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C.J. Foley & J.D. Holland
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Do Flying Beetles Respond to Human-Dominated Landscapes as Complex Mosaics or Binary Patterns?

Carolyn J. Foley & Jeffrey D. Holland*

Department of Entomology, Purdue University, 901 W. State St., West Lafayette, Indiana, USA 47907

cfoley@purdue.edu, jdhollan@purdue.edu

* Corresponding author

Abstract

Understanding and measuring functional connectivity for animals with habitats that have been fragmented by human activity requires that the biology and movement of the species be considered. We used least cost paths in GIS to test hypotheses regarding how different species of longhorned beetles likely connect habitats with dispersal. We predicted that there would be differences in the functional connectivity of landscapes depending on species larval niche breadth, adult feeding habits, and the potential for use of non-forest habitats. For the species with very specialized larvae, we developed a classification tree to determine areas likely to contain the appropriate species of host tree. Connectivity calculated using least cost paths did not out-perform Euclidean distances for three generalist beetles. This was also the case for the specialist beetle species when all forest was considered habitat. However, when we delineated habitat based on areas likely to support the host tree the functional connectivity incorporating least cost paths was a much better predictor than that using Euclidean distances. Generalists may respond to fragmented habitat in a binary habitat-matrix way while more specialized species may respond to a mosaic. These trends are obscured if habitat is defined by human perceptions rather than species biology.

Keywords:

Cerambycidae, functional connectivity, habitat, landscape mosaic, least-cost path, resistance surface

1 Introduction

Connectivity of the landscape is defined as "…the degree to which the landscape facilitates or impedes movement among habitat patches" (Taylor et al. 1993). Properly, then, connectivity is a function of the composition and configuration of landscape elements as well as the movement behaviours and abilities of the dispersing organism (Merriam 1984). It follows that presence of a species in a given location is subject to the composition of the surrounding landscape, which may be thought of as structurally connected by features such as corridors. It has been argued that connectivity should be defined from the point of view of an organism, paying particular attention to behavioural costs incurred by moving between habitat patches (Bélisle 2005). The non-habitat matrix that surrounds habitat patches is composed of various types of land cover, each providing differential probabilities of mortality, resources, and physical obstacles to an organism so this extra-habitat area is often better though of as a mosaic of different patches or land covers as opposed to a homogeneous "non-habitat." Bender & Fahrig (2005) used simulation models to show that if the matrix is heterogeneous and an organism responds to boundaries between different matrix cover types, the variance in distribution that is explained by patch size and isolation alone drops dramatically. This indicates that the composition of the matrix should be taken into consideration when planning large-scale ecological analyses.

One way of incorporating an organism's perception of the landscape into connectivity calculations is with effective distance measures, also known as friction, resistance or cost surfaces. When calculating the effective distance between habitat patches, different land cover types are assigned different costs and the simplest or least-cost path is calculated through them. Effective distance measures have been used to investigate the movement of ground beetles (Jopp & Reuter 2005), butterflies (Sutcliffe et al. 2003), amphibians (Ray et al. 2002; Stevens et al. 2006), squirrels (Verbeylen et al. 2003), and grizzly bears (Singleton et al. 2004) and have generally met with good success. We determined the connectivity of appropriately scaled landscapes for four species of longhorned beetle that occur in Indiana, U.S.A., in terms of both Euclidean and effective distances. The study species were the red-headed ash borer *Neoclytus acuminatus acuminatus* (Fabricius); the pole borer *Neandra brunnea* (Fabricius) (= Parandra brunnea brunnea); *Typocerus velutinus velutinus* (Olivier); and *Urographis despectus* (LeConte).

Neoclytus a. acuminatus and *N. brunnea* are considered pests of hardwood trees (Solomon 1995). They are both established alien species in Europe (Roques 2007; Mattson et al. 2007), and their life histories are relatively well known. The larvae of *N. a. acuminatus* develop in a variety of tree species that are weakened, dying, dead, or recently felled, and have been responsible for the destruction of over one million board feet of ash logs (Craighead 1950; Solomon 1995). Adults are short-lived and may not feed (Lacey et al. 2004) though they have been observed eating sap in laboratory studies (Waters 1981). The larvae of N. brunnea develop in the dead inner wood of live trees or in wood products, and their known hosts include maple, chestnut, poplar, pear, black oak, basswood, and elm (Linsley & Chemsak 1997). Adults eclose in midsummer, but usually remain in their pupal chambers for a few days before emerging (Solomon 1995). Many adults do not leave their natal piece of wood to mate and lay eggs (Kotinsky 1921; Craighead 1950), so dispersal may obviously be very limited in some cases. Females may deposit eggs in a wide variety of trees and wood products, including shade and ornamental trees, fruit trees, and telephone or power line poles (Solomon 1995).

Less is known about the ecology of the other study species. As they are not known pests, available data are limited to surveys done over the past 100 years. The larvae of *T. v. velutinus* feed on the deadwood of a few host species (Knull 1946; Hanula 1993). The adults are active fliers and feed on flowers (Blackman 1918; Knull 1946), and therefore may be involved in pollination. *Urographis despectus* is a larval habitat specialist on pignut hickory (Knull 1946; Linsley & Chemsak 1997), but adult feeding habits are unknown. Each of these species is a member of a different subfamily within the Cerambycidae (Tab. 1).

We hypothesized that longhorned beetles perceive the landscape as having features with differing levels of hospitality or cost rather than as a binary pattern of habitat and non-habitat matrix, and that the relative costs of moving through the landscape differ between the four study species. We assumed that forest was the best habitat for the generalist feeding species *N. a. acuminatus, N. brunnea* and *T. v. velutinus*, while other types of land cover may simply be crossed to get between habitat patches. For *U. despectus*, we tested two landscapes, one where habitat was forest and another where habitat was only areas likely to contain pignut hickory as described below. We predicted that incorporating both Euclidean and cost distances into functional connectivity calculations would explain significantly more variation in the distribution of each study species than using Euclidean distance alone. For example, in Fig. 1 the effective distance or accumulated cost of following path 2 would still be significant in a model of occurrence that already contained the Euclidean distance or cost of path 1. We also predicted that the best cost surfaces for each species would reflect aspects of their ecology: *N. a. acuminatus* would respond positively to urban areas as they provide additional wood resources such as stressed trees; *N. brunnea* would respond to urban and field areas, as they may contain damaged or stressed trees and utility poles; *T. v. velutinus* would respond to agriculture areas as they contain both large areas of flowers that serve as adult feeding sites and some decaying wood for larval habitat; and *U. despectus* would respond to habitat only as it is a specialized larval feeder. In Fig. 1, the specialist habitat is depicted as the areas containing trees with non-green foliage, patches 1 and i. For a beetle with larvae specialized on this species of tree, habitat is not all forest but those parts of the forest that contain the correct larval host (sections of forest i and 1 in Fig. 1). For beetles with generalist larvae, most forest should be habitat so that forests i, 1, and 2 in Fig. 1 should all serve as habitat. Paths 3 and 4 should indicate effective distances i-1 and i-2 depending on the cost of moving across different land cover types.

Table 1. Biological attributes of the four study species of longhorned beetles.

Species	**Neoclytus a. acuminatus**	**Neandra brunnea**	**Typocerus v. velutinus**	**Urographis despectus**
Subfamily	Lamiinae	Parandrinae	Lepturinae	Cerambycinae
Pest species?	Yes	Yes	No	No
Larval specialist?	No	No	No	Yes
Adults feed at flowers?	No	No	Yes	No?
Predicted habitat	Forest, Urban	Forest, Urban, Agriculture	Forest, Agriculture	Forest, Forest with pignut hickory

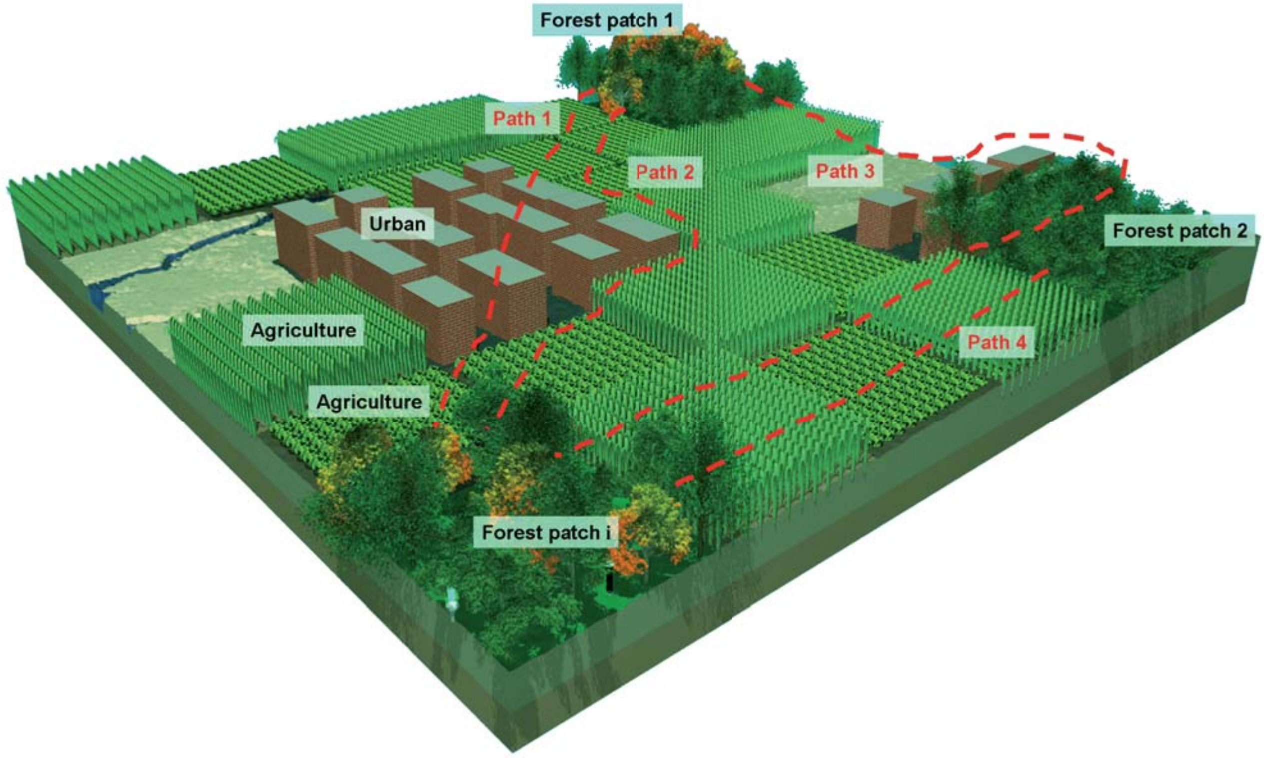


Figure 1. A hypothetical landscape with examples of Euclidean distances (Paths 1 and 4) and Effective distances (Paths 2 and 3) between habitat for generalist species (Forest patches i, 1, & 2) and specialist species (Patches i & 1). Larval host trees for a specialist species are indicated with non-green foliage. Two of the four beetle traps within sampling arrays are shown in the surveyed patch, i.

2 Methods

2.1 Sampling and Scaling

Adult beetle presence data were collected from 23 forest patches in northern Indiana over two summers (2005 & 2006, Fig. 2). Within these patches, one randomly chosen point was sampled in 2005 and two more were sampled in 2006. These points were at least 50 m apart and at least 50 m from the forest edge. Four flight intercept traps were placed around each point: two Lindgren funnel traps (Phero Tech Inc., Delta, Canada), one panel trap for bark beetles (Advanced Pheromone Technologies Inc., Portland, USA), and one window trap of JDH's design. Traps were placed approximately 10 m from the center point, one in each cardinal direction. Ethylene glycol was used as a killing fluid and preservative, and each trap was baited with 60 mL of 95% ethanol to mimic the odor of decaying wood (Brattli et al. 1988; Chénier and Philogène 1989a, 1989b). Nalgene bottles (125 mL) with four holes in the lid were used and these were refilled to 60 mL at each trap visit. Each trap was emptied three to four times between early May and early September, and a beetle species was recorded as present at a point if it showed up in any trap over the course of the summer. Using data from all three sampling points within a forest patch, we calculated the mean presence of the beetle in the patch, i.e., present at all points (1), present at two out of three points (0.67), present at one out of three points (0.33), or absent from all points (0).

Not every species responds to features in the landscape at the same spatial scale. We used the characteristic scale of response to habitat (Holland et al. 2004) of each beetle to determine the size of the landscapes within which we would calculate functional connectivity. The characteristic scales of response for each species, based on data collected in 2005 from 43 sampling points, are as follows: 1200 m for *N. a. acuminatus*, 135 m for *N. brunnea*, 1200 m for *T. v. velutinus* and 240 m for *U. despectus*. Each landscape was a circle around the sampling point with radius equal to the scale of response to forest habitat (n = 69, 23 patches x 3 sampling points) for that species. Because species may respond to different aspects of the landscape at different spatial scales (Bergin et al. 2000) we examined how the correlation between abundance of *U. despectus* changed with scale using habitat as defined for both generalist and specialist beetles (see below).

2.2 Movement Through the Landscape

We calculated the functional connectivity of each landscape with Hanski's connectivity measure, Si, (Hanski 1994; Eq. 1), which has been shown to increase the explanatory power of effective distance studies (Verbeylen et al. 2003). Patch i was a 30 m x 30 m cell around the sampling point. The S_i measure down-weights habitat according to distance as a negative exponential

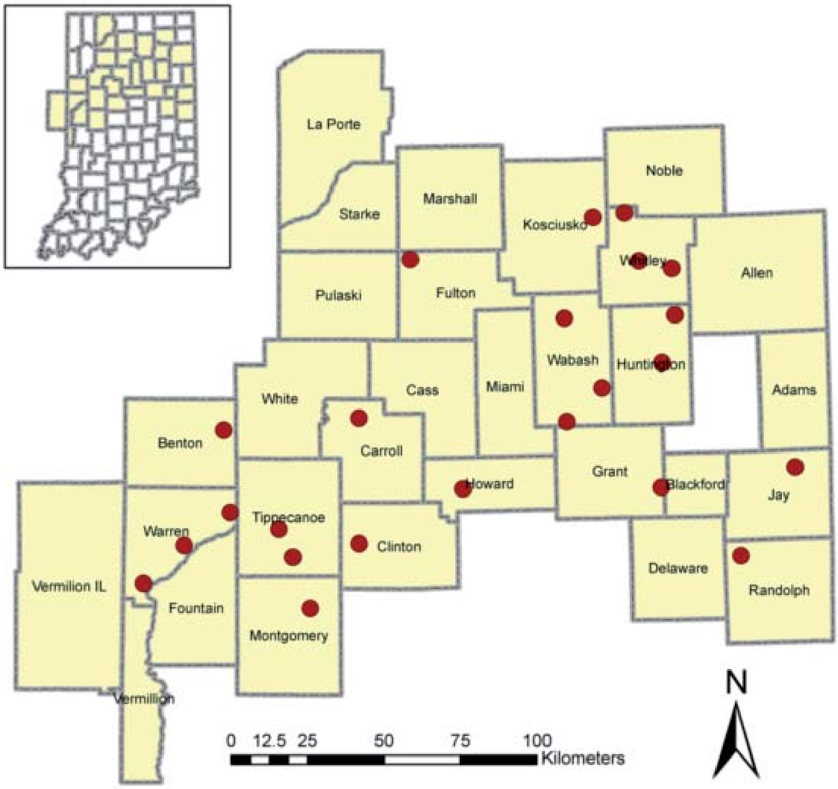


Figure 2. The counties sampled in northern Indiana, USA. Points indicate the location of a sampled forest patch. The total extent of these counties was used as a boundary when extracting land cover values from the National Land Cover Dataset. One county, Vermillion County, is in the neighbouring state of Illinois.

function scaled by the mean lifetime dispersal distance of the organism. We do not know the lifetime dispersal distance for our species (or most insect species). However, the spatial scale at which species respond most strongly to the surrounding landscape has been linked to the foraging ability and perception of the landscape of several groups of insects (Roland & Taylor 1997; Steffan-Dewenter et al. 2002). We therefore used the spatial scale of response to scale the distance between patches. The distance term dij was the least-cost distance to the patch j (see below), and we assumed that the surrounding patches in the landscape were occupied.

$$S_i = \sum_{i \neq j}^{n} (e^{-ad_{ij}})(A_j)(p_j) \qquad (1)$$

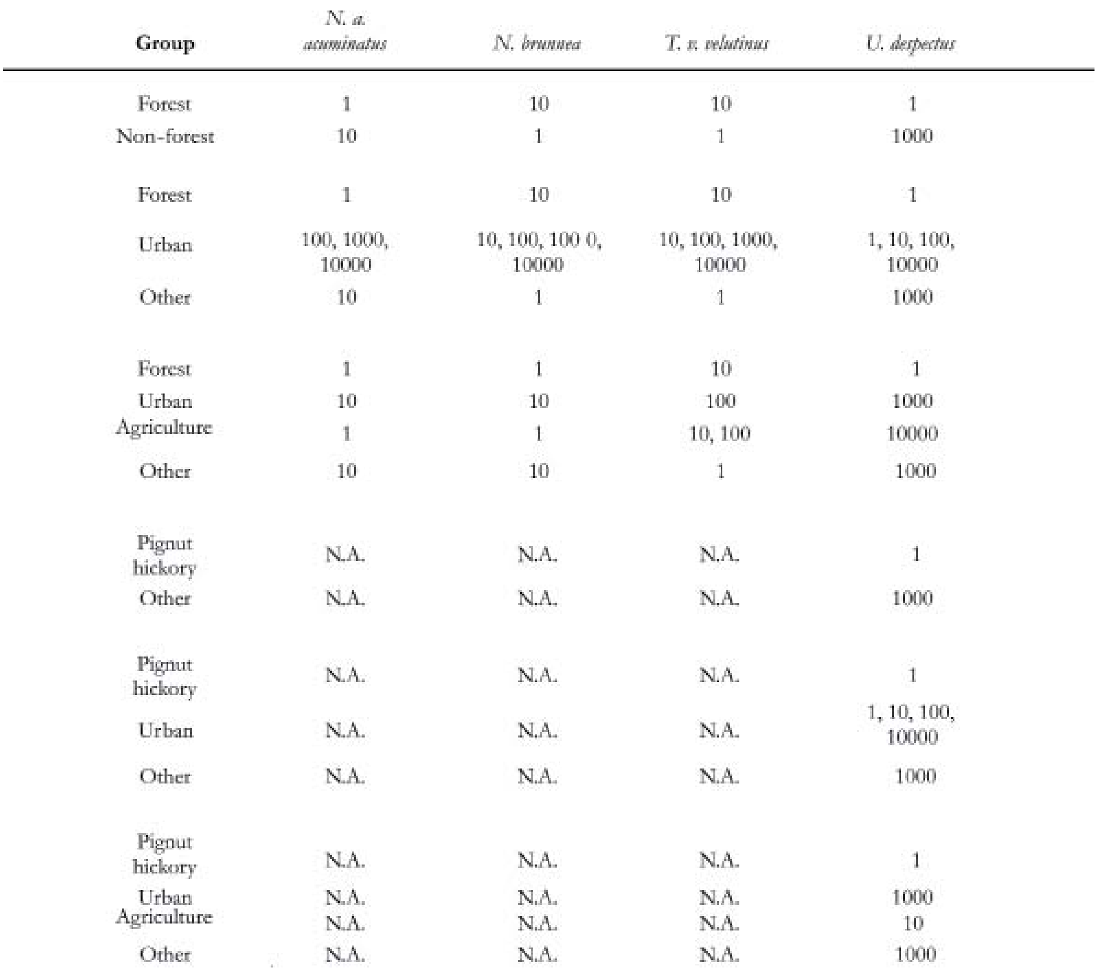
where n is the number of patches in the landscape; a is the inverse of the spatial scale of response of the species; d_{ij} is the distance between patch i and patch j; Aj is the area of patch j; and p_i is the probability that the patch j is occupied.

For functional connectivity calculations, we extracted land cover values from the National Land Cover Dataset (Vogelmann et al. 2001) for 29 counties in northern Indiana and one county in Illinois (Fig. 2). We grouped these land cover values into broad categories of forest (NLCD classes: deciduous forest, evergreen forest, mixed forest), urban areas (NLCD classes: low intensity residential, high intensity residential, commercial/industrial/transportation), and agriculture (NLCD classes: orchards/vineyards/other, pasture/hay, row crops, small grains, fallow) areas which were reclassified to create a suite of cost surfaces. Using a custom Python script and GIS software (Python Software Foundation 2001, ESRI 2005), we calculated least-cost distances from every sampling point to every forest patch within the appropriately-scaled landscape, and areas of each forest patch within the landscape. We then calculated the functional connectivity of the landscape surrounding each point (n = 69) for each cost surface and the mean functional connectivity for a forest patch (n = 23).

The first surface assumed all land cover types were equal (cost value = 1) before cost distances were calculated. This is approximately equal to calculating the Euclidean distance between patches, and we hereafter refer to the functional connectivity of a landscape calculated with this cost surface as S_i^{Euc}. For all additional surfaces, we varied the cost values for the three broad groups of land cover: forest and non-forest, urban and non-urban, and agriculture and non-agriculture (Tab. 2). We assessed one group at a time, including any information previously found to be important (after Verbeyelen et al. 2003). In lieu of expert opinion on the relative resistances of each land cover type to cerambycids (Adriansen et al. 2003; Sutcliffe et al. 2003), we tested a range of values in each broad group. We varied the cost values for each broad group by magnitudes of 10, ranging from 1 to 10000, and hereafter refer to the functional connectivity of a landscape where cost values differed from each other as S_i^{Eff}.

Cost distances between the sampling points and forest patches in the landscape are strongly correlated with Euclidean distances to the same patches. We performed linear regressions in SAS (PROC GLM; SAS Institute Inc. 2003) for each cost surface where mean S_i^{Eff} was the response variable and mean S_i^{Euc} was the predictor (n = 23). We standardized both the resulting residuals and the mean S_i^{Euc} values (PROC STDIZE, SAS Institute Inc. 2003), then used them as predictor variables in multiple multinomial regressions where the response variable was the mean presence of the beetle in the landscape. Including the residuals allowed us to keep cost distance information while ensuring independence of the predictor variables (Verbeylen et al. 2003) and examine the additional benefit of using least cost paths over simple Euclidean distance for flying beetles. We performed the multiple multinomial regressions in Statistica (Generalized Linear/Non-Linear Models Multiple Regression with Ordinal Multinomial Distribution and Logit Link, StatSoft Inc. 2007). For each cost surface, we assessed the fit of the predictor variables to the data by ensuring that the scaled deviance of the test divided by the degrees of freedom was not much greater than 1, and visually examining a plot of the residuals plotted against predicted values (Mazerolle 2004; Statsoft Inc. 2007).

Table 2. Values for the best-fitting cost surface(s) in each group. N.A., not applicable.



Group	*N. a. acuminatus*	*N. brunnea*	*T. v. velutinus*	*U. despectus*
Forest	1	10	10	1
Non-forest	10	1	1	1000
Forest	1	10	10	1
Urban	100, 1000, 10000	10, 100, 100 0, 10000	10, 100, 1000, 10000	1, 10, 100, 10000
Other	10	1	1	1000
Forest	1	1	10	1
Urban	10	10	100	1000
Agriculture	1	1	10, 100	10000
Other	10	10	1	1000
Pignut hickory	N.A.	N.A.	N.A.	1
Other	N.A.	N.A.	N.A.	1000
Pignut hickory	N.A.	N.A.	N.A.	1
Urban	N.A.	N.A.	N.A.	1, 10, 100, 10000
Other	N.A.	N.A.	N.A.	1000
Pignut hickory	N.A.	N.A.	N.A.	1
Urban	N.A.	N.A.	N.A.	1000
Agriculture	N.A.	N.A.	N.A.	10
Other	N.A.	N.A.	N.A.	1000

For each broad group of land cover types, the best-fitting surface was the one with the smallest value of negative two times the maximized log-likelihood. We used the log-likelihood value from the best-fitting surface overall, i.e., across all groups, to calculate the second order Akaike Information Criterion for that surface (AIC_c; Eq. 2). This is a modification of the Akaike Information Criterion used when sample sizes are low (Hurvich & Tsai 1989). We also calculated AIC_c values for the Euclidean distance surface for each species, and compared these to the best-fitting surfaces overall using Akaike weights (w_i; Eq. 3) and evidence ratios (Wagenmakers & Farrell 2004). In general, evidence ratios greater than 2.7 indicate that a model is a better fit than the one it is being compared to (Mazerolle 2004). Because the AIC_c is not a hypothesis test we assessed the overall significance of the best-fitting cost surface and the Euclidean distance surface with likelihood ratios.

$$AIC_c = -2LL + 2k + \frac{2k(k+1)}{(n-k-1)} \qquad (2)$$

where LL is the maximized log-likelihood, k is the number of parameters being estimated and n is the sample size.

$$w_i = \frac{\exp(-\Delta_i / 2)}{\sum_{r=1}^{R} \exp(-\Delta_r / 2)} \qquad (3)$$

where Δi is the difference between the AIC_c of model i and the smallest possible AIC_c and R is the total number of possible models.

We used the National Land Cover Dataset (Vogelmann et al. 2001) as the basis for reclassification of surfaces for *N. a. acuminatus, N. brunnea,* and *T. v. velutinus*, but tested additional surfaces for the specialist species, U. despectus. For this beetle, we calculated the functional connectivity of landscapes both with habitat defined as forest from the National Land Cover Dataset, and landscapes with habitat defined as areas conducive to the growth of pignut hickory. The radius of the landscapes around sampled points was determined separately for the analyses using forest patches and pignut hickory patches as habitat. We tested 17 cost surfaces each for *N. a. acuminatus, N. brunnea,* and *T. v. velutinus*. One was the Euclidean distance surface, eight were used in the first group of forest and non-forest, four were used in the second group that included urban effects, and four were used in the third group that included agricultural effects. We tested 34 cost surfaces for *U. despectus*, 17 with forest as larval habitat and 17 with pignut hickory habitat as larval habitat. We chose the best-fitting surface in a group by examining maximum likelihood values, and cost values for each group were informed by the previously best-fitting surface. If several surfaces had the same maximum likelihood, we retained the lowest possible value when assigning costs in the next group.

2.3 Locating Host Tree Habitat

Pignut hickory, the larval host of *U. despectus*, is an upland tree with a tendency to grow in well-drained soils (Deam 1931; Tirmenstein 1991; Farrer 1995) and along forest edges (Sork 1983). For the pignut hickory map, we included National Land Cover Data (NLCD; Vogelmann et al. 2001), floodplain data (FEMA 2006), soil data (Soil Survey Staff 2006), and location data for roads (INDOT 2006), railroads (NTAD 2003), and recreational hiking trails (IDNR 2002) in our analysis. Layers that were downloaded in vector format were converted to raster format and aligned with the NLCD. Linear features, such as roads and recreational trails, were buffered by appropriate distances before converting to raster (details in Foley 2008).

To determine which combination of layers best predicted the location of pignut hickory, we used data from preexisting tree inventories in a classification tree analysis. Tree location inventory data were taken across northern Indiana in the summers of 2001-2003 (Swihart et al. 2007). At each survey location (n = 934), all tree species present within 10 m of a central point were recorded. Locations of pignut hickory were tested for spatial autocorrelation in ArcGIS 9.1 (High/Low Clustering (Getis-Ord General G) tool; ESRI 2005). We combined raster layers depicting data that may influence growth preference to assess which combination of layers best predicted the location of pignut hickory (Foley 2008).

We created a classification tree (Partition procedure; SAS Institute Inc. 2003), where the response variable was presence of pignut hickory at a point (1 = present, 0 = not present), and the factors were the values of each GIS layer at the point (1 = preferred growth condition present, 0 = preferred growth condition not present). This method of analyzing categorical data is similar to a regression tree. We split the data into as many branches as possible then pruned these branches back. Splits were made one at a time, with more variation in the dataset being explained as the number of splits increased. We pruned the classification tree by plotting the total variance explained (R^2) against the split number and visually determining where this abruptly leveled-off, similar to using a scree plot.

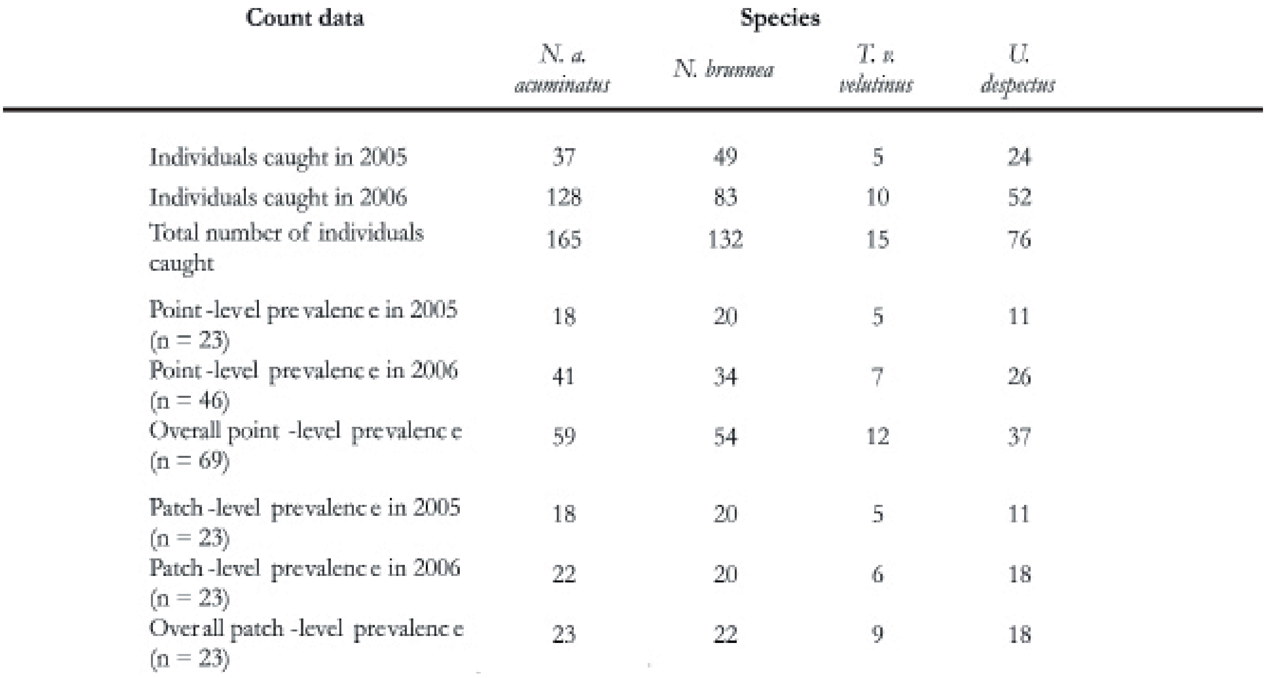
Each branch in the resulting classification tree contained a combination of growth conditions that could potentially be included in the pignut hickory map. If the cumulative probability of predicting the location of pignut hickory, calculated at the tip of a given branch, either had the higher probability of predicting the presence of pignut hickory in a couplet, or had the higher sample size in a respective couplet plus a probability of predicting the location of the tree that was greater than 0.1, information gleaned from that branch was included in the larval habitat map.

3 Results

We caught all four of our study species in several sampling sites within the human activity-dominated landscapes of Indiana (Tab. 3). Figure 3 depicts the change in maximum likelihood values for the different cost surfaces. When habitat was simply delineated as forest the overall best-fitting cost surfaces for all species were those that only distinguished between forest and non-forest (Tab. 4). For *T. v. velutinus* and *U. despectus* with forest as habitat, surfaces that included both urban and agricultural effects had the same maximum likelihood values as those that grouped forest and non-forest (Tab. 4).

Pignut hickories were found at 89 locations in the tree inventory survey (n = 934). Since pignut hickory abundance data were not found to be spatially autocorrelated (General G = 0.26, p > 0.10), data from all tree survey points were used to create the classification tree. The variance explained by the classification tree for areas likely to support pignut hickory levelled off abruptly after split number five (Fig. 4). Branches of the pruned tree (R2 = 0.085; Fig. 5) indicated that cells in the *U. despectus* larval habitat map should either be upland, forested areas with well-drained soil that were at least 90 m from the forest edge (n = 22, probability of correctly predicting presence of pignut hickory = 0.45); upland forest edge habitat that extended up to 90 m into the forest (n = 436, probability of correctly predicting presence of pignut hickory = 0.13); or upland field edge habitat that extended up to 60 m out of the forest (n = 224, probability of correctly predicting presence of pignut hickory = 0.08). Eighty-four of 89 locations inhabited by pignut hickories fell within the boundaries of the *U. despectus* larval habitat map (Fig. 6). The scale of response to habitat changed for *U. despectus* depending on the definition of habitat as forest or pignut hickory habitat. For *U. despectus* with habitat redefined as areas favouring pignut hickory

Table 3. Catch data for study species. Point-level prevalence refers to the number of trap arrays at which the species was caught. Patch-level prevalence refers to the number of forest patches within which the species was caught.



Count data	Species			
	N. a. acuminatus	*N. brunnea*	*T. v. velutinus*	*U. despectus*
Individuals caught in 2005	37	49	5	24
Individuals caught in 2006	128	83	10	52
Total number of individuals caught	165	132	15	76
Point-level prevalence in 2005 (n = 23)	18	20	5	11
Point-level prevalence in 2006 (n = 46)	41	34	7	26
Overall point-level prevalence (n = 69)	59	54	12	37
Patch-level prevalence in 2005 (n = 23)	18	20	5	11
Patch-level prevalence in 2006 (n = 23)	22	20	6	18
Overall patch-level prevalence (n = 23)	23	22	9	18

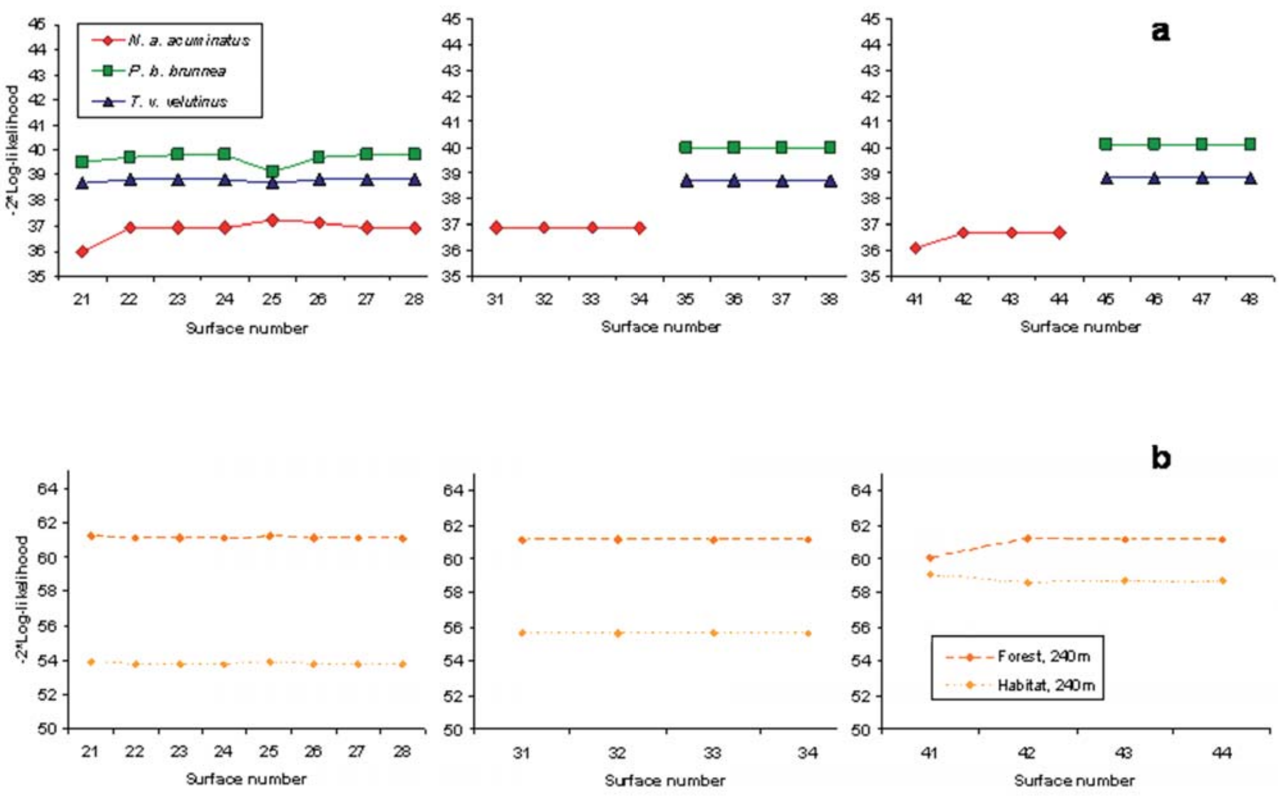


Figure 3. Log likelihood results for all cost surfaces in all broad groups. Forest/non-forest surface numbers start with 2, urban effect surface numbers start with 3, and agriculture surface numbers start with 4. The best-fitting cost surface in each group had the smallest y-value (-2*Log(likelihood)). Generalist species fits are depicted in (a), while all surfaces tested for the specialist *U. despectus*, i.e., forest as habitat at 240 m and pignut hickory as habitat at 240 m, are depicted in (b).

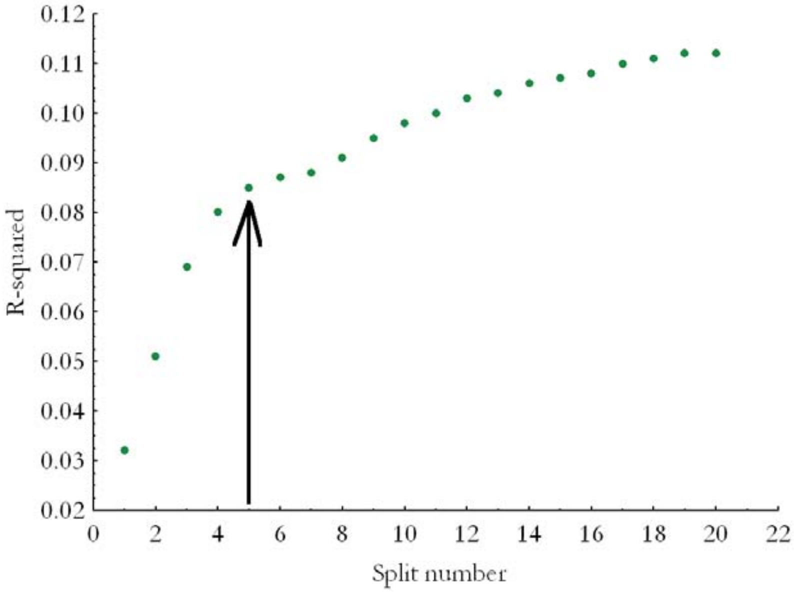


Figure 4. The variance explained (R^2) by the classification tree after each split in the data. The tree was pruned at the number of splits where the graphs abruptly level off, indicated by an arrow (here, split number five).

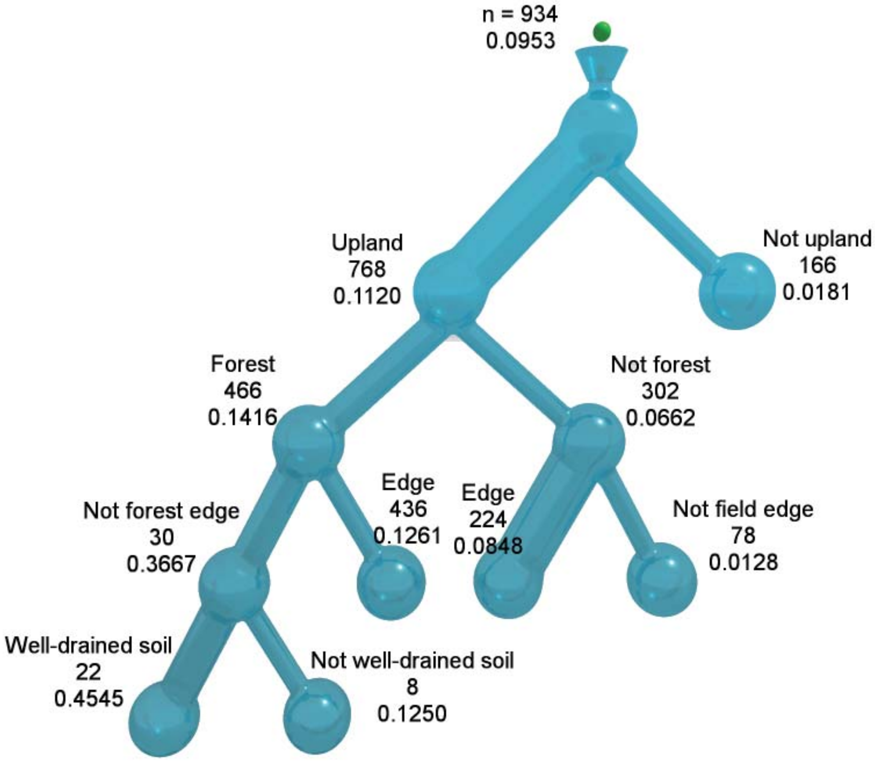


Figure 5. Final classification tree for locating areas likely to contain pignut hickory, the larval host tree of *Urographis despectus*. Numbers indicate group size (top number) and the probability that pignut hickory was present. Terminal nodes with yellow text indicate conditions used to determine the larval habitat maps. White text indicates intermediate or terminal nodes that were not included in the final map. At each split the relative cross-sectional areas of the tubes are proportional to the difference in the probabilities at the next nodes that pignut hickory was present.

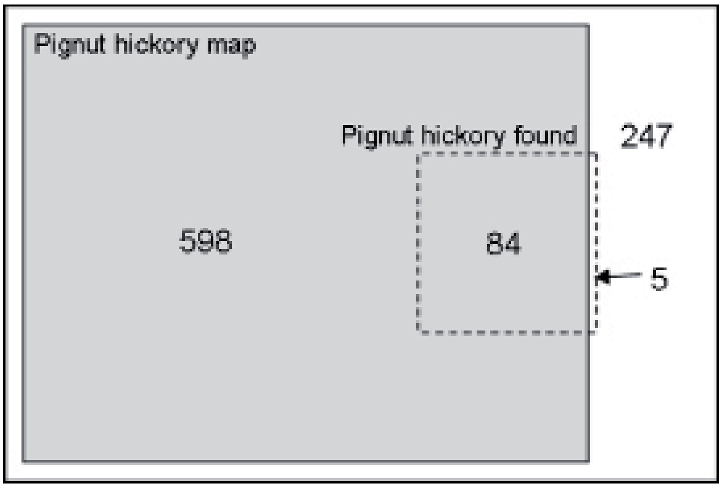


Figure 6. Venn diagram to demonstrate the predictive ability of the pignut hickory map. The large white rectangle symbolizes all sampled locations (n = 934), the smaller grey rectangle symbolizes the number of these locations that fell within the boundaries of the final habitat maps (n = 682), and the dashed rectangle symbolizes the number of sampled locations where pignut hickory was found (n = 89). The majority of the locations where pignut hickories were found fall within the boundaries of the final habitat map.

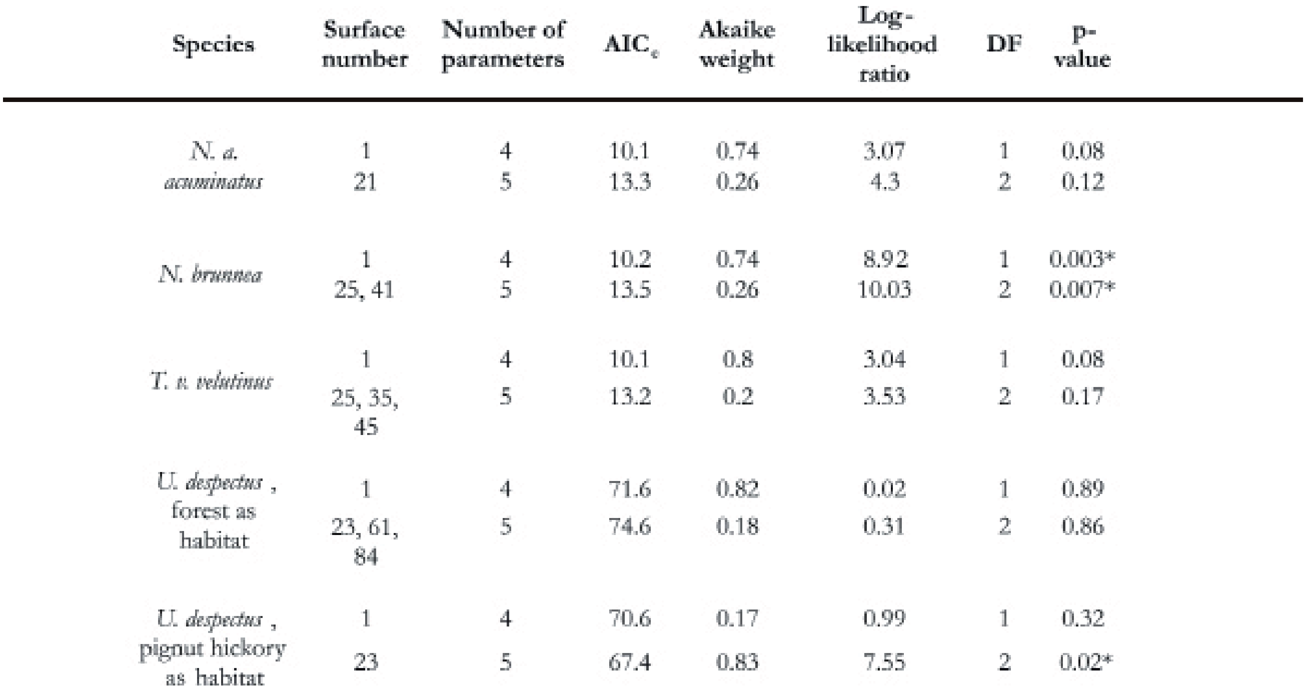
Table 4. Land cover cost values associated with the overall best Fitting surface(s) for each species (not including Euclidean distance).

	Species, Best Surface Number							
NLCD classification	*N. a. acuminatus*, 21	*N. brunnea*, 25	*T. v. velutinus*, 25	*T. v. velutinus*, 35	*T. v. velutinus*, 45	*U. despectus* [a], 23	*U. despectus* [a], 61	*U. despectus* [a], 84
Open Water	10	1	1	1	1	1000	1000	1000
Perennial Ice/Snow	10	1	1	1	1	1000	1000	1000
Low-Intensity Residential	10	1	1	10	100	1000	1	1000
High-Intensity Residential	10	1	1	10	100	1000	1	1000
Commercial/Industrial/Transportation	10	1	1	10	100	1000	1	1000
Bare Rock/Sand/Clay	10	1	1	1	1	1000	1000	1000
Quarries/Strip Mines/Gravel Pits	10	1	1	1	1	1000	1000	1000
Transitional	10	1	1	1	1	1000	1000	1000
Deciduous Forest	1	10	10	10	10	1	1	1
Evergreen Forest	1	10	10	10	10	1	1	1
Mixed Forest	1	10	10	10	10	1	1	1
Shrubland	10	1	1	1	10	1000	1000	10000
Orchards/Vineyards/Other	10	1	1	1	10	1000	1000	10000
Grasslands/Herbaceous	10	1	1	1	10	1000	1000	10000
Pasture/Hay	10	1	1	1	10	1000	1000	10000
Row Crops	10	1	1	1	10	1000	1000	10000
Small Grains	10	1	1	1	10	1000	1000	10000
Urban/Recreational Grasses	10	1	1	1	10	1000	1000	10000
Woody Wetlands	10	10	10	10	10	1	1	1
Emergent Herbaceous Wetlands	1	1	1	1	10	1000	1000	10000

[a] U. despectus with forest as habitat. With pignut hickory as habitat, the single best surface (23) had pignut hickory habitat 1, all else 1000.

growth, the best-fitting cost surface simply distinguished between pignut hickory habitat and non-pignut hickory habitat (Tab. 4). For all generalist species, the Euclidean distance surfaces were a better fit to the data than the overall best-fitting surfaces (Tab. 5). Evidence ratios indicate that Euclidean distance surfaces are 2.8 times more likely to explain the distributions of *N. a. acuminatus* and *N. brunnea*, respectively, than their best-fitting cost surfaces. The Euclidean distance surface is also 4 times more likely to explain the distribution of *T. v. velutinus* than the best-fitting cost surfaces for this species. Results for the specialist species differ depending on how habitat was defined. If habitat was defined as forest, the Euclidean distance surface was 4.5-5 times more likely to explain the distribution of *U. despectus* than the best-fitting cost surface (Tab. 5). If the definition of habitat was changed to pignut hickory habitat, the results reversed and the best-fitting cost surface was five times more likely to explain the species' distribution than the Euclidean distance surface. Both the Euclidean surface and the best-fitting cost surface significantly explained the variation in the distribution of *N. brunnea* (Tab. 5). The best-fitting cost surface for *U. despectus* when pignut hickory habitat was included as a land cover type was also significant (Tab. 5). No other surfaces showed significance, though the Euclidean distance surfaces for both *N. a. acuminatus* and *T. v. velutinus* were close to significance (Tab. 5).

Table 5. Goodness of fit and model significance statistics for each species for the Euclidean distance surface (1) and the best-fitting cost surface(s). Significant log-likelihood ratios are marked with an asterisk (*).



Species	Surface number	Number of parameters	AIC_c	Akaike weight	Log-likelihood ratio	DF	p-value
N. a. acuminatus	1	4	10.1	0.74	3.07	1	0.08
	21	5	13.3	0.26	4.3	2	0.12
N. brunnea	1	4	10.2	0.74	8.92	1	0.003*
	25, 41	5	13.5	0.26	10.03	2	0.007*
T. v. velutinus	1	4	10.1	0.8	3.04	1	0.08
	25, 35, 45	5	13.2	0.2	3.53	2	0.17
U. despectus , forest as habitat	1	4	71.6	0.82	0.02	1	0.89
	23, 61, 84	5	74.6	0.18	0.31	2	0.86
U. despectus , pignut hickory as habitat	1	4	70.6	0.17	0.99	1	0.32
	23	5	67.4	0.83	7.55	2	0.02*

4 Discussion

For all three generalist species, connectivity calculated with Euclidean distance was a much better predictor of presence in a landscape than the functional connectivity calculated with effective (least cost path) distance. The only exception was the pole borer *N. brunnea*, where the results between the best cost surface and the Euclidean distance surface were very similar to each other (Tab. 5). In contrast, when habitat was defined as pignut hickory for *U. despectus*, the best predictor of presence in a landscape was functional connectivity calculated with cost values of 1 for pignut hickory habitat and 1000 for all other types of habitat. The difference was dramatic, with no other cost surfaces being even close to statistical significance. The area of habitat patches, and thus the way they were defined, was more important to the functional connectivity calculations than the distances between them because landscape sizes were small compared to inter-patch distances.

The *U. despectus* results could indicate that they perceive the non-habitat matrix as inhospitable in terms of lack of resources. It is likely that this specialist species was selected over time to detect good larval habitat, since in other cerambycid species egg size, number of eggs and mating success (e.g., Hanks et al. 1996, 1998) are positively associated with adult size, and adult size is positively correlated with quality of larval host habitat (Hanks 1995). For species with generalist larvae, *N. a. acuminatus, N. brunnea,* and *T. v. velutinus*, we failed to reject the null hypothesis that adult beetles perceive the landscape as a binary matrix of forest and non-forest. At the same time, the Euclidean distance cost surfaces either significantly explained the distribution of each species (*N. brunnea*) or were quite close (*N. a. acuminatus, T. v. velutinus*). These results imply that future studies of cerambycid movement in Indiana need not measure anything more than Euclidean distance between habitat patches if the species being investigated are polyphagous as larvae.

Though the best cost surfaces did differ between species, we were unable to reject the null hypotheses relating cost values to the biology of each organism. The best cost surfaces were statistically significant for both *N. brunnea* and *U. despectus*, but only for *U. despectus* when habitat was redefined. The best cost surface for *N. brunnea* had forest slightly more costly than non-forest (Tab. 5), which may indicate that there are more and better resources for this species in non-forest areas. Though this makes sense when considering its common name, the pole borer, evidence ratios indicate that the Euclidean distance surface, i.e., that which assigns the same cost value to every land cover type, is the most probable. This renders any interpretation of cost values inappropriate. We must also avoid interpreting the best cost surface values for *N. a. acuminatus* and *T. v. velutinus*, respectively, as they were not good statistical fits to the distribution data and are less likely than their Euclidean distance counterparts.

The results outlined above are surprising, as they imply that adult feeding habits do not affect movement through the landscape for these species. The limited dispersal of adult *N. brunnea* indicates that adult feeding, if it occurs, takes place on or near larval hosts, as noted previously (Solomon 1995). So long as the hosts, e.g., utility poles or logs, are abundant, the consequent lack of prolonged movement in the landscape may mean that the composition of the landscape has little impact on persistence of the species if they rarely encounter the larger landscape around them and they have no need to disperse to feed. Adult *N. a. acuminatus* may not feed, but they and other cerambycid species do detect volatiles emitted by larval hosts (Hanks 1999; Allison et al. 2004), and communicate via aggregation pheromones (Lacey et al. 2004). Adults of the flower-feeding species, *T. v. velutinus*, may similarly be able to detect floral volatiles. If they behave as other pollinators do, they respond to the composition of a habitat patch rather than its area (Hunter 2002). These chemicals may not have great impacts over the spatial scales that we examined, as wind and other environmental factors would lead to dissipation over large distances. Still, the existence of these chemical signals indicates levels of communication that may not be reflected by our study design. Insect species previously studied with cost distances tend to either come into direct contact with their habitat through walking, e.g., ground beetles (Jopp & Reuter 2005), or be specialized to particular larval plants or adult feeding sites, e.g., butterflies (Sutcliffe et al. 2003). Those that walk can potentially perceive boundaries and decide which type of habitat that they prefer (Collinge et al. 2002), while those that are highly specialized must have developed ways of cueing into their habitat, much like the cerambycids studied here. Since trunk volatiles, leaf volatiles, floral volatiles, pheromones and kairomones are airborne, any perceived boundaries between habitat types are probably not purely related to physical boundaries defined by the National Land Cover Dataset. While tracing the boundaries of any type of land cover in a GIS is possible, it may not be the most feasible option when operating over areas as large as those investigated here. Alternatively, we could have altered the functional connectivity calculations by weighting habitat patches by not just area and distance, but also by quality (p_j in Eq. 1). It was not logistically possible for us to assess the probability of occupation of each patch in each landscape, so we assumed that all patches contained equally suitable habitat and set all p_j equal to 1. In reality, most cerambycids are able to distinguish the physiological state of a tree (Linsley 1959; Solomon 1995; Hanks 1999); all patches do not have the same suitability and the beetles can detect this. More appropriate values of p_j would weight each patch's contribution to the functional connectivity calculation differently, and including these may help researchers elucidate how the beetles actually perceive the landscape. Assessing the probability of occupation could be accomplished by ground surveys, or by examining aerial photos or remotely-sensed images (e.g., Jia et al. 2006).

GIS surfaces that combine many aspects of an organism's ecology tend to be the best at explaining its distribution (Sutcliffe et al. 2003; Verbeylen et al. 2003; Stevens et al. 2006). Here, we begin to examine the ecological factors that affect persistence of four species of flying beetle in a fragmented landscape. Our results support the idea that adult cerambycid movement in a landscape is shaped by location of larval host habitat, but could be supplemented with further information about the quality of that habitat. Our results also underline the importance of properly delineating habitat when dealing with specialist species, even if those species feed on plants that do not exist in well-defined monocultures. While human activities influence the location and size of habitats for all species, the patterns of human activities in non-habitat areas may not play a large role in structuring movement of some flying insects if they have a wide niche breadth.

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