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The Importance of Landscape Structure and Habitat Quality for Biodiversity of Invertebrates

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ABSTRACT

In fragmented landscape, migration of individuals from one fragment to another may be important for biodiversity of taxa and species. This thesis tests the importance of landscape connectivity of the Bohemian Karst (Central Bohemia, the Czech Republic) for three taxa - Carabidae, Lepidoptera, and Araneae. Many previous studies of connectivity did not account for variability in landscape matrix and measured connectivity just in Euclidean distance. However, individuals might use landscape matrix as a part of habitat which supports movement or conversely as an environment which impedes their movement between fragments.

Landscape connectivity was tested on 3 different levels: (1) a connectivity measured by Euclidean distance and least-cost distance for taxa Carabidae, Lepidoptera, and Araneae, (2) an importance of matrix, and (3) a comparison of connectivity and habitat quality. Different modifications of Incidence Function Model (IFM) were used - for Euclidean distance analyses and for least-cost analyses, which I calculated in ArcGIS 10. To test statistical significance of models, GLM and regression models with a dependent variable of species richness (according to Menhinick index) and a number of species were used. Statistical analysis with "step by selection" was done to test the significance of environmental variables on the habitat separately for each of the taxon groups. Results demonstrate that connectivity has different importance for each studied taxon. These taxa of invertebrates are able to move in the landscape independently on its matrix. Environmental variables connected to vegetation type and structure are more significant for biodiversity indices than connectivity alone. Nevertheless, in species level, connectivity partially explains distribution of some species in landscape. Because of its higher significance and lower sophistication, the simple IFM model for Euclidean distance (from sampling point to the nearest edge of each forest fragment) is optimal for studying connectivity of invertebrate species.

Key words: Landscape connectivity, matrix, IFM model, Euclidean distance, least-cost distance, GIS modeling, forest fragment, habitat structure, Carabidae, Lepidoptera, Araneae

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ABSTRAKT

Ve fragmentované krajině může hrát migrace jedinců mezi fragmenty důležitou roli pro taxony a druhy. Ve své práci jsem testovala důležitost konektivity krajiny Českého krasu (střední Čechy, Česká republika) pro tři taxony - Carabidae, Lepidoptera, and Araneae. Řada recentních studií nereflektovala variabilitu krajinné matrice a konektivita byla jejich autory měřena pouze pomocí eukleidovské vzdálenosti. Právě krajinná matrice však může být jedinci využívána jako součást biotopu, který podporuje pohyb, nebo jako prostředí, které brání jejich disperzi mezi fragmenty.

Konektivitu krajiny jsem testovala na 3 různých úrovních: (1) konektivita měřená eukleidovskou vzdáleností a *least-cost* vzdáleností pro taxony Carabidae, Lepidoptera, and Araneae; (2) důležitost matrice; a (3) srovnání konektivity a kvality biotopu. Pracovala jsem s různými modifikace *Incidence Function Model* (IFM) pro eukleidovskou vzdálenost a *least-cost* vzdálenost, které jsem vypočítala v programu ArcGIS 10. K testování statistické významnosti modelů jsem použila *Generalized Linear Model* (GLM) a regresní modely, kde závislou proměnnou byl index druhové pestrosti (podle Menhinicka) a počet druhů. K testování významnosti environmentálních faktorů stanoviště jsem použila metodu *step by* selekce pro každý ze studovaných taxonů zvlášť. Výsledky ukazují, že vliv konektivity je pro každý sledovaný taxon jiný. Vybrané skupiny bezobratlých jsou schopny se v krajině pohybovat nezávisle na její matrici. Lokální parametry prostředí související s typem vegetace a její strukturou jsou pro biodiverzitu významnější než samotná konektivita. Na druhové úrovni však konektivita částečně vysvětluje distribuci některých druhů v krajině. Díky vyšší významnosti a menší komplikovanosti se jako optimální pro studium konektivity bezobratlých jeví IFM model pro eukleidovskou vzdálenost (ze vzorkovacího místa k nejbližším okrajům všech lesních fragmentů).

Klíčová slova: Konektivita krajiny, matrice, IFM model, euklidovská vzdálenost, *least-cost* vzdálenost, GIS modelování, lesní fragment, struktura stanoviště, Carabidae, Lepidoptera, Araneae

Affirmation

I declare that I wrote this Master's thesis independently under the supervision of RNDr. Tomáš Kuras, PhD. and I used cited literature only.

In Olomouc, 2nd May, 2013 ....

Lenka Šprtová

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LIST OF ABBREVIATIONS

PLP	Public land register
COSMC	Czech Office for Surveying, Mapping and Cadastre
NCA CR	Nature Conservation Agency of the Czech Republic
IFM	Incidence Function Model
GLM	Generalized Linear Model
AIC	Akaike's Information Criterion

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1 INTRODUCTION

The fundamental effects of fragmentation on organisms are particularly a loss or reduction of a habitat, habitat alteration and increased habitat isolation of native species (Andren 1994, Wilcox and Murphy 2012). These processes create a mosaic landscape with spatial and time heterogeneity and thus more diversified vegetation structure. Area of natural habitat, spatial distribution, and rate of fragment isolation, number of fragments, and mean fragment size is important for survival of populations and formation of landscape biodiversity (Andren 1994, Fahrig 2003). In fragmented landscape, migration of individuals from one fragment to another is a vital process for survival of local subpopulations, because of high rate of population extinction and reestablishment (Hanski et al. 2000). Thus the strength of links among persisting fragments, known as "connectivity", becomes more and more important. If the connectivity is very low, it might not sustain viability of some species (Calabrese and Fagan 2004). Landscape connectivity is defined as "the degree to which the landscape facilitates or impedes movement among resource patches" (Taylor et al. 1993). The definition emphasizes that connectivity is landscape- and species-specific. (Adriaensen et al. 2003, Tischendorf and Fahrig 2000). There are two most important classes of landscape connectivity – structural and functional. Structural connectivity stresses the characteristics of the landscape such as size, shape, and location of a fragment, whereas functional connectivity considers the mobility of particular species (Adriaensen et al. 2003, Calabrese and Fagan 2004). Functional connectivity also includes the impact of the landscape matrix (Watts and Handley 2010).

An important role in calculation of fragment connectivity plays the cost to move between fragments (Moilanen et al. 2001, Tischendorf and Fahrig 2001). The simplest way to measure the cost is to utilize the Euclidean (which means the nearest neighbor) distance (Moilanen et al. 2001).

However, Euclidean distance does not account for differences in matrix or ecological processes (e.g. dispersal) (Tischendorf and Fahrig 2001, Kindlmann and Burel 2008, Kupfer 2012). Consequently, it might use identical dispersal characteristics for matrix and habitat components, even though the environments are different (Gustafson 1998, Kindlmann and Burel 2008). Nevertheless, there is a growing awareness that matrix can play an important role as a proportion of original habitat, because habitat fragments are a part of the landscape mosaic (Andren 1994). Matrix can be considered as a conduit (i.e. allowing the movement of individuals), a source, a sink or a barrier (blocking all movement) (Kupfer et al. 2006). Species do not always move in Euclidean distance between two fragments, they rather chose a simpler way through the matrix, where, for example a corridor, which can support connectivity of these fragments (Ellis et al. 2010). If the landscape is prevailed by a matrix that facilitate movement, it will have a higher connectivity than landscape with matrix impending movement (Kindlmann and Burel 2008). Another way of estimating inter-fragment distances which takes the matrix into account is least-cost distance (Chardon et al. 2003, Verbeylen et al. 2003). This approach allows to look at landscapes as a whole not only as a fragmented area and interfragment distance (Kupfer et al. 2006).

The primary aim of this thesis is to test how connectivity influences biodiversity indices (a number of invertebrate species and species richness) of species in fragments. Secondly, I would like to develop a least-cost methodology to test the influence of the matrix on the movement of species through the landscape. The third objective is to compare landscape connectivity to habitat quality and conclude which one of the two is a more important factor to determine overall landscape biodiversity.

2 METHODS

2.1 Study area and species data

To test the importance of landscape connectivity and matrix on invertebrates, Czech landscape is an essential area, because of its human-caused fragmentation. The modeled area is situated in the southwest part of PLA Bohemian Karst in the neighborhood of the village of Měňany. The landscape is a highly fragmented mosaic of forest biotopes with variable ecological quality. In the past, a much larger area was forested, however due to the human activity the forests became fragmented. Intensive agriculture largely modified and caused a degradation of the matrix among fragments. Studied forest fragments are prevailed by mesophilous and subxerothermic oak woods and oak-hornbeam woods. Their dominant species are Sessile Oak (*Quercus petraea*), Small-leaved Lime (*Tilia cordata*) and European Hornbeam (*Carpinus betulus*) (Chytrý et al. 2010).

For testing the connectivity of a landscape and the importance of a matrix, I used the data collected by Kuras, Zedek et al. in years 2008 – 2010 as a part of project VaV-SP 2d3/139/07. They studied three groups of organisms – Carabidae, Araneae, and Lepidoptera which are considered to be significant bioindicators. These groups are ecologically diverse taxa that have distinct abilities to get through the environment and different length of dispersal.

For modeled forest biotopes, I used the term “fragment”. When observing the local conditions of different qualities of each sampling point, I used the term “habitat quality”.

2.2 Landscape data

In the Czech Republic is a remarkable lack of environmentally significant spatial data for a modeling of species distribution or an arrangement of landscape elements. Thus, I first had to create a suitable land cover layer.

The studied area consists of 24 forest fragments which were selected and used in previous studies (Tyralík 2012; Zedek 2011). To further test the connectivity of broader landscape, I created a buffer zone of 3 km (selected by considering the species dispersal ability) around these fragments. Within this buffer zone I edited all forest fragments. The selection was based on combination of 3 data resources: (1) The Forest Management Institute (FMI) - Regional forest development plan[1], (2) Czech Office for Surveying, Mapping and Cadastre (COSMC) – Orthophoto[2], and (3) Nature Conservation Agency of the Czech Republic (NCA CR) - Biotopes[3]. If there was only a small part of a large polygon within this 3 km buffer zone, I included the whole polygon.

To define the matrix, I included 7 different layers: urban area, waterbody, arable land, dry grassland, meadow, golf course and quarry. The layer of meadows and arable land was downloaded from Public land register (PLR)[4]. Information about the waterbodies were obtained from T. G. Masaryk Water Research Institute, a public research institution[5]. I edited urban areas, golf course and quarry based on orthophoto. Layer of dry grassland was created based on a combination of orthophoto map and a layer of biotopes. Shrubby hillsides, xerotermic edges, and grasslands that are not cultivated were selected.

In ArcGIS, I combined all layers together and the gaps between them, I assigned the value of the cell that is most frequent in its neighborhood. Final land cover layer is in a raster format with cell size 5. For every analysis, I used the S-JTSK Krovak East North coordinate system.

2.3 Modeling approach

In my thesis, I will focus on the comparison of calculations of Incidence Function Model (IFM) for Euclidean distance with modification of IFM for least-cost analyses. IFM model for Euclidean distance ignores the impact of matrix whereas modified IFM model for least-cost analyses takes the matrix into account. To test the importance of connectivity for species richness and number of species of different groups of invertebrate, I used the following formula:

$$S_i = A_i^c \sum_{j \neq i} exp\,(-\alpha d_{ij}) A_j^b$$

[1] http://geoportal2.uhul.cz/wms_oprl?SERVICE=WMS
[2] http://geoportal.cuzk.cz/WMS_ORTOFOTO_PUB/WMService.aspx
[3] http://mapmaker.nature.cz/wmsconnector/com.esri.wms.Esrimap/aopk_ biotopy_wms
[4] http://eagri.cz/public/app/lpisext/lpis/verejny/
[5] http://www.dibavod.cz/index.php?id=27 – dib_A05_Vodni_nadrze.zip

This method was described by Moilanen and Nieminen (2002) for calculating with Euclidean distance as an extension of the measure originally proposed by Hanski (1994). Generalization of this formula was described by (Moilanen et al. 2001):

$$S_i = A_i^c \sum_{j \neq i} D\,(d_{ij}, \alpha, \ldots) A_j^b$$

In this formula *Si* is the connectivity of the fragment, *Ai* is the area of target fragment *i*, *Aj* is the area of source fragment *j*. Parameters *b* a *c* specify rate of emigration and immigration. *D(dij, α,…)* is the dispersal kernel which "scales the effect of distance on migration rate" (Moilanen et al. 2001), and *α* describes the dispersal ability of the species and modifies dispersal kernel (Moilanen et al. 2001, Ellis et al. 2010).

However, Euclidean distance might not explain the real path the organism would use to move through landscape. I compared the models which use Euclidean distance with those that use least-cost distance.

2.4 Connectivity that ignores landscape matrix

For the first group of models, I used Euclidean distance and IFM model (Table 1; Figure 1). In ArcGIS, I calculated near distance from each sampling point to each fragment of forest (nearest edge) within the buffer zone of 3 km (Model I). I used parameter α to modify the dispersal kernel. I set values of *α* to 0.5, 1, 1.5, 2, 2.5, 3, 3.5, 4, 4.5 and 5 to find the best model for connectivity and calculated connectivity according to IFM. I chose this range of parameter *α* according to known dispersal abilities of invertebrates along with published papers (Hanski 1994, Hanski et al. 1994, 2000)[6]. For parameters *b* and *c*, I used mean values (b = 0.3, c = 0.2) described by Hanski (1994) and Hanski et al. (2000). As an output, I obtained connectivity values for each *α* for each sampling point.

However, in the case when forest fragment is larger and contains more sampling points, the Euclidean distance of each sampling point to the nearest edge of other forest fragments can much differentiate. To moderate this impact of distance within a forest fragment, I further adjusted the model and calculated distance from edge of source fragment to the nearest edge of other forest fragments (Model II and III).

[6] Other ways to define *α* are summarized in Prugh (2009)

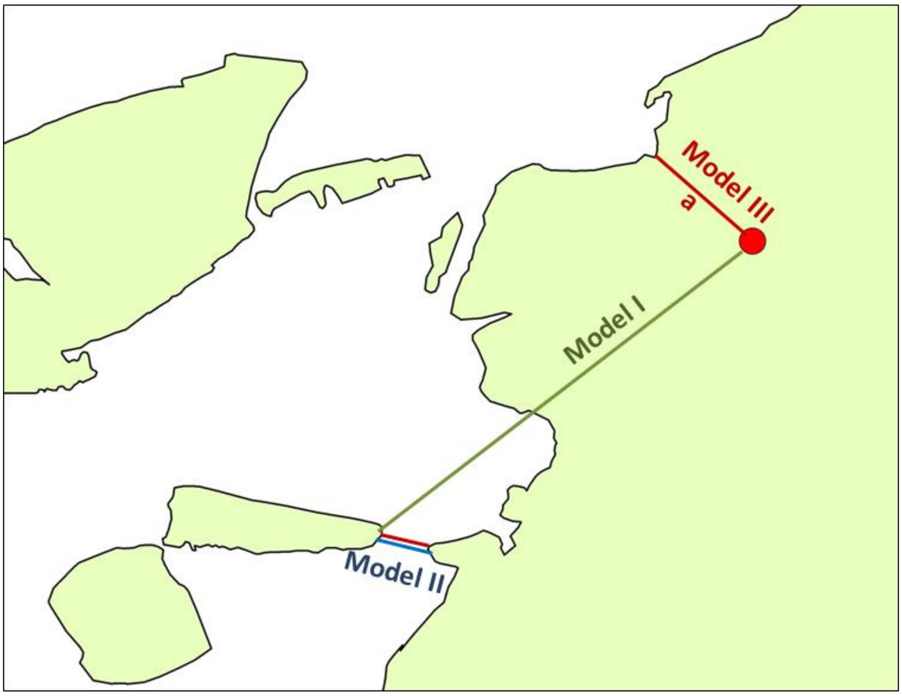

Figure 1. Euclidean distances measured by IFM models. Example for sampling point 653. (a) Covariate of distance from point to nearest edge of fragment (see Table 1).

Table 1. IFM models used for Euclidean distance

Name of model	Description of the model
Model I	Near distance from each sampling point to each fragment of forest (nearest edge)
Model II	Near distance from edge of source fragment to the nearest edge of other forest fragments
Model III	Near distance from edge of source fragment to the nearest edge of other forest fragments with covariate of distance from point to the nearest edge of fragment

See Figure 1

2.5 Connectivity that accounts for landscape matrix

While Euclidean distance does not take the landscape matrix into account, least-cost distance follows the importance of variability in landscape matrix. By using GIS, each grid cell of the landscape obtains a resistance value of how much this environment restrains or facilitates a movement process (Kupfer 2012). Resistance value is assign 1 for habitat (minimum cost). On a relative scale, the maximum value is assigned to areas that are highly unsuitable. These values are used to find a path between two fragments with minimal cost (Fall et al. 2007, Kupfer 2012).

The input for this model consists of two GIS layers: source layer and friction layer (Adriaensen et al. 2003). Source layer is composed of habitat fragments for which I calculated connectivity. In friction layer, I assigned resistance value to every grid cell depending on landuse of the studied area. The areas that might support the movement of organisms are given low resistance values, whereas the landuse that might impede movement get higher value (Chardon et al. 2003). Cost layer around the source fragment serves as the output of a cost-distance analysis (Adriaensen et al. 2003). As specified by Adriaensen et al. (2003), "a cost value of *n* indicates the cost of moving through *n* cells with a resistance value of 1, or through one cell with a resistance values of *n*, etc." (Figure 2).

By setting a various resistance values for landscape elements, I made two different groups of landscape scenarios: (1) values for matrix are set all the same - it does not play an important role, and (2) matrix is diversified and thus plays an important role in explanation of connectivity (Table 2).

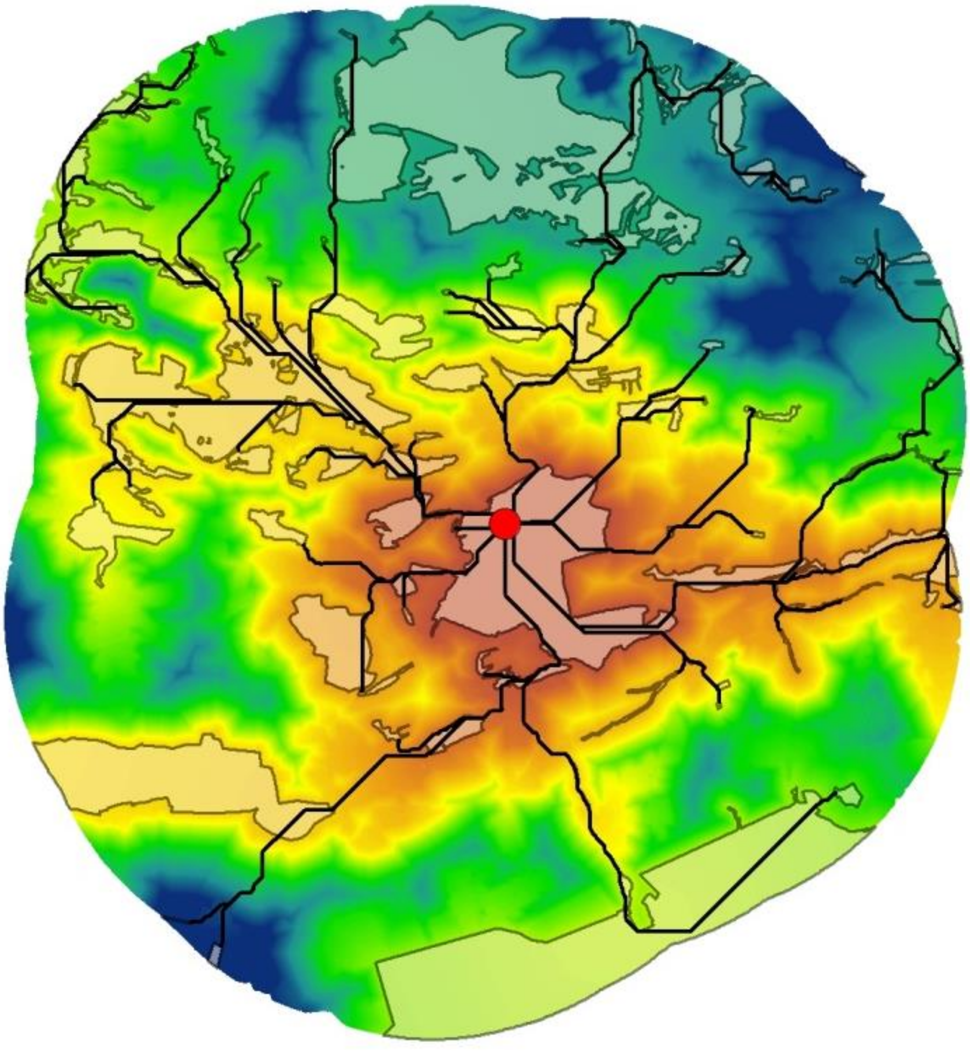

Figure 2. Example of cost distance surface for scenario 2_01, sampling point 653. Black lines show the least cost path from the sampling point to the each forest fragment.

I generated 20 raster friction surface layers which I consequently used for cost distance analyses. A value of forest was always set to 1, because the forest fragments are considered as a habitat. Except for scenario sc_1_10, I always set the highest value to 100 for waterbodies and quarries, whose behave more less as a barrier (Chardon et al. 2003, Verbeylen et al. 2003, Fall et al. 2007, Watts et al. 2010, Duggan et al. 2011, Kupfer 2012, Maag et al. 2013). In the first group of scenarios (sc_1_01 – sc_1_10), I test how prominent is friction of matrix which is seen by organisms as a homogenous. Value 10 for matrix means that it is easily permeable for invertebrates, value 90 signifies it is hardly permeable. Landscape elements in scenario sc_1_10 have all a resistance of 1, thus only distance without effect of matrix is taken into account (Verbeylen et al. 2003). This scenario acts as Euclidean distance and because of same relative scale as other scenarios in the section, it makes it comparable. In the second group of scenarios (sc_2_01 – sc_2_10), I randomly choose different values for different groups of landscape elements. I assigned different vales to urban area and arable land and I consistently grouped meadow, dry grassland, and golf course together. The values have ascending tendency from scenario sc_2_01 to sc_2_10. This group of scenarios tests if diversity of matrix plays important role in movement of invertebrate organisms through landscape.

I prepared a model (Appendix 3) which measures cost distance from every sampling point to the nearest edge of every forest fragment. An input of a model is a map of sampling points, friction surface (for scenarios sc_1_01 – sc_2_10), and a shape-file with forest fragments. The output of the whole analyses is tables of least cost values for all sampling points for all scenarios.

Table 2. Resistance values for two groups of landscape scenarios.

Least-cost scenario	Forest	Meadow Dry grassland Golf course	Urban area	Arable land	Waterbody Quarry
scenario 1					
sc_1_01	1	10	10	10	100
sc_1_02	1	20	20	20	100
sc_1_03	1	30	30	30	100
sc_1_04	1	40	40	40	100
sc_1_05	1	50	50	50	100
sc_1_06	1	60	60	60	100
sc_1_07	1	70	70	70	100
sc_1_08	1	80	80	80	100
sc_1_09	1	90	90	90	100
sc_1_10	1	1	1	1	1
scenario 2					
sc_2_01	1	20	10	50	100
sc_2_02	1	10	20	50	100
sc_2_03	1	20	30	50	100
sc_2_04	1	40	50	60	100
sc_2_05	1	30	40	70	100
sc_2_06	1	40	30	70	100
sc_2_07	1	60	50	70	100
sc_2_08	1	60	70	80	100
sc_2_09	1	60	50	80	100
sc_2_10	1	50	40	90	100

2.6 Adaptation of IFM formula for Least-cost analyses

In my model, I wanted to test the importance of variability of environment and matrix, rather than variability of dispersal of different species. Because I calculated the connectivity of different groups of invertebrate organisms, that might have various dispersal abilities, I did not use modifier α of dispersal kernel. In a similar way as described by Verbeylen et al. (2003), I replaced "αd_{ij}" by cost-distance calculated in ArcGIS. I set 20 different landscape scenarios, with varying resistance values to test, whether (a) connectivity plays significant role in explaining biodiversity indices (species richness and number of species) in the landscape and whether (b) variability of matrix can support/impede the movement of invertebrate species through landscape.

In Microsoft Excel 2000, I calculated connectivity of every sampling point for each of 20 landscape scenarios, according to formula:

$$S_i = A_i^c \sum_{j \neq i} exp\,(-\mathrm{c}d) A_j^b$$

where *cd* is a least-cost distance modeled in ArcGIS. Ai, the area of target fragment *i* and Aj, the area of source fragment *j* of all of the forest fragments were procured from ArcGIS as well.

2.7 Statistical analysis

For each of the three groups of organisms, Carabidae, Araneae, and Lepidoptera, I tested a total number of species and number of species specialized for forest habitat collected in every sampling point between 2009 and 2011. I also calculated index of species richness for all of the species and for forest species, according to Menhinick (1964):

$$D = \frac{S}{\sqrt{N}}$$

where *D* is an index, *S* is a number of species, and *N* is a total number of individuals.

I tested the effects of landscape scenarios and different dispersal abilities of groups of species with a generalized linear model (GLM) for normal distribution. I chose this model according to the lowest AIC. In GLM, I took a logarithm for a dependent variable – associated with biodiversity indices (number of species, species richness). As an independent variable served results from models for different landscape scenarios. For each model, I calculated regression coefficient, P, AIC, and when the result is significant also R^2.

For adjusted Euclidean distance model from the edge of source fragment to the nearest edge of other forest fragments (Model II), I included a distance of sampling point from the nearest edge of source fragment as another covariate in the statistical analyses (Model III). To test if a model with covariate is different than the one without covariate, I used ANOVA.

2.8 Analyses of selected species

Connectivity might have more significant impact on species level than on taxon level. Therefore, I selected 10 species from taxa Carabidae and Araneae and tested the connectivity for IFM (Model I) and for least-cost distance scenarios. The response variable was species abundance in each sampling point. To test if connectivity plays more important role for forest species than for non-forest species, I chose 5 forest and 5 non-forest species from each taxon with the highest abundance.

For analyses, I used GLM with Poisson distribution of error variability. Species abundance data were transformed by square root.

2.9 Analyses of environmental variables

To test if other environmental variables explain more variability than the connectivity alone, I prepared a model, which includes these factors. Factors were chosen by regression models based on step by selection, ordered from the lowest AIC to the highest, separately for each of the taxon groups. Combination of all selected factors thus explains the variability the best.

2.10 Software

I prepared the entire project in ArcGIS Desktop (ArcView) v10, ArcGIS Spatial Analyst Extension, v10 produced by Environmental Systems Research Institute, Redlands, CA. For calculations, I used Microsoft Excel 2000 and R 2.14.2.

3 RESULTS

I tested the importance of connectivity on biodiversity indices of invertebrates in Bohemian Karst, the Czech Republic. For testing the connectivity I used IFM and modified IFM for least-cost analyses. I calculated IFM in two different ways, i.e. from sampling point to all forest fragments (Model I) and from source fragment to the nearest edge of other forest fragments (Model II and III) for distinct values of alpha (from 0.5 to 5). I calculated least-cost for 20 scenarios which differ in friction of matrix. I display the results in tables.

3.1 Euclidean distance analyses

IFM results for Euclidean distance analyses calculated from sampling point to all forest fragments (Model I). I tested parameters species richness, number of species for all of the species and for forest species (Table 3). According to IFM, connectivity is significant for index of species richness for all of the species for all studied taxa. Carabidae show bimodal trend of data distribution. The best-fit α for Lepidoptera and Araneae is a high number, indicating poor dispersal ability. For taxon Araneae, this biodiversity index is also important only for group of forest species. While considering the total number of species, connectivity plays the role for Carabidae and Lepidoptera. Whereas, the number of forest species is significant for Lepidoptera and Araneae. Abundance of all species as well as forest species is a significant index for Lepidoptera and Araneae.

Results for Euclidean distance analyses calculated from source fragment to the nearest edge of other forest fragments (Model II; Tables 4-15) show that connectivity is significant for species richness for all of the species of taxa Carabidae and Araneae. For testing if the model with covariate (Model III) is different than the one without covariate (Model II), I used ANOVA. According to the results, Model III did not significantly explain connectivity for any of the indices. To have the whole Model III significant, both of its parts α*distance and IFM calculated from Model II has to be simultaneously significant.

The results did not indicate any significance of biodiversity indices solely for forest species. AIC for different dispersal parameter α did not notably differentiate, thus I could not specify the best-fit α.

Table 3. Diversity indices for species richness and number of species for all of the species and for forest species of invertebrates in Bohemian Karst calculated with IFM (Model I).

Dispersal parametr	**Studied invertebrate taxons (Model I.)**								
	Carabidae			Lepidoptera			Araneae		
	regress.coeff.		AIC	regress.coeff.		AIC	regress.coeff.		AIC
Index of species richness for all of the species									
alpha 0.5	-0.04	*	24.4	-0.01		-30.6	0.03	n.s.	-25.3
alpha 1	-0.10		26.5	-0.02		-29.7	0.06		-23.7
alpha 1.5	-0.07		28.6	0.03		-29.6	0.05		-21.6
alpha 2	0.06		28.8	0.12		-31.0	-0.05		-21.4
alpha 2.5	0.21		28.1	0.20	n.s.	-32.6	-0.15		-22.5
alpha 3	0.36		27.2	0.28	*	-33.9	-0.24		-23.7
alpha 3.5	0.52		26.3	0.36	*	-35.1	-0.32	n.s.	-24.6
alpha 4	0.70	n.s.	25.4	0.44	*	-36.1	-0.40	*	-25.3
alpha 4.5	0.89	*	24.4	0.53	**	-36.9	-0.47	*	-25.8
alpha 5	1.08	*	23.5	0.61	**	-37.5	-0.53	*	-26.1
Index of species richness for forest species									
alpha 0.5	-0.01		11.4	0.00		-10.4	0.02		29.1
alpha 1	-0.01		11.7	0.02		-10.5	-0.01		30.0
alpha 1.5	0.04		11.6	0.05		-10.7	-0.20		28.4
alpha 2	0.11		11.2	0.09		-11.0	-0.43	*	25.8
alpha 2.5	0.18		10.8	0.14		-11.4	-0.60	*	24.1
alpha 3	0.26		10.4	0.19		-11.9	-0.74	*	23.1
alpha 3.5	0.34		10.0	0.26		-12.4	-0.88	**	22.5
alpha 4	0.44		9.6	0.33		-12.9	-1.01	**	22.1
alpha 4.5	0.54		9.3	0.41	n.s.	-13.4	-1.15	**	21.9
alpha 5	0.64		8.9	0.50	n.s.	-13.9	-1.27	**	21.8
Total number of species									
alpha 0.5	-0.02		17.0	0.00		58.7	0.01		-19.0
alpha 1	-0.04		18.3	0.09		57.5	0.04		-19.7
alpha 1.5	0.04		18.7	0.40	*	52.5	0.11		-20.3
alpha 2	0.19		17.5	0.71	**	48.2	0.13		-19.9
alpha 2.5	0.33		16.1	0.90	***	46.8	0.11		-19.4
alpha 3	0.47	n.s.	15.0	1.05	***	46.4	0.09		-19.0
alpha 3.5	0.61	*	14.1	1.22	***	46.3	0.06		-18.8
alpha 4	0.75	*	13.4	1.39	***	46.4	0.03		-18.7
alpha 4.5	0.89	*	12.8	1.56	***	46.6	0.00		-18.7
alpha 5	1.03	*	12.5	1.73	***	46.8	-0.04		-18.7

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, n.s. $p < 0.1$

Table 3. Continued.

Dispersal parametr	**Studied invertebrate taxons (Model I.)**					
	Carabidae		Lepidoptera		Araneae	
	regress.coeff.	AIC	regress.coeff.	AIC	regress.coeff.	AIC
Number of forest species						
alpha 0.5	0.01	-27.9	0.03	64.9	0.02	5.2
alpha 1	0.02	-27.8	0.18 *	61.4	0.12 *	1.9
alpha 1.5	0.02	-27.6	0.53 **	56.4	0.33 **	-2.2
alpha 2	0.01	-27.5	0.76 **	55.8	0.44 **	-1.6
alpha 2.5	-0.01	-27.5	0.86 **	57.0	0.44 *	0.7
alpha 3	-0.04	-27.6	0.96 **	57.9	0.43 $^{n.s.}$	2.5
alpha 3.5	-0.07	-27.7	1.07 **	58.4	0.40	3.8
alpha 4	-0.10	-27.8	1.20 **	58.7	0.37	4.8
alpha 4.5	-0.14	-27.9	1.34 **	58.9	0.32	5.4
alpha 5	-0.18	-28.1	1.48 **	59.1	0.27	5.9
Abundance of all species						
alpha 0.5	0.04	78.5	0.02	102.3	-0.04	20.3
alpha 1	0.12	78.5	0.20 $^{n.s.}$	99.7	-0.04	22.6
alpha 1.5	0.22	78.6	0.74 **	93.3	0.12	22.4
alpha 2	0.25	78.9	1.18 ***	90.0	0.36 $^{n.s.}$	19.6
alpha 2.5	0.25	79.1	1.39 ***	90.4	0.53 *	17.6
alpha 3	0.22	79.2	1.55 **	91.4	0.65 *	16.7
alpha 3.5	0.18	79.4	1.72 **	92.3	0.76 *	16.4
alpha 4	0.11	79.4	1.89 **	93.1	0.85 *	16.5
alpha 4.5	0.01	79.4	2.07 **	93.8	0.92 *	16.9
alpha 5	-0.10	79.4	2.24 **	94.4	0.98 *	17.4
Abundance of forest species						
alpha 0.5	0.03	77.3	0.06	104.0	0.00	105.6
alpha 1	0.06	77.9	0.34 **	98.6	0.25	104.0
alpha 1.5	-0.02	78.1	0.97 ***	90.6	1.06 **	98.3
alpha 2	-0.20	77.7	1.34 ***	90.8	1.74 **	94.5
alpha 2.5	-0.38	77.2	1.45 ***	94.1	2.09 **	94.2
alpha 3	-0.59	76.7	1.52 **	96.5	2.33 **	94.8
alpha 3.5	-0.82	76.1	1.62 **	98.1	2.56 **	95.7
alpha 4	-1.08	75.5	1.73 **	99.2	2.76 **	96.7
alpha 4.5	-1.35	75.0	1.85 *	100.0	2.94 **	97.6
alpha 5	-1.64	74.5	1.98 *	100.6	3.08 **	98.5

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, $^{n.s.}$ $p < 0.1$

Table 4. Index of species richness for all of the species. Carabidae

Dispersal parameter	Model II.			Model III.			ANOVA
				distance	alfa*distance		
	regress. coeff.	R2	AIC	regress. coeff.	regress. coeff.	AIC	F
alpha 0.5	-0.02 *	0.14	23.4	-0.0041	0.0001	22.3	2.43
alpha 1	-0.03 *	0.14	23.1	-0.0039	0.0002	22.0	2.43
alpha 1.5	-0.05 *	0.15	22.8	-0.0039	0.0004	21.8	2.39
alpha 2	-0.07 **	0.15	22.5	-0.0038	0.0005	21.6	2.36
alpha 2.5	-0.09 **	0.16	22.3	-0.0038	0.0006	21.4	2.34
alpha 3	-0.11 **	0.16	22.2	-0.0038	0.0008	21.4	2.33
alpha 3.5	-0.13 **	0.16	22.2	-0.0038	0.0009	21.3	2.33
alpha 4	-0.15 **	0.16	22.2	-0.0038	0.0010	21.3	2.33
alpha 4.5	-0.17 **	0.16	22.3	-0.0037	0.0011	21.4	2.36
alpha 5	-0.19 **	0.16	22.4	-0.0037	0.0012	21.4	2.38

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, $^{n.s.}$ $p < 0.1$

Table 5. Index of species richness for forest species. Carabidae

Dispersal parameter	Model II.		Model III.			ANOVA
			distance	alfa*distance		
	regress. coeff.	AIC	regress. coeff.	regress. coeff.	AIC	F
alpha 0.5	-0.01	12.1	-0.004	0.0001	8.7	3.66 *
alpha 1	-0.01	12.2	-0.004 n.s.	0.0002	8.8	3.66 *
alpha 1.5	-0.02	12.1	-0.004 n.s.	0.0003	8.9	3.59 *
alpha 2	-0.02	12.1	-0.004 n.s.	0.0004	9.0	3.52 *
alpha 2.5	-0.03	12.0	-0.004	0.0005	9.0	3.45 *
alpha 3	-0.03	12.0	-0.003	0.0006	9.1	3.40 *
alpha 3.5	-0.04	12.0	-0.003	0.0007	9.1	3.37 *
alpha 4	-0.05	12.0	-0.003	0.0008	9.2	3.34 *
alpha 4.5	-0.05	12.0	-0.003	0.0009	9.2	3.33 *
alpha 5	-0.06	12.0	-0.003	0.0010	9.2	3.32 *

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, $^{n.s.}$ $p < 0.1$

Table 6. Total number of species. Carabidae

Dispersal parameter	Model II.		Model III.				ANOVA
			distance	alfa*distance			
	regress. coeff.	AIC	regress. coeff.	regress. coeff.	R^2	AIC	F
alpha 0.5	-0.01 n.s.	16.1	-0.008 ***	0.0003 *	0.48	-4.1	14.78 ***
alpha 1	-0.02	16.1	-0.007 ***	0.0004 *	0.47	-3.9	14.69 ***
alpha 1.5	-0.03	16.2	-0.007 ***	0.0006 *	0.47	-3.7	14.61 ***
alpha 2	-0.04	16.3	-0.007 ***	0.0008 *	0.47	-3.6	14.56 ***
alpha 2.5	-0.05	16.4	-0.007 ***	0.0010 *	0.47	-3.4	14.52 ***
alpha 3	-0.06	16.5	-0.007 ***	0.0012 *	0.47	-3.3	14.48 ***
alpha 3.5	-0.07	16.5	-0.006 ***	0.0014 *	0.47	-3.3	14.46 ***
alpha 4	-0.08	16.6	-0.006 ***	0.0016 *	0.46	-3.2	14.44 ***
alpha 4.5	-0.09	16.6	-0.006 ***	0.0018 *	0.46	-3.1	14.42 ***
alpha 5	-0.10	16.6	-0.006 ***	0.0019 *	0.46	-3.1	14.41 ***

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, $^{n.s.}$ $p < 0.1$

Table 7. Number of forest species. Carabidae

Dispersal parameter	Model II.		Model III.			ANOVA
			distance	alfa*distance		
	regress. coeff.	AIC	regress. coeff.	regress. coeff.	AIC	F
alpha 0.5	0.003	-29.6	-0.0017	0.0001	-27.5	0.87
alpha 1	0.005	-29.7	-0.0015	0.0001	-27.5	0.85
alpha 1.5	0.008	-29.7	-0.0015	0.0001	-27.5	0.85
alpha 2	0.010	-29.7	-0.0014	0.0002	-27.5	0.84
alpha 2.5	0.013	-29.7	-0.0014	0.0002	-27.5	0.82
alpha 3	0.015	-29.7	-0.0014	0.0003	-27.4	0.80
alpha 3.5	0.017	-29.6	-0.0013	0.0003	-27.3	0.77
alpha 4	0.019	-29.6	-0.0013	0.0004	-27.2	0.74
alpha 4.5	0.020	-29.6	-0.0013	0.0004	-27.1	0.71
alpha 5	0.021	-29.5	-0.0012	0.0005	-27.0	0.68

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, $^{n.s.}$ $p < 0.1$

Table 8. Index of species richness for all of the species. Lepidoptera

Dispersal parameter	Model II.		Model III.			ANOVA
			distance	alfa*distance		
	regress. coeff.	AIC	regress. coeff.	regress. coeff.	AIC	F
alpha 0.5	-0.01	-32.2	-0.0022 $^{n.s.}$	0.0001	-34.6	3.15 $^{n.s.}$
alpha 1	-0.01	-32.1	-0.0021 $^{n.s.}$	0.0001	-34.7	3.21 *
alpha 1.5	-0.01	-32.1	-0.0020 $^{n.s.}$	0.0002	-34.7	3.23 *
alpha 2	-0.02	-32.0	-0.0020 $^{n.s.}$	0.0002	-34.6	3.27 *
alpha 2.5	-0.02	-31.9	-0.0020 $^{n.s.}$	0.0003	-34.6	3.32 *
alpha 3	-0.03	-31.7	-0.0019 $^{n.s.}$	0.0004	-34.6	3.39 *
alpha 3.5	-0.03	-31.6	-0.0019 $^{n.s.}$	0.0004	-34.6	3.45 *
alpha 4	-0.03	-31.4	-0.0019 $^{n.s.}$	0.0005	-34.6	3.52 *
alpha 4.5	-0.04	-31.3	-0.0019 $^{n.s.}$	0.0005	-34.5	3.57 *
alpha 5	-0.04	-31.2	-0.0018 $^{n.s.}$	0.0006	-34.5	3.62 *

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, $^{n.s.}$ $p < 0.1$

Table 9. Index of species richness for forest species. Lepidoptera

Dispersal parameter	Model II.		Model III.			ANOVA
			distance	alfa*distance		
	regress. coeff.	AIC	regress. coeff.	regress. coeff.	AIC	F
alpha 0.5	-0.001	-10.5	-0.0007	0.00001	-8.0	0.71
alpha 1	-0.002	-10.5	-0.0006	0.00001	-8.0	0.70
alpha 1.5	-0.003	-10.5	-0.0006	0.00001	-8.0	0.69
alpha 2	-0.004	-10.5	-0.0006	0.00001	-8.0	0.72
alpha 2.5	-0.003	-10.5	-0.0006	0.00001	-8.1	0.76
alpha 3	-0.002	-10.5	-0.0005	0.00000	-8.2	0.81
alpha 3.5	-0.001	-10.5	-0.0005	-0.00001	-8.3	0.87
alpha 4	0.001	-10.5	-0.0005	-0.00002	-8.4	0.92
alpha 4.5	0.003	-10.5	-0.0005	-0.00003	-8.5	0.96
alpha 5	0.005	-10.5	-0.0005	-0.00005	-8.6	1.00

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, $^{n.s.}$ $p < 0.1$

Table 10. Total number of species. Lepidoptera

Dispersal parameter	Model II.		Model III.					ANOVA	
			distance		alfa*distance				
	regress. coeff.	AIC	regress. coeff.		regress. coeff.	R^2	AIC	F	
alpha 0.5	-0.007	59.7	-0.0059	*	0.0002	0.20	52.8	5.63	**
alpha 1	-0.011	59.8	-0.0056	*	0.0003	0.20	52.6	5.75	**
alpha 1.5	-0.015	59.9	-0.0054	*	0.0004	0.20	52.6	5.84	**
alpha 2	-0.019	60.0	-0.0052	*	0.0005	0.20	52.5	5.94	**
alpha 2.5	-0.020	60.0	-0.0051	*	0.0007	0.21	52.4	6.05	**
alpha 3	-0.021	60.1	-0.0050	*	0.0008	0.21	52.2	6.15	**
alpha 3.5	-0.022	60.2	-0.0049	*	0.0009	0.21	52.1	6.24	**
alpha 4	-0.022	60.2	-0.0048	*	0.0009	0.21	52.0	6.31	**
alpha 4.5	-0.023	60.2	-0.0048	*	0.0010	0.21	52.0	6.37	**
alpha 5	-0.023	60.2	-0.0047	*	0.0011	0.21	51.9	6.41	**

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, $^{n.s.}$ $p < 0.1$

Table 11. Number of forest species. Lepidoptera

Dispersal parameter	Model II.		Model III.			ANOVA	
			distance	alfa*distance			
	regress. coeff.	AIC	regress. coeff.	regress. coeff.	AIC	F	
alpha 0.5	0.002	67.6	-0.0018	-0.00001	66.5	2.49	n.s.
alpha 1	0.004	67.6	-0.0018	-0.00002	66.5	2.45	n.s.
alpha 1.5	0.006	67.6	-0.0017	-0.00004	66.5	2.47	n.s.
alpha 2	0.010	67.6	-0.0016	-0.00008	66.3	2.54	n.s.
alpha 2.5	0.015	67.5	-0.0015	-0.00012	66.1	2.63	n.s.
alpha 3	0.021	67.5	-0.0015	-0.00017	65.9	2.71	n.s.
alpha 3.5	0.027	67.4	-0.0014	-0.00023	65.7	2.78	n.s.
alpha 4	0.034	67.4	-0.0014	-0.00028	65.6	2.83	n.s.
alpha 4.5	0.040	67.4	-0.0014	-0.00033	65.5	2.87	n.s.
alpha 5	0.045	67.4	-0.0013	-0.00038	65.4	2.89	n.s.

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, $^{n.s.}$ $p < 0.1$

Table 12. Index of species richness for all of the species. Araneae

Dispersal parameter	Model II.				Model III.			ANOVA
					distance	alfa*distance		
	regress. coeff.		R^2	AIC	regress. coeff.	regress. coeff.	AIC	F
alpha 0.5	0.01	n.s.	0.09	-26.9	-0.0014	0.0001	-24.0	0.51
alpha 1	0.02	*	0.10	-26.9	-0.0011	0.0001	-23.9	0.43
alpha 1.5	0.03	*	0.10	-27.0	-0.0009	0.0001	-23.8	0.37
alpha 2	0.03	*	0.10	-27.0	-0.0008	0.0002	-23.7	0.32
alpha 2.5	0.04	n.s.	0.09	-26.8	-0.0008	0.0002	-23.5	0.28
alpha 3	0.05	n.s.	0.09	-26.6	-0.0007	0.0002	-23.2	0.25
alpha 3.5	0.06	n.s.	0.09	-26.4	-0.0006	0.0003	-23.0	0.24
alpha 4	0.06	n.s.	0.08	-26.3	-0.0006	0.0003	-22.8	0.23
alpha 4.5	0.07	n.s.	0.08	-26.1	-0.0006	0.0003	-22.6	0.23
alpha 5	0.07	n.s.	0.08	-26.0	-0.0005	0.0004	-22.5	0.23

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, $^{n.s.}$ $p < 0.1$

Table 13. Index of species richness for forest species. Araneae

Dispersal parameter	Model II.		Model III.			ANOVA
			distance	alfa*distance		
	regress. coeff.	AIC	regress. coeff.	regress. coeff.	AIC	F
alpha 0.5	0.01	27.6	0.0039	-0.0001	26.5	2.46 n.s.
alpha 1	0.02	27.8	0.0037	-0.0002	26.4	2.58 n.s.
alpha 1.5	0.03	27.9	0.0037	-0.0003	26.4	2.66 n.s.
alpha 2	0.04	28.1	0.0037 n.s.	-0.0004	26.4	2.74 n.s.
alpha 2.5	0.05	28.3	0.0037 n.s.	-0.0006	26.5	2.82 n.s.
alpha 3	0.06	28.5	0.0036 n.s.	-0.0007	26.5	2.88 n.s.
alpha 3.5	0.07	28.6	0.0036 n.s.	-0.0008	26.6	2.94 n.s.
alpha 4	0.08	28.7	0.0036 n.s.	-0.0009	26.6	2.97 n.s.
alpha 4.5	0.08	28.8	0.0036 n.s.	-0.0010	26.6	3.00 n.s.
alpha 5	0.09	28.8	0.0035 n.s.	-0.0011	26.6	3.01 n.s.

*** p < 0.001, ** p < 0.01, * p < 0.05, n.s. p < 0.1

Table 14. Total number of species. Araneae

Dispersal parameter	Model II.		Model III.			ANOVA
			distance	alfa*distance		
	regress. coeff.	AIC	regress. coeff.	regress. coeff.	AIC	F
alpha 0.5	0.0001	-20.3	-0.0026 n.s.	0.0001 n.s.	-19.6	1.57
alpha 1	0.0007	-20.3	-0.0096 n.s.	0.0002 n.s.	-19.5	1.52
alpha 1.5	0.0019	-20.3	-0.0021 n.s.	0.0003	-19.4	1.45
alpha 2	0.0034	-20.3	-0.0020	0.0004	-19.3	1.40
alpha 2.5	0.0047	-20.3	-0.0020	0.0005	-19.3	1.36
alpha 3	0.0057	-20.3	-0.0019	0.0006	-19.2	1.35
alpha 3.5	0.0064	-20.3	-0.0019	0.0007	-19.2	1.34
alpha 4	0.0067	-20.3	-0.0018	0.0007	-19.2	1.35
alpha 4.5	0.0067	-20.3	-0.0018	0.0008	-19.2	1.36
alpha 5	0.0062	-20.3	-0.0018	0.0009	-19.3	1.38

*** p < 0.001, ** p < 0.01, * p < 0.05, n.s. p < 0.1

Table 15. Number of forest species. Araneae

Dispersal parameter	Model II.		Model III.			ANOVA
			distance	alfa*distance		
	regress. coeff.	AIC	regress. coeff.	regress. coeff.	AIC	F
alpha 0.5	0.001	6.1	0.00037	-0.00005	9.0	0.49
alpha 1	0.002	6.1	0.00019	-0.00007	9.0	0.48
alpha 1.5	0.004	6.1	0.00016	-0.00011	9.0	0.50
alpha 2	0.007	6.0	0.00015	-0.00015	8.9	0.52
alpha 2.5	0.009	6.0	0.00013	-0.00019	8.9	0.52
alpha 3	0.012	6.0	0.00010	-0.00022	8.9	0.52
alpha 3.5	0.013	6.0	0.00006	-0.00024	8.9	0.51
alpha 4	0.014	6.0	0.00003	-0.00026	8.9	0.49
alpha 4.5	0.015	6.0	0.00000	-0.00028	9.0	0.47
alpha 5	0.014	6.0	-0.00002	-0.00029	9.1	0.45

*** p < 0.001, ** p < 0.01, * p < 0.05, n.s. p < 0.1

3.2 Least-cost analyses

Least-cost distance analyses take into account the variability in the landscape matrix. However, results for least-cost analyses calculated from sampling point to all forest fragments (Tables 16-18) did not demonstrate a significance of matrix for studied taxa. The index of species richness for all of the species was significant for Carabidae and Araneae. In both taxa, the scenario sc_1_10, where resistance value was set to 1 for all landscape elements (it behaves as Euclidean distance), had high R^2 value. While considering second group of scenarios with different resistance values for various elements, the highest values was calculated for scenarios sc_2_01 and sc_2_02. These scenarios were very similar and are characterized by low resistance values of landscape elements.

The index of species richness for forest species was significant only for Araneae, with highest R^2 value for scenario sc_1_10. The results demonstrated that matrix was not an important indicator for them. According to the least-cost analyses, connectivity did not explain the number of species within fragments.

The results of least-cost analyses were partially consistent with the results of the Euclidean analyses (Model I and Model II) and supported the relevance of IFM models. In each model, the index of species richness for all of the species was significant for Carabidae and Araneae. In IFM Model I, results for index of species richness for forest species were also in concordance with least-cost model. However, compared to least-cost model, results of IFM Model I are significant also for index of species richness for all of the species of Lepidoptera, and for number of species of some taxa.

Table 16. Index of species richness for all of the species

Least-cost scenario	**Carabidae**			**Lepidoptera**		**Araneae**		
	regress. coeff.	**R^2**	**AIC**	**regress. coeff.**	**AIC**	**regress. coeff.**	**R^2**	**AIC**
sc_1_10	-0.012 *	0.14	23.0	-0.0044 $^{\text{n.s.}}$	-33.7	0.007 *	0.14	-28.8
sc_1_01	-0.013 *	0.14	23.1	-0.0046 $^{\text{n.s.}}$	-33.3	0.008 *	0.13	-28.6
sc_1_02	-0.014 *	0.14	23.2	-0.0047 $^{\text{n.s.}}$	-33.0	0.008 *	0.13	-28.3
sc_1_03	-0.015 *	0.14	23.3	-0.0048	-32.6	0.009 *	0.12	-28.1
sc_1_04	-0.016 *	0.14	23.4	-0.0049	-32.4	0.009 *	0.12	-27.8
sc_1_05	-0.017 *	0.13	23.5	-0.0050	-32.1	0.009 *	0.11	-27.6
sc_1_06	-0.018 *	0.13	23.6	-0.0051	-31.9	0.010 *	0.11	-27.4
sc_1_07	-0.019 *	0.13	23.7	-0.0051	-31.7	0.010 *	0.10	-27.2
sc_1_08	-0.020 *	0.13	23.8	-0.0051	-31.5	0.011 *	0.10	-27.0
sc_1_09	-0.021 *	0.13	23.8	-0.0051	-31.4	0.011 $^{\text{n.s.}}$	0.09	-26.8
sc_2_01	-0.015 *	0.15	22.9	-0.0049 $^{\text{n.s.}}$	-32.9	0.008 *	0.12	-28.2
sc_2_02	-0.015 *	0.15	22.6	-0.0051 $^{\text{n.s.}}$	-33.3	0.008 *	0.12	-28.1
sc_2_03	-0.016 *	0.15	22.7	-0.0051 $^{\text{n.s.}}$	-33.3	0.009 *	0.11	-27.7
sc_2_04	-0.017 *	0.14	23.1	-0.0052	-32.3	0.009 *	0.11	-27.4
sc_2_05	-0.018 *	0.15	22.6	-0.0054	-32.5	0.009 *	0.10	-27.3
sc_2_06	-0.017 *	0.14	23.0	-0.0052	-32.3	0.010 *	0.12	-28.1
sc_2_07	-0.018 *	0.14	23.4	-0.0052	-31.9	0.010 *	0.10	-27.2
sc_2_08	-0.020 *	0.14	23.3	-0.0054	-31.9	0.010 *	0.10	-27.0
sc_2_09	-0.019 *	0.14	23.2	-0.0053	-31.9	0.010 *	0.10	-27.0
sc_2_10	-0.019 *	0.15	22.9	-0.0054	-32.0	0.010 *	0.10	-27.0

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, $^{\text{n.s.}}$ $p < 0.1$

Table 17. Index of species richness for forest species.

Least-cost scenario	**Carabidae**		**Lepidoptera**		**Araneae**		
	regress. coeff.	**AIC**	**regress. coeff.**	**AIC**	**regress. coeff.**	**R^2**	**AIC**
sc_1_10	-0.0037	12.0	-0.0020	-11.0	0.012 *	0.11	25.3
sc_1_01	-0.0039	12.1	-0.0019	-10.8	0.013 *	0.10	25.7
sc_1_02	-0.0040	12.1	-0.0017	-10.7	0.013 $^{\text{n.s.}}$	0.09	26.1
sc_1_03	-0.0041	12.2	-0.0015	-10.6	0.014 $^{\text{n.s.}}$	0.08	26.5
sc_1_04	-0.0042	12.3	-0.0012	-10.6	0.014 $^{\text{n.s.}}$	0.08	26.8
sc_1_05	-0.0044	12.3	-0.0010	-10.5	0.014 $^{\text{n.s.}}$	0.07	27.1
sc_1_06	-0.0045	12.4	-0.0007	-10.5	0.015	0.06	27.4
sc_1_07	-0.0046	12.4	-0.0004	-10.5	0.015	0.06	27.7
sc_1_08	-0.0046	12.5	-0.0001	-10.5	0.015	0.05	27.9
sc_1_09	-0.0047	12.5	0.0002	-10.5	0.015	0.05	28.1
sc_2_01	-0.0045	12.0	-0.0016	-10.7	0.013 $^{\text{n.s.}}$	0.08	26.5
sc_2_02	-0.0046	12.0	-0.0018	-10.7	0.013 $^{\text{n.s.}}$	0.09	26.4
sc_2_03	-0.0047	12.0	-0.0015	-10.6	0.013 $^{\text{n.s.}}$	0.08	26.8
sc_2_04	-0.0049	12.2	-0.0010	-10.5	0.014	0.07	27.3
sc_2_05	-0.0051	12.1	-0.0012	-10.5	0.013	0.06	27.4
sc_2_06	-0.0049	12.2	-0.0010	-10.5	0.014	0.07	27.3
sc_2_07	-0.0047	12.3	-0.0006	-10.5	0.014	0.06	27.5
sc_2_08	-0.0052	12.3	-0.0005	-10.5	0.015	0.06	27.7
sc_2_09	-0.0050	12.3	-0.0006	-10.5	0.014	0.06	27.7
sc_2_10	-0.0054	12.2	-0.0007	-10.5	0.014	0.05	27.8

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, $^{\text{n.s.}}$ $p < 0.1$

Table 18. Total number of species.

Least-cost scenario	Carabidae		Lepidoptera		Araneae	
	regress. coeff.	AIC	regress. coeff.	AIC	regress. coeff.	AIC
sc_1_10	-0.007 n.s.	16.0	-0.006	59.0	0.0004	-20.3
sc_1_01	-0.008 n.s.	16.0	-0.006	59.2	0.0005	-20.3
sc_1_02	-0.008 n.s.	16.0	-0.006	59.4	0.0006	-20.3
sc_1_03	-0.009 n.s.	16.1	-0.006	59.6	0.0007	-20.3
sc_1_04	-0.010	16.2	-0.005	59.8	0.0009	-20.3
sc_1_05	-0.010	16.2	-0.005	59.9	0.0010	-20.4
sc_1_06	-0.011	16.3	-0.005	60.0	0.0012	-20.4
sc_1_07	-0.011	16.3	-0.004	60.1	0.0014	-20.4
sc_1_08	-0.012	16.4	-0.004	60.2	0.0016	-20.4
sc_1_09	-0.013	16.4	-0.003	60.2	0.0018	-20.4
sc_2_01	-0.009 n.s.	16.0	-0.006	59.5	0.0007	-20.3
sc_2_02	-0.009 n.s.	15.9	-0.007	59.4	0.0006	-20.3
sc_2_03	-0.009 n.s.	16.0	-0.006	59.6	0.0007	-20.3
sc_2_04	-0.011 n.s.	16.1	-0.006	59.9	0.0009	-20.3
sc_2_05	-0.010 n.s.	16.0	-0.006	59.8	0.0009	-20.3
sc_2_06	-0.011 n.s.	16.1	-0.005	59.9	0.0019	-20.5
sc_2_07	-0.011	16.2	-0.005	60.0	0.0012	-20.4
sc_2_08	-0.012	16.2	-0.005	60.1	0.0012	-20.4
sc_2_09	-0.012	16.2	-0.005	60.0	0.0012	-20.4
sc_2_10	-0.012	16.1	-0.005	60.0	0.0012	-20.4

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, n.s. $p < 0.1$

Table 19. Number of forest species.

Least-cost scenario	Carabidae		Lepidoptera		Araneae	
	regress. coeff.	AIC	regress. coeff.	AIC	regress. coeff.	AIC
sc_1_10	0.0017	-29.7	0.0001	67.6	0.001	6.1
sc_1_01	0.0018	-29.7	0.0007	67.6	0.001	6.0
sc_1_02	0.0020	-29.7	0.0015	67.6	0.002	6.0
sc_1_03	0.0021	-29.7	0.0023	67.5	0.002	6.0
sc_1_04	0.0022	-29.6	0.0033	67.5	0.003	5.9
sc_1_05	0.0024	-29.6	0.0042	67.4	0.003	5.9
sc_1_06	0.0026	-29.6	0.0052	67.3	0.004	5.8
sc_1_07	0.0027	-29.6	0.0063	67.2	0.004	5.7
sc_1_08	0.0029	-29.6	0.0074	67.1	0.005	5.7
sc_1_09	0.0030	-29.6	0.0085	67.0	0.006	5.6
sc_2_01	0.0021	-29.7	0.0020	67.6	0.002	5.9
sc_2_02	0.0022	-29.7	0.0014	67.6	0.002	6.0
sc_2_03	0.0023	-29.7	0.0025	67.5	0.002	5.9
sc_2_04	0.0026	-29.7	0.0041	67.4	0.003	5.9
sc_2_05	0.0026	-29.7	0.0037	67.5	0.003	5.8
sc_2_06	0.0026	-29.7	0.0042	67.4	0.005	5.6
sc_2_07	0.0027	-29.7	0.0054	67.3	0.004	5.8
sc_2_08	0.0029	-29.7	0.0060	67.3	0.004	5.8
sc_2_09	0.0028	-29.7	0.0057	67.3	0.004	5.8
sc_2_10	0.0029	-29.7	0.0054	67.3	0.004	5.8

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, n.s. $p < 0.1$

3.3 Analyses of selected species

Landscape connectivity is a significant factor for abundance of some of the studied species. From the non-forest species of Carabidae, connectivity is important for *Carabus cancellatus* and *Pseudoophonus rufipes* (Appendix 4), from forest species for *Abax parallelepipedus* and *Carabus glabratus* (Appendix 5). From the non-forest species of Araneae, connectivity is important for *Pardosa lugubris*, *Trochosa terricola*, *Tenuiphantes flavipes* and *Drassyllus villicus* (Appendix 6), from forest species for *Lepthyphantes flavipes* and *Panamomops affinis* (Appendix 7). In general, IFM Model I explains the connectivity better than least-cost models. For least-cost analyses, the highest R^2 value always appears for scenario sc_1_10 (with no differences between habitat and matrix) and for scenarios with the lowest friction of matrix (sc_1_01, sc_1_02). In case where both models are significant, IFM Model I shows overall higher R^2 than least-cost models.

3.4 Analyses of environmental variables

The environmental factors were tested by GLM, the order of factors was set from the lowest AIC by step by selection. GLM had Gaussian distribution of error variability. The model chose different significant environmental variables for each taxon (Table 20). As a result, in all tree taxonomic groups the most important variables were connected to the vegetation type and structure. Species were determined especially by local environment conditions, compared to global conditions. The species occurred in all fragments. For Carabidae, the model explained 96% (Table 21), for Lepidoptera 85% (Table 22), and for Araneae 45% (Table 23) of variability of response variable (index of species richness for all of the species).

Table 20. Environmental variables chosen by “step by selection” for models for Carabidae, Lepidoptera, and Araneae

Abbreviation	Description of environmental variables
alfa1_5	IFM connectivity calculated for alpha 1.5
alpha3_5	IFM connectivity calculated for alpha 3.5
area	area of fragment
azimuth	azimuth measured in the field
C_N_org	C:N ratio
coverage_E1	coverage of the herb layer (E1)
coverage_E2	coverage of the shrub layer (E2)
coverage_E3	coverage of the tree layer (E3)
distance_edge_1840	distance of the sampling point from edge of the fragment in 1840
distance_edge_recent	distance of the sampling point from recent edge of the fragment
open_45	canopy openness in the fragment with an angular height of 45°
openness	canopy openness – the proportion of uncovered pixels from the total area of hemispherical image (in%)
perimeter	perimeter of the fragment
sc_2_01	modeled least-cost scenario
species_number_E1	number of species in herb layer (E1)
species_number_E2	number of species in shrub layer (E2)
species_number_E3	number of species in tree layer (E3)
vegetation_type	vegetation type

Table 21. Analysis of deviance table for Carabidae. Used model is Gaussian, link is identity. Response variable is index of species richness for all of the species. Terms were added sequentially (first to last).

Environmental variables^{+}	Df	Deviance	Resid. Df	Resid. Dev.	F	
NULL			41	2.11		
vegetation type	7	1.03	34	1.08	14.98	***
poly(coverage_E3, 3)	3	0.33	31	0.74	11.26	**
poly(distance_edge_recent, 2)	2	0.21	29	0.53	10.87	**
poly(open_45, 3)	3	0.10	26	0.43	3.30	n.s.
poly(C_N_org, 3)	3	0.08	23	0.35	2.82	n.s.
poly(alpha3_5, 3)	3	0.06	20	0.29	1.93	
poly(perimeter, 2)	2	0.02	18	0.27	0.98	
poly(azimuth, 3)	3	0.02	15	0.25	0.74	
poly(coverage_E2, 3)	3	0.04	12	0.21	1.51	
poly(area, 2)	2	0.04	10	0.17	1.82	
distance_edge_1840	1	0.08	9	0.09	8.33	n.s.

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, $^{n.s.}$ $p < 0.1$, $^{+}$ *poly* is a polynomial function with a number of polynomials

Table 22. Analysis of deviance table for Lepidoptera. Used model is Gaussian, link is identity. Response variable is index of species richness for all of the species. Terms were added sequentially (first to last).

Environmental variables^{+}	**Df**	**Deviance**	**Resid. Df**	**Resid. Dev.**	**F**	
NULL			52	22.42		
vegetation type	7	7.50	45	14.92	6.19	***
coverage_E2	1	0.04	44	14.87	0.26	
poly(azimuth, 2)	2	1.79	42	13.08	5.17	*
poly(species_number_E2, 3)	3	2.75	39	10.33	5.30	**
poly(open_45, 3)	3	1.01	36	9.32	1.95	
slope	1	2.27	35	7.05	13.15	**
species_number_E1	1	0.84	34	6.21	4.84	*
species_number_E3	1	0.09	33	6.12	0.50	
openess	1	0.68	32	5.45	3.93	*
distance_edge_recent	1	0.33	31	5.12	1.91	
distance_edge_historical	1	0.19	30	4.93	1.08	
coverage_E1	1	0.08	29	4.85	0.48	
C_N_org	1	0.00	28	4.84	0.02	

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, $^{n.s.}$ $p < 0.1$, $^{+}$ *poly* is a polynomial function with a number of polynomials

Table 23. Analysis of deviance table for Araneae. Used model is Gaussian, link is identity. Response variable is index of species richness for all of the species. Terms were added sequentially (first to last).

Environmental variables^{+}	**Df**	**Deviance**	**Resid. Df**	**Resid. Dev.**	**F**	
NULL			40	4.08		
species_number_E1	1	0.46	39	3.62	6.00	*
poly(area, 3)	3	0.72	36	2.90	3.13	*
poly(sc_2_01, 3)	3	0.51	33	2.39	2.23	
poly(alfa1_5, 2)	2	0.05	31	2.33	0.35	
poly(coverage_E2, 2)	2	0.11	29	2.22	0.74	

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, $^{n.s.}$ $p < 0.1$, $^{+}$ *poly* is a polynomial function with a number of polynomials

4 DISCUSSION

Many previous studies have examined importance of connectivity for a specific species, but only a few analyses have focused on the importance of connectivity on the form of biotic communities and biodiversity indices. Similarly, much work has been done on testing connectivity between fragments without considering the importance of landscape matrix.

4.1 How connectivity influences biodiversity of species in fragments

My results suggest that connectivity is an important factor in explaining the spatial distribution of taxa. However, the importance of connectivity is different for each of the studied taxa. The only biodiversity index which constantly showed significant dependence on connectivity was species richness for all of the species of Carabidae and Araneae.

For the taxon Carabidae for index of species richness, results from Model I show variable data distribution for α, whereas data for Model II and least-cost model are all significant. Thus, the results demonstrate the importance of connectivity for Carabidae. However, it may also result from heterogeneity of studied taxon which contains species with different abilities of dispersion: brachypterous (e.g. *Carabus coriaceus*, *Molops elatus*), macropterous (e.g. *Pterostichus oblongopunctatus*, *Harpalus rufipalpis*), and polymorphic (e.g. *Notiophilus rufipes*, *Pterostichus melanarius*).

Results for Lepidoptera suggest that this taxon is rather sedentary. However, according to the known characteristics, Lepidoptera is a taxon with a good mobility. From studied taxa, Lepidoptera is the only herbivore group. These species are bound to woody species and a higher variability of them should lead to a higher biodiversity of Lepidoptera. In accordance with Tyralík (2012), if parameter α is higher the relative importance of the biggest fragments rises. The biggest fragments have higher species/area ratio (Cain 1938). Thus higher α gives higher weights to the biggest fragment which is the most important one for Lepidoptera because of the highest number of woody species. In this case, dispersal does not play a role, crucial is a simple area of fragment and a trophic relationship.

According to results, the studied taxon Araneae contains species which do not disperse for longer distances and are rather epigeic. Thus, the heterogeneity and local conditions of forest habitat are not crucial for them. Compared to the other studied taxa, connectivity is significant for index of species richness for forest species (Model I, least-cost scenario). In conclusion, connectivity partially explains the biodiversity of Araneae within fragments.

4.2 Is matrix important?

In my thesis, I utilized 2 different groups of models to test if matrix is important in movement of taxa from fragment to fragment. The Euclidean distance models (especially Model I) which do not distinguish differences in matrix explain the data with the highest significance. Results do not show considerable variance between IFM Model II for different α and least-cost distance analyses for different scenarios. In that sense, the models do not suggest that matrix is important for these taxa. Therefore, individuals can move through variable environments.

When comparing Model I and least-cost model for selected species of Carabidae and Araneae, Model I usually displays higher R^2 values. From least-cost analyses, the highest R^2 value always appears for scenario sc_1_10 (no differences in matrix). These results show that most of the species move through landscape without taking matrix into account.

When comparing the use of and least-cost models, the effectiveness of Euclidean models for invertebrate species in Bohemian Karst was much higher than for least-cost models. Preparation of the landscape data and modeling scenarios for least-cost analyses is complex and time consuming process with results not better than those using simple IFM models for Euclidean distance. As Ricketts (2001) concluded, matrix resistance and species response to it might be variable for different species. It should correspond to the way species read the environment (Adriaensen et al. 2003). The implementation of more sophisticated models is restrained by lack of essential data and deficiency of land cover data (Watts and Handley 2010). Consistent with other reviewed studies, least-cost models are still not commonly used (Schooley and Branch 2011) even though conclusions supported by least-cost analyses might be better than simple Euclidean distances (Chardon et al. 2003, Watts et al. 2010).

4.3 Heterogeneity of the environment

The results might be affected by heterogeneity on different levels which are not captured in the models. For models which count with biodiversity indices (species richness and number of species), there are two main sources of heterogeneity: (1) within fragments, and (2) within taxon (because of different movement abilities, foraging behavior etc.).

Connectivity indices are significant for Lepidoptera only in Model I. Model II, which considers only the Euclidean distance between two fragments, does not explain the data. Because Model I includes also the distance within inner environment of fragment, the results suggest that the inner heterogeneity of fragments may be important in restricting or facilitating the movement of individuals.

Landscape of Bohemian Karst is characterized by many heterogeneous fragments with variable size and distance from each other. In some cases, the distance from a sampling point to the nearest edge of the next fragment might include higher percentage of habitat comparing to matrix that species would have to cross (Figure 1). I did not integrate the potential heterogeneity and fragment quality into my models, however, some studies highlight its importance (Yamanaka et al. 2009, Dugong et al. 2011, Schooley and Branch 2011). For some species, the difference in quality of fragments is important or only a part of studied fragment might be suitable. Thus, Schooley and Branch (2011) suggest that fragment-weighted areas might better predict the dispersion of individuals and they should be included into IFM by substituting fragment areas with effected fragment areas.

Models which include environmental conditions explained more variability of the response variable (i.e. the index of species richness for all of the species) than those considering only connectivity. Step by selection for Carabidae and Lepidoptera did not include any connectivity metrics into the models. This suggests that environmental conditions alone are more important than connectivity for these taxa. While for Araneae, model contains also connectivity. One of the possible explanations could be that the species occurred almost everywhere in the fragments and thus the connectivity is not a crucial factor for biodiversity of the studied taxa. However, it is concordant with other studies that environmental conditions have moderately stronger impact than connectivity (Yamanaka et al. 2009, Ellis et al. 2010).

4.4 Conclusions

Results demonstrate that connectivity is a parameter which explains biodiversity but differently for each taxon. The studied taxa of invertebrates are able to move in the landscape independently on its matrix. Habitat quality and local environmental variables are more significant for biodiversity indices than landscape structure alone. However, connectivity partially clarifies the distribution of some species in the landscape. For further studies, I suggest to use the simple IFM model for Euclidean distance (Model I – from sampling point to the nearest edge of each forest fragment), because of its higher significance and lower sophistication.

Further a research of invertebrates in Bohemian Karst is needed to test the trends within least cost analyses. One of the possible approaches might be to adapt least-cost scenarios according to tendencies demonstrated in tables. In subsequent research of the studied area, I propose to study the importance of spatial heterogeneity of fragments on biodiversity of species with more detailed analyses of local environmental variables. Because in Euclidean distance analysis, parameter α is rather species-specific, I suggest studying each of the species separately and consequently group them according to similar α.

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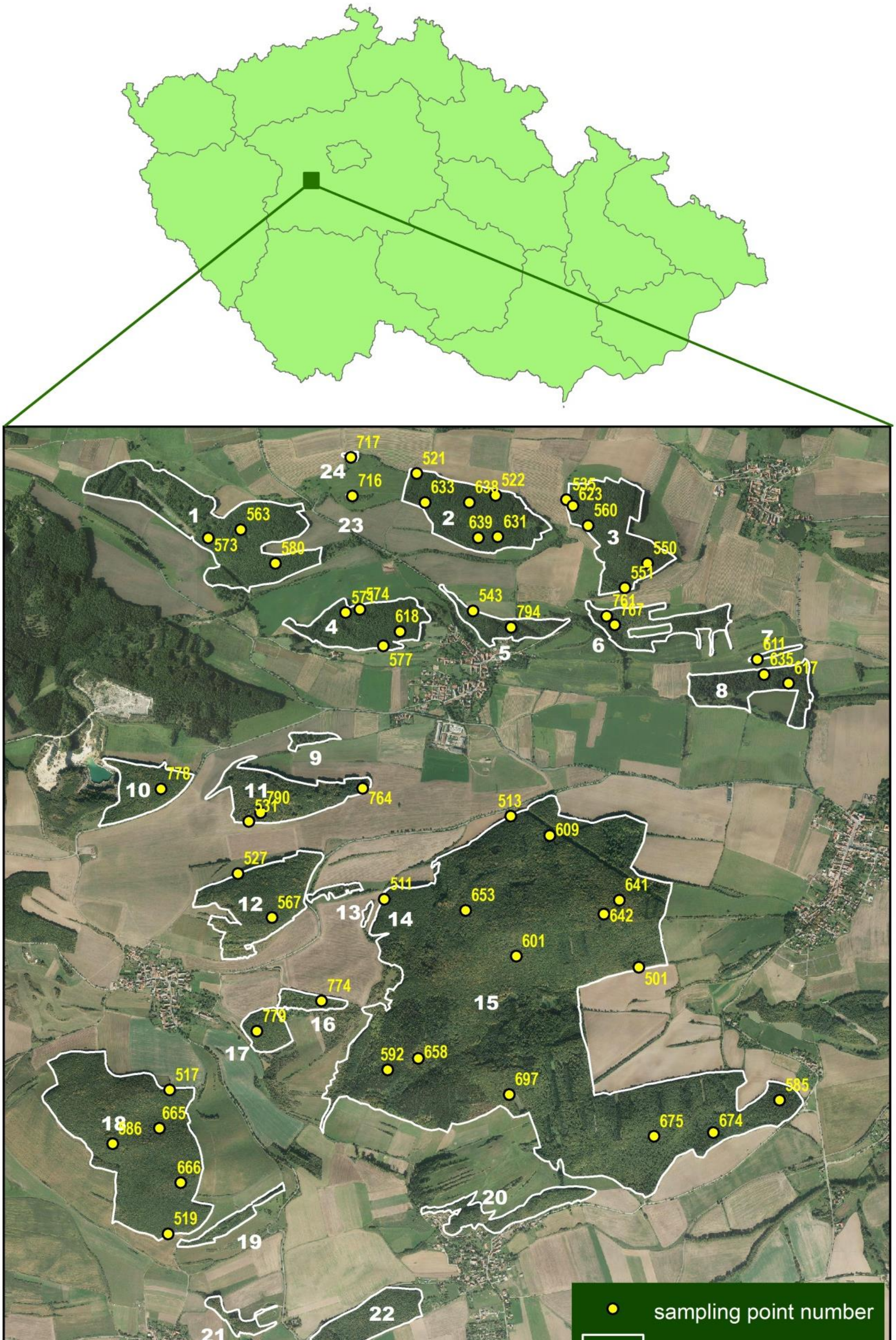
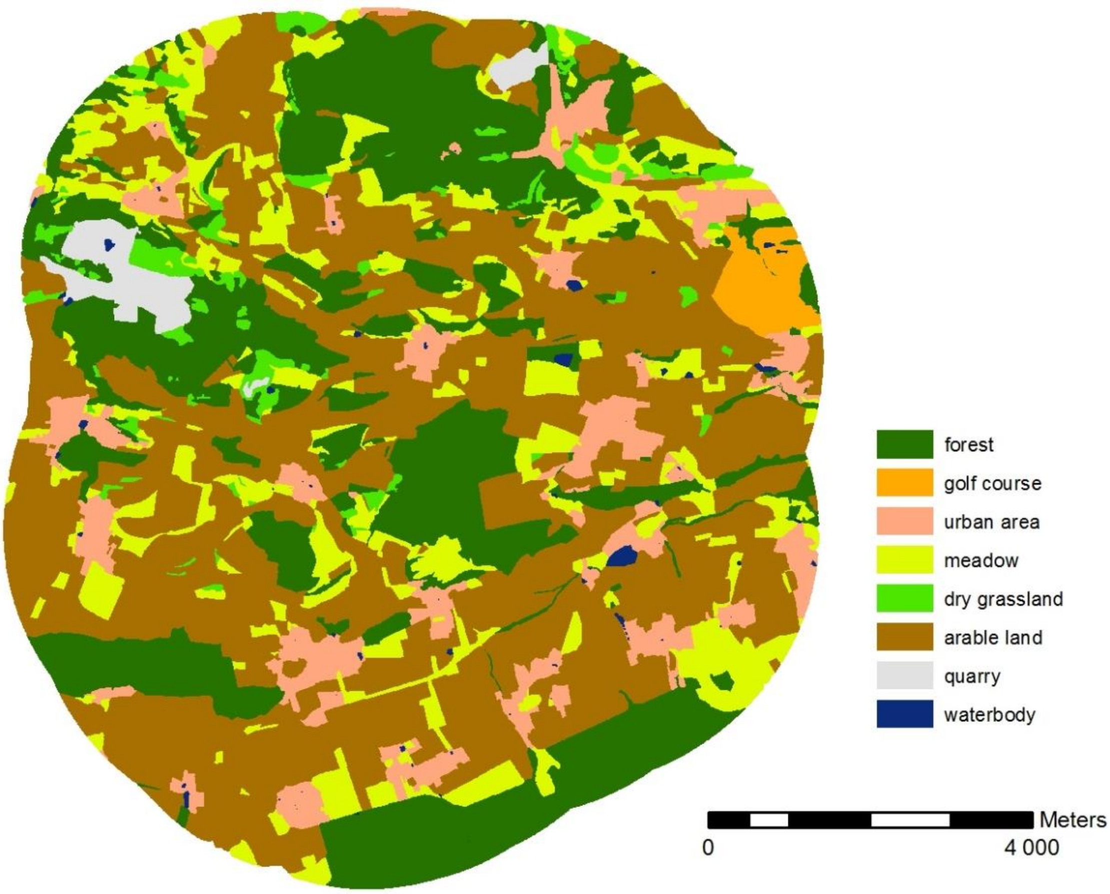
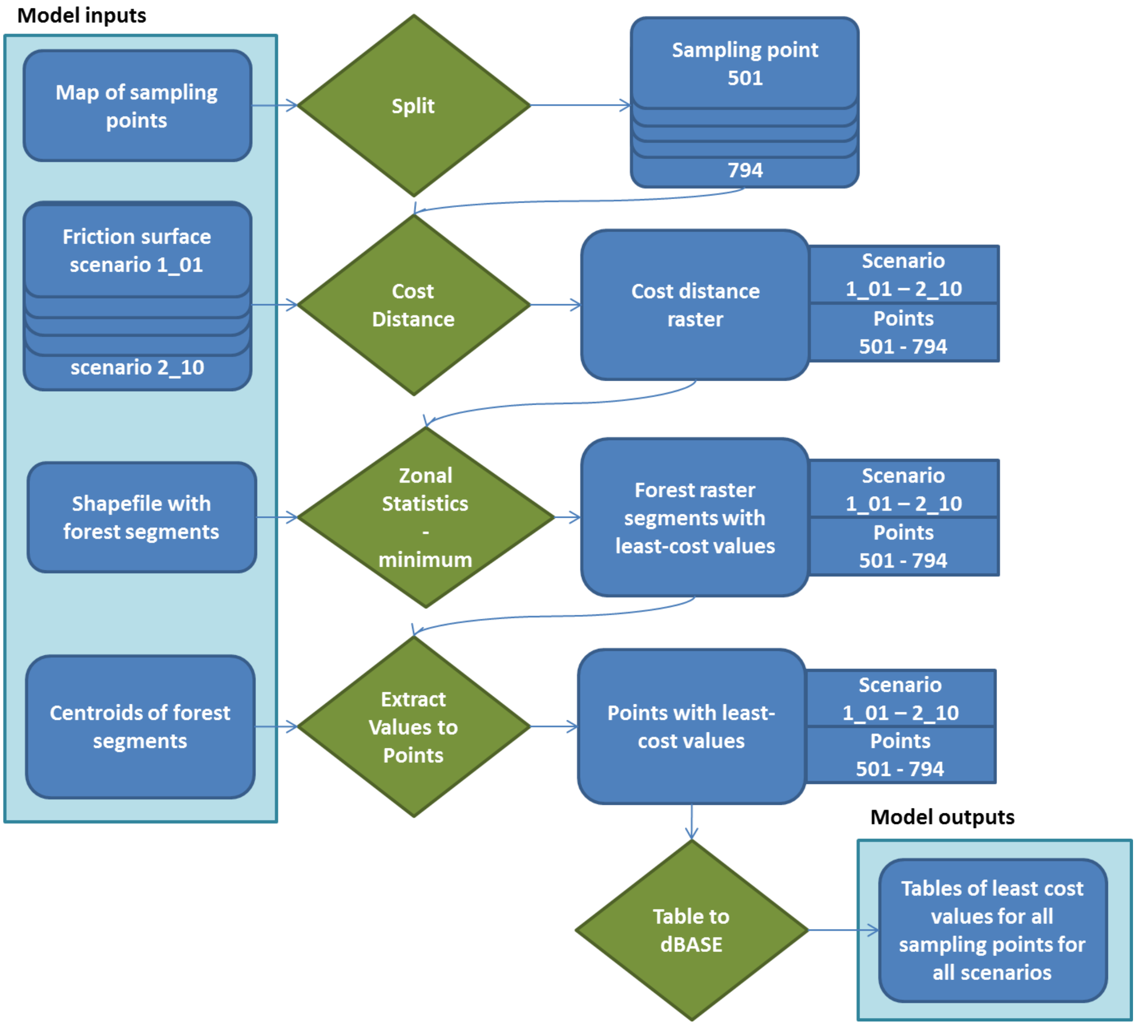
6 APPENDICES



Appendix 1. Scheme of studied area with numbers of fragments and sampling points (http://geoportal.cuzk.cz, http://www.diva-gis.org).



Appendix 2. Land cover



Appendix 3. Model for obtaining tables of least cost for all sampling points within each scenario.

Appendix 4. Dependence of connectivity on abundance of selected non-forest species of Carabidae.

Dispersal parameter	**Non-forest species**							
	Carabus cancellatus			***Abax parallelus***	***Pseudoophonus rufipes***			***Pterostichus burmeisteri***	***Carabus nemoralis***
	reg.coeff.		**R^2**	**reg.coeff.**	**reg.coeff.**		**R^2**	**reg.coeff.**	**reg.coeff.**
IFM Model I									
alpha 0.5	-0.08			0.01	-0.08			0.06	-0.85 n.s.
alpha 1	-0.13			0.01	-0.07			0.20	-0.04
alpha 1.5	0.18			-0.03	0.44			0.36	-0.11
alpha 2	0.77	n.s.		-0.10	1.25	n.s.		0.29	-0.15
alpha 2.5	1.26	*	0.10	-0.16	1.93	*	0.12	0.12	-0.16
alpha 3	1.66	*	0.13	-0.20	2.52	*	0.15	-0.03	-0.16
alpha 3.5	2.02	**	0.15	-0.25	3.05	**	0.16	-0.17	-0.16
alpha 4	2.33	**	0.15	-0.29	3.50	**	0.17	-0.29	-0.17
alpha 4.5	2.59	**	0.15	-0.34	3.88	**	0.17	-0.39	-0.18
alpha 5	2.81	**	0.14	-0.38	4.19	**	0.16	-0.48	-0.19
Least-cost scenario									
sc_1_01	-0.028	*	0.10	0.003	-0.025			0.014	-0.002
sc_1_02	-0.030	*	0.10	0.003	-0.026			0.014	-0.002
sc_1_03	-0.032	*	0.10	0.003	-0.027			0.014	-0.002
sc_1_04	-0.034	*	0.09	0.003	-0.028			0.013	-0.002
sc_1_05	-0.037	*	0.09	0.003	-0.029			0.013	-0.003
sc_1_06	-0.039	n.s.		0.004	-0.030			0.013	-0.003
sc_1_07	-0.041	n.s.		0.004	-0.031			0.013	-0.003
sc_1_08	-0.043	n.s.		0.004	-0.031			0.012	-0.003
sc_1_09	-0.045	n.s.		0.004	-0.032			0.012	-0.003
sc_1_10	-0.026	*	0.10	0.003	-0.023			0.013	-0.002
sc_2_01	-0.032	*	0.10	0.003	-0.027			0.014	-0.003
sc_2_02	-0.031	*	0.10	0.003	-0.027			0.015	-0.003
sc_2_03	-0.033	*	0.09	0.003	-0.027			0.014	-0.003
sc_2_04	-0.037	*	0.09	0.004	-0.030			0.014	-0.003
sc_2_05	-0.036	*	0.09	0.004	-0.029			0.014	-0.003
sc_2_06	-0.036	n.s.		0.003	-0.027			0.013	-0.004
sc_2_07	-0.040	n.s.		0.004	-0.030			0.013	-0.003
sc_2_08	-0.042	n.s.		0.004	-0.032			0.013	-0.003
sc_2_09	-0.041	n.s.		0.004	-0.031			0.013	-0.003
sc_2_10	-0.040	n.s.		0.004	-0.030			0.013	-0.003

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, n.s. $p < 0.1$

Appendix 5. Dependence of connectivity on abundance of selected forest species of Carabidae.

Dispersal parameter	*Carabus hortensis*	*Abax parallelepipedus*			*Brachinus crepitans*	*Carabus glabratus*			*Amara ovata*	
	reg.coeff.	reg.coeff.		R^2	reg.coeff.	reg.coeff.		R^2	reg.coeff.	
IFM Model I										
alpha 0.5	0.00	0.01			0.07	0.12	**	0.14	-0.07	
alpha 1	0.01	-0.02			0.27	0.30	*	0.09	-0.13	
alpha 1.5	0.08	-0.21	n.s.		0.64	0.26			0.02	
alpha 2	0.14	-0.42	*	0.10	0.97	-0.18			0.38	
alpha 2.5	0.14	-0.54	*	0.11	1.30	-0.61			0.68	
alpha 3	0.11	-0.61	*	0.11	1.70	-0.96	n.s.		0.91	
alpha 3.5	0.05	-0.68	*	0.10	2.13	-1.29	n.s.		1.12	
alpha 4	-0.03	-0.74	*	0.09	2.56	-1.60	*	0.08	1.30	
alpha 4.5	-0.13	-0.80	*	0.08	2.97	-1.92	*	0.09	1.45	
alpha 5	-0.25	-0.85	n.s.		3.36	-2.24	*	0.10	1.58	
Least-cost scenario										
sc_1_01	-0.0002	0.008	n.s.		0.018	0.031	**	0.17	-0.022	
sc_1_02	-0.0005	0.008			0.021	0.034	**	0.17	-0.023	
sc_1_03	-0.0009	0.008			0.023	0.036	**	0.17	-0.025	
sc_1_04	-0.0014	0.009			0.026	0.039	**	0.17	-0.026	
sc_1_05	-0.0018	0.009			0.029	0.042	**	0.17	-0.028	
sc_1_06	-0.0023	0.009			0.032	0.044	**	0.17	-0.029	
sc_1_07	-0.0028	0.010			0.034	0.047	**	0.17	-0.030	
sc_1_08	-0.0033	0.010			0.037	0.050	**	0.17	-0.032	
sc_1_09	-0.0039	0.010			0.041	0.053	**	0.17	-0.033	
sc_1_10	0.0001	0.007	n.s.		0.016	0.029	**	0.17	-0.020	n.s.
sc_2_01	0.0000	0.008			0.021	0.035	**	0.17	-0.024	
sc_2_02	0.0002	0.008			0.021	0.035	**	0.17	-0.024	
sc_2_03	-0.0001	0.009			0.023	0.037	**	0.16	-0.025	
sc_2_04	-0.0011	0.009			0.028	0.042	**	0.16	-0.028	
sc_2_05	-0.0003	0.009			0.027	0.040	**	0.16	-0.027	
sc_2_06	-0.0008	0.008			0.032	0.041	**	0.16	-0.025	
sc_2_07	-0.0021	0.010			0.032	0.045	**	0.17	-0.029	
sc_2_08	-0.0020	0.010			0.034	0.047	**	0.16	-0.031	
sc_2_09	-0.0020	0.010			0.033	0.046	**	0.17	-0.030	
sc_2_10	-0.0012	0.010			0.031	0.045	**	0.16	-0.029	

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, n.s. $p < 0.1$

Appendix 6. Dependence of connectivity on abundance of selected non-forest species of Araneae.

Dispersal parameter	**Non-forest species**														
	Pardosa lugubris			***Coelotes terrestris***		***Trochosa terricola***			***Tenuiphantes flavipes***			***Drassyllus villicus***		
	reg.coeff.		**R^2**	**reg.coeff.**		**reg.coeff.**		**R^2**	**reg.coeff.**		**R^2**	**reg.coeff.**		**R^2**
IFM Model I															
alpha 0.5	-0.05	n.s.		0.05		-0.13			0.13			-0.16	n.s.	
alpha 1	-0.09			0.15		-0.13			0.02			-0.29		
alpha 1.5	0.07			0.17		0.37			-1.04			-0.07		
alpha 2	0.37			-0.02		1.08	n.s.		-2.62	**	0.17	0.50		
alpha 2.5	0.62	*	0.11	-0.25		1.60	*	0.10	-3.67	**	0.23	0.97		
alpha 3	0.83	*	0.14	-0.45		2.02	*	0.11	-4.31	**	0.25	1.37		
alpha 3.5	1.02	**	0.17	-0.64		2.36	*	0.12	-4.91	**	0.26	1.72		
alpha 4	1.18	**	0.18	-0.81		2.63	*	0.12	-5.57	**	0.26	2.02	n.s.	
alpha 4.5	1.33	**	0.18	-0.98		2.83	*	0.11	-6.29	**	0.25	2.29	n.s.	
alpha 5	1.46	**	0.18	-1.13		2.97	*	0.10	-7.05	**	0.24	2.50	n.s.	
Least-cost scenario															
sc_1_01	-0.017	*	0.12	0.017	n.s.	-0.053	*	0.13	0.056	*	0.12	-0.06	*	0.17
sc_1_02	-0.018	*	0.11	0.017		-0.055	*	0.12	0.057	*	0.11	-0.07	*	0.16
sc_1_03	-0.019	*	0.11	0.018		-0.057	*	0.11	0.059	*	0.10	-0.07	*	0.16
sc_1_04	-0.019	*	0.10	0.018		-0.059	*	0.10	0.060	*	0.09	-0.08	*	0.15
sc_1_05	-0.020	n.s.		0.019		-0.060	*	0.09	0.061	n.s.		-0.08	*	0.14
sc_1_06	-0.020	n.s.		0.019		-0.061	n.s.		0.062	n.s.		-0.08	*	0.13
sc_1_07	-0.021	n.s.		0.019		-0.062	n.s.		0.063	n.s.		-0.09	*	0.13
sc_1_08	-0.021	n.s.		0.020		-0.062	n.s.		0.064			-0.09	*	0.12
sc_1_09	-0.022	n.s.		0.020		-0.062	n.s.		0.064			-0.09	*	0.11
sc_1_10	-0.016	*	0.13	0.016	n.s.	-0.050	*	0.14	0.054	*	0.13	-0.06	**	0.18
sc_2_01	-0.018	*	0.11	0.017		-0.057	*	0.11	0.057	*	0.10	-0.07	*	0.15
sc_2_02	-0.018	*	0.11	0.018		-0.056	*	0.12	0.059	*	0.11	-0.07	*	0.16
sc_2_03	-0.019	*	0.10	0.018		-0.057	*	0.10	0.058	*	0.09	-0.07	*	0.15
sc_2_04	-0.020	n.s.		0.019		-0.061	*	0.09	0.061	n.s.		-0.08	*	0.14
sc_2_05	-0.019	n.s.		0.018		-0.058	*	0.09	0.060	n.s.		-0.08	*	0.13
sc_2_06	-0.018	n.s.		0.017		-0.056	n.s.		0.057	n.s.		-0.08	*	0.14
sc_2_07	-0.020	n.s.		0.019		-0.062	n.s.		0.062	n.s.		-0.08	*	0.13
sc_2_08	-0.021	n.s.		0.020		-0.063	n.s.		0.064	n.s.		-0.09	*	0.12
sc_2_09	-0.021	n.s.		0.019		-0.062	n.s.		0.062	n.s.		-0.08	*	0.13
sc_2_10	-0.020	n.s.		0.019		-0.061	n.s.		0.061	n.s.		-0.08	*	0.12

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, n.s. $p < 0.1$

Appendix 7. Dependence of connectivity on abundance of selected forest species of Araneae.

Dispersal parameter	**Forest species**									
	Lepthyphantes flavipes			***Panamomops affinis***			***Zora nemoralis***	***Microneta viaria***	***Hahnia pusilla***	
	reg.coeff.		**R^2**	**reg.coeff.**		**R^2**	**reg.coeff.**	**reg.coeff.**	**reg.coeff.**	
IFM Model I										
alpha 0.5	-0.01			0.04			-0.02	0.01	0.08	
alpha 1	0.17			0.31			0.01	0.06	0.40	
alpha 1.5	0.78	*	0.07	1.02	**	0.14	0.16	0.20	1.01	n.s.
alpha 2	1.38	*	0.12	1.54	**	0.18	0.33	0.39	1.38	n.s.
alpha 2.5	1.81	**	0.14	1.83	**	0.17	0.45	0.56	1.56	
alpha 3	2.18	**	0.15	2.03	**	0.15	0.53	0.72	1.68	
alpha 3.5	2.52	**	0.15	2.16	*	0.13	0.60	0.87	1.75	
alpha 4	2.82	**	0.15	2.23	*	0.11	0.64	0.99	1.76	
alpha 4.5	3.07	**	0.14	2.24	*	0.09	0.66	1.08	1.71	
alpha 5	3.28	**	0.14	2.20	n.s.		0.66	1.14	1.60	
Least-cost scenario										
sc_1_01	-0.02			0.004			-0.011	-0.003	0.009	
sc_1_02	-0.02			0.006			-0.012	-0.002	0.012	
sc_1_03	-0.02			0.007			-0.012	-0.001	0.015	
sc_1_04	-0.02			0.009			0.013	0.000	0.018	
sc_1_05	-0.02			0.011			-0.013	0.002	0.022	
sc_1_06	-0.02			0.013			-0.013	0.003	0.026	
sc_1_07	-0.02			0.016			-0.014	0.004	0.030	
sc_1_08	-0.02			0.018			-0.014	0.005	0.034	
sc_1_09	-0.02			0.021			-0.014	0.007	0.038	
sc_1_10	-0.02			0.003			-0.011	-0.003	0.006	
sc_2_01	-0.02			0.007			-0.012	-0.001	0.014	
sc_2_02	-0.02			0.007			-0.012	-0.001	0.015	
sc_2_03	-0.02			0.009			-0.012	0.000	0.019	
sc_2_04	-0.02			0.011			-0.013	0.002	0.024	
sc_2_05	-0.02			0.012			-0.013	0.002	0.025	
sc_2_06	-0.02			0.012			-0.013	0.004	0.023	
sc_2_07	-0.02			0.014			-0.014	0.003	0.027	
sc_2_08	-0.02			0.016			-0.014	0.004	0.032	
sc_2_09	-0.02			0.015			-0.014	0.004	0.030	
sc_2_10	-0.02			0.015			-0.014	0.004	0.031	

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, $^{n.s.}$ $p < 0.1$