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ORIGINAL PAPER

Habitat quality of source patches and connectivity in fragmented landscapes

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Abstract Because spatial connectivity is critical to dispersal success and persistence of species in highly fragmented landscapes, the way that we envision and measure connectivity is consequential for biodiversity conservation. Connectivity metrics used for predictive modeling of spatial turnover and patch occupancy for metapopulations, such as with Incidence Function Models (IFM), incorporate distances to and sizes of possible source populations. Here, our focus is on whether habitat quality of source patches also is considered in these connectivity metrics. We propose that effective areas (weighted by habitat quality) of source patches should be better surrogates for population size and dispersal potential compared to unadjusted patch areas. Our review of a representative sample of the literature revealed that only 12.5% of studies incorporated habitat quality of source patches into IFM-type connectivity metrics. Quality of source patches generally was not taken into account in studies even if habitat quality of focal patches was included in analyses. We provide an empirical example for a metapopulation of a rare wetland species, the round-tailed muskrat (*Neofiber alleni*), demonstrating that a connectivity metric based on effective areas of source patches better predicts patch colonization and occupancy than a metric that used simple patch areas. The ongoing integration of landscape ecology and metapopulation dynamics could be hastened by incorporating habitat quality of source patches into spatial connectivity metrics applied to species conservation in fragmented landscapes.

Keywords Colonization · Connectivity · Fragmentation · Habitat heterogeneity · Metapopulation · Patch quality · *Neofiber alleni*

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Introduction

Habitat connectivity is crucial to dispersal success, persistence, and genetic diversity of species in fragmented landscapes. Exactly how we conceptualize and quantify connectivity is important for understanding spatial population processes and for conserving biodiversity. Patch connectivity, the inverse of patch isolation, should index the likelihood of immigration into a focal habitat patch (Tischendorf and Fahrig 2000; Moilanen and Hanski 2006). Metapopulation studies frequently use patch connectivity metrics to model recolonization of patches and demographic rescue of small populations (Moilanen and Hanski 2001; Moilanen and Nieminen 2002). In contrast, landscape connectivity applies to whole landscapes (Tischendorf and Fahrig 2000) and is the degree to which landscape structure promotes or impedes movements of individuals among resource patches (Taylor et al. 1993). Our emphasis is on patch connectivity as used for predictive modeling of metapopulations in highly fragmented environments. Another less subtle distinction is between structural connectivity and functional connectivity (Taylor et al. 1993; Tischendorf and Fahrig 2000; Baguette and Van Dyck 2007). Structural connectivity measures the spatial patterning of habitat based on mappable landscape features. Functional connectivity is a species-specific measure that considers how movement behavior and dispersal capacity of species interact with structural connectivity.

Previous assessments of spatial connectivity metrics have produced valuable insights. Moilanen and Nieminen (2002) demonstrated that the nearest neighbor measure (i.e., distance from focal patch to nearest source patch) can be inferior to buffer metrics and Incidence Function Model (IFM) metrics for predicting colonization (see also Moilanen and Hanski 2006). Buffer metrics sum all occupied habitat areas within a specified distance of a focal patch to index potential sources of dispersers. However, buffer measures are sensitive to the selected buffer radius and do not consider explicit spatial locations of source patches within the buffer (Moilanen and Nieminen 2002). IFM connectivity metrics perform well by incorporating the distances to and sizes of potential source populations. Patch areas of source populations are used as a surrogate for local population sizes. Simulation studies also support the superiority of area-informed connectivity metrics relative to distance-only measures (Bender et al. 2003; Tischendorf et al. 2003). In contrast, Prugh (2009) recently evaluated connectivity measures for 24 metapopulations and concluded that nearest neighbor measures can perform as well as IFM metrics if distance to the nearest occupied patch is used as a source instead of distance to any nearest patch. Winfree et al. (2005) determined that none of the simple connectivity metrics were good predictors of colonization for several empirical systems and suggested that more detailed biological information should be included in metrics. Relative performance of connectivity metrics also can depend on spatial scaling of the system (i.e., dispersal ability of species relative to interpatch distances; Matter et al. 2005). Finally, existing connectivity metrics can be ordered so as to display a progression from structural to functional measures and to represent a tradeoff between information content and data requirements (Calabrese and Fagan 2004; Fagan and Calabrese 2006).

Our focus is on habitat quality of suitable patches and its effect on patch connectivity. Researchers now recognize that quality of focal patches can affect local extinctions, colonizations, and occupancy (Thomas 1994; Hokit et al. 1999; Fleishman et al. 2002; Franken and Hik 2004; Armstrong 2005; Thornton et al. 2011). Patch areas can be weighted by habitat quality to create a more ecologically relevant measure termed ‘effective patch areas’ (Hanski 1994; Hokit et al. 2001). However, we posit that habitat quality of source patches typically is ignored when patch connectivity metrics are constructed. For instance, IFM metrics use patch areas of source patches and not their effective patch areas. Habitat-weighted areas often should be better surrogates for population sizes and thus better predictors of dispersal potential.

Our objectives were twofold. First, we reviewed relevant literature to determine how often habitat quality of source patches was incorporated into patch connectivity metrics applied to fragmented landscapes. Second, we analyzed empirical data for a mammal metapopulation and directly compared the abilities of IFM connectivity metrics that either used raw areas or effective areas of source patches to predict colonization and patch occupancy. Previous reviews have discussed possible extensions of current connectivity metrics but have not underscored the importance of habitat quality of source patches (Moilanen and Nieminen 2002; Bender et al. 2003; Calabrese and Fagan 2004; Winfree et al. 2005; Fagan and Calabrese 2006; Moilanen and Hanski 2006; Kindlmann and Burel 2008; Kadoya 2009; Prugh 2009; but see Visconti and Elkin 2009).

Mini-review

Our goal was to survey a representative sample of literature in spatial ecology in which IFM-type connectivity metrics were applied. We excluded from our review any studies that used a nearest-neighbor measure or a habitat buffer because our experience was that habitat quality of sources was rarely included in these simpler connectivity metrics. We were particularly interested in whether there were changes over time in how researchers dealt with habitat quality of patches when measuring connectivity. Therefore, we first revisited the literature survey conducted by Moilanen and Nieminen (2002) in which they reviewed all 1998–2000 issues of six representative journals in ecology and conservation: *American Naturalist*, *Conservation Biology*, *Ecology*, *Journal of Animal Ecology*, *Landscape Ecology*, and *Oikos*. Moilanen and Nieminen (2002) excluded studies of population genetic structure. We inspected 20 papers from Moilanen and Nieminen's (2002) review in which researchers had used some type of IFM connectivity metric. We removed five papers from our survey in which connectivity was measured using only summed distances to source patches but not patch areas (e.g., Nekola 1999), or by weighting source patches with direct estimates of population sizes instead of with indirect estimates from patch areas (e.g., Thomas and Kunin 1999). Hence, we reviewed 15 papers from 1998 to 2000 (Appendix).

Next, we repeated the literature survey procedures of Moilanen and Nieminen (2002) for the same six journals for all 2005–2008 issues. We included papers that used some form of IFM metric. As before, we did not review studies in which the response variable was genetic similarity. We reviewed 25 papers from 2005 to 2008 (Appendix). A quantitative meta-analysis (e.g., Prugh et al. 2008) was not possible because information needed to estimate effect sizes—relative performances of connectivity metrics with and without quality of source patches—was missing from nearly all studies (see also Mortelliti et al. 2010). Moreover, a meta-analysis was not necessary to make our main points (see "Results" section).

For the total of 40 papers in our mini-review, we asked two main questions. (1) Was habitat quality of source patches included in connectivity metrics through the use of effective patch areas or some similar weighting? (2) Was habitat quality of focal patches considered in studies? An affirmative answer to the second question would indicate researchers were aware of the potential importance of habitat quality of suitable patches for their system. We classified papers as belonging to the early period (1998–2000) or the late period (2005–2008). We also classified papers based on whether the response variable was typical of metapopulation studies (occupancy, extinction, colonization, metapopulation persistence) or some other response (see Appendix). We used logistic regression (Proc Genmod, SAS 2002) to examine whether the proportion of studies that included habitat quality of source patches depended on time period and the type of response variable. We conducted a separate analysis with logistic regression to ask if the likelihood that a study included habitat quality of focal patches depended on time period and the response variable. We used an Akaike Information Criterion (AIC_c) to select the best model for each response variable and to rank the others (Burnham and Anderson 2002). We present results as AIC differences ($\Delta_i = AIC_i - \text{minimum AIC}$) so that the best model has $\Delta_i = 0$. We also report Akaike weights (w_i) that are normalized relative likelihoods that model i is the best model.

Effect of matrix heterogeneity on connectivity was not the focus of our review. Nevertheless, we kept track of whether investigators used Euclidean distances or effective distances modified by the matrix (Ricketts 2001; Chardon et al. 2003; Verbeylen et al. 2003) to measure interpatch distances as an additional gauge of whether habitat heterogeneity was being incorporated into spatial ecology.

Mini-review results

Overall, only 5 of 40 (12.5%) studies incorporated habitat quality of source patches into connectivity metrics using effective patch areas or a related approach (Appendix). There was little evidence that time period or response type had an effect on whether studies included source patch quality (Table 1). The top-ranked model was the intercept-only model. The only other competitive model ($\Delta_i \leq 2$) included time period as a predictor, but this model did not alter the log-likelihood much compared to the intercept-only model (Table 1).

Table 1 Ranking of logistic regression models to evaluate how habitat quality of patches was treated in published papers in spatial ecology (see Appendix)

Response variable and model[a]	K	Log-likelihood	AIC_c	
			Δ_i	w_i
Source patch				
Intercept-only	1	−15.07	0.00	0.50
Time	2	−14.67	1.41	0.25
Response	2	−15.03	2.14	0.17
Time, response	3	−14.56	3.54	0.08
Focal patch				
Intercept-only	1	−27.68	0.00	0.37
Time	2	−26.70	0.26	0.32
Response	2	−27.53	1.59	0.16
Time, response	3	−26.31	1.83	0.15

Source patch refers to whether habitat quality of sources was included in connectivity metrics. Focal patch refers to whether habitat quality of target patches was considered. K = no. estimable parameters, $\Delta_i = AIC_{ci} - \text{minimum } AIC_c$, and w_i are Akaike weights

[a] Predictor variables include time period of study that was either 1998–2000 or 2005–2008 (time), and whether the response variable was typical of metapopulation studies or not (response)

Nineteen of 40 (47.5%) studies included habitat quality of focal patches in their analyses (Appendix). We detected no strong effects of time period or response type on whether studies included focal patch quality (Table 1). The top-ranked model again was the intercept-only model. The Δ_i values and log-likelihoods, however, suggested a weak effect of time period. There was an increase over time in the likelihood that studies considered focal patch quality (1998–2000 = 33.3%, 2005–2008 = 56.0%). Overall, in 14 of 19 (73.7%) studies in which habitat quality of focal patches was considered, habitat quality of source patches was ignored when measuring connectivity (Appendix). We are responsible for such an inconsistent treatment of patch quality in some of our own research (Hokit et al. 1999; Schooley and Wiens 2005; but see Hokit et al. 2001; Schooley and Branch 2007, 2009).

Only 3 of 40 (7.5%) reviewed studies used effective distances modified by intervening matrix type or topography to measure inter-patch distances (Moilanen and Hanski 1998; Schooley and Wiens 2005; Snäll et al. 2008). Euclidean distances remained the norm for measuring patch isolation.

Empirical example: source quality and connectivity for muskrats

To determine whether including habitat quality of source patches improved predictions of patch occupancy and colonization, we investigated spatial dynamics of round-tailed muskrats (*Neofiber alleni*) at Avon Park Air Force Range in central Florida (see Schooley and Branch 2009). Suitable habitat for muskrats covered <5% of the landscape and consisted of small (median = 0.9 ha), geographically isolated depression marshes. The round-tailed muskrat is a rare, nocturnal, semi-aquatic herbivore with a restricted geographic distribution (Florida and southern Georgia) that has been proposed as a Species of Special Concern due to extensive loss of wetland habitat (Lefebvre and Tilmant 1992). Muskrats displayed metapopulation dynamics at Avon Park in which patch occupancy was stable between years, despite substantial local turnover, because extinctions were balanced by recolonizations (Schooley and Branch 2009).

In central Florida, round-tailed muskrats typically occur within zones of maidencane grass (*Panicum hemitomon*) in wetlands, often use maidencane to build lodges, and maidencane is their main diet item (Birkenholz 1963; Schooley and Branch 2009). Hence, we developed a maidencane index as a measure of patch quality (Schooley and Branch 2009). For each suitable wetland, we recorded cover and density of maidencane grass and then calculated an index that ranged from 0 (no maidencane) to 1 (pure maidencane with an estimated cover of 81–100%). The mean maidencane index for wetlands was 0.18 (SD = 0.16, min. = 0, max. = 0.88). Our study area included a strong gradient in habitat quality of patches (Schooley and Branch 2007; Mortelliti et al. 2010).

We surveyed 457 wetlands for presence-absence of muskrats during fall–winter in each of 2 years (2002–2003, 2003–2004). Patch occupancy was determined reliably based on presence of active lodges constructed by muskrats. False absences were unlikely (Schooley and Branch 2005) so use of occupancy modeling techniques was unnecessary (MacKenzie et al. 2003). Instead, we used ordinal logistic regression (Proc Genmod, SAS 2002) to model patch occupancy in which the response variable was the number of years a wetland was occupied (0, 1, 2). We used binary logistic regression to model colonization probability. Local extinctions were not strongly related to connectivity (Schooley and Branch 2009), so we do not evaluate extinction models here.

We focused on two key predictors for metapopulations—patch area and connectivity—in our logistic regression models. We included either patch area or effective patch area of the focal patch. Effective area (EA_i) for patch i was calculated as Q_iA_i/Q^*, where Q_i was the habitat quality (maidencane index) of patch i and Q^* was the maximal habitat quality of any patch (Hanski 1994; Hokit et al. 2001). Our spatial connectivity metrics either used patch areas of source patches (Connectivity_A) or effective patch areas of source patches that incorporated habitat quality (Connectivity_EA). Connectivity_A (Ca_i) of patch i was defined as

$$Ca_i = \sum_{j \neq i} p_j \exp(-\alpha d_{ij}) A_j^b \qquad (1)$$

where p_j is the likelihood that patch j was occupied the previous year, α is a parameter that scales the effect of distance on migration, d_{ij} is the distance (km) between centers of patches i and j (for $d_{ij} \leq 2$ km), A_j is the area of patch j, and b is a scaling parameter relating abundance to area. We set p_j equal to 0 for patches unoccupied in both years, 0.5 for patches occupied in 1 year, and 1 for patches occupied in both years. We estimated α as 0.5 by using logistic regression to model colonization of patches in 2003–2004 as a function of $\exp(-\alpha d)$, where d was distance to nearest potential source patch (Hokit et al. 2001), and selecting the value of α that minimized the deviance of model fit. Emigration is unlikely to scale linearly with patch area, so we assumed a value of 0.5 for b, which is a more reasonable expectation (Moilanen and Nieminen 2002). Model performance is relatively insensitive to changes in b (Moilanen and Nieminen 2002; Prugh 2009). We calculated connectivity using only source patches within 2 km because our study area was not an isolated patch network and a minor edge adjustment was needed (Schooley and Branch 2009). We used a buffer radius of 2 km because only 2% of vacant wetlands located >2 km from a source patch were colonized between years (Schooley and Branch 2007).

We calculated Connectivity_EA (Cea_i) for patch i where all variables are as defined in Eq. 1 except that we replaced area of source patches (A_j) with effective area of source patches (EA_j). As before, effective area (EA_j) for patch j was calculated as Q_jA_j/Q^*, where Q_j was the habitat quality of patch j and Q^* was the maximal patch quality.

We used AIC_c to rank the logistic regression models for occupancy and colonization (Burnham and Anderson 2002). For each response variable, we evaluated eight models with covariates (Area, Effective Area, Connectivity_A, Connectivity_EA, Area + Connectivity_A, Area + Connectivity_EA, Effective Area + Connectivity_A, Effective Area + Connectivity_EA) plus the intercept-only model.

Results

In each year, 26% of suitable patches ($n = 457$) were occupied. The only competitive model for predicting occupancy (Table 2) included the effective area of the focal patch ($\beta = 1.624$, SE = 0.270) and Connectivity_EA ($\beta = 0.185$, SE = 0.027). The spatial connectivity metric that included habitat quality of source patches was superior to the metric that ignored habitat quality. The best patch occupancy model explained a reasonable amount of variation ($R^2 = 0.34$). All models with a single covariate (not shown in Table 2) had no support ($\Delta_\text{i} \geq 48.27$, $\text{w}_\text{i} = 0.00$).

Table 2 Ranking of logistic regression models for predicting patch occupancy and colonization of wetlands for a metapopulation of round-tailed muskrats

Response variable and model[a]	K	Log-likelihood	AIC_c	
			Δ_i	w_i
Occupancy				
Effective area, Connectivity_EA	4	−332.53	0.00	0.98
Effective area, Connectivity_A	4	−336.26	7.45	0.02
Area, Connectivity_EA	4	−349.54	34.00	0.00
Area, Connectivity_A	4	−353.49	41.90	0.00
Intercept-only	2	−409.60	150.07	0.00
Colonization				
Effective area, Connectivity_EA	3	−110.18	0.00	0.84
Effective area, Connectivity_A	3	−111.86	3.36	0.16
Area, Connectivity_EA	3	−116.33	12.30	0.00
Area, Connectivity_A	3	−118.47	16.59	0.00
Intercept-only	1	−134.75	45.09	0.00

K = no. estimable parameters, $\Delta_i = AIC_{ci} -$ minimum AIC_c, and w_i are Akaike weights. The top four models plus the intercept-only model are shown

[a] Predictor variables include patch area of focal patch (Area), effective patch area of focal patch (Effective area), spatial connectivity measured using patch areas of source patches (Connectivity_A), and spatial connectivity measured using effective patch areas of source patches (Connectivity_EA). Effective patch areas are weighted by habitat quality

Of the 340 wetlands that were vacant in 2002–2003, 46 (13.5%) were colonized by 2003–2004. Again, the only competitive model for predicting patch colonization (Table 2) included effective area of the focal patch ($\beta = 2.206$, SE $= 0.499$) and Connectivity_EA ($\beta = 0.188$, SE $= 0.042$). Larger and more connected patches were more likely to be colonized between years (Fig. 1; $R^2 = 0.25$). All models with a single covariate had no support ($\Delta_i \geq 18.75$, $w_i = 0.00$).

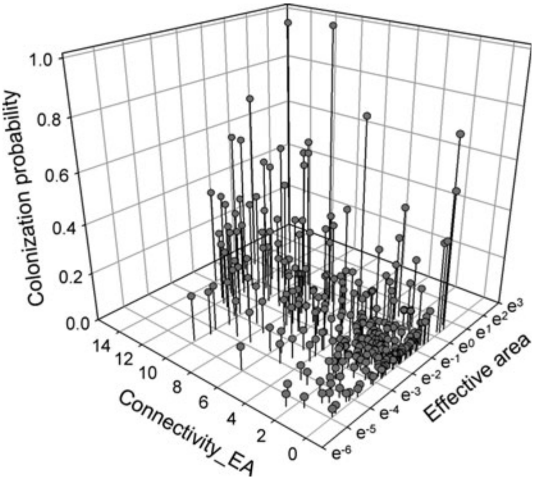

Fig. 1 Combined influences of effective patch area and spatial connectivity on probability of vacant wetlands being colonized by round-tailed muskrats. Effective patch area (modified by habitat quality) of focal patches is plotted on a natural log scale. Connectivity_EA is a metric that includes effective patch areas of source patches. Colonization probabilities are predicted values from a logistic regression model [logit (Colonization) = −3.38 + 2.206 (effective area) + 0.188 (Connectivity_EA)]

Discussion

Our literature review of spatial ecology studies revealed that habitat quality of source patches generally was not included in connectivity metrics even when variation in quality of focal patches was recognized. This omission occurred even though effective patch areas of sources should be better predictors of patch colonization, occupancy, and abundance for most systems. Recently, Visconti and Elkin (2009) demonstrated via simulation modeling that connectivity metrics that included patch quality performed better in all scenarios, especially in environments with high variance in patch quality and spatial clustering of good quality patches. Our empirical example of round-tailed muskrats demonstrated the superiority of a habitat-informed connectivity metric for a metapopulation that includes substantial variation in patch quality and positive spatial autocorrelation of patch quality (Schooley and Branch 2007).

Habitat quality of source patches can be included in IFM connectivity metrics merely by replacing patch areas with effective patch areas (Hanski 1994) as in our empirical example. Alternatively, Jaquiéry et al. (2008) included habitat quality of source patches instead of their areas, but this substitution only marginally improved explanatory power of occupancy and did not account for variance in colonization. For graph-theoretic approaches to connectivity, which might provide an ideal balance between information content and data requirements (Calabrese and Fagan 2004), nodes can be habitat patches described by their areas or by some index of habitat quality or productivity (Urban and Keitt 2001; Visconti and Elkin 2009). However, inclusion of effective areas when applying graph theory to conservation is not the norm. Buffer connectivity metrics can be reasonable predictors of colonization if buffer radii reflect dispersal abilities of focal species (Moilanen and Nieminen 2002). Habitat quality can be considered when measuring isolation with buffers (e.g., González-Varo et al. 2008), but this practice is rare. Finally, connectivity models derived from circuit theory could be extended by giving greater weight to high-quality source patches that release more current (McRae et al. 2008).

The simplest way to convert patch areas to effective patch areas is to use the relative weighting method suggested by Hanski (1994) and applied to our muskrat metapopulation. This approach is perhaps best suited to systems in which one, or a few, environmental variables can be identified as important drivers of habitat quality. For instance, Hokit et al. (2001) calculated effective patch areas for the Florida scrub lizard (*Sceloporus woodi*) using percentages of open, sandy habitat within patches. Likewise, Moilanen and Hanski (2006) created effective patch areas by summing coverages of two host-plant species within patches for the Glanville fritillary butterfly (*Melitaea cinxia*), and Rabasa et al. (2007) used modified patch areas that accounted for fruit production by the host plant for the butterfly *Iolana iolas*. More complicated functions of environmental variables could be used to index patch quality (Moilanen and Hanski 1998) as could measures from ecological-niche factor analysis (Jaquiéry et al. 2008) or occupancy modeling that accounts for imperfect detection (Cosentino et al. 2010).

Conservation of species in fragmented landscapes often is guided by metapopulation theory (Hanski and Gaggiotti 2004). A long-awaited fusion of metapopulation biology and landscape ecology has begun (Hanski and Gaggiotti 2004; With 2004; Armstrong 2005). Our literature review indicated researchers integrate habitat quality of focal patches into simple patch-matrix perspectives fairly often. However, habitat quality of source patches generally is disregarded when quantifying connectivity. Moreover, effects of the matrix on dispersal are ignored in favor of using straight-line distances to measure patch isolation. The unresolved question centers on how much we can simplify landscapes (Pellet et al. 2007; Prugh et al. 2008), and dispersal behavior (Baguette and Van Dyck 2007), and still retain predictive measures of spatial connectivity (Calabrese and Fagan 2004; Winfree et al. 2005). In our view, overlaying habitat quality of suitable patches onto binary landscapes is a complexity that will improve predictions and conservation efforts for many metapopulations. Nevertheless, a patch-matrix approach remains a practical starting point for evaluating connectivity if habitat quality is not well understood for a species, obtaining data on habitat quality is too costly, or patch area is correlated with resource quantity and population size (Rabasa et al. 2007).

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Appendix

See Table 3.

Table 3 Papers reviewed to examine how patch quality was treated in spatial ecology studies

Reference	Response[a]	Patch quality included?	
		Connectivity metric	Focal patch
American Naturalist			
Moilanen et al. (1998)	C	No	No
Facon and David (2006)	O, C	No	No
Brooks et al. (2008)	D	No	No
Snäll et al. (2008)	D	No	No
Urban et al. (2008)	I	No	No
Conservation Biology			
Foppen et al. (2000)	O, C, E, A	No	Yes
Schultz and Crone (2005)	O, M	No	No
Ecology			
Moilanen (1999)	M	No	No
Moilanen and Hanski (1998)	O, C, E	Yes	Yes
Doak (2000)	A	No	No
Hanski et al. (2000)	M	No	No
Johnson (2005)	O	No	No
Johnson and Horvitz (2005)	C	No	No
Schooley and Wiens (2005)	O, A	No	Yes
Schtickzelle et al. (2006)	M	No	No
Vellend et al. (2006)	O	No	Yes
Ewers et al. (2007)	A, R	No	Yes
Tremlová and Münzbergová (2007)	O	No	Yes
Jaquiéry et al. (2008)	O, E, C, A	Yes	Yes
Steffan-Dewenter and Schiele (2008)	A	No	No

Table 3 continued

Reference	Response[a]	Patch quality included?	
		Connectivity metric	Focal patch
Journal of Animal Ecology			
Lei and Hanski (1998)	O, C	No	No
van Nouhuys and Hanski (1999)	O, C, E	No	Yes
Menéndez and Thomas (2000)	O	No	Yes
Moilanen (2000)	M	No	No
Landscape Ecology			
Bastin and Thomas (1999)	O	No	Yes
Price et al. (2005)	O	No	Yes
Ranius and Kindvall (2006)	E	Yes	Yes
Verheyen et al. (2006)	R	Yes	Yes
Vergara and Marquet (2007)	A	No	Yes
Mortelliti and Boitani (2008)	O	No	Yes
Renfrew and Ribic (2008)	A	No	Yes
Thiele et al. (2008)	O, A	No	Yes
Oikos			
Hanski (1998)	O	No	No
Kuussaari et al. (1998)	A	No	No
Hanski (1999)	M	No	No
Lindenmayer et al. (1999)	O	No	No
Laaksonen et al. (2008)	O	No	Yes
Matter et al. (2005)	C	No	No
Schtickzelle et al. (2005)	O, C, P	No	No
Rabasa et al. (2007)	P	Yes	Yes

References are listed in chronological order within each of six ecological or conservation journals. Tallies indicate whether habitat quality of source patches was included in spatial connectivity metrics, and whether habitat quality of focal patches was considered

[a] Response variables included patch occupancy (O), patch colonization (C), patch extinction (E), patch abundance or density (A), disease dynamics (D), invasion speed (I), metapopulation model parameters (M), metapopulation persistence (P), species richness (R)

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