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Can landscape indices predict ecological processes consistently?

Lutz Tischendorf

*Ottawa-Carleton Institute of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, Canada K1S 5B6;
(Current address: Busestrasse 76, 28213 Bremen, Germany, E-mail: tischendorf@clavis-bremen.de)

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Abstract

The ecological interpretation of landscape patterns is one of the major objectives in landscape ecology. Both landscape patterns and ecological processes need to be quantified before statistical relationships between these variables can be examined. Landscape indices provide quantitative information about landscape pattern. Response variables or process rates quantify the outcome of ecological processes (e.g., dispersal success for landscape connectivity or Morisita's index for the spatial distribution of individuals). While the principal potential of this approach has been demonstrated in several studies, the robustness of the statistical relationships against variations in landscape structure or against variations of the ecological process itself has never been explicitly investigated. This paper investigates the consistency of correlations between a set of landscape indices (calculated with Fragstats) and three response variables from a simulated dispersal process across heterogeneous landscapes (cell immigration, dispersal success and search time) against variation in three experimental treatments (control variables): habitat amount, habitat fragmentation and dispersal behavior. I found strong correlations between some landscape indices and all three response variables. However, 68% of the statistical relationships were highly inconsistent and sometimes ambiguous for different landscape structures and for differences in dispersal behavior. Correlations between one landscape index and one response variable could range from highly positive to highly negative when derived from different spatial patterns. I furthermore compared correlation coefficients obtained from artificially generated (neutral) landscape models with those obtained from Landsat TM images. Both landscape representations produced equally strong and weak statistical relationships between landscape indices and response variables. This result supports the use of neutral landscape models in theoretical analyses of pattern-process relationships.

Introduction

Landscape ecology examines relationships between landscape patterns and ecological processes (Forman and Godron 1986; Turner 1989; Gustafson 1998). In order to quantify these relationships, we need to quantify both landscape patterns and ecological processes. Landscape patterns are quantified by landscape indices (e.g., contagion index). Ecological processes are measured by response variables (process rates), such as dispersal success or survival probability of populations. Statistical methods are then used to relate landscape indices and response variables to each

other. High correlation scores indicate that the corresponding landscape indices provide information about landscape patterns with particular importance to an ecological process. This information could then be used to manage landscape patterns with a predictable effect on ecological processes. This approach seems to have become common practice, supported by the increasing availability of remotely sensed landscape data, Geographic Information Systems and computer programs to calculate landscape indices. However, there are some major problems associated with the generalization of relationships between landscape patterns and ecological processes.

What are these problems and what do we already know about landscape indices? Our current knowledge about landscape indices is attributed to many studies conducted over the past two decades. We know that many commonly used landscape indices provide redundant information about spatial patterns (O'Neill et al. 1988; Riitters et al. 1995; Hargis et al. 1998; Giles and Trani 1999; Traub and Kleinn 1999). Factor analysis techniques have been used to reduce redundancy in the information provided by sets of landscape indices (e.g., McGarigal and McComb 1995; Riitters et al. 1995; Cain et al. 1997). Other studies revealed that some landscape indices provide ambiguous information about spatial patterns, i.e. one landscape index may have the same numerical value for different spatial patterns (Gustafson and Parker 1992; Hargis et al. 1998) (Figure 1). It has also been shown that landscape indices are sensitive to the spatial resolution (scale) at which they are calculated (Turner et al. 1991; Baker and Cai 1992; Cullinan and Thomas 1992; Plotnick et al. 1993; Leduc et al. 1994; Qi and Wu 1996; Cain et al. 1997; Nikora et al. 1999).

Landscape indices have been applied to compare heterogeneity between different landscapes (O'Neill et al. 1988; Hulshoff 1995; Skinner 1995; Garrabou et al. 1998; Pan et al. 1999; Trani and Giles 1999) and to predict response variables of ecological processes, such as dispersal success (Gustafson and Gardner 1996; Schumaker 1996), abundance (McGarigal and McComb 1995; Hamazaki 1996), distribution (With and Crist 1995; With et al. 1997) and survival probability (Fahrig 1997; Fahrig 1998) of species or populations in heterogeneous landscapes. Most of these studies revealed significant statistical relationships between some landscape indices and response variables, suggesting the general potential of landscape indices to predict ecological processes. However, relationships between landscape indices and response variables of ecological processes may be nonlinear (With and Crist 1995; Wiens et al. 1997), including thresholds at which ecological processes may change dramatically. For instance, the survival probability of a population may dramatically decrease after a certain proportion of habitat is removed from the landscape (Fahrig 1998).

To summarize, while landscape indices have been found to be statistically related to ecological processes, generalization of such relationships is problematic. Thresholds, nonlinearity, ambiguity and sensitivity to spatial resolution are associated with the use of landscape indices. Furthermore statistical relation-

ships are usually not based on the complete numerical range of a landscape index (i.e., not the whole spectrum of pattern variation is included in the analysis) and many statistical relationships are based on artificially generated landscape patterns, which must not necessarily represent realistic landscape patterns. Facing these problems, we need to identify how robust and consistent statistical relationships between landscape indices and response variables really are. We furthermore need to key out those landscape indices which provide the most consistent relationships with response variables.

The primary focus of this paper is to examine the consistency of correlations between 26 landscape indices and 3 response variables against variations in both landscape pattern and ecological process. This examination is based on simulating dispersal of four hypothetical species across a set of artificial (neutral) landscape models and across a set of realistic landscapes derived from Landsat TM images. Landscape indices for each landscape model were calculated by using the spatial pattern analysis program 'Fragstats' (McGarigal and Marks 1995). I simulated dispersal of hypothetical specialist and generalist species to vary the ecological process, i.e., a specialist's dispersal strategy is different from a generalist species. I measured three response variables that have been used to quantify the success of dispersal in heterogeneous landscapes: dispersal success (Schumaker 1996), search time (Doak et al. 1992; Ruckelshaus et al. 1997) and cell immigration (Tischendorf and Fahrig 2000).

The results provide answers to the following research questions. (1) What is the overall potential of the landscape indices to predict the response variables: dispersal success, search time and cell immigration? (2) How robust are the correlations between landscape indices and response variables against variation in (a) habitat amount, (b) habitat fragmentation, and (c) dispersal process (i.e. different disperser types)? (3) Are there general patterns in the variation of the correlations between landscape indices and response variables? (4) Can artificial model landscapes substitute for realistic landscapes in theoretical analyses?

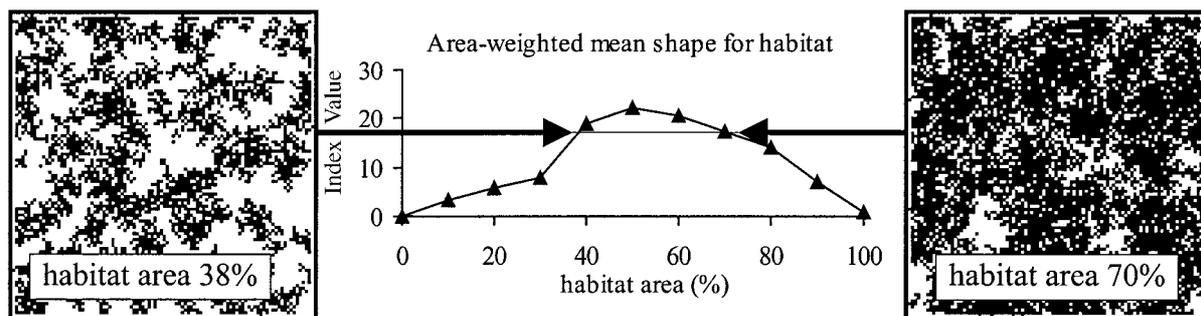


Figure 1. Relationship between the area-weighted mean shape index for habitat ($AWMSI_H$) and the habitat area (black area) in artificial landscape models. This relationship indicates that there is no one-to-one relationship between spatial pattern and the landscape index $AWMSI_H$. $AWMSI_H$ can have the same numerical value for patterns emerging from different proportions of habitat.

Methods

Experimental design – Overview

The experiment is based on simulating dispersal across two sets of heterogeneous, mosaic landscape models. The first set comprises artificially generated (neutral) landscape models. For the second set I used Landsat Thematic Mapper (TM) images. Landscape models in both sets were composed of three landcover types: habitat, hospitable matrix and inhospitable matrix. For each landscape model a set of landscape indices was calculated. I then simulated dispersal of four hypothetical species across each landscape model. For each simulation run I measured the success of dispersal by means of three different response variables: dispersal success, search time and cell immigration. Data analysis comprised the following steps. At first I pooled the data over all artificial landscape models and over all four hypothetical species and examined the statistical relationships between each landscape index and each response variable. In a second step I investigated these statistical relationships separately for each hypothetical species and for subsets of the artificial landscape models, e.g., for all landscapes with a certain habitat amount or habitat fragmentation. I used type III sums of squares to quantify the relative importance of habitat amount, habitat fragmentation and hypothetical disperser type to the variation in the statistical relationships between each landscape index and each response variable. Finally, I compared the statistical relationships obtained from simulations on artificial landscape models with those obtained from simulations on realistic (Landsat TM images) landscape models. I analyzed the conditions under which statistical relationships between landscape indices and

Table 1. Landscape parameters and their factorial combinations. H_{COV} is the proportion of the grid in habitat while HM_{COV} is the proportion in hospitable matrix. HM_{COV} can not exceed the difference between the total area and habitat amount. The factorial variation therefore depends on the actual habitat amount, i.e., $1-H_{COV}$. Fragmentation for habitat amount and hospitable matrix is controlled by H_{FRAG} and HM_{FRAG} respectively. All factorial combinations make up 1632 landscapes.

Parameter name	Range	Step	Variations
H_{COV}	0.1–0.8	0.1	8
H_{FRAG}	0.05–1	0.19	6
HM_{COV}	$0-(1-H_{COV})$	0.1	10, 9, ..., 3
HM_{FRAG}	0.05–1	0.19	6

response variables were similar to those obtained from realistic landscapes.

Landscape model

All landscape models were represented by a square grid of 40,000 cells. The state of each cell was defined by one of three landcover types: habitat (H), hospitable matrix (HM) and inhospitable matrix (IM). I created two sets of landscapes. One set was artificially generated by a placement algorithm, which assigned the three landcover types to cells of the grid. (Figure 2, Table 1, see also Fahrig 1997, 1998; Tischendorf and Fahrig in press). The second set of landscapes comprised 60 non-overlapping subsets (5 km × 5 km, i.e. 200 × 200 pixels of 25 m pixel size) of a Landsat Thematic Mapper (TM) image covering the St. Lawrence Region east of Lake Ontario in June 1993. I reclassified the processed image into three landcover types by combining forest and wetlands into habitat, agri-

cultural landuse classes into hospitable matrix, and urban land-use classes into inhospitable matrix. Four examples of these landscape models are shown in Figure 3. For all of the artificially generated and realistic landscape grids I combined adjacent (orthogonal and diagonal) cells of the same landcover type to patches. In the final landscapes each cell of the grid belongs to a single patch, which is defined by its cover type and an identification number.

Dispersal model

I developed an individual-based model to simulate dispersal of four hypothetical species across the landscape models. The four hypothetical species mimic dispersal behavior of specialist and generalist species. I associate specialist (or escape) dispersal behavior with faster movement and less convoluted movement patterns on matrix (e.g., Baars 1979; Rijnsdorp 1980; Wallin and Ekblom 1988; Wegner and Merriam 1990; Hansson 1991; Andreassen et al. 1996; Matter 1996; Charrier et al. 1997; Collins and Barrett 1997; Rosenberg et al. 1997), higher mortality risk on matrix (e.g., Lidicker 1975; Gaines and McGlenaghan 1980; Krohne and Dubbs 1984; Krohne and Burgin 1987; Garrett and Franklin 1988; Henein and Merriam 1990; Johansen 1994; Fahrig et al. 1995; Schippers et al. 1996; Charrier et al. 1997; Poole 1997; Sakai and Noon 1997; Bonnet et al. 1999), and low probability to cross boundaries from habitat to matrix (e.g., Mader 1984; Wiens et al. 1985; Bakowski and Kozakiewicz 1988; Merriam et al. 1989; Duelli et al. 1990; Mader et al. 1990; Frampton et al. 1995; Mauremooto et al. 1995; Charrier et al. 1997; Sakai and Noon 1997; Haddad 1999). I assume that generalist species show a less pronounced response to different landcover and boundary types. The generalist disperser types are therefore more likely to cross boundaries between habitat and matrix, experience lower mortality risk on matrix, and exhibit slower and less directed movement patterns on matrix. The parameter definitions and values of the four hypothetical disperser types on all landcover and boundary types are listed in Table 2.

Dispersal for each hypothetical species was described by three sets (one for each landcover type) of probabilistic movement, mortality and boundary crossing parameters. The actual value of these parameters depends on the individual's position within the landscapes. That is, movement pattern, mortality rates and boundary crossing probabilities vary among the

3 landcover and the 6 boundary types (Table 2). The position of each individual is defined by a pair of x , y coordinates, which allows for defining movement steps as vectors using two parameters: step length and step angle (Kareiva and Shigesada 1983; Turchin et al. 1991). Decision on mortality (per movement step) was made by comparing the current value of the mortality parameter (depending on the individual's position) with a random number between 0 and 1. If the random number was smaller than the parameter value, the individual 'died' and was deleted. When an individual encountered a boundary between two cover types, a random number between 0 and 1 was compared to the corresponding boundary crossing parameter (see Table 2) to determine whether the individual proceeds or returns into the previous patch. If the random number was smaller than the parameter value, boundary crossing was denied and the individual returned to the previous patch by reversing its movement direction.

Individuals perceived the landscape models as a torus (i.e., when individuals approached a landscape border, they reentered the landscape at the opposite border). This torus perception assumes that the region of interest is isolated from other regions, because there are no net losses or gains due to emigration from or immigration into the landscape (Haefner et al. 1991). The dispersal model is density independent (Gaines and McGlenaghan 1980; Krohne and Dubbs 1984).

Simulation

The experiment consisted of simulation runs of 1000 movement steps for each of 800 individuals across all artificial ($N = 1632$, see Table 1) and all realistic ($N = 60$, see above) landscape models. At the beginning of each simulation run individuals were randomly distributed across habitat area of the landscapes. Each simulation run was replicated ten times. Response variables (see below) were averaged over the ten replicate simulation runs and transformed into per capita rates (actual values divided by the number of simulated individuals, 800).

Landscape indices

I used the spatial pattern analysis program Fragstats (McGarigal and Marks 1995) to calculate a set of landscape indices for all artificial and realistic landscape models used in this experiment. Fragstats calculates landscape indices separately for (i) individual patches (patch-level indices), (ii) landcover types (class-level

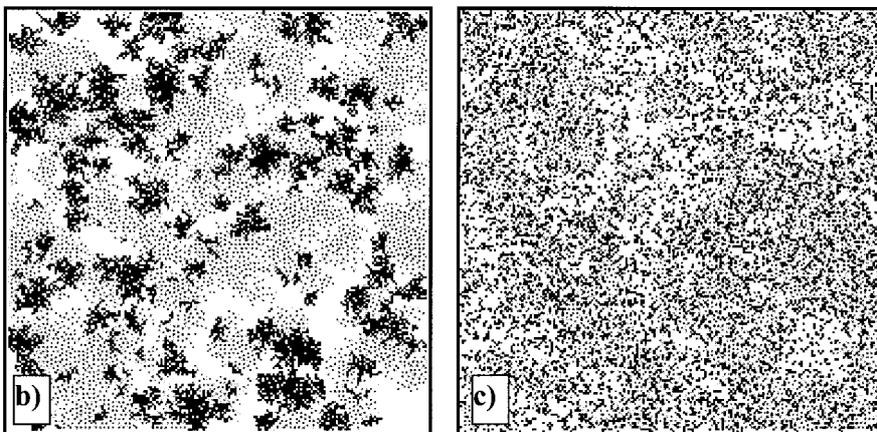
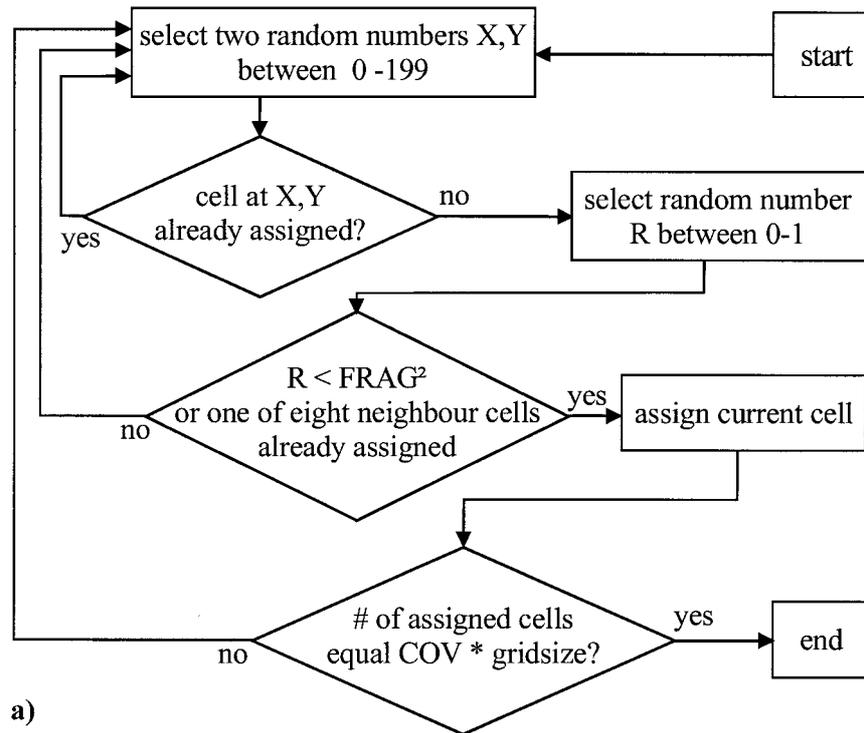


Figure 2. (a) Flow diagram of the placement algorithm used to assign first cover type habitat (H) and subsequently hospitable matrix (HM; see text) to cells of the grid. The algorithm is therefore executed twice and governed by two principal parameters: Cover (COV) and Fragmentation (FRAG). COV in the flow diagram stands for H_{COV} and HM_{COV} in Table 1. Equally, FRAG stands for H_{FRAG} and HM_{FRAG} in Table 1. We squared the value of FRAG within the algorithm to achieve a linear reduction of the number of patches with decreasing FRAG. (b) Small values of FRAG (near zero) prioritize assignment of H or HM adjacent to already assigned cells. This results in clumped patterns compared to a more fragmented distribution of H when FRAG is large, i.e., near 1 (c).

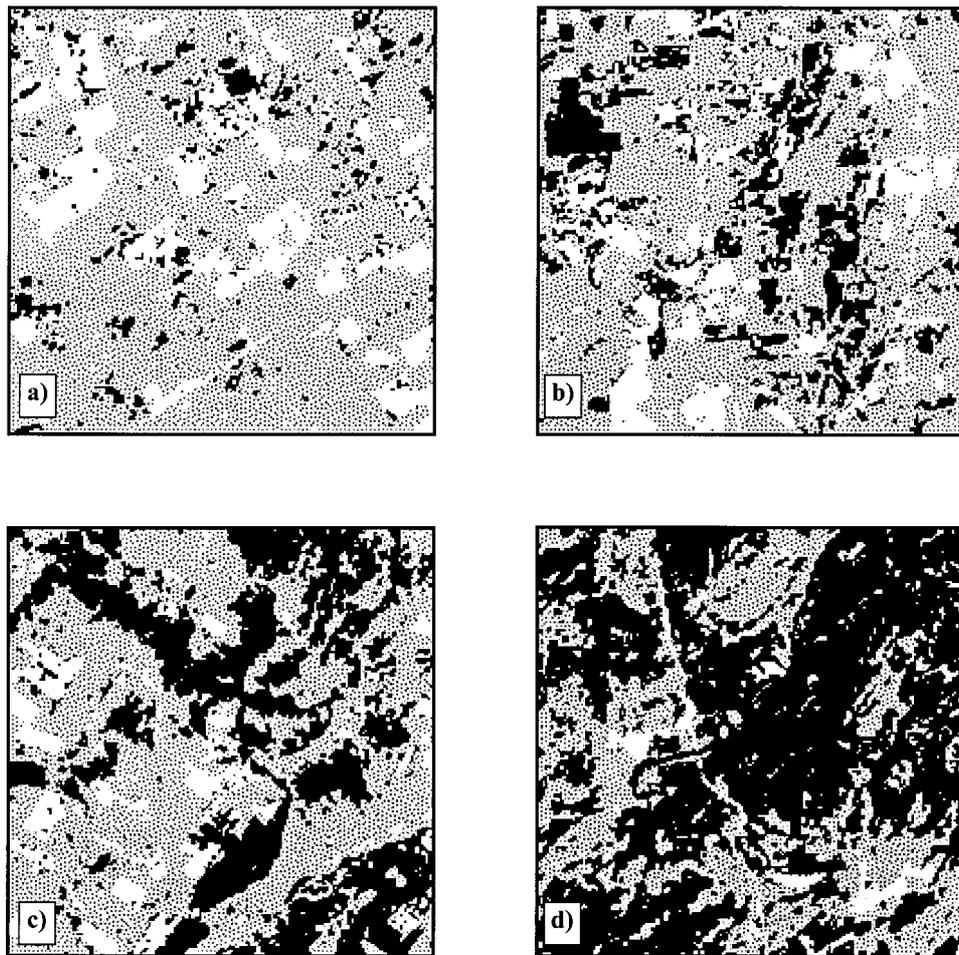


Figure 3. Sample landscapes as obtained from a Landsat TM image covering the St. Lawrence Region east of lake Ontario in June 1993. Black area corresponds with habitat (forest and wetlands), gray area is hospitable matrix (agricultural landuse), and white area corresponds to inhospitable matrix (urban landuse).

indices), and (iii) for the entire landscape (landscape-level indices). I selected a subset of landscape-level and (habitat) class-level indices out of the entire set of landscape indices calculated by Fragstats. I excluded those indices which were highly correlated ($r > 0.8$) (e.g., different versions of diversity and evenness indices) from the analysis. Variable names and descriptions for all landscape indices included in this analysis are listed in Table 3. A full explanation and mathematical formulas are provided elsewhere (McGarigal and Marks 1995). I furthermore calculated the habitat class-level index 'patch cohesion', which was introduced and related to dispersal success by Schumaker (1996), see also (Gustafson 1998).

Response variables

From the simulation runs I measured three response variables, which have been used to quantify the success of dispersing individuals across landscapes in simulation models: dispersal success (Schumaker 1996), search time (Doak et al. 1992; Ruckelshaus et al. 1997) and cell immigration (Tischendorf and Fahrig 2000). Although all three response variables refer to the same ecological process (dispersal across heterogeneous landscapes), they are differently related to the set of landscape indices used in this analysis. The comparison of these relationships will demonstrate the importance of quantifying ecological processes consistently to achieve general insights

Table 2. Each disperser type is defined by a set of parameters defining its dispersal characteristics in each of the three different cover types in the landscape model. Step length is the expected value of a negative exponential distribution. Step angle is drawn from a uniform probability distribution. Boundary crossing probability defines the probability that an individual crosses that boundary type on each encounter.

Disperser type	Parameters	Cover type		
		Habitat (H)	Hospitable matrix (HM)	Inhospitable matrix (IM)
Extreme specialist 'es'	mortality (rate per 1000 movement steps)	0.1	0.5	1
	step length	1	3	5
	step angle	$\pm 180^\circ$	$\pm 45^\circ$	$\pm 5^\circ$
	boundary crossing probability	H \rightarrow HM: 0.3 H \rightarrow IM: 0.1	HM \rightarrow H: 1 HM \rightarrow H: 0.2	IM \rightarrow H: 1 IM \rightarrow HM: 1
Moderate specialist 'ms'	mortality (rate per 1000 movement steps)	0.1	0.4	0.8
	step length	1	2	4
	step angle	$\pm 180^\circ$	$\pm 90^\circ$	$\pm 45^\circ$
	boundary crossing probability	H \rightarrow HM: 0.5 H \rightarrow IM: 0.3	HM \rightarrow H: 1 HM \rightarrow IM: 3	IM \rightarrow H: 1 IM \rightarrow HM: 1
Moderate generalist 'mg'	mortality (rate per 1000 movement steps)	0.1	0.3	0.6
	step length	1	1	3
	step angle	$\pm 180^\circ$	$\pm 135^\circ$	$\pm 45^\circ$
	boundary crossing probability	H \rightarrow HM: 0.7 H \rightarrow IM: 0.5	HM \rightarrow H: 1 HM \rightarrow IM: 0.5	IM \rightarrow H: 1 IM \rightarrow HM: 1
Extreme generalist 'eg'	mortality (rate per 1000 movement steps)	0.1	0.2	0.5
	step length	1	1	2
	step angle	$\pm 180^\circ$	$\pm 180^\circ$	$\pm 135^\circ$
	boundary crossing probability	H \rightarrow HM: 0.9 H \rightarrow IM: 0.7	HM \rightarrow H: 1 HM \rightarrow IM: 0.7	IM \rightarrow H: 1 IM \rightarrow HM: 1

into the effects of landscape patterns on ecological processes.

Dispersal success is the total number of immigration events of all individuals into all habitat patches. An immigration event is the first entry of an individual into a habitat patch not previously visited. In other words, dispersal success was incremented by one when an individual entered a new (not yet visited) habitat patch during the simulation run. Individuals were allowed to return into previously visited habitat patches. This did not, however, contribute to incrementing dispersal success.

Search time corresponds to the average number of movement (time) steps individuals needed to move between any two habitat patches. I quantified search time as the average number of steps taken by individuals

who successfully dispersed between any two habitat patches.

Cell immigration quantifies the number of immigration events into habitat grid cells (e.g. equally sized territories). Similar to the measurement of dispersal success, only the first entry of an individual into a habitat grid cell is counted as immigration event for that individual. Any subsequent return into a previously visited habitat grid cell does not contribute to cell immigration. This response variable is sensitive to movement within and between habitat patches, since a habitat patch is composed of habitat grid cells.

Data analysis

I conducted simple linear regression analyses between landscape indices (Table 3) and three response vari-

Table 3. Landscape indices used in the analysis. I excluded highly redundant landscape indices (i.e., $r > 0.8$) from the entire set of landscape indices calculated by Fragstats. The numerical ranges (min and max) were obtained from the values of all artificial (1632) model landscapes and from all 60 realistic (GIS) landscapes.

Abbreviation	Description	Artificial landscapes		Realistic landscapes	
		Min	Max	Min	Max
<i>landscape-level indices</i>					
LPI (%)	largest patch index	2.75	90	12.86	71.94
NP	number of patches	145	5909	403	1061
MPS (cells)	mean patch size	10	300	40	990
PSCV (%)	patch size coefficient of variation	354	5761.4	628.61	1771.2
TE (cell edges)	total edge between all landcover types	7381	52744	7430	16919
AWMSI	area-weighted mean shape index	6.4	69.37	4.78	11.98
DFLD	double log fractal dimension	1.6	1.77	1.318	1.414
AWMPFD	area-weighted mean patch fractal dimension	1.46	1.85	1.392	1.503
MNN (cell edges)	mean nearest-neighbor distance	1	3.66	1.626	3.14
NNCV (%)	nearest-neighbor coefficient of variation	0	136.53	64.5	108.35
SIDI	Simpson's diversity index	0.18	0.66	0.41	0.67
IJI (%)	interspersion and juxtaposition index	54.57	99.99	55.54	99.88
CONTAG (%)	contagion index	0	58.39	21.97	51.3
<i>habitat class-level indices</i>					
CA _H (%)	habitat area	10	80	7.25	68
LPI _H (%)	largest habitat patch index	0.02	80	0.45	56.78
NP _H	number of habitat patches	1	3006	101	507
MPS _H (cells)	mean habitat patch size	2	32000	8	269
PSCV _H (%)	habitat patch size coefficient of variation	0	1755.3	201.5	1290.8
TE _H	total habitat edge	7272	40208	4280	12450
AWMSI _H	area-weighted mean shape for habitat	1.22	69.55	1.57	10.24
DLFD _H	habitat related double log fractal dimension	0	1.92	1.299	1.44
AWMPFD _H	area-weighted mean habitat patch fractal dimension	1.315	1.85	1.259	1.491
MNN _H	mean nearest-neighbor distances between	0	9.055	1.354	3.559
(cell edges)	habitat patches				
NNCV _H (%)	coefficient of variation for nearest-neighbor distances between habitat patches	0	147.43	49.44	98.24
IJI _H (%)	habitat related juxtaposition and interspersion index	26.8	100	42.1	99.87
PCOH _H	patch cohesion (see Schumaker 1996)	0	1	0.755	1

ables (see above). In a first step I pooled data obtained from simulations on all artificial landscape models and all disperser types and calculated the Pearson product-moment correlation coefficients between each landscape index and each response variable.

In a second step I conducted ANCOVA's (SAS Institute 1990) to test for differences in the slopes of the regression lines (between each landscape index and each response variable) at different values of three control (class) variables: habitat amount, habitat fragmentation, and disperser type. Differences between slopes of the regression lines at different values of the

control variables are indicated by significant effects of the interaction terms (landscape index vs. control variable) in the statistical models.

Based on the ANCOVA results, I calculated Pearson product-moment correlation coefficients between all landscape indices and all three response variables separately for each value of the three control variables (habitat amount, habitat fragmentation, disperser type). For instance, correlation coefficients were calculated separately for 8 values of habitat amount (e.g. 10, 20, ..., 80%), for 6 values of habitat fragmentation and for 4 disperser types (192 correlation

coefficients altogether). From these sets of correlation coefficients I extracted the minimum and maximum values to identify the overall range of possible correlations values.

Finally, I compared the statistical relationships between landscape indices and response variables for the realistic landscape models (landsat TM images) and a subset of the artificial landscape models. The subset comprised those artificial landscape models whose habitat patterns were similar to the realistic landscapes with respect to the range of habitat amount and the range of the mean patch sizes. I included only artificial landscape models with habitat amounts up to 70% (maximum $H_{COV} = 0.7$, see Table 1 and Table 3) and with low habitat fragmentation ($H_{FRAG} = 0.05, 0.24$) in this analysis. These settings produced landscape patterns similar to the realistic landscapes. The correlation coefficients were obtained for the extreme specialist disperser type only, because the specialist disperser type produced the highest correlation scores and allowed for a better comparison.

Results

Overall pattern-process relationships

The overall Pearson product-moment correlation coefficients between all landscape indices and all three response variables are shown in the Figures 4a, 5a and 6a. Dispersal success (Figure 4a) was strongly correlated with patch cohesion ($PCOH_H$), number of habitat patches (NP_H) and area weighted mean versions of both shape index ($AWMSI_H$) and patch fractal dimension ($AWMPFD_H$). Search time (Figure 5a) was highly correlated with the habitat class-level nearest-neighbor indices (MNN_H and $NNCV_H$) as well as habitat edge (TE_H). Cell immigration (Figure 6a) elicited strong correlations with the habitat class-level indices: mean nearest-neighbor distance and its coefficient of variation (MNN_H and $NNCV_H$ respectively), habitat edge (TE_H) and habitat amount (CA_H). In general, habitat class-level indices were often better correlated to the response variables than their landscape-level counterparts.

Consistency

I tested the robustness of the overall correlation coefficients against variations in habitat amount, habitat fragmentation and dispersal behavior. This was achieved by examining the interaction effects between

each landscape index and three control (class) variables: habitat amount, habitat fragmentation and disperser type on each of the three response variables. For example, a significant interaction effect between the landscape index LPI and the control variable habitat amount on the response variable cell immigration indicates different slopes of the regression lines between LPI and cell immigration for different values (levels) of habitat amount. The results of the ANCOVA's revealed that all possible interaction effects (i.e., all landscape indices vs. all control variables on all three response variables) are significant at $p < 0.001$. Consequently, statistical relationships between all examined landscape indices and all three response variables depend on the actual values of habitat amount, habitat fragmentation and disperser type. The relative importance of these interaction effects corresponds directly to their type III sums of square values in the statistical models. Higher type III sums of square values indicate stronger interaction effects. The actual type III sums of square values are comparable within one statistical model, but not necessarily between two or more statistical models. I therefore transformed the actual type III sums of square values into proportions, which are shown in Figures 4b, 5b and 6b. Figure 4b shows that habitat amount accounts for most of the variations in the relationships between landscape indices and dispersal success. These relationships are otherwise quite robust against variations in habitat fragmentation and dispersal behavior. However, correlations between the two habitat class-level indices NP_H and $NNCV_H$ and dispersal success are most sensitive to disperser type and habitat fragmentation respectively. Correlations between landscape indices and search time (Figure 5b) depend mostly on habitat fragmentation. However, type III sums of square values were highest for interactions with habitat amount (e.g., LPI_H , MPS_H) and disperser type (MNN_H). Finally, relationships between landscape indices and cell immigration (Figure 6b) vary mainly with habitat amount and between disperser types. Type III sums of square values were lowest for most interaction effects between landscape indices and habitat fragmentation.

I was also interested in the absolute variations of the correlation coefficients. I calculated correlation coefficients between all landscape indices and all three response variables separately for each value (level) of each control variable (see section 'data analysis' above). From these sets of correlation coefficients I extracted the minima and maxima, which bound the error bars in Figures 4a, 5a and 6a. For most of

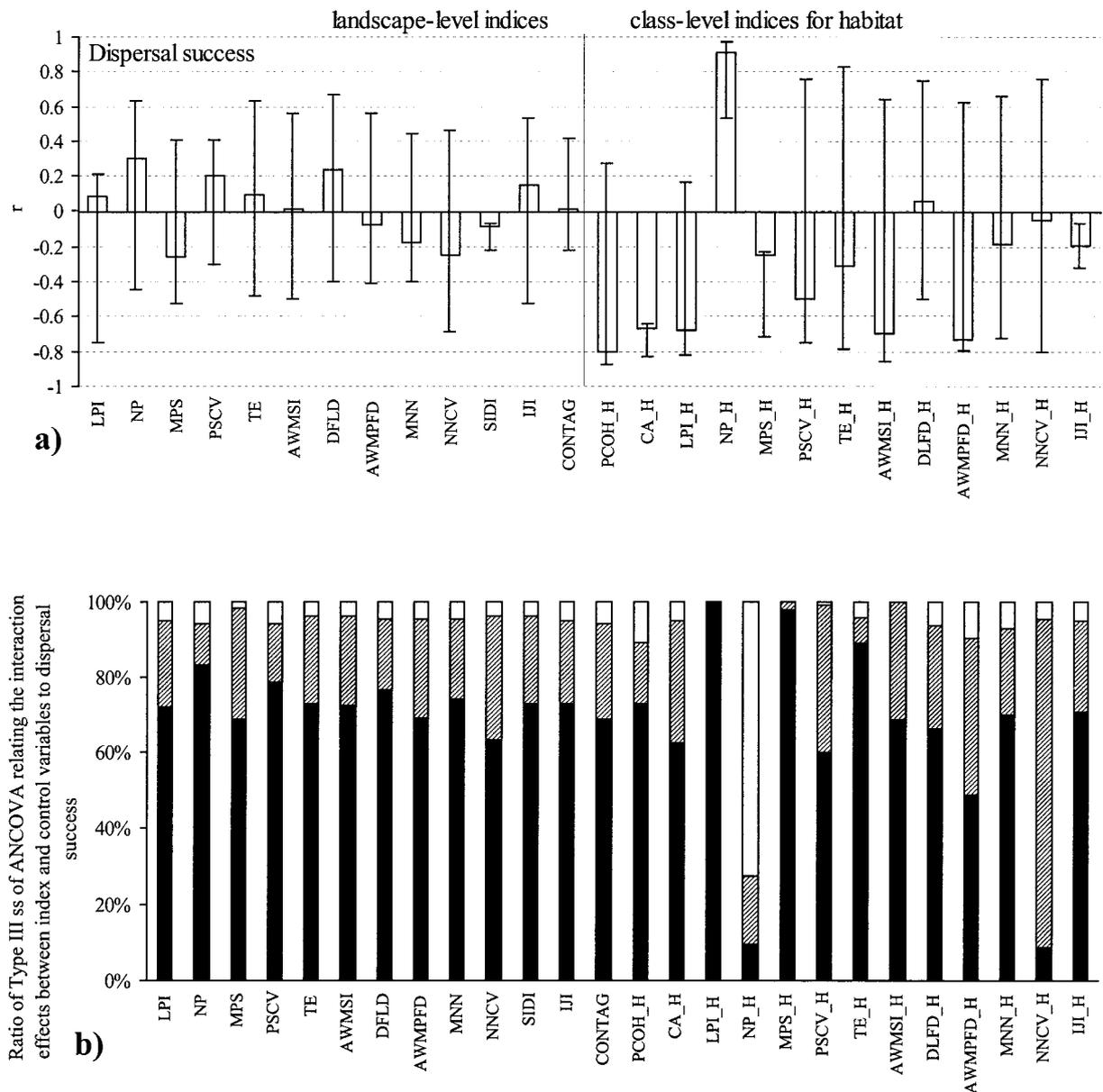


Figure 4. (a) Bars show the values of the Pearson product-moment correlation coefficients between landscape indices and the response variable 'Dispersal success' pooled over all 1632 model landscapes (see Table 1) and all 4 disperser types (see Table 2). The error bars indicate minimum and maximum correlation coefficients when calculated separately for each level of the control variables (i.e., habitat amount, habitat fragmentation and disperser type, see text). (b) Ratio of the type III sums of square values of a statistical model relating the interaction effects between landscape indices and habitat amount (black bar), habitat fragmentation (striped bar) as well as disperser type (white bar) to the response variable 'Dispersal success' (see text for further explanation). The proportion (lengths of a colored bar) corresponds with the relative importance of this interaction effect after controlling for the other two interaction effects.

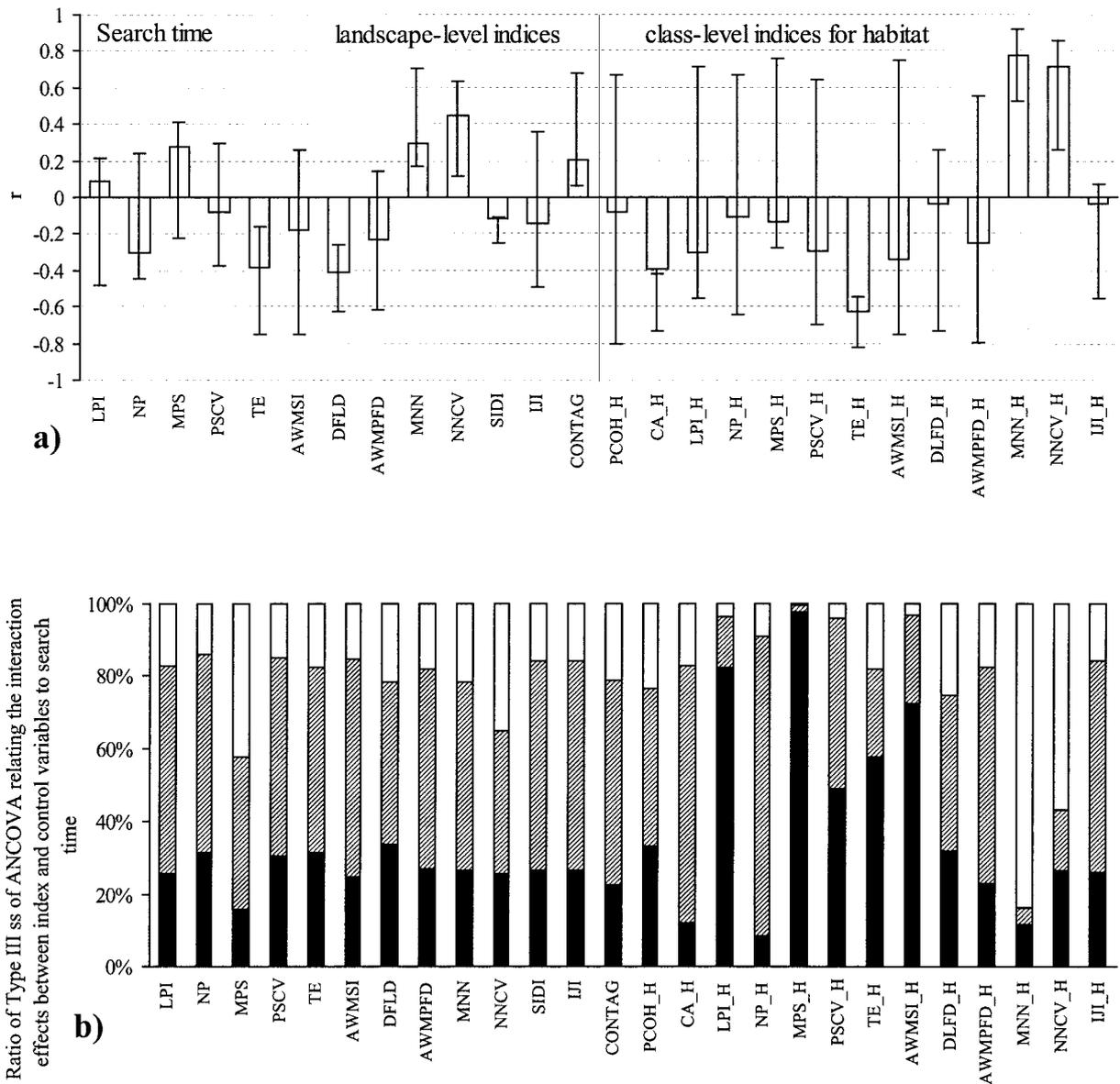


Figure 5. (a) Bars show the values of the Pearson product-moment correlation coefficients between landscape indices and the response variable ‘Search time’ pooled over all 1632 model landscapes (see Table 1) and all 4 disperser types (see Table 2). The error bars indicate minimum and maximum correlation coefficients when obtained separately for each level of the control variables (i.e. habitat amount, habitat fragmentation and disperser type, see text). (b) Ratio of the type III sums of square values of a statistical model relating the interaction effects between landscape indices and habitat amount (black bar), habitat fragmentation (striped bar) as well as disperser type (white bar) to the response variable ‘Search time’ (see text for further explanation). The proportion (lengths of a colored bar) corresponds with the relative importance of this interaction effect after controlling for the other two interaction effects.

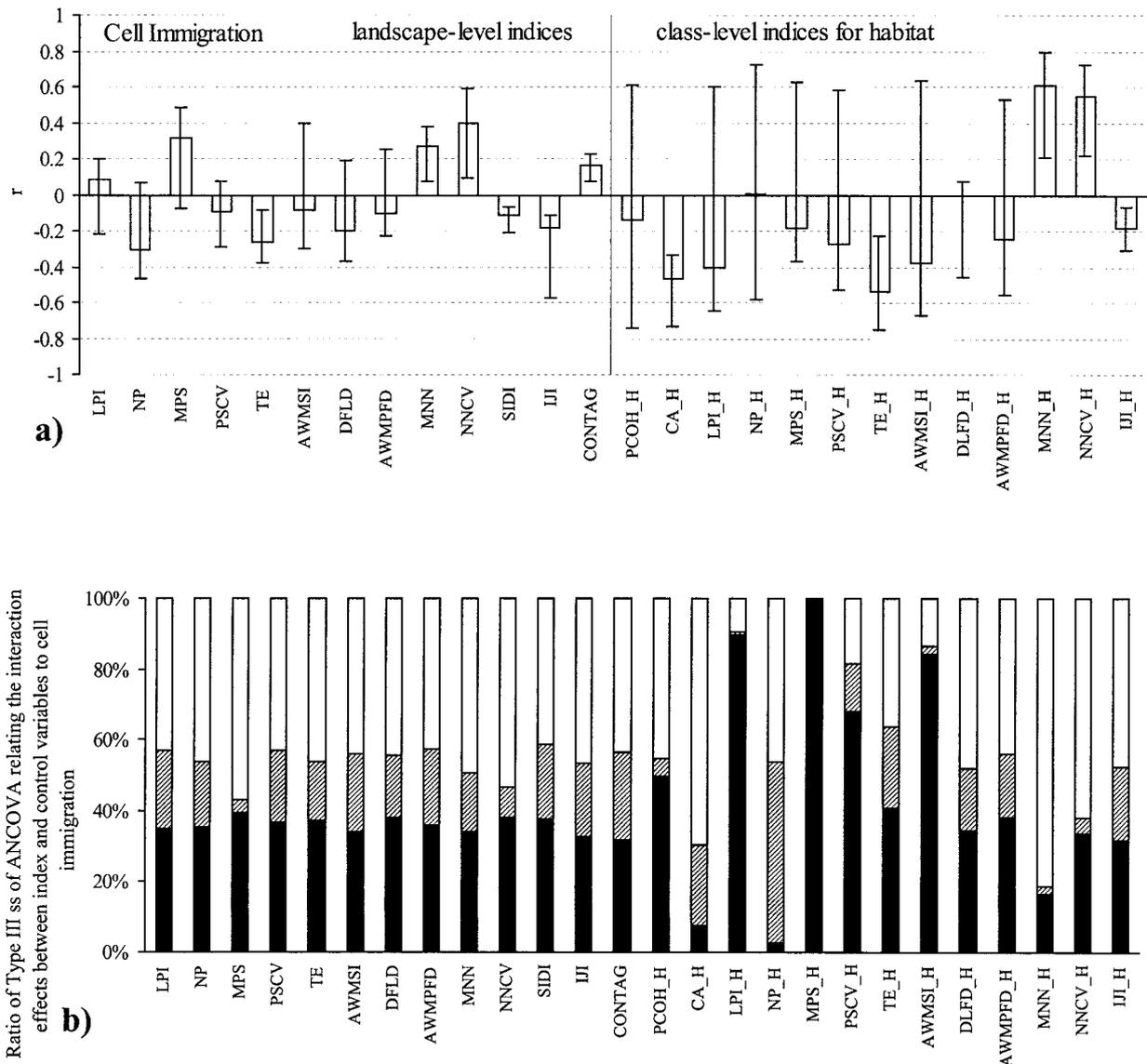
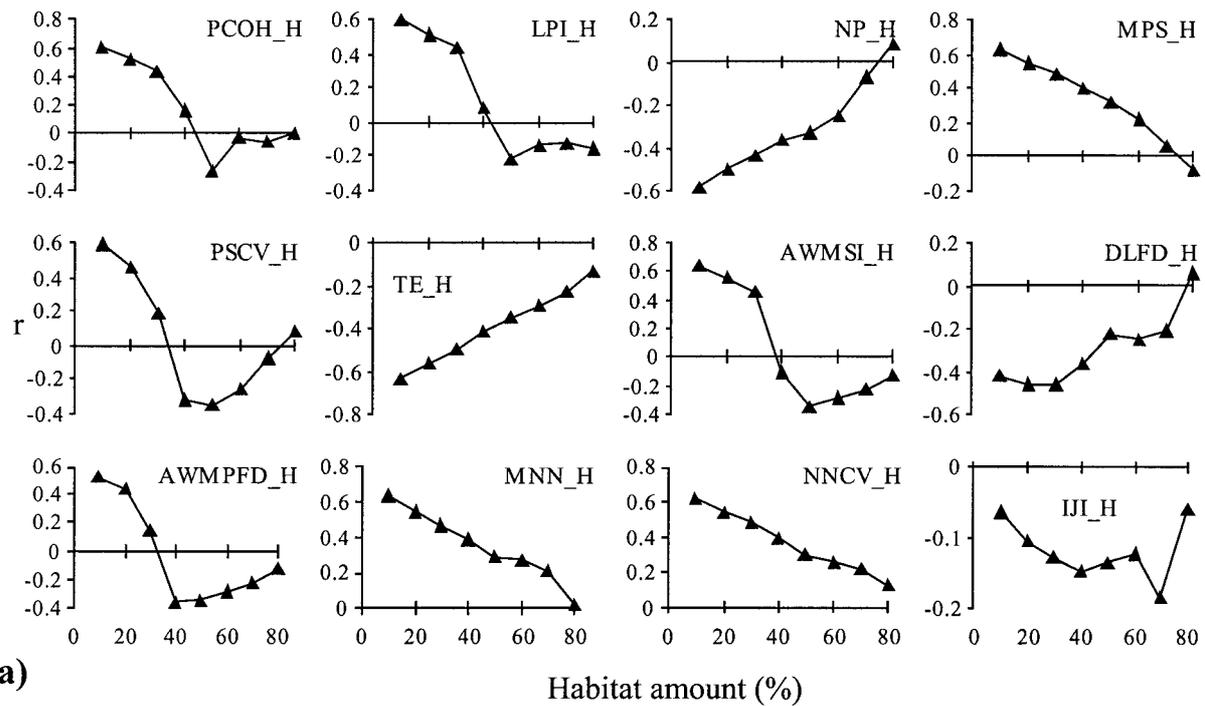


Figure 6. (a) Bars show the values of the Pearson Product Moment correlation coefficients between landscape indices and the response variable 'Cell immigration' pooled over all 1632 model landscapes (see Table 1) and all 4 disperser types (see Table 2). The error bars indicate minimum and maximum correlation coefficients when obtained separately for each level of the control variables (i.e., habitat amount, habitat fragmentation and disperser type, see text). (b) Ratio of the type III sums of square values of a statistical model relating the interaction effects between landscape indices and habitat amount (black bar), habitat fragmentation (striped bar) as well as disperser type (white bar) to the response variable 'Cell immigration' (see text for further explanation). The proportion (lengths of a colored bar) corresponds with the relative importance of this interaction effect after controlling for the other two interaction effects.

the relationships between landscape indices and response variables, correlation coefficients covered a wide range of possible values. Some correlation coefficients varied between high positive and high negative values indicating a strong ambiguous predictive potential. Habitat amount (CA_H) was consistently correlated to all three response variables. Mean nearest

neighbor indices (MNN_H, NNCV_H) and habitat edge (TE_H) predicted cell immigration and search time consistently. Dispersal success was consistently predicted by the number of habitat patches (NP_H), and mean habitat patch size (MPS_H).



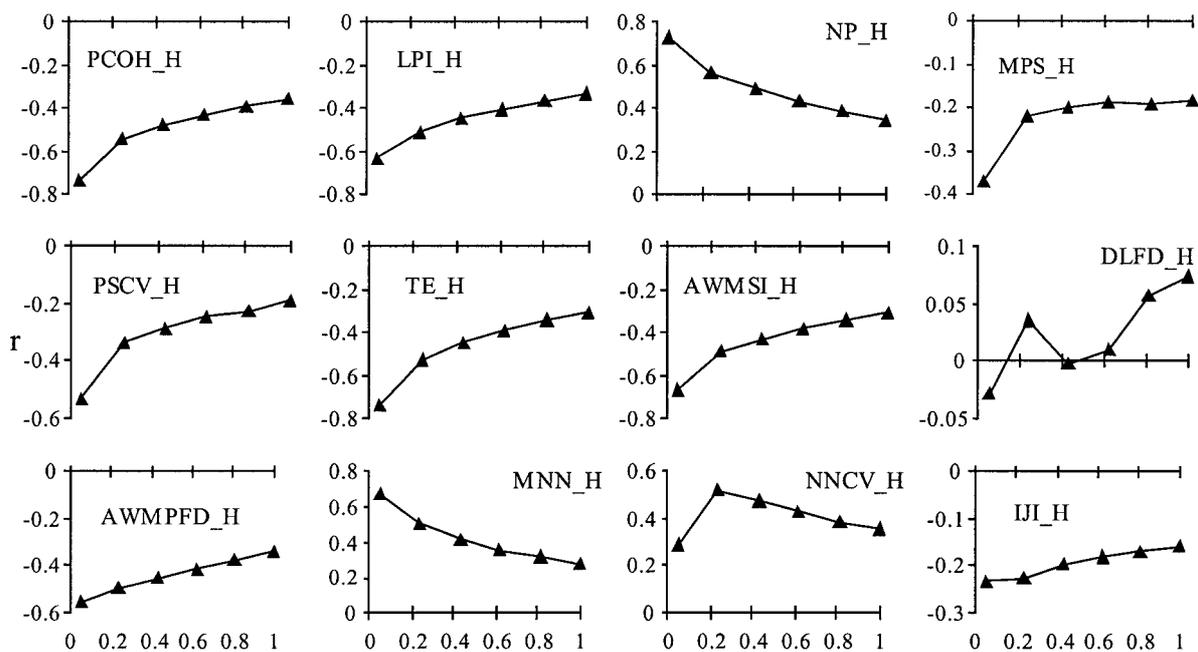
a) Figure 7. (a) Pearson product-moment correlation coefficients between selected habitat class-level indices and the response variable 'Cell immigration' calculated separately for different levels of the control variable 'Habitat amount' (pooled over all levels of H_{FRAG}). Most habitat class-level indices elicit higher correlation scores at low habitat amounts. Some correlation coefficients change from highly positive to negative at habitat amounts between 30 and 50% (e.g., LPI_H , $PSCV_H$, $AWMSI_H$, $AWMPFD_H$). (b) Correlation coefficients between selected habitat class-level indices and 'Cell immigration' calculated separately for different levels of the control variable 'Habitat fragmentation' (pooled over all levels of H_{COV}). Most habitat class-level indices produce stronger correlations with 'Cell immigration' when habitat fragmentation is low, i.e., near zero. (c) Correlation coefficients between selected habitat class-level indices and 'Cell immigration' calculated separately for each disperser type (see Table 2). Higher correlation scores are mostly associated with the specialist disperser types.

Patterns

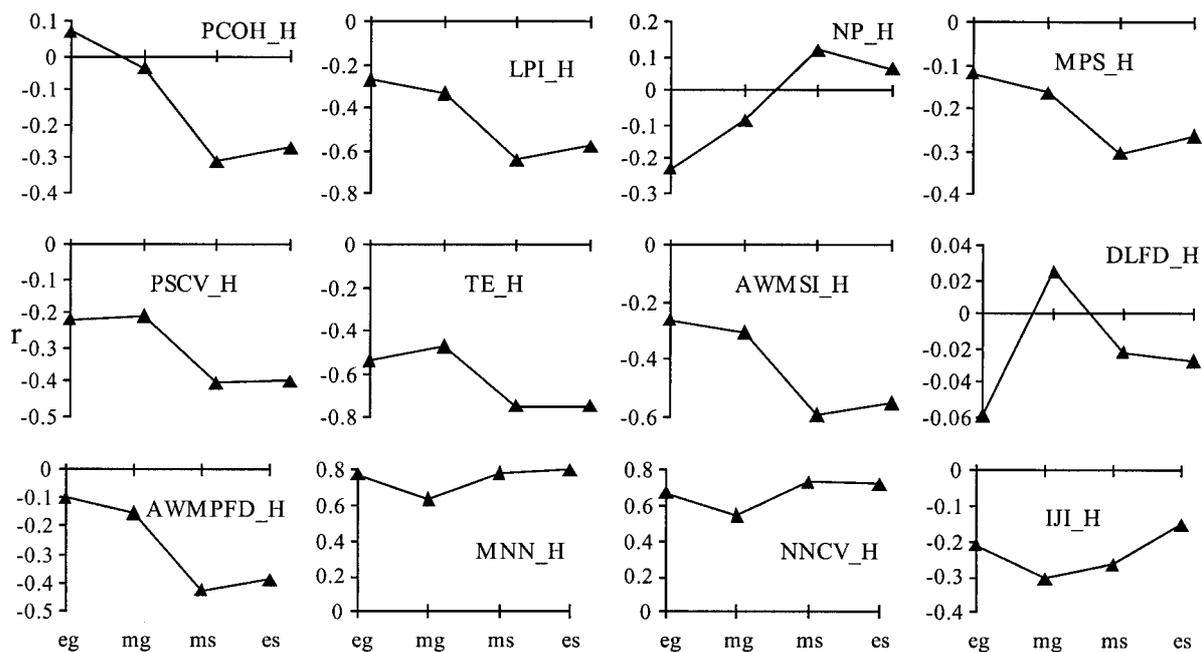
The results give rise to the question; can we predict the variation in these statistical relationships along with changes in the control variables? I visually examined all correlation coefficients against the values of the control variables. Figure 7 shows a subset of these graphs of the relationships between habitat class-level indices and cell immigration. Generally, correlation coefficients declined with increasing habitat amount (Figure 7a) and with increasing habitat fragmentation (Figure 7b) (i.e., lowest values correspond with pure random habitat distributions). Correlations were also stronger for the specialist disperser types (Figure 7c) due to their more pronounced response to landscape structure. However, not all of the examined correlation coefficients follow these patterns. For example, relationships between the habitat class-level indices LPI_H , $PSCV_H$ and $AWMPFD_H$ (see Table 3) and cell immigration changed from positive to negative at different values of habitat amount (Figure 7a).

Artificial vs. realistic landscapes

Figure 8 shows the comparison of correlation coefficients obtained from simulations on a subset of the artificially generated landscape models and on the realistic landscapes. Habitat class-level indices were similarly correlated to all three response variables for both artificial and realistic landscapes. Landscape-level indices (based on all landcover types) performed generally better in the realistic landscape models. I examined the numerical ranges of all landscape-level indices. Large differences in the statistical relationships between artificial and realistic landscapes were mostly attributed to differences in the numerical range of the landscape indices. For instance, double log fractal dimension (DLFD) was highly correlated with cell immigration and search time ($r = -0.65$ and $r = -0.74$, respectively) in realistic landscapes but was not in artificial landscapes. The numerical range of DLFD obtained from the realistic landscapes was 1.318–1.414 compared to 1.63–1.74 as obtained from



b) Habitat fragmentation (H_FRAG)



c) Disperser type

Figure 7. Continued.

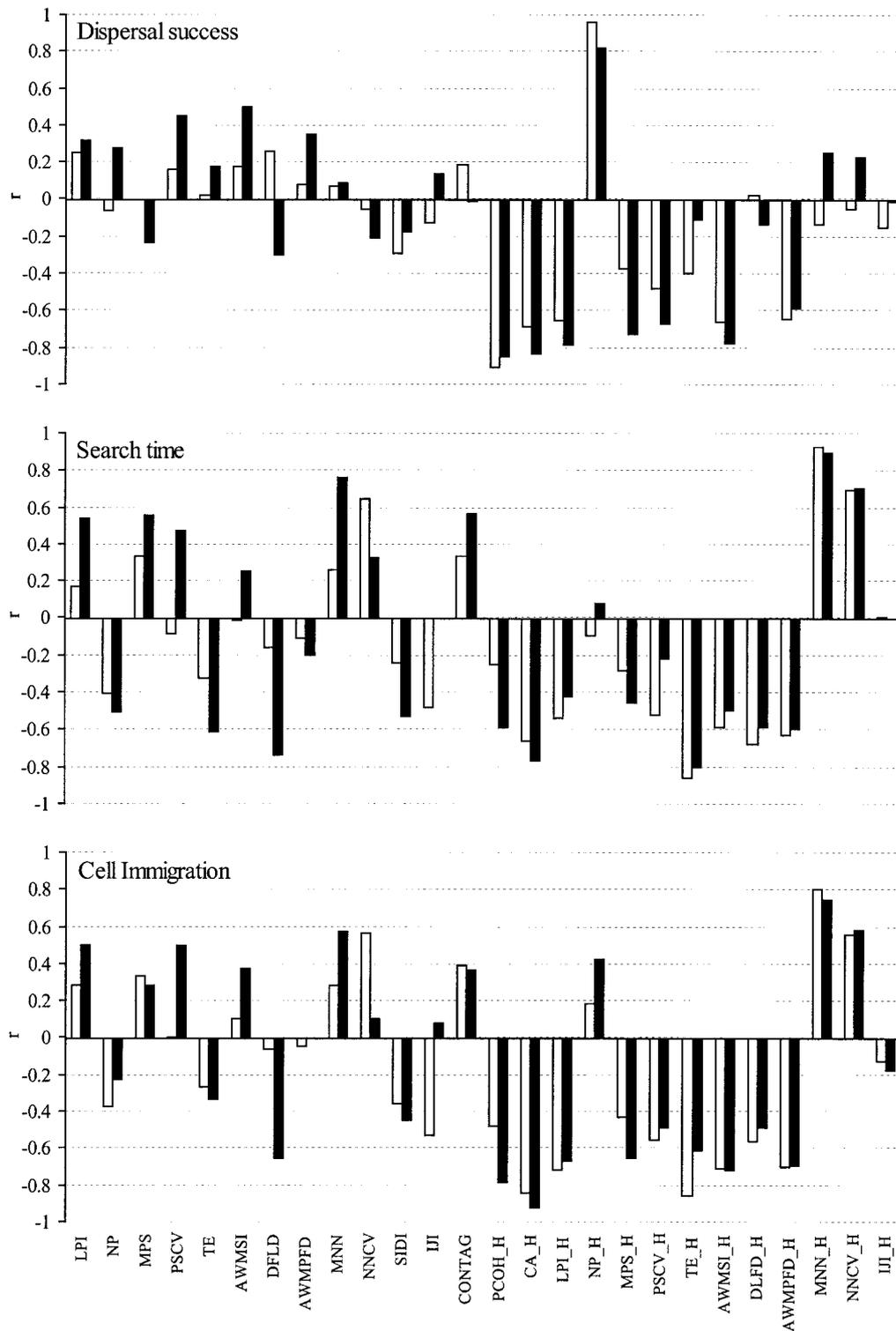


Figure 8. Comparison of the Pearson product-moment correlation coefficients between landscape indices and all three response variables obtained from artificial model landscapes (white bars) and realistic landscapes (black bars). Habitat class-level indices produced equally strong correlations for both landscape types. In contrast, most landscape-level indices predicted the response variables much better in realistic landscapes.

the selected subset of artificial landscapes (compare with Table 3).

Discussion

How well are landscape-level and class-level indices doing?

Habitat class-level indices were generally more strongly correlated with all three response variables than landscape-level indices. This is logical since the calculation of all response variables refers exclusively to habitat. Remember that dispersal success and search time are based on immigration events into habitat patches and cell immigration was incremented by immigration events into habitat grid cells. Matrix structure is not explicitly considered in the calculation of these response variables, but is included in the calculation of landscape-level indices. Consequently, landscape-level indices contain information which is not crucial to the habitat class-level specific response variables. For instance, the number of all patches in a landscape (i.e., patches of all three landcover types) explains much less of dispersal success compared to the number of habitat patches (see Figure 4a, NP, NP_H). This effect will likely increase when landscapes comprise more than just three landcover types.

Dispersal success was highly correlated with patch cohesion (PCOH_H), area-weighted mean shape index (AWMSI_H) and area-weighted mean habitat patch fractal dimension (AWMPFD_H). Although I determined dispersal success in a somewhat different way than Schumaker (1996), my results confirm the potential of these landscape indices, in particular patch cohesion, to predict dispersal success. The most consistent correlations, however, are attributed to the number of habitat patches (NP_H) and the habitat amount (CA_H) of the landscapes (Figure 4a). Dispersal success is determined by inter-patch movements. The more patches there are, the shorter are the inter-patch distances and, consequently, more patch immigration can occur. The number of habitat patches declines with increasing habitat amount ($r = -0.66$, $p < 0.001$, $df = 1631$) which accounts for the negative relationship between habitat amount and dispersal success.

Search time and cell immigration were strongly correlated with nearest-neighbor indices (MNN_H, NNCV_H), habitat amount (CA_H) and habitat edge (TE_H). Search time is positively correlated with inter-patch distances, because more movement steps are

required to cover longer distances between habitat patches. Longer inter-patch distances are in turn related to a smaller number of habitat patches, which corresponds to less fragmentation. In other words, fewer and more compact habitat patches increase search time. Increasing habitat amount, however, decreases mean-nearest neighbor distances (MNN_H) ($r = -0.35$, $p < 0.001$, $df = 1631$), and is therefore negatively correlated with search time.

The calculation of cell immigration is not based on habitat patches, which is reflected in the lack of a relationship to NP_H (see Figure 6a). Cell immigration responds positively to inter-patch distances (MNN_H, NNCV_H) and negatively to habitat edge (TE_H) as well as habitat amount (CA_H). Less habitat edge combined with longer inter-patch distances corresponds to less habitat fragmentation. The negative effect of habitat amount on cell immigration is attributed to the habitat specific response of the modeled individuals. All disperser types express a random walk on habitat area with an overall low displacement potential. More habitat area results in more random walk movement based on which fewer new habitat grid cells are entered. Hence, the overall displacement potential, which is crucial for cell immigration, is reduced in landscapes with more habitat amount.

Finally, statistical relationships varied considerably among the three response variables. This is an interesting result itself, since all three response variables quantify the success of dispersal and refer to the same ecological process. Consequently, pattern-process relationships may depend on the way we quantify ecological processes. Consistent quantification of ecological processes is necessary to allow for comparisons of pattern-process relationships between different studies.

Altogether, landscape indices, and in particular, class-level indices do have the potential to explain class-specific response variables of dispersal across heterogeneous landscapes. However, as the results indicate, ecological interpretation of one single landscape index is unlikely to completely explain the response of an ecological process to landscape structure.

How consistent are correlations between landscape indices and response variables?

Consistency in statistical relationships between landscape indices and response variables of ecological processes is the prerequisite for generalizations. Surprisingly, this question has rarely been addressed in

previous studies, mostly because of the lack of appropriate and independent control variables against which consistency could be examined. Gustafson (1998) recommended exploring the response of landscape indices to changes in landscape heterogeneity by using neutral landscape models. I went one step further and examined the robustness (response) of the ecological interpretations of landscape indices against changes in landscape pattern and the ecological process itself. The results revealed that only 25 out of the 78 analyzed statistical relationships were unambiguous (i.e., clearly positive or clearly negative) for all variations of the three control variables. Correlation coefficients of the remaining 53 statistical relationships ranged from highly negative to highly positive values indicating low consistency with variations in landscape structure and/or dispersal process. Consequently, these landscape indices do not provide the potential for general interpretations with respect to the process of dispersal. The inconsistencies of the examined statistical relationships across all three response variables emphasize the dangerous potential for inappropriate interpretations of landscape indices. A careful examination of the (range of) conditions under which a certain statistical relationship was established, can help to avoid the derivation of improper generalizations or conclusions.

Do correlations between landscape indices and process variables vary in a predictable way?

Most of the minima and maxima enclosing the potential ranges of the correlation coefficients are attributed to extreme values of the control variables (i.e. to landscapes with low amounts of habitat (Figure 7a), low habitat fragmentation (Figure 7b) and the extreme specialist disperser type (es, Figure 7c). Two principal patterns emerged for the relationships of the correlation coefficients with habitat amount. Correlation coefficients either declined linearly with increasing habitat amount (e.g., NP_H , TE_H , $NVCV_H$ in Figure 7a) or changed from high positive values to negative values near a common threshold at the habitat amount scale (e.g., $PCOH_H$, LPI_H , $AWMSI_H$ in Figure 7a). The location of the threshold at the habitat amount scale (between 30% and 50%, see Figure 7a), and the fact that threshold behavior is restricted to habitat area dependent class-level indices, suggest a relationship to percolation thresholds (e.g., Gardner et al. 1987; Gardner and O'Neill 1991; Lavorel et al. 1993; With et al. 1997). It is likely that the fundamental differences in habitat structure below and above the

percolation threshold may cause a turnover in the statistical relationships between some habitat class-level indices and response variables of ecological processes.

Increasing habitat fragmentation resulted in lower correlation coefficients for most of the statistical relationships examined. The lowest values of the correlation coefficients were mostly associated with a pure random distribution of habitat (see Figure 7b, $H_{FRAG} = 1$). Using habitat fragmentation as a control variable, however, is problematical, since (to my knowledge) there is no commonly used measure for habitat fragmentation (but see McGarigal and McComb 1995; Trzcinski et al. 1999 for statistical measures). This result is particularly interesting in light of the potential for random (neutral) landscape models to substitute for realistic landscape pattern in theoretical analyses. Analyses based on pure random distributions of habitat area will definitely underestimate the predictive potential of landscape indices (compare to Schumaker 1996).

The variation in the dispersal process (i.e., the differences in the dispersal behavior between the modeled hypothetical species) affected statistical relationships between landscape indices and cell immigration (see Figure 6b). In most cases, correlation coefficients were higher for the more specialist disperser types, which is likely caused by their more pronounced response (i.e., larger differences between the dispersal parameters for different landcover types) to landscape structure.

In summary, statistical relationships between landscape indices and response variables varied in a predictable way along with changes in the control variables. Low habitat amount and low habitat fragmentation account for most of the extreme values of the correlation coefficients. The qualitative change of habitat pattern near potential percolation thresholds is likely to cause dramatic changes in statistical relationships between habitat area dependent landscape indices and response variables of ecological processes.

Can artificial landscape models substitute for realistic landscapes in theoretical analyses?

There is no general answer to this question, since many different algorithms have been used to generate artificial (neutral) landscape models (e.g., Li and Reynolds 1994; With et al. 1997; Hargis et al. 1998; Meisel and Turner 1998) and there are no general patterns in realistic landscapes, e.g., natural patterns may differ substantially from human landuse (e.g.,

agricultural) patterns (e.g., O'Neill et al. 1988; Hulshoff 1995). I examined the statistical relationships between landscape indices and the response variables for a range of natural and human dominated landscape pattern (compare Figures 3a and 3d), and I compared the correlation coefficients with those obtained from a subset of the artificially generated landscape models. I found very similar relationships between habitat class-level indices and all three response variables for both landscape representations. In fact, high values of the correlation coefficients based on artificial landscape models were always confirmed by realistic landscapes. These results (Figure 8) support the idea of using artificial landscape models for analyzing statistical relationships between landscape indices and response variables of ecological processes (see also With and King 1997). Substantial differences between correlation coefficients (e.g., DLFD in Figure 8a,c) were mostly attributed to differences in their actual numerical range (see results). It is therefore likely that not all aspects of spatial patterns of realistic landscapes are reflected in their artificial counterparts. However, since the values of the correlation coefficients based on realistic landscapes were mostly higher than those obtained from artificial landscape models, estimates from artificial landscape models may be considered as conservative.

Implications for further studies

The results of this study revealed the potential but also the pitfalls of using landscape indices to predict ecological processes. How can we use this potential and how can we avoid improper interpretations of landscape indices? First of all, we need to avoid automatism. Rather than 'plugging' all available landscape indices (as calculated by computer programs) into statistical analyses, we need to propose hypothetical relationships followed by statistical tests. That means to select those landscape indices, which are likely to be relevant to the ecological process in question. This pre-selection requires understanding of mechanisms that would lead us to expect certain statistical relationships. In some cases it might be appropriate to develop new landscape indices which contain specific information about landscape patterns with particular importance to the ecological process in question (e.g., Schumaker 1996; Jaeger 2000). Second, it should be mandatory for any further study dealing with this subject to report the numerical ranges of the landscape indices. This would allow to restrict the validity of

a detected pattern-process relationship and ease comparisons across different studies. Finally, I recommend one visually examining (scatter plot) relationships between landscape indices and response variables. It might be that statistical tests other than linear correlation analysis are more suitable to reflect a certain pattern-process relationship.

Conclusions

The results obtained from my simulation experiments support the following conclusions:

1. Landscape indices appear statistically related to response variables of ecological processes. Class-level indices show generally stronger statistical relationships with response variables than landscape-level indices.
2. Dispersal success is consistently explained by habitat amount and the number of habitat patches. Patch cohesion as well as area weighted mean versions of shape index and habitat patch fractal dimension elicit overall strong but less consistent correlations with dispersal success.
3. Search time responds consistently to the mean nearest neighbor distance between habitat patches and to habitat edge.
4. Cell immigration is best and consistently correlated to the mean nearest-neighbor distance between habitat patches, habitat edge and habitat amount.
5. Most landscape indices appear to have the potential for inconsistent and ambiguous statistical relationships with response variables of ecological processes. Careful examination and report of the range of conditions for which statistical relationships were obtained may prevent misleading ecological interpretations of landscape indices.
6. Class-level indices tend to provide stronger correlations with response variables of ecological processes at low amounts and low fragmentation of the corresponding landcover type (class, e.g., habitat in this analysis).
7. Neutral landscape models do have the potential for studying the effects of spatial patterns on dispersal across heterogeneous landscapes. However, a close match of the artificially generated patterns with their realistic counterparts (i.e., equal number of landcover types, similar range of the amount of landcover types, etc.) and the use of clumping al-

gorithms are necessary to obtain reliable statistical relationships with response variables.

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