

An evaluation of patch connectivity measures

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Abstract. Measuring connectivity is critical to the study of fragmented populations. The three most commonly used types of patch connectivity measures differ substantially in how they are calculated, but the performance of these measures has not been broadly assessed. Here I compare the ability of nearest neighbor (NN), buffer, and incidence function model (IFM) measures to predict the patch occupancy and colonization patterns of 24 invertebrate, reptile, and amphibian metapopulations. I predicted that NN measures, which have been criticized as being overly simplistic, would be the worst predictors of species occupancy and colonization. I also predicted that buffer measures, which sum the amount of habitat in a radius surrounding the focal patch, would have intermediate performance, and IFM measures, which take into account the areas and distances to all potential source patches, would perform best. As expected, the simplest NN measure (distance to the nearest habitat patch, NH_i) was the poorest predictor of patch occupancy and colonization. Contrary to expectations, however, the next-simplest NN measure (distance to the nearest occupied [source] patch, NS_i) was as good a predictor of occupancy and colonization as the best-performing buffer measure and the general IFM measure S_i . In contrast to previous studies suggesting that area-based connectivity measures perform better than distance-based ones, my results indicate that the exclusion of vacant habitat patches from calculations is the key to improved measure performance. I highlight several problems with the parameterization and use of IFM measures and suggest that models based on NS_i are equally powerful and more practical for many conservation applications.

Key words: connectivity; fragmentation; incidence function model; isolation; logistic regression; meta-analysis; metapopulation dynamics; model selection; occupancy.

INTRODUCTION

Habitat loss and fragmentation are widely recognized as major threats to biodiversity (Baille et al. 2004). Ecological theory and empirical evidence both show that species occupancy and colonization probabilities are lower in habitat patches that are smaller and more isolated (MacArthur and Wilson 1967, Prugh et al. 2008). Thus, the study of connectivity (i.e., the converse of isolation) is one of the most prolific fields in conservation ecology today (Crooks and Sanjayan 2006). Much debate has surrounded the definition of connectivity, leading to distinctions between structural, functional, landscape, patch, and habitat connectivity, among others (Tischendorf and Fahrig 2000b, Moilanen and Hanski 2001, Lindenmayer and Fischer 2007). Within each of these subcategories, a variety of methods have been used to measure connectivity, including grid-based, area-based, distance-based, and movement-based methods. Because different methods can produce conflicting connectivity estimates (Tischendorf and

Fahrig 2000a), choosing an appropriate measure is a challenging and critical step in fragmentation studies.

To some extent, the choice of an appropriate measure depends on the study design. One of the most commonly used fragmentation study designs is patch-based monitoring, wherein species occupancy is recorded in a network of discrete habitat patches of varying size and isolation. This is the standard design used by metapopulation ecologists, and it is also used by many conservation biologists. Attributes of the habitat patches, intervening matrix areas, and/or the species of interest are used in a modeling framework to determine how strongly connectivity and other factors influence species occupancy, colonization, or extinction probabilities. In this design, connectivity is considered to be a patch-specific attribute and is often referred to as “patch connectivity” (Moilanen and Hanski 2001, Tischendorf and Fahrig 2001). Patch connectivity (or isolation) can be measured in a variety of ways, from the simplest nearest-neighbor distance to more complex formulas that include patch distances, areas, species dispersal abilities, and other scaling parameters (known as incidence function model measures; Hanski 1994b).

Because nearest-neighbor (NN) measures are so easy to calculate, they have been used extensively by ecologists and conservation planners. However, these measures do not take into account the area of surrounding habitat

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patches and have been criticized as being overly simplistic (Moilanen and Nieminen 2002). Because interpatch distances are usually calculated from center to center, the shapes and areas of patches could strongly influence connectivity; patch edges may be close together if the patches are large, even if the patch centers are far apart. Thus, some researchers have advocated and used area-based buffer measures, which sum the amount of habitat in a given radius around a focal patch (Saari et al. 1998, Beard et al. 1999, Pope et al. 2000, Bender et al. 2003, Tischendorf et al. 2003). However, buffer measures do not include any information about distances between patches, and they may also be sensitive to the radius size (Moilanen and Nieminen 2002, Bender et al. 2003). Incidence function model (IFM) measures take into account both the areas of and distances to surrounding patches, and use of IFM measures has increased following a study showing their superior performance in comparison to buffer and NN measures (Moilanen and Nieminen 2002). A more recent study found little difference in the performance of NN, buffer, and IFM measures, however, calling into question the necessity of using the more complex IFM measures (Winfree et al. 2005). Both of these studies were limited in their scope, using two to three metapopulations to evaluate connectivity measure performance. Differences in scale, vagility, habitat, and other variables among species and sites limit the applicability of narrow evaluations, and a broader test is needed to adequately examine these connectivity measures.

In this study, I evaluated the performance of six NN, buffer, and IFM measures using occupancy data from 24 invertebrate, reptile, and amphibian metapopulations from around the world. I used logistic regression models to predict species occupancy and colonization probabilities using each connectivity measure, and I compared model performance using three robust techniques: Akaike Information Criterion (AIC) weights, explained deviance (pseudo- R^2), and Wald tests (regression coefficients divided by their errors). Two of the metapopulations included in this study were those used by Moilanen and Nieminen (2002) in their evaluation of patch connectivity measures. Of the six connectivity measures evaluated here, two are nearest-neighbor (nearest habitat, NH_i , and nearest source, NS_i), two are buffer (buffer habitat, BH_i , and buffer source, BS_i), and two are IFM (S_i and AS_i) measures (see Table 1 for formulas). These measures were chosen primarily because of their frequent use in the literature, but I will briefly highlight some other important characteristics.

The NN measure NH_i and buffer measure BH_i are both calculated without regard to the occupancy status of patches, whereas only occupied patches (i.e., potential source patches) are included in calculations of NS_i , BS_i , S_i , and AS_i . Several other formulations of S_i have been used in studies (see Bonte et al. 2004, Pellet et al. 2007), but the one used here is the most common (Hanski 1994a). Previous evaluations have categorized patch connectivity measures primarily as area-based or dis-

tance-based (Moilanen and Nieminen 2002, Bender et al. 2003, Winfree et al. 2005). While I also highlight this important distinction, this is the first evaluation to directly compare measures that include all habitat patches in their calculations of connectivity with analogous measures that include surrounding patches only if they are occupied.

As stated above, another important distinction among connectivity metrics is the unit of measure. Nearest-neighbor measures are in units of distance, whereas buffer and IFM measures are in units of area. Note that, in contrast to the other connectivity measures, NN measures increase as connectivity decreases. Thus, NN measures are perhaps more accurately described as isolation measures. Although IFM measures include interpatch distances in the calculations, these distances are divided by the migration distance of the species; thus, IFM measures are scaled by distance but are fundamentally area-based. As a result of this scaling, IFM measures have more parameters than the others (Table 1).

Unlike the other five measures, the IFM measure AS_i has not been commonly used in the literature. I evaluated it primarily because it was the best-performing measure evaluated by Moilanen and Nieminen (2002). While the other area-based measures quantify the amount of habitat surrounding a focal patch, this measure also takes into account the potential positive effect that focal patch area has on connectivity and metapopulation dynamics (e.g., larger patches should supply and intercept more dispersers). I also evaluated multiple regression models that included the connectivity measure and focal patch area as independent predictors. Because focal patch area arguably has an impact on metapopulation dynamics that is largely separate from connectivity, I focus primarily on evaluating the connectivity measures without terms for focal patch area (NH_i , BH_i , NS_i , BS_i , and S_i ; Table 1).

I expected that IFM measures would perform better than buffer and NN measures for three main reasons. First, IFM measures contain more information about the patch network and species' dispersal abilities. Second, the negative exponential dispersal kernel used in IFM measures is well justified biologically and rooted in metapopulation theory (Hanski 1994b). Third, Moilanen and Nieminen (2002) found that IFM measures were superior to buffer and NN measures using two of the metapopulations included in this study. Because inaccuracy in the additional biological information could potentially have strong effects on the performance of IFM measures, I also examined the effect of varying parameters α and b for several metapopulations (see Plate 1).

METHODS

Data acquisition

The 24 metapopulations included in this study are a subset of a larger meta-analysis (Prugh et al. 2008). Studies were found by a comprehensive search using the

TABLE 1. Description of the models and connectivity measures evaluated.

Model	Model formula	Connectivity measure formula	Measure type	Description of measure
BH	$\ln\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 \text{BH}_i + \varepsilon$	$\text{BH}_i = \sum_{d_{ij} \leq r} A_j$	buffer	area of all habitat within a radius
BS	$\ln\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 \text{BS}_i + \varepsilon$	$\text{BS}_i = \sum_{d_{ij} \leq r} A_j \times k$	buffer	area of occupied habitat within a radius
<i>S</i>	$\ln\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 S_i + \varepsilon$	$S_i = \sum_{j \neq i} \exp(-\alpha d_{ij}) A_j^b \times k$	IFM	distance-weighted area of occupied habitat
<i>AS</i>	$\ln\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 AS_i + \varepsilon$	$AS_i = A_i^c \times S_i$	IFM	S_i multiplied by the scaled area of patch i
NH	$\ln\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 \text{NH}_i + \varepsilon$	$\text{NH}_i = \min(d_{ij})$	nearest neighbor	distance to the nearest patch
NS	$\ln\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 \text{NS}_i + \varepsilon$	$\text{NS}_i = \min(d_{ij}) \times k$	nearest neighbor	distance to the nearest occupied patch
$A \times \text{NS}$	$\ln\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 \text{NS}_i + \beta_2 A_i + \beta_3 \text{NS}_i A_i + \varepsilon$	$\text{NS}_i = \min(d_{ij}) \times k$	nearest neighbor	NS_i multiplied by the area of patch i in a multiple regression model

Notes: Abbreviations are: p , probability of occupancy or colonization; β_0 , intercept; β_x , regression coefficient of variable x ; ε , error term; A_i , area of focal patch (patch i); A_j , area of patch j (patch j is any other patch in the landscape; patch $j \neq i$); d_{ij} , distance between focal patch i and patch j ; r , radius of buffer around focal patch i (in this study, $r = 1/\alpha$, the mean migration distance of the species); k , occupancy or colonization status of patch (1 = occupied or colonized, 0 = not occupied or colonized); α , 1/average migration distance of the species (but see *Discussion* for other definitions); b , a parameter scaling the effect of emigration to area; c , a parameter scaling the effect of immigration to area.

Web of Science in March 2005 with the terms “patch occupancy,” “habitat occupancy,” “metapopulation,” “island biogeography,” and “incidence function.” Forward and backward citations of articles found in these searches were also used to locate studies. Studies were included if 10 or more discrete terrestrial habitat patches were surveyed and raw occupancy data for birds, mammals, invertebrates, reptiles, or amphibians could be obtained (either from the published papers or directly from the authors). Data were available to calculate buffer and IFM measures for 24 of the 1015 metapopulations included in the larger meta-analysis. These metapopulations occurred in 13 different landscapes; some studies recorded occupancy data for multiple species in a landscape. The fragmented populations included in this study all showed evidence of metapopulation dynamics through documented colonizations, extinctions, and/or interpatch dispersal events. All metapopulations occurred in moderate to highly fragmented landscapes, with habitat patches comprising 2% of the landscape area on average (range < 0.01–17%, $n = 13$ landscapes). The number of patches in each landscape ranged from 32 to 1716 (Table 2).

Connectivity measure calculations and parameter evaluation

The distance matrix \mathbf{d}_{ij} was calculated using patch coordinate data for each metapopulation. I wrote code to calculate \mathbf{d}_{ij} and each connectivity measure in program R (R Development Core Team 2007). Patch

coordinates were not provided for three metapopulations, and I used the NS_i and S_i calculations provided by the authors in these cases (metapopulations 1, 4, and 22; Table 2).

Published values for parameters α , b , and c were used to calculate S_i when available (Table 2). In a few cases, I used published mean dispersal distances to calculate α . Parameter values were set to 1 if information was not available. Excluding metapopulations without estimates of α did not change any results. In calculating the buffer measures, I set the radius equal to the average migration distance of the focal species ($1/\alpha$), because that radius led to the best-performing buffer measure among those evaluated by Moilanen and Nieminen (2002).

To examine the effect of α and b on the performance of S_i , I varied α from 0.01 to 100 while holding b constant at its published value and varied b from 0 to 1 while holding α constant at its published value. This analysis was conducted for the three metapopulations with published estimates for both α and b and patch coordinate data (metapopulations 15, 23, and 24; Table 2). I did not examine the scaling parameter c because it was rarely estimated or used in studies.

Logistic regression analyses

Logistic regression analyses were run in program R for each metapopulation using each of the six connectivity measures as predictors and either occupancy or colonization as the dependent variable. Colonization events could be recorded only in cases in which more than one

TABLE 2. Metapopulations used in this study.

Metapopulation	Reference	Species	Taxon	Location	N patches	N years	α	b	c
1	Biedermann (2005)	<i>Gonioctena olivacea</i>	beetle	Germany	237	3	1†‡	0.5	1
2	Eber and Brandl (2003)	<i>Urophora cardui</i>	fly	Germany	512	5	1§	1	1
3	Fleishman et al. (2002)	<i>Speyeria nokomis</i>	butterfly	Nevada, USA	39	11	0.25	1	1
4	Hanski et al. (1994)	<i>Melitaea cinxia</i>	butterfly	Finland	47	1	1§	0.3	1
5	Hjermann and Ims (1996)	<i>Decticus verrucivorus</i>	cricket	Norway	70	2	0.02¶‡	1	1
6	Hokit et al. (1999)	<i>Sceloporus woodi</i>	reptile	Florida, USA	95	3	10	1	1
7	Hokit et al. (1999)	<i>Cnemidophorus sexlineatus</i>	reptile	Florida, USA	95	3	1	1	1
8	James et al. (2003)	<i>Pseudophilotes sinaicus</i>	butterfly	Egypt	41	2	2	1	1
9	Knapp et al. (2003)	<i>Rana muscosa</i>	amphibian	California, USA	1716	3	1	1	1
10	Maes and Bonte (2006)	<i>Oedipoda caerulea</i>	grasshopper	Belgium	133	2	25	1	1
11	Maes and Bonte (2006)	<i>Alopecosa fabrilis</i>	spider	Belgium	133	2	4	1	1
12	Maes and Bonte (2006)	<i>Xysticus sabulosus</i>	spider	Belgium	133	2	4	1	1
13	Maes and Bonte (2006)	<i>Hipparchia semele</i>	butterfly	Belgium	133	2	2	1	1
14	Maes and Bonte (2006)	<i>Issoria lathonia</i>	butterfly	Belgium	133	2	2	1	1
15	Hanski (1994b)	<i>Scolitantides orion</i>	butterfly	Finland	70	3	0.35	0.3	0.2
16	Schmidt (2005)	<i>Alytes obstetricans</i>	amphibian	Switzerland	32	2	1¶	1	1
17	Schmidt (2005)	<i>Bufo calamita</i>	amphibian	Switzerland	32	2	1	1	1
18	Schmidt (2005)	<i>Triturus helveticus</i>	amphibian	Switzerland	32	2	1	1	1
19	Schmidt (2005)	<i>Triturus alpestris</i>	amphibian	Switzerland	32	2	1	1	1
20	Schmidt (2005)	<i>Bombina variegata</i>	amphibian	Switzerland	32	2	1	1	1
21	Schmidt (2005)	<i>Rana lessonae</i>	amphibian	Switzerland	32	2	1	1	1
22	Valimaki and Itamies (2003)	<i>Parnassius mnemosyne</i>	butterfly	Finland	58	1	9	1	1
23	Wahlberg et al. (1996)	<i>Melitaea diamina</i>	butterfly	Finland	94	1	4.9	0.2	1
24	Wahlberg et al. (2002a)	<i>Euphydryas aurinia</i>	butterfly	Finland	113	2	0.42	0.1	1

Notes: Distance was measured in kilometers unless otherwise noted. Parameter values (α , b , and c) used to calculate S_i are shown. A value of 1 was used when published parameter values were not available.

† Value used in original study, not based on dispersal estimates.

‡ Distance was measured in meters.

§ Value used in original study, based on dispersal estimates.

¶ Estimated based on published dispersal estimates.

year of occupancy data were provided ($n = 15$ metapopulations; Appendix B). In these cases, patch occupancy was recorded as the number of years occupied vs. the number of years surveyed, and colonization was recorded as having occurred if an empty patch became occupied.

As a convention throughout the paper, I refer to each logistic regression model using the same notation that was used for the predicting connectivity measure, but without the subscript i . For example, the model that used NH_i as a predictor is referred to as model NH (Table 1). I evaluated simple logistic regression models for each connectivity measure and multiple regression models that included focal patch area A_i as a predictor in addition to the connectivity measure. In this way, the independent and combined influences of focal patch area and surrounding patches were examined. I calculated these multiple regression models as an alternative to the measure AS_i , which included A_i in the calculation of the connectivity measure itself. Because all of the simple regression models were improved similarly by the addition of A_i , I show results for one multiple regression model only, $A \times NS$. In this model, NS_i and A_i , as well as their interaction, were used as predictors (Table 1).

Model comparison

Three metrics were calculated to evaluate model performance for each metapopulation: (1) pseudo- R^2 values, (2) Akaike Information Criterion (AIC) values, and (3) Wald tests. The pseudo- R^2 measures the amount of deviance (i.e., variation) in occupancy or colonization that is explained by each model. This statistic is analogous to the R^2 of linear regression (Hagler and Mitchell 1992) and was calculated as:

$$\text{pseudo-}R^2 = \frac{\text{null deviance} - \text{residual deviance}}{\text{null deviance}}.$$

The AIC is commonly used to rank competing models, with the best model having the lowest AIC value and highest model weight (w_i). The AIC values and w_i were calculated using standard techniques (Burnham and Anderson 2001). The Wald statistic (Z) was calculated as C/SE , where C is the coefficient of the logistic regression and SE is the associated standard error (Sokal and Rohlf 1995). The Z values were calculated for the six simple regression models only. Because the multiple regression model $A \times NS$ has three Z values (one each for NS_i , A_i , and $NS_i \times A_i$), this metric was not used.

The overall performance of each model was evaluated across metapopulations using mixed-model ANOVAs.

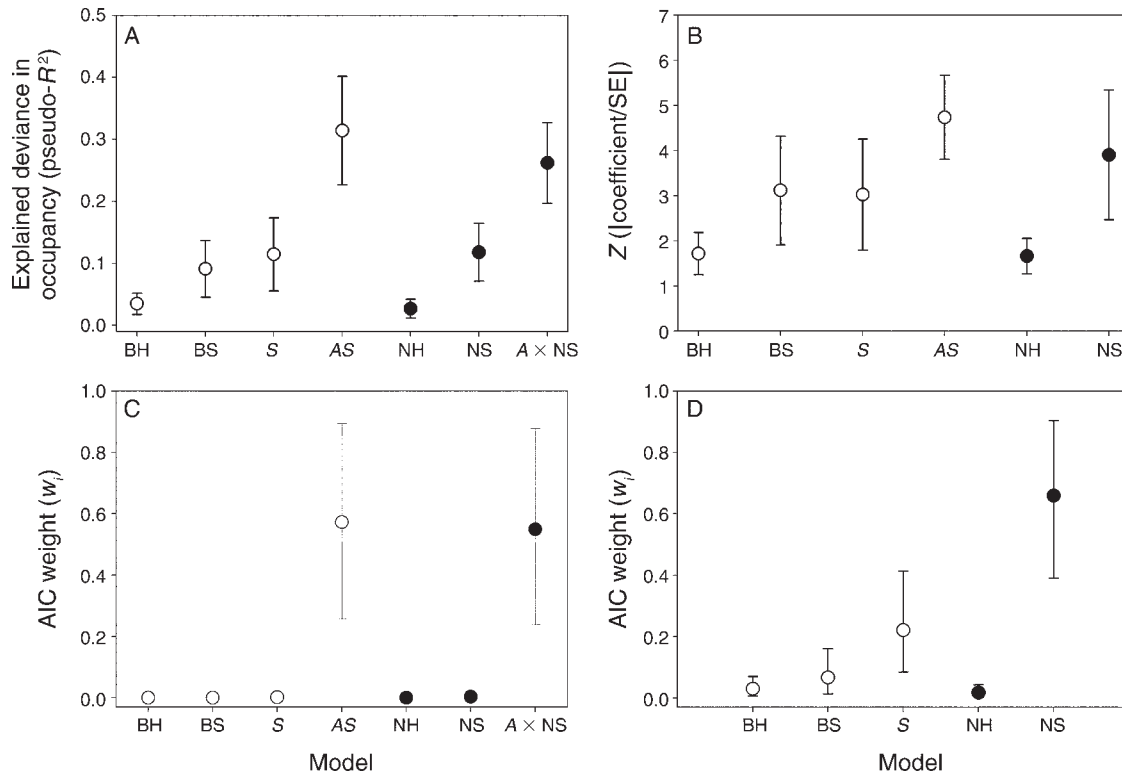


FIG. 1. Ability of connectivity measures to predict occupancy probabilities across 24 metapopulations. Six simple logistic regression models (BH, BS, S, AS, NH, and NS) and one multiple regression model ($A \times NS$) were evaluated using three model comparison techniques: (A) the amount of deviance in patch occupancy explained by each model (pseudo- R^2), (B) Wald tests, and (C, D) Akaike Information Criterion (AIC) model weights (w_i). See Table 1 for descriptions of the connectivity measures, which are either area-based (open circles) or distance-based (solid circles). Means and 95% confidence intervals are shown. Absolute values of Z values (logistic regression coefficient/SE) from Wald tests are shown for the six simple models in (B). The AIC weights are shown for (C) all seven models and (D) the five connectivity models without terms for focal patch area.

“Study” was included as a random effect to account for the non-independence of data (some metapopulations were reported in the same studies; Table 2), and “connectivity model” was included as a fixed effect. Proportions (pseudo- R^2 values and AIC weights) were arcsine square-root transformed prior to analyses.

In traditional meta-analyses, effect sizes are weighted by the inverse of their associated error estimates to evaluate hypotheses across studies (Hedges and Olkin 1985). The Z values are in essence weighted effect sizes: the regression coefficients (C) indicate how strongly occupancy or colonization changes with connectivity, and these effect sizes are divided by their associated error estimates (SE). Nearest-neighbor measures have negative coefficients because connectivity decreases with increasing distance, whereas buffer and IFM measures have positive coefficients (connectivity increases as BH_i , BS_i , S_i , and AS_i values increase). Thus, absolute values were used to compare Z values among models.

RESULTS

The six connectivity measures differed significantly in their ability to explain patterns of occupancy across the 24 metapopulations, and the three model comparison

techniques (pseudo- R^2 , AIC, and Wald tests) ranked the competing models similarly (Figs. 1 and 2). The simplest NN measure, NH_i , and the simplest buffer measure, BH_i , were the poorest predictors of occupancy and colonization in all comparisons (Figs. 1 and 2, Table 3). The NN measure NS_i , buffer measure BS_i , and IFM measure S_i (all of which excluded vacant patches) consistently performed better than NH_i and BH_i (which included all patches).

Contrary to expectations, S_i did not outperform NS_i or BS_i . Measures NS_i , BS_i , and S_i explained similar amounts of deviance in occupancy and colonization (Figs. 1A and 2A) and had similar Z values (Figs. 1B and 2B). Model NS had a significantly higher AIC weight than S when models with terms for focal patch area were excluded (Fig. 1D, Tukey tests). Models AS and $A \times NS$ were better predictors of occupancy than the other models, likely due to the term for focal patch area in these models (Fig. 1). Interestingly, these models were not better predictors of colonization than S, NS, and BS, which lack the focal patch area term (Fig. 2).

Parameters α and b both affected the performance of S_i , and all three metapopulations evaluated showed the same general patterns (Fig. 3). The Z values decreased

from 0 to a low of -8 as α increased from 0.01 to 0.1, then sharply increased as α increased from 0.1 to 1, and continued to increase until reaching peak values when α was 20–40 (Fig. 3A, C, E). Realistic values of α (up to 0.25) led to significant negative Z values in all three metapopulations, with the interpretation that occupancy actually decreases with increasing connectivity. Significant positive Z values were obtained when α was >1.5 for all metapopulations. The Z values were far from their peaks when α was 1, a value that is often used by default when dispersal information is unavailable. Published values of α , which were based on mark-recapture studies (Hanski et al. 2000, Moilanen and Nieminen 2002, Wahlberg et al. 2002a), led to nonsignificant Z values in two of the three metapopulations. The Z values did not change as dramatically in response to variation in parameter b , but in all cases Z values steadily declined as b increased from 0.01 to 1 (Fig. 3B, D, F).

DISCUSSION

Using a quantitative meta-analysis of 24 invertebrate, reptile, and amphibian metapopulations and three robust techniques to evaluate performance, I demonstrate that incidence function model (IFM) measures are not better than buffer or nearest-neighbor (NN) measures at predicting patch occupancy and colonization probabilities. This finding is quite surprising, given that NN measures include very little information about the patch network and no species-specific information. Logic and theory tell us that it should matter whether neighboring patches are large or small, how many of them surround the focal patch, how close they are, and how far the species can disperse. The IFM measures elegantly include this information in equations that account for the exponential decay typical of dispersing propagules, as well as the relationships between immigration, emigration, and patch area, which are likely to be nonlinear and species-specific. The S_i measure relates directly to other metapopulation models and has strong theoretical justification (Hanski 1994a). These logical and theoretical advantages, however, do not translate into an empirical advantage when it comes to predicting patch occupancy and colonization probabilities. This study shows that, in most cases, the distance to the nearest source patch (NS_i) contains sufficient information to predict patterns of species occupancy and colonization in comparison to S_i .

Comparison of model performance

Not all of the NN measures performed well. The simplest NN measure, distance to nearest habitat patch (NH_i), was a poor predictor of occupancy, as was the simplest buffer measure, the area of all habitat within a given radius (BH_i , where the radius equals the average migration distance of the species). By altering calculations to exclude vacant patches, however, the performance of both the nearest neighbor and the buffer

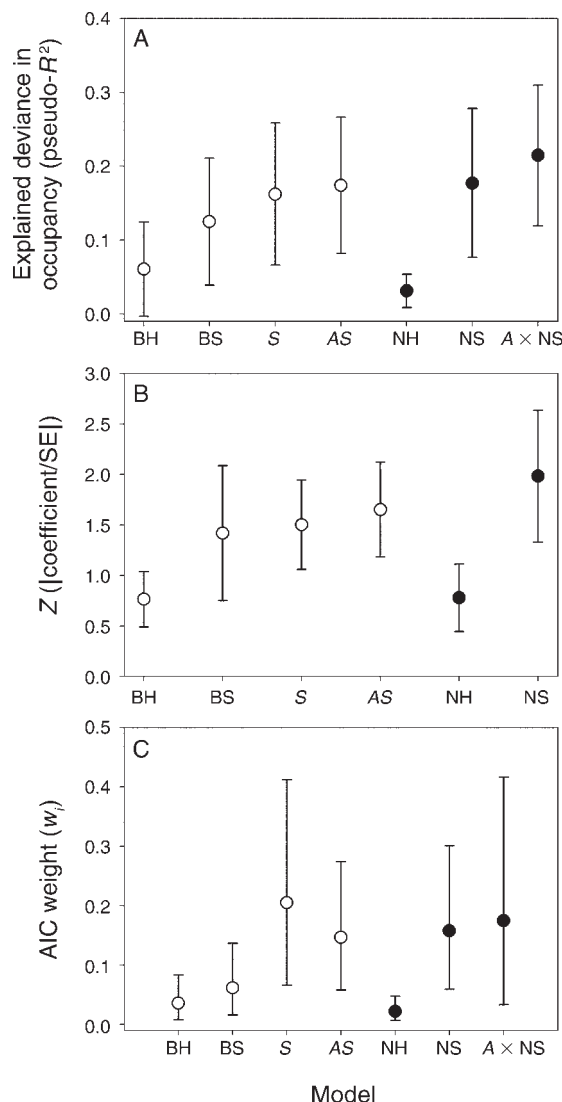


FIG. 2. Ability of connectivity measures to predict colonization probabilities across 15 metapopulations. Six simple logistic regression models (BH, BS, S, AS, NH, and NS) and one multiple regression model ($A \times NS$) were evaluated using three model comparison techniques: (A) the amount of deviance in patch occupancy explained by each model (pseudo- R^2), (B) Wald tests, and (C) Akaike Information Criterion (AIC) model weights (w_i). Absolute values of Z values (logistic regression coefficient/SE) from Wald tests are shown for the six simple models in (B). See Table 1 for descriptions of the connectivity measures, which are either area-based (open circles) or distance-based (solid circles). Means and 95% confidence intervals are shown.

measures were greatly improved (NS_i and BS_i , respectively). Likewise, Bastin and Thomas (1999) found that NS_i was better than NH_i at predicting the occurrence of 22 tree species in a fragmented urban landscape. This finding is consistent with metapopulation and island biogeography theory, because the proximity of source populations rather than habitat patches per se should most strongly affect the probability of colonization and

TABLE 3. Results of mixed-model ANOVAs comparing the ability of seven models to predict species' occupancy and colonization probabilities (see Table 1 for model descriptions).

Comparison method	Occupancy			Colonization		
	<i>F</i>	df	<i>P</i>	<i>F</i>	df	<i>P</i>
Explained deviance (pseudo- R^2)	23.9	6, 139	<0.0001	4.7	6, 89	<0.0001
AIC weight (w_i)	14.2	4, 92	<0.0001	2.4	6, 89	0.03
Wald test (<i>Z</i> value)	13.9	5, 115	<0.0001	6.9	5, 78	<0.0001

Notes: Three techniques were used to evaluate model performance: (1) pseudo- R^2 values (the amount of deviance in occupancy or colonization explained), (2) Akaike Information Criterion (AIC) weights, and (3) Wald tests (*Z* values, regression coefficient/SE). For occupancy, results are shown for the AIC comparison that excluded the two models with terms for focal patch area (*AS* and $A \times NS$). Data from some metapopulations were reported in the same studies, so "study" was included as a random effect and "connectivity model" was included as a fixed effect in the ANOVAs.

occupancy (MacArthur and Wilson 1967, Gilpin and Diamond 1976).

Unlike Moilanen and Nieminen (2002), who concluded that all NN measures were inferior and recommended using S_i or AS_i , I found in my broader comparison that the NN measure NS_i performed as well as S_i did, if not better. Across the 24 metapopulations used to evaluate model performance, NS_i and S_i explained a similar amount of deviance in patch occupancy and colonization probabilities, their mean *Z* values were not significantly different, and model *NS* had a higher average AIC weight than model *S* (Fig. 1D). Although these results appear to conflict with those reported by Moilanen and Nieminen (2002), a closer look reveals general consistency between studies. Two of the 24 metapopulations in my analysis were used by Moilanen and Nieminen (2002) to evaluate models (metapopulations 3 and 15; Table 2), and our results for these metapopulations were similar. Although their literature survey showed that studies using NN measures were less likely to find a significant effect of connectivity than studies using IFM and buffer measures, most of these studies (24/35) used NH_i rather than NS_i . This result is therefore consistent with my quantitative meta-analysis showing a weaker effect of NH_i in comparison to NS_i and S_i .

The role of focal patch area

The IFM model *AS* and the NN-based multiple regression model $A \times NS$ were by far the best performing occupancy models (Fig. 1), but they were not better than models *S*, *NS*, and *BS* at predicting colonization (Fig. 2). The key feature that distinguished models *AS* and $A \times NS$ from the others was the inclusion of a term for focal patch area, A_i (Table 1). While inclusion of A_i improved the prediction of occupancy probabilities for nearly all metapopulations (Appendix A), its inclusion improved the prediction of colonization probabilities for less than half of the metapopulations (Appendix B). Thus, focal patch area appears to consistently improve occupancy models and inconsistently improve colonization models. Other studies not included in this meta-analysis have been similarly divided, with some finding that larger patches are more likely to be colonized (e.g., Saari et al. 1998,

Crone et al. 2001, Crooks et al. 2001, Ferraz et al. 2007) and others finding no effect of focal patch area (e.g., Cronin 2004, Franken and Hik 2004). In general, however, results of this study suggest that properties of source patches surrounding an empty focal patch are more important than the size of the focal patch in determining its likelihood of being colonized.

While focal patch area A_i affected the performance of occupancy and colonization models differently, the way in which A_i was included in the models did not have a strong impact on performance. The A_i measure was included in the models in two distinct ways: either directly in the calculation of the connectivity metric (AS_i), as in Moilanen and Nieminen (2002), or as a separate factor in a multiple regression model ($A \times NS$). Both types of models performed similarly, but AS_i requires seven parameters for its calculation vs. three parameters for model $A \times NS$ (Table 1). Moreover, the validity of AS_i as a metric is questionable. Because AS_i includes two terms for patch area (focal patch area A_i and surrounding patch A_j ; Table 1), its units are area^2 , which is difficult to interpret biologically. I feel the use of a multiple regression model such as $A \times NS$ is a better way to examine the influence of focal patch area, from both biological and statistical standpoints. Biologically, the predictors in the multiple regression model have units that make sense. Statistically, the independent and interactive effects of the predictors can be examined. This is advantageous because focal patch area is arguably a patch covariate that is distinct from connectivity, and some may argue that it should not be included in connectivity calculations. Additionally, the multiple regression model is penalized for the added parameter when using model comparison techniques such as AIC, whereas the additional parameters that go into calculating the IFM measures are basically hidden.

Potential drawbacks of IFM measures

The primary advantage of IFM measures is also a potential drawback: they contain more information about the patch network and dispersal abilities of species than NN measures, but this detail requires more parameterization. Parameter estimates for α , b , and c should ideally be based on mark-recapture data (Hanski et al. 2000, Wahlberg et al. 2002b). These data are

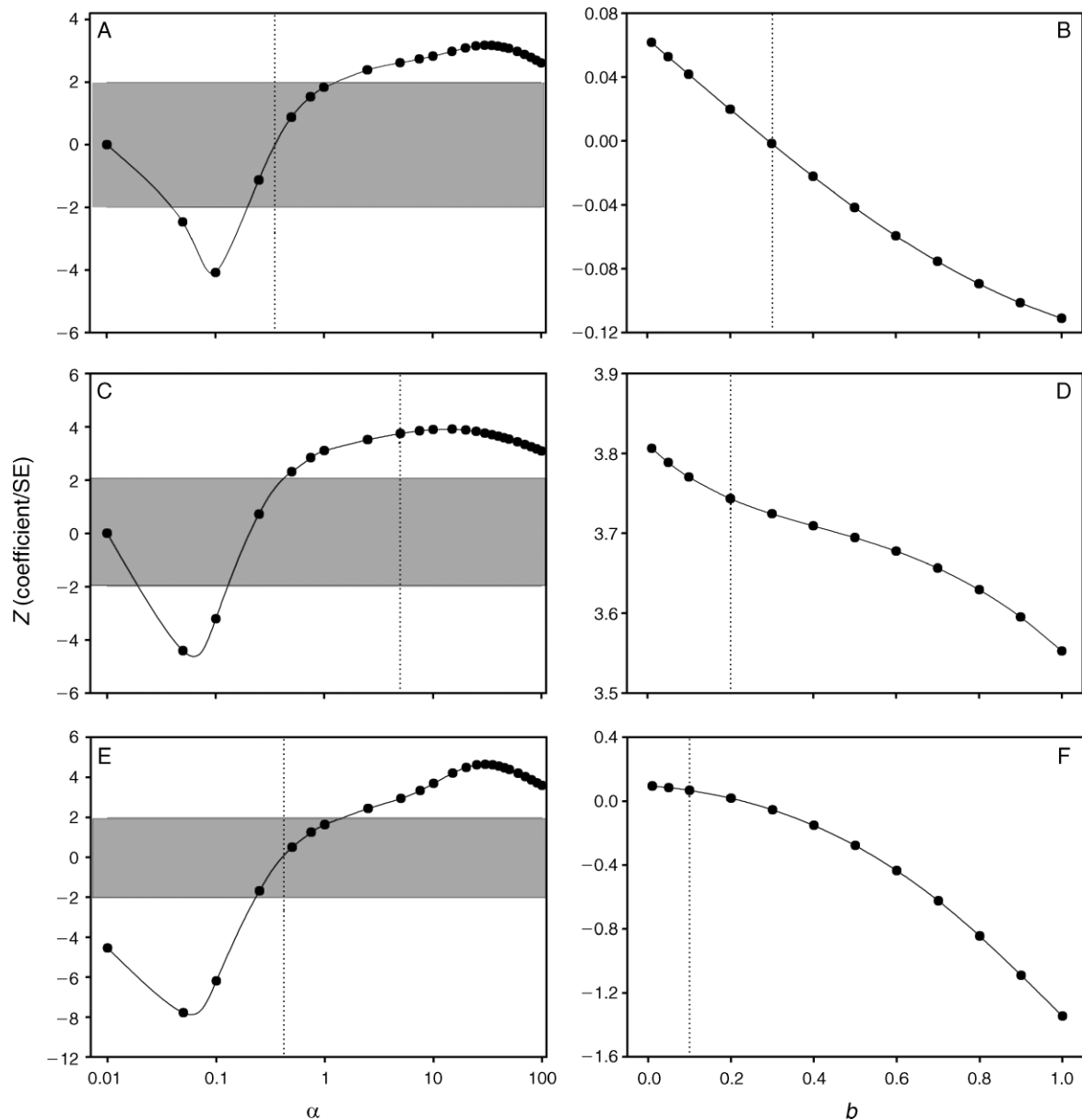


FIG. 3. Effect of parameters α and b on the S model Wald statistic for (A, B) the *Scolitantides orion* metapopulation, (C, D) the *Melitaea diamina* metapopulation, and (E, F) the *Euphydryas aurinia* metapopulation. The Wald statistic, or Z value, is the coefficient from the logistic regression analysis divided by its standard error. Areas shaded in gray indicate the range of Z values that are nonsignificant. Vertical dotted lines in panels A, C, and E show the published value of α , and vertical dotted lines in panels B, D, and F show the published value of b .

usually unavailable, and conservation ecologists often lack the resources to conduct such detailed species-specific studies. Thus, many researchers ignore these parameters when calculating S_i (e.g., Steffan-Dewenter and Tscharrntke 2000, Cronin 2004). Fortunately, I found that S_i performance was relatively insensitive to changes in b , and c has also been shown to have little effect on S_i (Moilanen and Nieminen 2002). Thus, if information is not available for these scaling parameters, the performance of S_i should not be strongly affected.

In contrast, α is an important component of the negative exponential dispersal kernel and should not be ignored. Performance of S_i was strongly affected by α , and I found that both estimated and default α values led to S_i values with low predictive ability. Moreover, inaccurate estimates of α could easily lead to the false conclusion that increased connectivity decreases the likelihood of occupancy (see Fig. 2). Moilanen and Nieminen (2002) also found nonlinear changes in Z values as they varied α from 0 to 5. Consistent with my



PLATE 1. A metapopulation of the Marsh fritillary butterfly *Euphydryas aurinia* (shown here) that occurred in patchy meadows in Finland was included in this study. Photo credit: Niklas Wahlberg.

findings, they report that the maximum Z value was obtained when α was far greater than the estimated value for *Scolitantides orion*. Likewise, Hokit et al. (2001) found that the performance of S_i was sensitive to changes in α for the lizard *Sceloporus woodi* (metapopulation 6; Table 2). These findings suggest that the migration distances used to calculate α may often be inaccurate. According to Wahlberg et al. (2002b), these distances should be mean daily movement rates (but see alternative definitions of α in the following paragraph). However, daily movement rates are rarely available and annual movements are often used to calculate α . Because α is the inverse of the migration distance, overestimation of migratory ability due to use of annual movement data could explain the general tendency for α to be far below the optimal value. Estimation of α from the occupancy data themselves may be the most practical way to optimize IFM connectivity measures (Pellet et al. 2007).

Aside from the difficulties associated with estimating α and S_i sensitivity, there are two problems with the way α has been implemented in the literature to date: (1) many definitions have been published for α , and (2) the units that are used for α are important but rarely specified. Definitions of α include: a distance-dependent survival rate (Hanski 1994a), migration rate (Moilanen and Nieminen 2002, Wahlberg et al. 2002b), or colonization rate (Wahlberg et al. 2002a); a parameter that “determines the effect of distance on isolation” (Hanski et al. 2000); and “a species-specific parameter (or several parameters) describing the dispersal ability of the species” (Moilanen and Hanski 2001). The two published equations for α are incompatible:

$$\alpha = 1/\text{average distance moved} \quad (1)$$

$$\alpha = 30.94 \times e^{-0.004 \times \text{average distance}} \quad (2)$$

(Wahlberg et al. 2002b). Not surprisingly, this confusing variety of definitions and equations has led to almost no consistency among studies in the way α (and hence S_i) is calculated (e.g., Valimaki and Itamies 2003, Franken and Hik 2004, Maes and Bonte 2006).

Perhaps because of the confusion surrounding α and scarcity of data required to calculate it, α is often left out of S_i calculations altogether, which gives it a value of 1 (e.g., Reunanen et al. 2002, Krauss et al. 2003, Biedermann 2005). This practice is problematic, not only because a default value of 1 can lead to poor S_i performance, but also because α is not a unitless scaling parameter (Winfree et al. 2005). The units of α should be distance⁻¹ to cancel out d_{ij} , leaving S_i in units of area. An α value of 1 in a study with distance measured in kilometers is 1000 times different than an α of 1 in a study with distance measured in meters. Thus, the fact that units of α (and often d_{ij}) are rarely specified can lead to poor model construction that is easy to overlook without close scrutiny. These problems are not inherent to the parameter, and they could be avoided in the future if a single definition (and equation) for α is agreed upon and authors ensure that units are always specified.

What is the best measure of patch connectivity for applied conservation?

The best measure of patch connectivity depends largely on the level of spatial detail needed to address the conservation problem. Measures of IFM are useful for detailed modeling of metapopulation dynamics, whereas buffer and NN measures are not. If the contribution of specific habitat patches to metapopulation viability needs to be determined, for example, an IFM measure may be necessary (Wahlberg et al. 1996). For applied conservation problems that are not spatially explicit, BS_i or NS_i may be preferable measures of patch

connectivity. Although these buffer and NN measures lack the biological detail of IFM measures, simplicity does not appear to decrease their ability to predict patterns of patch occupancy and colonization. Additionally, they are easier to compute, avoid the problems associated with IFM measures, and provide results that are easier to compare among species and studies. The NN measure NS_i is particularly attractive because it requires no data beyond patch coordinates and occupancy data, whereas buffer measures often use species dispersal data (which are notoriously inaccurate) to determine the buffer radius.

Models NS and $A \times NS$ can be used effectively to address several applied conservation problems. For example, the relative influence of focal patch area (A_i) and isolation are often of interest to conservation ecologists (Fahrig 1997, Fleishman et al. 2002, James et al. 2003, Krauss et al. 2003), and the independent and combined effects of these factors can be assessed statistically using model $A \times NS$. This framework facilitates testing of significant interactions between patch area and isolation, which could lead to important ecological insights. For example, the theory of island biogeography predicts that area effects should be stronger on islands that are more isolated and that isolation effects should be stronger on smaller islands (MacArthur and Wilson 1967:24–32); this prediction could be tested using $A \times NS$. Another practical application of NS and $A \times NS$ is the use of regression coefficients to determine the minimum size and maximum isolation values that correspond to a given probability of occupancy or colonization (Hinsley et al. 1996, Biedermann 2003). At the very least, researchers would be wise to determine whether using an incidence function model measure would improve their study before abandoning robust, simple, and useful nearest-neighbor measures.

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LITERATURE CITED

- Baile, J., C. Hilton-Taylor, and S. N. Stuart. 2004. 2004 IUCN red list of threatened species: a global assessment. International Union for the Conservation of Nature and Natural Resources, Cambridge, UK.
- Bastin, L., and C. D. Thomas. 1999. The distribution of plant species in urban vegetation fragments. *Landscape Ecology* 14:493–507.
- Beard, K. H., N. Hengartner, and D. K. Skelly. 1999. Effectiveness of predicting breeding bird distributions using probabilistic models. *Conservation Biology* 13:1108–1116.
- Bender, D. J., L. Tischendorf, and L. Fahrig. 2003. Using patch isolation metrics to predict animal movement in binary landscapes. *Landscape Ecology* 18:17–39.
- Biedermann, R. 2003. Body size and area–incidence relationships: Is there a general pattern? *Global Ecology and Biogeography* 12:381–387.
- Biedermann, R. 2005. Incidence and population dynamics of the leaf beetle *Gonioctena olivacea* in dynamic habitats. *Ecography* 28:673–681.
- Bonte, D., L. Baert, L. Lens, and J. P. Maelfait. 2004. Effects of aerial dispersal, habitat specialisation, and landscape structure on spider distribution across fragmented grey dunes. *Ecography* 27:343–349.
- Burnham, K. P., and D. R. Anderson. 2001. Kullback-Leibler information as a basis for strong inference in ecological studies. *Wildlife Research* 28:111–119.
- Crone, E. E., D. Doak, and J. Pokki. 2001. Ecological influences on the dynamics of a field vole metapopulation. *Ecology* 82:831–843.
- Cronin, J. T. 2004. Host–parasitoid extinction and colonization in a fragmented prairie landscape. *Oecologia* 139:503–514.
- Crooks, K. R., and M. Sanjayan. 2006. Connectivity conservation. Cambridge University Press, New York, New York, USA.
- Crooks, K. R., A. V. Suarez, D. T. Bolger, and M. E. Soule. 2001. Extinction and colonization of birds on habitat islands. *Conservation Biology* 15:159–172.
- Eber, S., and R. Brandl. 2003. Regional patch dynamics of *Cirsium arvense* and possible implications for plant–animal interactions. *Journal of Vegetation Science* 14:259–266.
- Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* 61:603–610.
- Ferraz, G., J. D. Nichols, J. E. Hines, P. C. Stouffer, R. O. Bierregaard, and T. E. Lovejoy. 2007. A large-scale deforestation experiment: effects of patch area and isolation on Amazon birds. *Science* 315:238–241.
- Fleishman, E., C. Ray, P. Sjogren-Gulve, C. L. Boggs, and D. D. Murphy. 2002. Assessing the roles of patch quality, area, and isolation in predicting metapopulation dynamics. *Conservation Biology* 16:706–716.
- Franken, R. J., and D. S. Hik. 2004. Influence of habitat quality, patch size and connectivity on colonization and extinction dynamics of collared pikas *Ochotona collaris*. *Journal of Animal Ecology* 73:889–896.
- Gilpin, M. E., and J. M. Diamond. 1976. Calculation of immigration and extinction curves from the species–area–distance relation. *Proceedings of the National Academy of Sciences (USA)* 73:4130–4134.
- Hagler, T. M., and G. E. Mitchell. 1992. Goodness-of-fit measures for probit and logit. *American Journal of Political Science* 36:762–784.
- Hanski, I. 1994a. Patch-occupancy dynamics in fragmented landscapes. *Trends in Ecology and Evolution* 9:131–135.
- Hanski, I. 1994b. A practical model of metapopulation dynamics. *Journal of Animal Ecology* 63:151–162.
- Hanski, I., J. Alho, and A. Moilanen. 2000. Estimating the parameters of survival and migration of individuals in metapopulations. *Ecology* 81:239–251.
- Hanski, I., M. Kuussaari, and M. Nieminen. 1994. Metapopulation structure and migration in the butterfly *Melitaea cinxia*. *Ecology* 75:747–762.
- Hedges, L. V., and I. Olkin. 1985. Statistical methods for meta-analysis. Academic Press, New York, New York, USA.
- Hinsley, S. A., P. E. Bellamy, I. Newton, and T. H. Sparks. 1996. Influences of population size and woodland area on bird species distributions in small woods. *Oecologia* 105:100–106.
- Hjermann, D. O., and R. A. Ims. 1996. Landscape ecology of the wart-biter *Decticus verrucivorus* in a patchy landscape. *Journal of Animal Ecology* 65:768–780.
- Hokit, D. G., B. M. Stith, and L. C. Branch. 1999. Effects of landscape structure in Florida scrub: a population perspective. *Ecological Applications* 9:124–134.
- Hokit, D. G., B. M. Stith, and L. C. Branch. 2001. Comparison of two types of metapopulation models in real and artificial landscapes. *Conservation Biology* 15:1102–1113.

- James, M., F. Gilbert, and S. Zalut. 2003. Thyme and isolation for the Sinai baton blue butterfly (*Pseudophilotes sinaicus*). *Oecologia* 134:445–453.
- Knapp, R. A., K. R. Matthews, H. K. Preisler, and R. Jellison. 2003. Developing probabilistic models to predict amphibian site occupancy in a patchy landscape. *Ecological Applications* 13:1069–1082.
- Krauss, J., I. Steffan-Dewenter, and T. Tschardt. 2003. How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? *Journal of Biogeography* 30:889–900.
- Lindenmayer, D. B., and J. Fischer. 2007. Tackling the habitat fragmentation panchreston. *Trends in Ecology and Evolution* 22:127–132.
- MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.
- Maes, D., and D. Bonte. 2006. Using distribution patterns of five threatened invertebrates in a highly fragmented dune landscape to develop a multispecies conservation approach. *Biological Conservation* 133:490–499.
- Moilanen, A., and I. Hanski. 2001. On the use of connectivity measures in spatial ecology. *Oikos* 95:147–151.
- Moilanen, A., and M. Nieminen. 2002. Simple connectivity measures in spatial ecology. *Ecology* 83:1131–1145.
- Pellet, J., E. Fleishman, D. S. Dobkin, A. Gander, and D. D. Murphy. 2007. An empirical evaluation of the area and isolation paradigm of metapopulation dynamics. *Biological Conservation* 136:483–495.
- Pope, S. E., L. Fahrig, and N. G. Merriam. 2000. Landscape complementation and metapopulation effects on leopard frog populations. *Ecology* 81:2498–2508.
- Prugh, L. R., K. E. Hodges, A. R. E. Sinclair, and J. S. Brashares. 2008. Effect of habitat area and isolation on fragmented animal populations. *Proceedings of the National Academy of Sciences (USA)* 105:20770–20775.
- R Development Core Team. 2007. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reunanen, P., A. Nikula, M. Monkkonen, E. Hurme, and V. Nivala. 2002. Predicting occupancy for the Siberian flying squirrel in old-growth forest patches. *Ecological Applications* 12:1188–1198.
- Saari, L., J. Aberg, and J. E. Swenson. 1998. Factors influencing the dynamics of occurrence of the hazel grouse in a fine-grained managed landscape. *Conservation Biology* 12:586–592.
- Schmidt, B. R. 2005. Monitoring the distribution of pond-breeding amphibians when species are detected imperfectly. *Aquatic Conservation* 15:681–692.
- Sokal, R. R., and F. J. Rohlf. 1995. Biometry. Third edition. W.H. Freeman, New York, New York, USA.
- Steffan-Dewenter, I., and T. Tschardt. 2000. Butterfly community structure in fragmented habitats. *Ecology Letters* 3:449–456.
- Tischendorf, L., D. J. Bender, and L. Fahrig. 2003. Evaluation of patch isolation metrics in mosaic landscapes for specialist vs. generalist dispersers. *Landscape Ecology* 18:41–50.
- Tischendorf, L., and L. Fahrig. 2000a. How should we measure landscape connectivity? *Landscape Ecology* 15:633–641.
- Tischendorf, L., and L. Fahrig. 2000b. On the usage and measurement of landscape connectivity. *Oikos* 90:7–19.
- Tischendorf, L., and L. Fahrig. 2001. On the use of connectivity measures in spatial ecology: a reply. *Oikos* 95:152–155.
- Valimaki, P., and J. Itamies. 2003. Migration of the clouded Apollo butterfly *Parnassius mnemosyne* in a network of suitable habitats: effects of patch characteristics. *Ecography* 26:679–691.
- Wahlberg, N., T. Klemetti, and I. Hanski. 2002a. Dynamic populations in a dynamic landscape: the metapopulation structure of the marsh fritillary butterfly. *Ecography* 25:224–232.
- Wahlberg, N., T. Klemetti, V. Selonen, and I. Hanski. 2002b. Metapopulation structure and movements in five species of checkerspot butterflies. *Oecologia* 130:33–43.
- Wahlberg, N., A. Moilanen, and I. Hanski. 1996. Predicting the occurrence of endangered species in fragmented landscapes. *Science* 273:1536–1538.
- Winfrey, R., J. Dushoff, E. E. Crone, C. B. Schultz, R. V. Budny, N. M. Williams, and C. Kremen. 2005. Testing simple indices of habitat proximity. *American Naturalist* 165:707–717.

APPENDIX A

Comparison of seven connectivity models used to predict the patch occupancy patterns of 24 metapopulations (*Ecological Archives* A019-051-A1).

APPENDIX B

Comparison of seven connectivity models used to predict the colonization patterns of 15 metapopulations (*Ecological Archives* A019-051-A2).