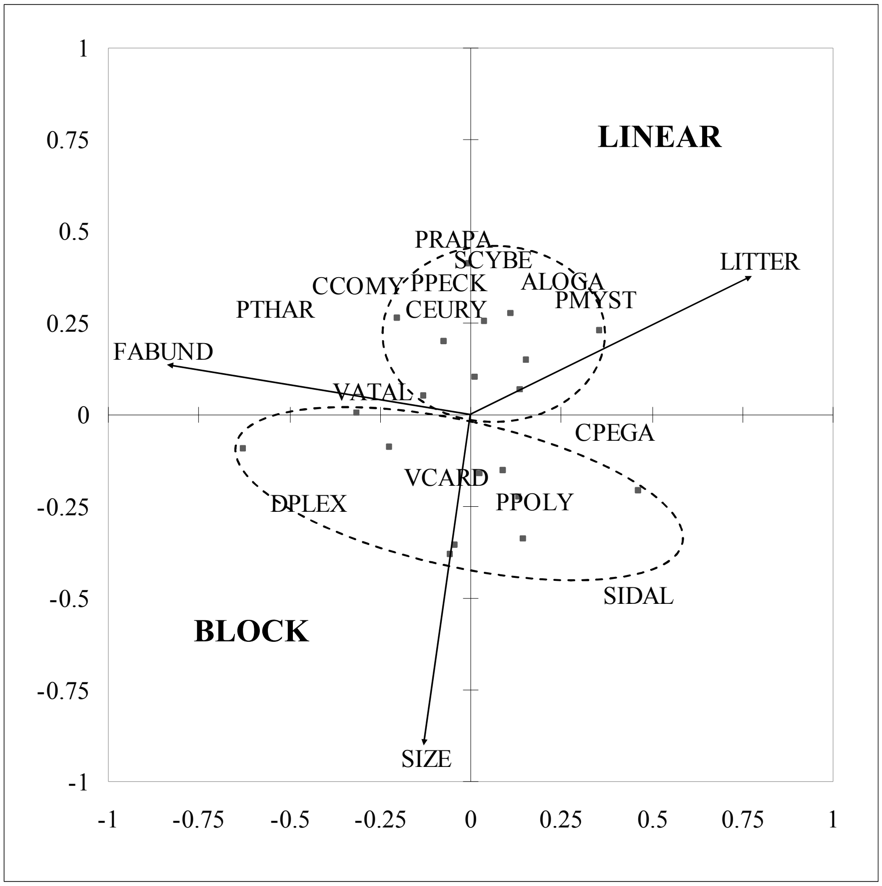
1.4
1.2
1.0
0.8
0.6
0.4
0.2
VIP
0.5
1.0
1.5
2.0
Extent (km)

IV.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CCOMY
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FABUND
VATAL
CPEGA
VCARD
DPLEX
PPOLY
SIDAL
SIZE
1
0.75
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-0.25
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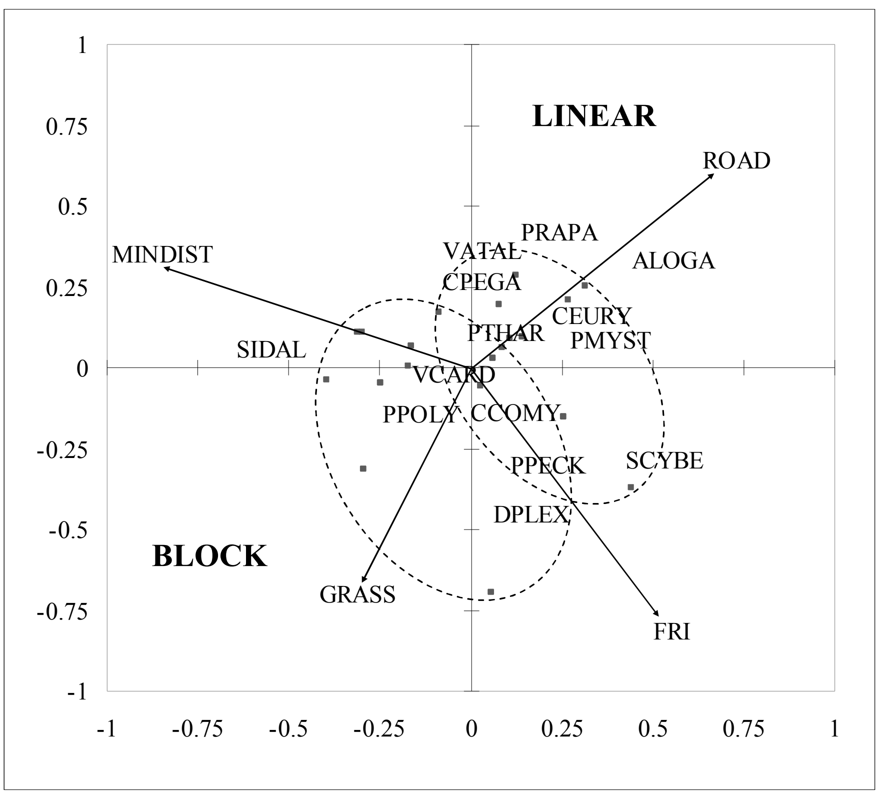
1


LINEAR
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CCOMY
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SCYBE
DPLEX
GRASS
FRI
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0.5
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-0.5
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-1
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-0.25
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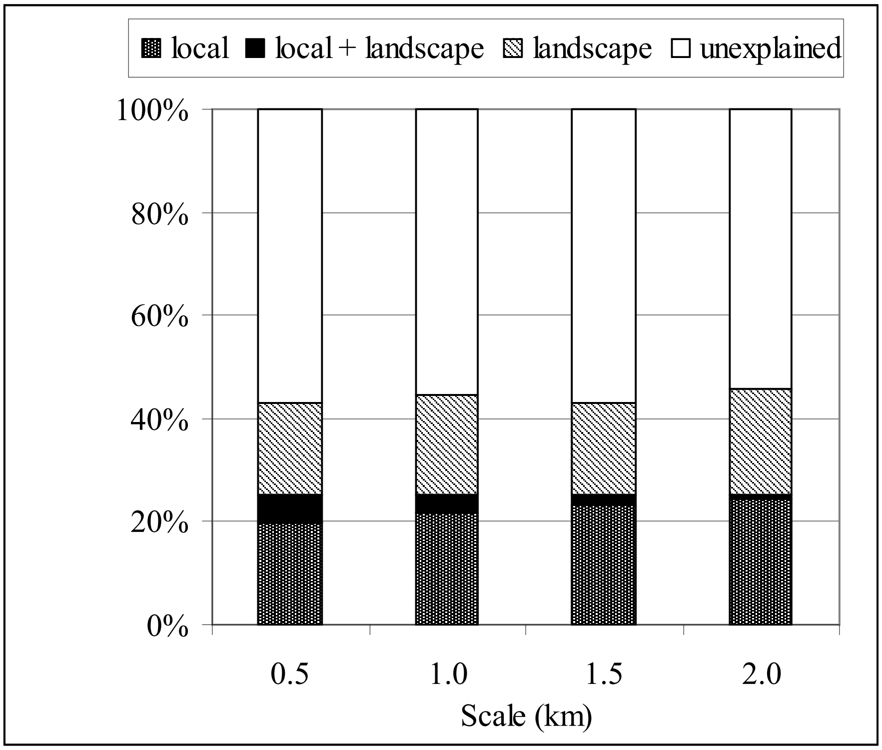
0.75
1

V.


local
local + landscape
landscape
unexplained
100%
80%
60%
40%
20%
0%
0.5
1.0
1.5
2.0
Scale (km)

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