

# Empirical evidence for source–sink populations: a review on occurrence, assessments and implications

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## ABSTRACT

Assessing the role of local populations in a landscape context has become increasingly important in the fields of conservation biology and ecology. A growing number of studies attempt to determine the source–sink status of local populations. As the source–sink concept is commonly used for management decisions in nature conservation, accurate assessment approaches are crucial. Based on a systematic literature review of studies published between 2002 and 2013, we evaluated *a priori* predictions on methodological and biological factors that may influence the occurrence of source or sink populations. The review yielded 90 assessments from 73 publications that included qualitative and quantitative evidence for either source or sink population(s) for one or multiple species. Overall, sink populations tended to occur more often than source populations. Moreover, the occurrence of source or sink populations differed among taxonomic classes. Sinks were more often found than sources in mammals, while there was a non-significant trend for the opposite to be true for amphibians. Univariate and multivariate analyses showed that the occurrence of sources was positively related to connectivity of local populations. Our review furthermore highlights that more than 25 years after Pulliam's widely cited publication on 'sources, sinks, and population regulation', in-depth assessments of the source–sink status of populations based on combined consideration of demographic parameters such as fecundity, survival, emigration and immigration are still scarce. To increase our understanding of source–sink systems from ecological, evolutionary and conservation-related perspectives, we recommend that forthcoming studies on source–sink dynamics should pay more attention to the study design (i.e. connectivity of study populations) and that the assessment of the source–sink status of local populations is based on  $\lambda$  values calculated from demographic rates.

**Key words:** systematic review, animals, source, sink, local populations, demography, conservation, meta-analysis.

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## I. INTRODUCTION

Many species occur in heterogeneous landscapes as networks of local populations amidst unsuitable matrix habitat. Such heterogeneous landscapes may consist of naturally fragmented habitat or might result from anthropogenically induced destruction of habitat (Fischer & Lindenmayer, 2007). In such landscapes, local populations residing in habitat fragments can form patchy populations (Harrison, 1991) or metapopulations (Hanski, 1999). Local populations embedded in such networks are known to be less prone to extinction than isolated populations as local extinction may be prevented by immigration (Brown & Kodric-Brown, 1977; Stacey & Taper, 1992). Furthermore, extirpated populations might be readily recolonized by immigrants from adjacent local populations of the network (Hanski, 1999). In a highly cited paper Pulliam (1988) presented a framework stating that populations in poor ‘sink’ habitats would rely on inputs from good ‘source’ habitats to persist (Hull, Morzillo & Liu, 2011). Such source populations must be more than self-supporting, which means that reproduction must exceed mortality and emigration must be higher than immigration (Shmida & Ellner, 1984; Pulliam, 1988). Pulliam (1988) argued that many individuals may live in sink habitats where local recruitment would not replace local losses arising from either mortality or emigration. However, local populations in sink habitats might persist due to immigration from other local populations (Holt, 2011). Theoretical models demonstrated that such source–sink dynamics can emerge in temporally varying environments through passive dispersal that equalizes population density (Holt, 1985). Moreover, in animals it might be beneficial for ‘subordinate’ individuals to disperse from source to sink habitats in order to gain direct fitness benefits (i.e. survival and reproduction; Hamilton, 1964*a,b*). Thus, apart from dispersal being a necessary consequence of natural selection’s struggle for existence, dispersal away from source habitats or source populations may be an adaptive strategy in source–sink systems. According to habitat selection theory, source–sink regulation can evolve when individuals maximize their inclusive fitness (Morris, Lundberg & Ripa, 2001), which may lead to fluctuating populations with reciprocating pulses of dispersal (Morris & Diffendorfer, 2004). Such dispersal by subordinates can be mediated by different mechanisms,

including for example direct eviction by dominant individuals (Cant *et al.*, 2010) or indirect effects of breeding-site privilege (Pulliam & Danielson, 1991). However, emigration induced by source–sink dynamics can also be non-beneficial to actively emigrating individuals (Morris, 2011).

In conservation planning, source populations (and source habitats) are typically considered important as they hold thriving local populations and thus represent priority areas for species conservation. Determining the source–sink status of certain local populations (or habitats) by calculating the local site’s contribution to a larger population network has become popular among biologists and resource managers (Crowder *et al.*, 2000). To distinguish source from sink populations, a local population growth rate  $\lambda$  is usually calculated based on reproductive rates and survival (Pulliam, 1988). If Pulliam’s  $\lambda$  is larger than 1, the population or habitat is considered to be a source, otherwise it is deemed to be a sink. However, this approach may lead to an incorrect assessment of the source–sink status for at least three reasons. Firstly, not all individuals leaving a local population die, which results in an underestimation of survival rates and thus also of Pulliam’s  $\lambda$ . Secondly, the exchange among local populations is not taken into account and their contributions to a population network cannot thus be adequately assessed (Runge, Runge & Nichols, 2006). As an example, a local population may be classified as a sink based on its Pulliam’s  $\lambda$ , even though it provides individuals to other populations in a network, for which it may therefore act as a source. Runge *et al.* (2006) proposed the new  $C'$  metric to calculate the demographic contribution of a local population to a population network. In addition to reproductive rates and (apparent) survival, the  $C'$  metric includes emigration rates, which greatly enhances the accuracy of source–sink assessments of local populations. However, the approach of Runge *et al.* (2006) has so far been relatively rarely applied (Pasinelli, Runge & Schiegg, 2011; Newby *et al.*, 2013). Thirdly, to distinguish source from sink populations, it may be advantageous to estimate immigration, which however is often neglected. Nevertheless, immigration might allow differentiating independent sources from dependent sources (Hixon, Pacala & Sandin, 2002), when  $\lambda$  is  $> 1$ .

The need quantitatively to assess the status of local populations to evaluate their relevance for conservation is ever increasing (Crowder *et al.*, 2000; Loreau *et al.*, 2013). Despite

this, little is known about the circumstances influencing the occurrence of source or sink populations. Here we present results of a systematic literature review conducted to evaluate what factors potentially affect source–sink occurrence in animals. Specifically, our aims were to assess, (i) how often source and sink populations were detected in various taxa, (ii) under which circumstances source and sink populations were found, and (iii) whether methodology applied to assess source–sink status affected aims (i) and (ii). A previous review by Runge *et al.* (2006) primarily addressed methodological issues and presented an improved approach to assessing source–sink status. Our study goes a step further by evaluating biological and methodological predictions.

## II. METHODS

A literature search was conducted to shed light on factors influencing source–sink occurrence and dynamics of animal populations. A number of *a priori* predictions were evaluated using published data determining the source–sink status of local populations. Following each prediction, we provide explanations below as to why we expected to find the predicted pattern. The predictions are arranged thematically in a methodological section and a biological section, respectively.

### (1) Methodological predictions

(1) We predicted that evidence for source populations had been provided less often than evidence for sink populations. Detailed demographic data are needed to assess adequately the source–sink status of local populations (Runge *et al.*, 2006). However, for logistic and financial reasons, most studies are conducted on spatial scales covering only a tiny part of a species' range, and often for only a few years. Particularly for mobile taxa (e.g. butterflies, birds, bats), survival rates and emigration rates will be underestimated and consequently the chance of a local population to be misclassified as sink increases.

(2) The spatial scale of the studies was predicted to affect the occurrence of source and sink populations. Specifically, sources were expected to be found more often than sinks in large-scale studies, while sinks were predicted to occur more often than sources in small-scale studies. Similar to prediction (1), marked individuals leaving a small study area will hardly ever be observed again and thus be considered to be dead, resulting in decreased apparent survival compared to true survival and consequently underestimation of  $\lambda$ . By contrast, the chance of re-observing or catching marked individuals in studies conducted at a larger spatial scale is increased, because local dispersal events are more likely to be observed than in studies at a smaller spatial scale (e.g. Cilimburg *et al.*, 2002; Schaub *et al.*, 2006; Perlut *et al.*, 2008). As a consequence, estimates of apparent survival are approaching true survival and  $\lambda$  is more accurately estimated. Note that apparent survival is defined as the

product of true survival and the probability of remaining at the site (Burnham, 1993). Apparent survival is typically estimated from capture–mark–recapture/re-observation data, while true survival may be estimated for example from band-recovery data (Burnham, 1993), radio-tracking data (Powell *et al.*, 2000) and spatial capture–recapture data (Schaub & Royle, 2014, and references therein).

(3) Source populations were expected to be found more often in studies including several local populations compared to studies including only one or a few local populations. The likelihood of observing or catching marked individuals is higher in studies analysing multiple local populations compared to studies investigating only one or very few local populations. Dispersal events are more likely to be observed, and thus estimates of apparent survival are approaching true survival (e.g. Cilimburg *et al.*, 2002; Schaub & Royle, 2014). Conversely, sink populations are predicted to be found more often in studies including one or a few local populations compared to studies including several local populations.

### (2) Biological predictions

(1) Sources were expected to be found more often in species with stable or increasing local populations than in species with decreasing local populations. In turn, we expected sinks to be found more often in species with decreasing populations than in stable or increasing ones. Reproduction, survival, emigration and immigration influence the growth rate of a local population (Williams, Nichols & Conroy, 2002). While in particular cases a local population may be growing due to sustained immigration (Schaub, Jakober & Stauber, 2013), stable or increasing populations are typically characterized by good reproduction and survival as well as substantial emigration (e.g. Bodkin *et al.*, 2002). On the other hand, declining populations often exhibit reduced reproduction and survival rates (e.g. Altwegg *et al.*, 2014).

(2) Sources were expected to be found more often in resident than in migratory species. Conversely, we expected sink populations to be found more often in migratory species than in resident species. Migratory species tend to have better dispersal abilities than resident species (e.g. Weatherhead & Forbes, 1994). Increased dispersal may result in decreased population-specific apparent survival rate (compared to true survival), which is often included to identify source–sink status of populations (e.g. Runge *et al.*, 2006). As a consequence, decreased apparent survival negatively affects assessment of  $\lambda$  and hence source–sink status.

(3) Source populations were predicted to be found more often in species with limited dispersal abilities than in well-dispersing species. On the other hand, sink populations were expected to be found more often in species with good dispersal abilities than in species with limited dispersal abilities. Survival probability estimates are often biased low because dispersal away from the local population cannot

be separated from mortality (Cilimburg *et al.*, 2002; but see Schaub & Royle, 2014). It was shown that the inclusion of local dispersal observations can increase apparent survival estimates substantially (Perlut *et al.*, 2008). Individuals of good dispersers may leave their natal area quickly and cover long distances before settling, often without ever being seen again. Many individuals with good dispersal abilities will thus be considered dead. Consequently, apparent survival will be estimated low compared to true survival, which leads to an underestimation of  $\lambda$ . Offspring of species with limited dispersal abilities may stay longer and/or regularly settle in their natal area. Therefore, estimates of their apparent survival rate could be higher than those of offspring from good dispersers.

(4) Source populations were predicted to be found more often in studies with well-connected than with badly connected local populations. Conversely, we expected to find a negative relationship between the likelihood of sink occurrence and population connectivity. It has been shown that local populations embedded in networks are less prone to extinction than isolated populations. Local extinction may be prevented by immigration (Brown & Kodric-Brown, 1977; Schaub *et al.*, 2010) or empty fragments can be recolonized from nearby local populations (Hanski, 2005). Furthermore, it was shown that habitat fragmentation may reduce population size (e.g. Herbener *et al.*, 2012). Small populations can suffer from reduced reproductive performance and/or survival of individuals (e.g. Burke & Nol, 2000; Luck, 2003; Diaz *et al.*, 2005; Mazgajski & Rejt, 2006). Such Allee effects (Courchamp, Berec & Gascoigne, 2008) might potentially lead to sink situations in badly connected populations.

(5) We predicted that for habitat generalists, who can thrive in a wide variety of environmental conditions and can make use of a variety of resources (Krebs & Davies, 1993), more source than sink populations would be found. By contrast, habitat specialists can only thrive in a narrow range of environmental conditions and/or have a limited diet (Krebs & Davies, 1993). As a consequence of variation in quality of the habitat for the specialist species, few source populations but many sink populations are expected to exist. Thus, we predicted to find more sink than source populations among habitat specialists.

(6) Sources were expected to occur more often than sinks in the core of a species range, while sinks were expected to be more common than sources in the range periphery. Several lines of evidence suggest that for many species conditions at the range periphery are less optimal than at the range centre. For example, patch occupancy, abundance and population density tend to be greatest near the centre of the range and to decline towards range edges (e.g. Brown, 1984; Gibbons, Reid & Chapman, 1993; Blackburn & Gaston, 2006). In terms of genetic variation across species' geographical ranges, more populations located at range margins show reduced genetic diversity compared to geographically central populations, perhaps as a consequence of smaller effective population sizes at range margins (Eckert, Samis & Loughheed, 2008). Finally, stochasticity of biotic and

abiotic factors limiting population size of species is generally considered to be greater in the range periphery than in the range core, resulting in pronounced fluctuations at range edges. Strong fluctuations in population size, however, increase the likelihood of population extinction (Mills, 2013). Collectively, these findings suggest that source populations are more likely to occur in the centre of a species' range while sink populations should be more common at the range periphery.

### (3) Review protocol and data extraction

We aimed to find studies addressing the source–sink status of one or multiple local populations of invertebrate and vertebrate species. From these studies, we then extracted the necessary data to investigate the methodology used to assess the source–sink status (methodological predictions 1–3) and the biological circumstances which might affect the source–sink status of particular populations (biological predictions 1–6). To compile the protocol we followed the guidelines for systematic reviews outlined by Pullin & Stewart (2006). Based on the methodology of a recently published review on sources and sinks (Runge *et al.*, 2006), we browsed the online databases *Web of Science* and *Wildlife & Ecology Studies Worldwide* to search for studies containing the following key words: 'dispersal sink(s)', 'source habitat(s)', 'sink habitat(s)', 'source population(s)', 'sink population(s)', 'mortality sink(s)' and 'source-sink'. We limited our search to the period of January 2002 to late February 2013 as studies published previously had been reviewed by Runge *et al.* (2006).

We also extracted relevant data from book chapters (Liu *et al.*, 2011). Only empirical studies were considered. Initially, 1087 studies matching our criteria were transferred into a reference manager database (Reference manager®, Thompson Reuters). From these studies, we used a subset of 290 studies providing data from 357 species for further analyses. This subset only contained studies where authors clearly stated how the source–sink status was assessed (Table 1). Studies providing evidence for both source and sink populations for a given species in the same study were removed, thus we retained only studies where authors stated qualitative and quantitative evidence for either source or sink population(s) for one or multiple species (see online Appendix S1). Finally, as some taxa were the subject of multiple studies, we randomly selected one study per taxon for statistical independence, resulting in 90 source–sink assessments from 73 studies for the statistical analyses. We call this data set the 'full data set'. For a second analysis, we reduced the data set once again by exclusively considering studies that assessed the source–sink status of population(s) quantitatively based on  $\lambda$  values, with  $\lambda > 1$  being sources and  $\lambda < 1$  sinks. Fourteen studies used demographic parameters such as birth, survival, emigration or immigration rates to calculate  $\lambda$  (henceforth referred to as  $\lambda_D$ ) in 16 source–sink assessments and two studies calculated  $\lambda$  based on abundance or density ( $\lambda_{ND}$ ) in two assessments. We call this data set 'the reduced data set' ( $N = 18$  assessments).



Table 1. Variables and associated parameters included in our study. Numerical code in the data source column: 1, based on publication; 2, based on expert opinion; 3, based on biological handbook.

Variable name and explanation	Parameter	Data source
Species name	Scientific name	1
Taxon	Phylum and class	1
Size: spatial scale of the study	Square kilometre (km <sup>2</sup> )	1
Local populations: number of local populations studied	Number of populations	1
Trend: population trend of the species in the study site and during the study period	Increasing (IC), stable (ST), decreasing (DC)	1
Migratory status	Migratory (MI), resident (RE)	1, 3
Dispersal ability	Good (GD), bad (BD)	1, 2, 3
Connectivity: degree of connectivity of a local population with other local populations	Good (GC), bad (BC)	1, 3
Habitat specialization: habitat generalist or specialist	High specialization (H), low specialization (L)	1, 2, 3
Range: relative location of study site(s) within geographic range of species	Peripheral (P), non-peripheral (NP)	1, 2
Approach to assessing source–sink status	Abundance (A), birth rate (B), emigration (E), immigration (I), molecular (ML), mortality (MR), occurrence (OC), density (R), survival (S)	1

To gain insights into the factors possibly influencing source–sink dynamics of animals, we extracted parameter values of specific taxonomic, ecological, demographic and behavioural variables for species included in the full data set and the reduced data set, respectively (Table 1). To classify the connectivity of local populations we used the following criteria. We considered local populations as ‘well connected’ if authors of the original publications did not indicate bad connectivity *via* the text and/or figures. We classified local populations as ‘badly connected’ when authors mentioned that local populations were badly connected due to the following reasons: local population located on an island (number 32, 42; see online Appendix S1); migration/dispersal routes of local population mostly blocked (47, 48, 77, 78); local population at seashore and fragmented (64); local populations patchy distributed and fragmented (96); local population isolated and small (76, 84, 94); local population at the edge of range and surrounded by fragmented or unsuitable habitat (94, 95). To classify the location of local populations as peripheral or non-peripheral we included the authors’ assessment or compared the location of the local population with maps of the species’ distribution provided by biological handbooks and defined local population as peripheral if the study site was located at the range boundary and non-peripheral otherwise.

The original publications did not always provide information on the parameter values required for our analyses. In these cases (see Table 1), we extracted data from handbooks (e.g. del Hoyo, Elliott & Christie, 2007) and papers (Jehle & Sinsch, 2007; Mims *et al.*, 2010). In addition, we asked experts for specific taxa to rate species in terms of habitat specialization and dispersal ability, as information on these variables was particularly hard to find. Ursina Tobler and Josh van Buskirk provided information on European amphibian species, Josh van Buskirk and Raymond Semlitsch on North American amphibian species, Alexandre Gouskov

on European fish species, Colden Baxter and Julian Olden on North American fish species, and Jeff Walters on North American bird species.

#### (4) Statistical analyses

All statistical analyses were performed using R 3.0.1 (The R Foundation for Statistical Computing: <http://www.r-project.org>).

##### (a) Univariate analyses

We assessed each prediction separately with non-parametric Mann–Whitney U-tests, Fisher’s exact tests and chi-squared tests. Based on our predictions, one-tailed Mann–Whitney U-tests were conducted. The full data set could be used for the analyses of the explanatory variables ‘Local populations’, ‘Migratory status’, ‘Connectivity’, and ‘Range’ (Table 1). The explanatory variables ‘Size’, ‘Trend’ and ‘Dispersal ability’ were analysed with a reduced sample size as not all authors provided the details necessary for our analyses and we were unable to obtain the respective information elsewhere. Sample sizes are indicated where the respective test results are shown. With the reduced data set (which only contained studies having assessed source–sink status of the population(s) quantitatively based on  $\lambda_D$  and  $\lambda_{ND}$  values, see Section II.3), we conducted Fisher’s exact tests and Mann–Whitney U-tests and used the same variables as mentioned above.

##### (b) Multivariate analyses

A generalized linear mixed-effect model (GLMM, see Crawley, 2002; Bolker *et al.*, 2009) with a binary response variable (source or sink), binomial error structure and logit-link function was used to estimate the effects of the different explanatory variables on source–sink status. We

used the study as a random factor in the model to control for among-study variance, because some studies provided data on more than one species (see online Appendix S1). We used the function ‘glmmPQL’ from the package nlme (Pinheiro *et al.*, 2012) to fit the model. As explanatory variables, we used the categorical (binary) variables ‘Migratory status’, ‘Connectivity’, ‘Habitat specialization’ and ‘Range’ as well as the continuous variable ‘Local populations’. The latter was standardized prior to analyses so that the mean equalled 0 and standard deviation equalled 0.5. Scaling with two times the standard deviation was done to make the effect sizes comparable between the binary and the continuous variables (see Fig. 3) (Gelman & Hill, 2007). The variables ‘Size’, ‘Trend’ and ‘Dispersal ability’ were excluded from the GLMMs because few studies provided the respective parameter values. To analyse the subgroup of studies that assessed the source–sink status of population(s) based on  $\lambda_D$  and  $\lambda_{ND}$  values, we used a generalized linear model (GLM) with binomial error structure and logit-link function. Explanatory variables were ‘Local populations’, ‘Trend’, ‘Migratory status’, ‘Connectivity’ and ‘Habitat specialization’. ‘Range’, ‘Size’ and ‘Dispersal ability’ were excluded as only few studies provided data on these two variables.

III. RESULTS

Across the 90 source–sink assessments found in the 73 studies from the full data set (see online Appendix S1), survival was used in 38 assessments, birth rate in 29 assessments, abundance in 27 assessments, density in 26 assessments, occurrence in 12 assessments, molecular data in eight assessments, immigration in seven assessments, emigration in four assessments and mortality in two assessments. 45 assessments used only one demographic parameter to determine the source–sink status of the studied populations, 31 assessments used a combination of two parameters, 11 assessments used three parameters and three assessments used four or more parameters (Table 2).

Table 2. Number of assessments using one, two, three or at least four parameters to determine source–sink status of populations according to our review of 73 studies (full data set).

One parameter	Two parameters	Three parameters	Four or more parameters
A: 9, ML: 7, MR: 1, OC: 6, R: 15, S: 7	A + B: 1, A + E: 1, A + M: 1, A + OC: 5, A + R: 1, B + MR: 1, B + S: 15, E + I: 1, I + R: 2, I + S: 1, OC + R: 1, R + S: 1	A + B + S: 5, A + R + S: 1, B + E + S: 1, B + R + S: 4	A + B + I + S: 2, A + E + I + R + S: 1

A, abundance; B, birth rate; E, emigration; I, immigration; ML, molecular; MR, mortality; OC, occurrence; R, density; S, survival.

Assessments using the approach of Pulliam (1988), i.e. determining the source–sink status from reproductive rate and survival rate, were more common (15) than assessments additionally including emigration (1) as proposed by Runge *et al.* (2006) or immigration (2, in combination with abundance).

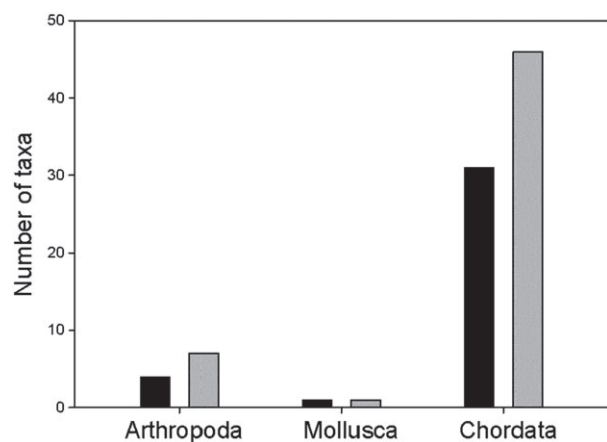
(1) Univariate analyses

(a) Methodological predictions

Across taxa, sink populations tended to occur more often than source populations when considering the full data set (36 sources *versus* 54 sinks,  $\chi^2 = 3.600$ , d.f. = 1,  $P = 0.059$ ). Similarly, sinks tended to be found more often than sources in the reduced data set (5 sources *versus* 13 sinks,  $\chi^2 = 3.556$ , d.f. = 1,  $P = 0.059$ ). In the full data set, the occurrence of source or sink populations did not differ significantly among taxonomic phyla ( $\chi^2 = 0.146$ , d.f. = 2,  $P = 0.930$ ,  $N = 90$ , Fig. 1). By contrast, the likelihood of finding source or sink populations differed among taxonomic classes ( $\chi^2 = 14.774$ , d.f. = 7,  $P = 0.039$ ,  $N = 90$ , Fig. 2). Within taxonomic classes, sinks were more likely to be found in Mammalia ( $\chi^2 = 7.539$ , d.f. = 1,  $P = 0.006$ ), while in Amphibia sources tended to occur more often than sinks ( $\chi^2 = 3.571$ , d.f. = 1,  $P = 0.059$ ). No difference in source–sink occurrence was found for Insecta, Actinopterygii and Aves (Fig. 2). No tests on the distribution of sources and sinks across phyla and classes were possible in the reduced data set.

(b) Biological predictions

In both the full and the reduced data sets (Table 3), there was no significant difference in the occurrence of source and sink populations in relation to spatial scale of the study (size), number of local populations studied (local populations), population trend, migratory status, dispersal ability, habitat specialization and range. However, sources and sinks differed in terms of population connectivity in the full data set (Table 3A), with populations revealing



**Fig. 1.** The distribution of source (black bars) and sink (grey bars) populations among taxonomic phyla based on 90 assessments found in 73 studies.

sources being better connected than those revealing sinks. By contrast, this difference was not found in the reduced data set (Table 3B).

## (2) Multivariate analyses

In the full data set, the occurrence of source and sink populations was related to connectivity of local populations (Table 4). Source populations were more likely to occur with increasing connectivity of local populations (Fig. 3). However, in the reduced data set, source–sink occurrence was not related to any of the predictor variables (Table 5).

## IV. DISCUSSION

### (1) Main findings

Across taxa, sink populations tended to be found more often than source populations when considering both the full and the reduced data sets although the *P* values at 0.059 just failed to reach significance. The likelihood of finding source or sink populations differed among taxonomic classes, with sinks more likely to be found than sources in mammals. There was a non-significant trend for sources to be found more often than sinks in amphibians. Furthermore, in the univariate analysis with the full data set, connectivity of

Table 3. The relationships of explanatory variables and the source–sink status of reviewed study species based on (A) the full data set and (B) the reduced data set (i.e. source–sink assessment based on  $\lambda_D$  and  $\lambda_{ND}$ ).

Variable	Source	Sink	<i>N</i>	Statistic	<i>P</i>	Test
(A) Size (km <sup>2</sup> ) <sup>a</sup>	650; 72.5–56875	4910; 155–78650	34	W = 256	0.564	Mann–Whitney U
Local populations <sup>a</sup>	1.5; 1–10.5	1; 1–4	90	W = 235	0.312	Mann–Whitney U
Trend	IC or ST: 13 DC: 3	IC or ST: 21 DC: 14	51	—	0.203	Fisher's exact
Migratory status	MI: 10 RE: 26	MI: 17 RE: 37	90	$\chi^2 = 0.02$	0.888	Chi-squared test
Dispersal ability	GD: 14 BD: 10	GD: 18 BD: 11	53	$\chi^2 = 0$	1	Chi-squared test
Connectivity	GC: 35 BC: 1	GC: 43 BC: 11	90	—	0.024	Fisher's exact
Habitat specialization	H: 18 L: 18	H: 21 L: 33	90	$\chi^2 = 0.681$	0.409	Chi-squared test
Range	NP: 33 P: 3	NP: 37 P: 17	90	—	0.68	Fisher's exact
(B) Size (km <sup>2</sup> ) <sup>a</sup>	332; 5–26032	124; 24–425	8	W = 18	1	Mann–Whitney U
Local populations <sup>a</sup>	1; 1–1.5	1; 1–22	18	W = 36	0.196	Mann–Whitney U
Trend	IC or ST: 5 DC: 0	IC or ST: 6 DC: 7	18	—	0.101	Fisher's exact
Migratory status	MI: 3 RE: 2	MI: 6 RE: 7	18	—	1	Fisher's exact
Dispersal ability	GD: 3 BD: 1	GD: 6 BD: 4	14	—	1	Fisher's exact
Connectivity	GC: 5 BC: 0	GC: 12 BC: 1	18	—	1	Fisher's exact
Habitat specialization	H: 3 L: 2	H: 7 L: 6	18	—	1	Fisher's exact
Range	NP: 5 P: 0	NP: 13 P: 0	18	—	NA	Fisher's exact

BC, bad connectivity; BD, bad dispersal ability; DC, decreasing; GC, good connectivity, GD, good dispersal ability; H, high specialization; IC, increasing; L, low specialization; MI, migratory; *N* = number of source–sink assessments; NA, not available (no variance in data); NP, non-peripheral; P, peripheral; RE, resident; ST, stable.

<sup>a</sup>Median; 25–75% quartile.

Table 4. Source–sink occurrence probability in relation to one methodological (local populations) and four biological explanatory variables assessed using a GLMM for the full data set ( $N = 90$ ). Modelled as source = 1.

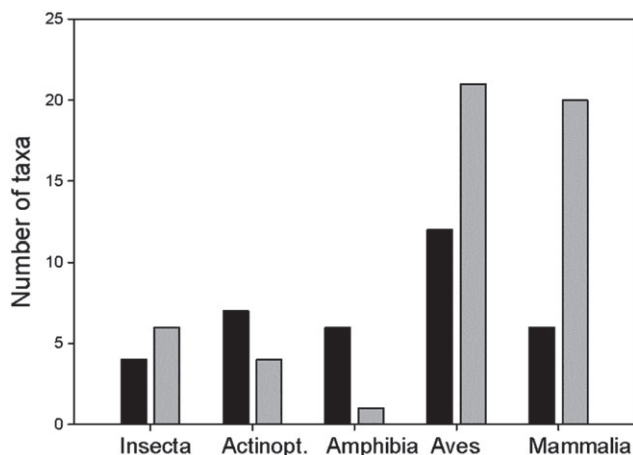
Source	Estimate $\pm$ S.E.	d.f.	<i>t</i>	<i>P</i>
Intercept	$-3.299 \pm 1.421$	84	$-2.321$	0.022
Local populations	$0.135 \pm 0.301$	84	0.120	0.656
Migratory status <sup>a</sup>	$0.266 \pm 0.538$	84	0.495	0.621
Connectivity <sup>b</sup>	$2.681 \pm 1.356$	84	1.977	0.051
Habitat specialization <sup>c</sup>	$0.369 \pm 1.356$	84	0.728	0.469
Range <sup>d</sup>	$1.628 \pm 1.347$	84	1.209	0.230

<sup>a</sup>Modelled as 1 = resident.

<sup>b</sup>Modelled as 1 = good connectivity.

<sup>c</sup>Modelled as 1 = high habitat specialization.

<sup>d</sup>Modelled as 1 = peripheral.

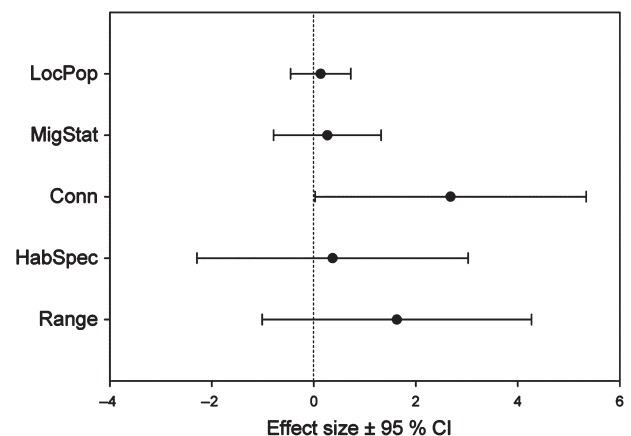


**Fig. 2.** The distribution of source (black bars) and sink (grey bars) populations among taxonomic classes based on 90 assessments found in 73 studies. The classes Bivalvia, Gastropoda and Malacostraca each had only one taxon studied and were therefore omitted from the graph. Actinopt., Actinopterygii.

populations differed in source and sink situations, with sources more likely to be found in well-connected populations and sinks more likely to occur in poorly connected populations. Multivariate analysis of the full data set confirmed the relationship between the source–sink status of local populations and population connectivity, as sources were more likely to be found in well-connected populations.

## (2) Taxonomic differences

Our results revealed that in mammals, sink populations were more often found than source populations, whereas in amphibians there was a tendency for source populations to be found more often (although with a small sample size). These opposing results might be linked to differences in the ecologies of amphibians and mammals. Many amphibian species are associated with spatially distinct breeding habitats and exhibit relatively high degrees of philopatry by adults and juveniles (Wells, 2010). Both spatially distinct breeding habitats and high degrees of philopatry, coupled with often short-distance



**Fig. 3.** Effect sizes and 95% confidence intervals for the five explanatory variables used in the GLMM with the full data set (see Table 4). Conn, connectivity; HabSpec, habitat specialization; LocPop, local populations; MigStat, migratory status. To allow comparison of estimates of the categorical and continuous variables, we scaled the continuous variable ‘LocPop’ using twice the standard deviation (Gelman & Hill, 2007).

movements of individuals that do disperse (Wells, 2010), increase the likelihood of recapture or re-observation of marked individuals. As a consequence, accurate estimation of demographic parameters such as survival or emigration will be promoted. By contrast, mammals often occur at comparatively low density throughout the landscape, range over wide areas, and are often nocturnal and relatively secretive. These combined characteristics might impede (re-)observation of marked individuals and thus render estimation of demographic parameters in mammals particularly difficult.

Another explanation for the different frequency of sources and sinks in amphibians and mammals might be related to the concept of  $r/K$  strategies (MacArthur & Wilson, 1967) and to how  $r/K$  strategies are distributed among these two taxa. According to theory, animals that follow the  $r$  strategy invest in the quantity of offspring at the expense of parental care and typically have relatively low survival rates both as young and adults. In addition,  $r$ -selected species



Table 5. Source–sink occurrence probability in relation to one methodological (local populations) and four biological explanatory variables assessed using a GLM for the reduced data set ( $N = 18$ ). Modelled as source = 1.

Source	Estimate $\pm$ S.E.	d.f.	<i>t</i>	<i>P</i>
Intercept	1.958 $\pm$ 0.453	12	4.319	0.001
Local populations	0.014 $\pm$ 0.017	12	0.809	0.434
Trend <sup>a</sup>	−0.461 $\pm$ 0.308	12	−1.496	0.161
Migratory status <sup>b</sup>	0.278 $\pm$ 0.353	12	0.782	0.449
Connectivity <sup>c</sup>	−0.144 $\pm$ 0.504	12	−0.285	0.781
Habitat specialization <sup>d</sup>	−0.082 $\pm$ 0.371	12	−0.221	0.828

<sup>a</sup>Modelled as 1 = increasing or stable.

<sup>b</sup>Modelled as 1 = resident.

<sup>c</sup>Modelled as 1 = good connectivity.

<sup>d</sup>Modelled as 1 = high habitat specialization.

should occur in unpredictable and ephemeral habitats (Begon, Harper & Townsend, 1991). Animals pursuing the *K* strategy are characterized by a reduced quantity of offspring with a correspondingly increased parental investment and are relatively long lived. Further, *K*-selected species should occur in relatively constant and predictable habitats. Given their high investment in reproduction and occurrence in relatively unpredictable and ephemeral habitats, many amphibians might be considered to be *r*-selected species. This might explain why sources tended to be found more often than sinks in amphibians, because the relative contribution of survival to  $\lambda$  is small in species with high investment in reproduction (Mills, 2013), such as *r*-selected species ('fast life-history' species: Bennett & Owens, 2002), and an underestimation of survival rates thus has a relatively small effect on source–sink assessment. In mammals, the situation is reversed as typically they are *K*-selected species ('slow life-history' species), in which the relative contribution of survival to  $\lambda$  is large (Mills, 2013). Hence, an underestimation of survival rates has a relatively large effect on source–sink assessment, which might explain why we found more sink than source populations in mammals.

### (3) Methodological predictions

Our first methodological prediction was that evidence for source populations had been provided less often than evidence for sink populations. This prediction was supported for both data sets, because sinks tended to be found more often than sources.

When looking at parameters that were used to evaluate source–sink status we found that 30 out of 54 (56%) assessments reporting sink status included demographic parameters such as birth rate, survival rate or both to determine source–sink status (see online Appendix S1), while only 10 out of 36 (28%) assessments reporting source populations did so. This may suggest that sinks were more reliably identified than sources. As not that many assessments (and thus studies) reporting sources included demographic data in their source–sink assignment, the number of assessments reporting sources in both data sets might have been inflated. Therefore, sinks may in reality

occur significantly more often than sources. In future studies, it is thus important to include demographic parameters, such as reproductive rates, survival rates and emigration rates, in source–sink assessments. By contrast, parameters such as abundance, occurrence and density are thought to be poor predictors of source–sink status (see Runge *et al.*, 2006).

At the same time, we note that source–sink assessments based on the use of demographic parameters to calculate  $\lambda_D$  may also not always be accurate. In particular when studies are conducted at small spatial scales and only during a short period, both of which are common, demographic parameters such as reproductive rates, survival rates and emigration rates may often be underestimated (Runge *et al.*, 2006). Therefore, the opportunity for local dispersal (emigration) to be observed should whenever possible be included in the study design, as such observations can increase apparent survival rates (Perlut *et al.*, 2008). Furthermore, the survival of study individuals is commonly underestimated as capture–recapture models often fail to discriminate between mortality and emigration. This problem can now be avoided by using spatial Cormack–Jolly–Seber models that allow the estimation of true survival (Schaub & Royle, 2014). As previously stated by Runge *et al.* (2006), we advocate that detailed demographic data, specifically on fecundity/mortality and immigration/emigration rates, are required to accurately determine source–sink status.

Our second and third methodological predictions were not supported. Thus, it appears that neither the spatial scale of the study nor the number of local populations examined were strong predictors of source–sink status.

### (4) Biological predictions

The fourth biological prediction was supported by analysis of the full data set. Connectivity of a local population with adjoining populations appears to be important for the occurrence of source populations. Sources were more likely to be found in well-connected than in badly connected populations, both in the multivariate analysis and in the univariate analysis. This pattern was not found in analyses of the reduced data set. Metapopulation theory and the development of source–sink dynamics have emphasized

the importance of connectivity between seemingly isolated local populations (Levins, 1969; Kritzer & Sale, 2006). For example, local populations of the northern flying squirrel (*Glaucomys sabrinus* Shaw, 1801) were less likely to occur at sites surrounded by increased proportions of unsuitable habitat that did not host other conspecific populations (Ritchie *et al.*, 2009). Local populations embedded in networks are known to be less prone to extinction than isolated populations, as local extinction may be prevented by immigration (Brown & Kodric-Brown, 1977). Also, empty fragments can be recolonized from nearby local populations (Hanski, 2005). Current source populations might have been sink populations previously and their extinction may have been prevented due to past immigration from nearby populations (Stacey & Taper, 1992). Furthermore, predation may lead to population oscillations but a network of populations can help to increase survival of both predator and prey (Real & Brown, 1991). Thus, patchy populations or metapopulations consisting of well-connected local populations could often be an important prerequisite for the occurrence of source populations.

All other biological predictions (1, 2, 3, 5, 6) were not supported by our analyses. Source–sink status of local populations was not related to population trend, migratory status, dispersal ability, habitat specialization and location in range. That we did not find more sink than source populations in migratory species and in species with good dispersal abilities is intriguing. It might be that resident species and bad dispersers still mostly disperse beyond the limits of often fairly small study sites. Estimates of population-specific survival rates may thus be biased similarly low in resident species and bad dispersers as in migratory species and good dispersers.

Research into the source–sink status of populations might have been biased towards species or populations of conservation relevance which often show declining trends. As a consequence, sinks might have been expected to occur more often than sources simply because of the species or populations selected for study by researchers. However, our analyses revealed that the source–sink status was not linked to population trends of the studied species or populations. Moreover, our data set comprised twice as many source–sink assessments with stable or increasing populations than declining populations. This suggests that our data set was neither biased towards declining species of conservation relevance nor towards species with stable or increasing populations.

### (5) Shortcomings in the assessment of source–sink status

The role of local populations in a landscape context has been increasingly the focus of ecological research (Loreau *et al.*, 2013). A steadily growing number of scientific articles investigate aspects of source–sink dynamics of populations (see Runge *et al.*, 2006; Liu *et al.*, 2011). However, examples providing empirical evidence for either source or sink populations based on rates of birth, death, emigration and/or immigration (Holt, 1984; Pulliam, 1988) have been rare

in the past (Diffendorfer, 1998) and remain so nowadays. Out of the papers published on this topic between 2002 and 2013 and included in our analyses (73 studies), we only found 16 assessments from 14 studies providing  $\lambda_D$  values (and two other assessments/studies providing  $\lambda_{ND}$  values), seven assessments from six studies providing data on immigration and only four assessments from four studies providing data on emigration. To assess the source–sink status of populations, one should not only focus on processes within local populations but also take processes among populations into account (Pasinelli *et al.*, 2011). A metric recently proposed by Runge *et al.* (2006), the  $C'$  metric, combines processes within and among populations by assessing the relative demographic contribution of a focal local population to itself and to all other local populations in the network of interest simultaneously. Yet, only one study analysed here provided data on survival, reproduction and emigration necessary to calculate the  $C'$  metric. In order to shed light on factors that influence the source–sink status of populations it is imperative that future studies apply metrics such as  $C'$  to assess comprehensively the source–sink status of populations. In addition, source–sink assessments should (if possible) be conducted on a time scale appropriate to the study species (e.g. on an annual basis for many passerine bird species). The temporal dynamics of sources and sinks may prove to be as important as the spatial dynamics.

### (6) Conservation implications

Due to ever-increasing human populations and subsequent land hunger, the conservation of specific populations is becoming increasingly important. Protected areas, where ecological processes and native species ought to be maintained, can be critical for conservation (Possingham *et al.*, 2006). However, many protected areas are not functioning quite as envisioned (Hansen, 2011). In many protected areas, ecological processes have been altered and native species have been lost (Newmark, 1995; Rivard *et al.*, 2000; Parks & Harcourt, 2002). Application of source–sink theory has the potential to enhance our understanding of such ecological processes and of factors influencing the function of protected areas (Crowder *et al.*, 2000). Knowledge about which local populations serve as sources will become more important in the future, as conservation managers may primarily aim at conserving source habitats (Crowder *et al.*, 2000; Semlitsch, 2000). However, prioritizing only areas containing source populations for conservation may be inadequate, as sinks can play a key role in sustaining viable metapopulations by serving as breeding habitat, thereby potentially contributing to the overall population network, and by functioning as stepping stones to facilitate dispersal among subpopulations (Pulliam, 1988; Pearson & Fraterrigo, 2011). Thus, in natural source–sink systems both sources and sinks are crucial to population regulation. In order to avoid misleading source–sink assessments of local populations, it is critical to take population demography into account. By assessing source–sink status with methods ignoring population demography, an apparently stable or

growing sink population can be misidentified as a source (Delibes, Gaona & Ferreras, 2001; Hansen, 2011) and wrong decisions may be made by authorities. Likewise, to avoid misclassifying a population as a 'pseudosink' (Watkinson & Sutherland, 1995) or 'dependent source' (Hixon *et al.*, 2002), the estimation of demographic parameters is fundamental. Finally, source–sink status of local populations might vary over time (Boughton, 1999; Johnson, 2004). Consequently, assessment of source–sink status needs to be based on studies conducted over a time span adequately taking the generation time of the study species into account.

## V. CONCLUSIONS

(1) Few of the 90 source–sink assessments taken from the 73 studies included in the analyses of our review were based on  $\lambda$  values (18); emigration (4) and immigration (7) were taken into account even less often. Thus, we note a substantial lack of empirical evidence in source–sink assessment.

(2) Our analyses demonstrate that good connectivity of local populations seems to foster the occurrence of source populations. Therefore, studies aiming at investigating the source–sink status of local populations should consider connectivity of local populations.

(3) Our study demonstrates that more than 25 years after Pulliam's (1988) seminal paper on 'sources, sinks, and population regulation', we still lack empirical data assessing the source–sink status of populations. Clearly, a thorough assessment of source–sink dynamics can have profound consequences for our ability to understand, predict, and manage species and ecosystems (Loreau *et al.*, 2013). Future studies must ensure that source–sink assessments are based on demographic rates, including survival, emigration and/or immigration, and  $\lambda$ .

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## VII. REFERENCES

References marked with asterisk have been cited within the supporting information.  
 \*ACOSTA, C. A. & PERRY, S. A. (2002). Spatio-temporal variation in crayfish production in disturbed marl prairie marshes of the Florida Everglades. *Journal of Freshwater Ecology* **17**, 641–650.

\*ADAMSKI, P. & WITKOWSKI, Z. J. (2007). Effectiveness of population recovery projects based on captive breeding. *Biological Conservation* **140**, 1–7.  
 \*ALISAUSKAS, R. T., DRAKE, K. L., CASWELL, J. H. & KELLETT, D. K. (2012). Movement and persistence by Ross's Geese (*Chen rossii*) in Canada's arctic. *Journal of Ornithology* **152**, S573–S584.  
 ALTWEGG, R., DOUTRELANT, C., ANDERSON, M. D., SPOTTISWOODE, C. N. & COVAS, R. (2014). Climate, social factors and research disturbance influence population dynamics in a declining sociable weaver metapopulation. *Oecologia* **174**, 413–425.  
 \*ASKINS, R. A., FOLSOM-O'KEEFE, C. M. & HARDY, M. C. (2012). Effects of vegetation, corridor width and regional land use on early successional birds on powerline corridors. *PLoS One* **7**, e31520.  
 \*BADER, T. J. & BEDNARZ, J. C. (2009). Reproductive success and causes of nest failures for Mississippi kites: a sink population in eastern Arkansas? *Wetlands* **29**, 598–606.  
 \*BEATTY, R. J., RAHEL, F. J. & HUBERT, W. A. (2009). Complex influences of low-head dams and artificial wetlands on fishes in a Colorado River tributary system. *Fisheries Management & Ecology* **16**, 457–467.  
 BEGON, M., HARPER, J. L. & TOWNSEND, C. R. (1991). *Ökologie: Individuen, Populationen, Lebensgemeinschaften*. Birkhäuser, Basel.  
 BENNETT, P. M. & OWENS, I. P. F. (2002). *Evolutionary Ecology of Birds: Life Histories, Mating Systems, and Extinction*. Oxford University Press, Oxford.  
 BLACKBURN, T. M. & GASTON, K. J. (2006). There's more to macroecology than meets the eye. *Global Ecology and Biogeography* **15**, 537–540.  
 BODKIN, J. L., BALLACHEY, B. E., DEAN, T. A., FUKUYAMA, A. K., JEWETT, S. C., McDONALD, L., MONSON, D. H., O'CLAIR, C. E. & VANBLARIGOM, G. R. (2002). Sea otter population status and the process of recovery from the 1989 'Exxon Valdez' oil spill. *Marine Ecology Progress Series* **241**, 237–253.  
 BOLKER, B. M., BROOKS, M. E., CLARK, C. J., GEANGE, S. W., POULSEN, J. R., STEVENS, M. & WHITE, J. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* **24**, 127–135.  
 BOUGHTON, D. A. (1999). Empirical evidence for complex source–sink dynamics with alternative states in a butterfly metapopulation. *Ecology* **80**, 2727–2739.  
 \*BRAND, L. A. & NOON, B. R. (2011). Seasonal fecundity and source–sink status of shrub-nesting birds in a southwestern riparian corridor. *Wilson Journal of Ornithology* **123**, 48–58.  
 \*BREININGER, D. R., NICHOLS, J. D., CARTER, G. M. & ODDY, D. M. (2009). Habitat-specific breeder survival of Florida Scrub-Jays: inferences from multistate models. *Ecology* **90**, 3180–3189.  
 BROWN, J. H. (1984). On the relationship between abundance and distribution of species. *American Naturalist* **124**, 253–279.  
 BROWN, J. H. & KODRIC-BROWN, A. (1977). Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* **58**, 445–449.  
 \*BROYER, J. (2009). Whinchat *Saxicola rubetra* reproductive success according to hay cutting schedule and meadow passerine density in alluvial and upland meadows in France. *Journal for Nature Conservation* **17**, 160–167.  
 BURKE, D. M. & NOL, E. (2000). Landscape and fragment size effects on reproductive success of forest-breeding birds in Ontario. *Ecological Applications* **10**, 1749–1761.  
 BURNHAM, K. (1993). A theory for combined analyses of ring recovery and recapture data. In *Marked Individuals in the Study of Bird Population* (eds J. D. LEBRETON and P. M. NORTH), pp. 199–213. Birkhäuser, Basel.  
 \*CAMERON, G. N., WILLIAMS, J. M. & KRUCHEK, B. L. (2009). Seasonal dynamics of small mammals and vegetation in a gulf cordgrass community. *Southwestern Naturalist* **54**, 237–247.  
 CANT, M. A., HODGE, S. J., BELL, M. B. V., GILCHRIST, J. S. & NICHOLS, H. J. (2010). Reproductive control via eviction (but not the threat of eviction) in banded mongooses. *Proceedings of the Royal Society B: Biological Sciences* **277**, 2219–2226.  
 \*CARTER, S. P. & BRIGHT, P. W. (2003). Reedbeds as refuges for water voles (*Arvicola terrestris*) from predation by introduced mink (*Mustela vison*). *Biological Conservation* **111**, 371–376.  
 \*CHRISTEN, W. (2007). Population trend and migration of the northern lapwing *Vanellus vanellus* in the Aare plain near Solothurn. *Der Ornithologische Beobachter* **104**, 173–188.  
 CILIMBURG, A. B., LINDBERG, M. S., TEWKSURY, J. J. & HEJL, S. J. (2002). Effects of dispersal on survival probability of adult yellow warblers (*Dendroica petechia*). *Auk* **119**, 778–789.  
 \*COLSON, I. & HUGHES, R. N. (2004). Rapid recovery of genetic diversity of dogwhelk (*Nucella lapillus* L.) populations after local extinction and recolonization contradicts predictions from life-history characteristics. *Molecular Ecology* **13**, 2223–2233.  
 \*CONWAY, C. J., GARCIA, V., SMITH, M. D., ELLIS, L. A. & WHITNEY, J. L. (2006). Comparative demography of Burrowing Owls in agricultural and urban landscapes in southeastern Washington. *Journal of Field Ornithology* **77**, 280–290.  
 \*COOLEY, H. S., WIELGUS, R. B., KOEHLER, G. & MALETZKE, B. (2009). Source populations in carnivore management: cougar demography and emigration in a lightly hunted population. *Animal Conservation* **12**, 321–328.  
 COURCHAMP, F., BEREK, J. & GASCOIGNE, J. (2008). *Allee Effects in Ecology and Conservation*. Oxford University Press, Oxford.



- CRAWLEY, M. J. (2002). *Statistical Computing: An Introduction to Data Analysis Using S-Plus*. Wiley-Blackwell, Chichester.
- \*CRONIN, J. T. (2007). From population sources to sieves: the matrix alters host-parasitoid source–sink structure. *Ecology* **88**, 2966–2976.
- CROWDER, L. B., LYMAN, S. J., FIGUEIRA, W. F. & PRIDDY, J. (2000). Source–sink population dynamics and the problem of siting marine reserves. *Bulletin of Marine Science* **66**, 799–820.
- \*DE BLOCK, M., GEENEN, S., JORDAENS, K., BACKELJAU, T. & STOKS, R. (2005). Spatiotemporal allozyme variation in the damselfly, *Lestes viridis* (Odonata: Zygoptera): gene flow among permanent and temporary ponds. *Genetica* **124**, 137–144.
- DELIBES, M., GAONA, P. & FERRERAS, P. (2001). Effects of an attractive sink leading into maladaptive habitat selection. *American Naturalist* **3**, 277–285.
- DIAZ, J. A., PEREZ-TRIS, J., TELLERIA, J. L., CARBONELL, R. & SANTOS, T. (2005). Reproductive investment of a lacertid lizard in fragmented habitat. *Conservation Biology* **19**, 1578–1585.
- DIFFENDORFER, J. E. (1998). Testing models of source–sink dynamics and balanced dispersal. *Oikos* **81**, 417–433.
- ECKERT, C. G., SAMIS, K. E. & LOUGHEED, S. C. (2008). Genetic variation across species' geographical ranges: the central marginal hypothesis and beyond. *Molecular Ecology* **17**, 1170–1188.
- \*ESSELSTYN, J. A., AMAR, A. & JANEKE, D. (2006). Impact of post-typhoon hunting on Mariana fruit bats (*Pteropus mariannus*). *Pacific Science* **60**, 531–539.
- \*FAUTH, P. T. & CABE, P. R. (2005). Reproductive success of Acadian Flycatchers in the blue ridge mountains of Virginia. *Journal of Field Ornithology* **76**, 150–157.
- \*FAUVELOT, C., CLEARY, D. F. R. & MENKEN, S. B. J. (2006). Short-term impact of disturbance on genetic diversity and structure of Indonesian populations of the butterfly *Drupadia theda* in East Kalimantan. *Molecular Ecology* **15**, 2069–2081.
- FISCHER, J. & LINDENMAYER, D. B. (2007). Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography* **16**, 265–280.
- \*GARDALI, T. & NUR, N. (2006). Site-specific survival of black-headed grosbeaks and spotted towhees at four sites within the Sacramento Valley, California. *Wilson Journal of Ornithology* **118**, 178–186.
- GELMAN, A. & HILL, J. (2007). *Data Analysis Using Regression and Multilevel/Hierarchical Models*. Cambridge University Press, Cambridge.
- \*GENTRY, D. J. & VIERLING, K. T. (2007). Old burns as source habitats for Lewis's woodpeckers breeding in the Black Hills of South Dakota. *Condor* **109**, 122–131.
- GIBBONS, D. W., REID, J. B. & CHAPMAN, R. A. (1993). *The New Atlas of Breeding Birds in Britain and Ireland: 1988–1991*. Poyser, London.
- \*GILLIS, E. A., HIK, D. S., BOONSTRA, R., KARELS, T. J. & KREBS, C. J. (2005). Being high is better: effects of elevation and habitat on arctic ground squirrel demography. *Oikos* **108**, 231–240.
- \*GLORVIGEN, P., ANDREASSEN, H. P. & IMS, R. A. (2013). Local and regional determinants of colonisation-extinction dynamics of a riparian mainland-island root vole metapopulation. *PLoS One* **8**, e56462.
- \*GOUDIE, R. I. & GILLILAND, S. G. (2008). Aspects of distribution and ecology of Harlequin Ducks on the Torment River, Newfoundland. *Waterbirds* **31**, 92–103.
- \*GOVINDAN, B. N., KERY, M. & SWIHART, R. K. (2012). Host selection and responses to forest fragmentation in acorn weevils: inferences from dynamic occupancy models. *Oikos* **121**, 623–633.
- \*GRIBBEN, P. E., WRIGHT, J. T., O'CONNOR, W. A. & STEINBERG, P. (2009). Larval settlement preference of a native bivalve: the influence of an invasive alga versus native substrata. *Aquatic Biology* **7**, 217–227.
- HAMILTON, W. D. (1964a). The genetical evolution of social behaviour I. *Journal of Theoretical Biology* **7**, 1–16.
- HAMILTON, W. D. (1964b). The genetical evolution of social behaviour II. *Journal of Theoretical Biology* **7**, 17–52.
- HANSEN, A. (2011). Contribution of source–sink theory to protected area science. In *Sources, Sinks and Sustainability* (eds J. LIU, V. HULL, A. T. MORZILLO and J. A. WIENS), pp. 339–360. Cambridge University Press, Cambridge.
- HANSKI, I. (1999). *Metapopulation Ecology*. Oxford University Press, Oxford.
- HANSKI, I. (2005). *The Shrinking World: Ecological Consequences of Habitat Loss*. International Ecology Institute, Oldendorf/Luhe.
- \*HARIHAR, A., PRASAD, D. L., RI, C., PANDAV, B. & GOYAL, S. P. (2009). Losing ground: tigers *Panthera tigris* in the north-western Shivalik landscape of India. *Oryx* **43**, 35–43.
- HARRISON, S. (1991). Local extinction in a metapopulation context – an empirical evaluation. *Biological Journal of the Linnean Society* **42**, 73–88.
- HERBENER, K. W., TAVENER, S. J., HOBBS, N. T. & THOMPSON, N. (2012). The distinct effects of habitat fragmentation on population size. *Theoretical Ecology* **5**, 73–82.
- HIXON, A., PACALA, S. W. & SANDIN, S. A. (2002). Population regulation: historical context and contemporary challenges of open versus closed systems. *Ecology* **83**, 1490–1508.
- \*HOFFMANN, I. E., MILLES, E., HUBER, S., EVERTS, L. G. & DITTAMI, J. P. (2003a). Population dynamics of European ground squirrels (*Spermophilus citellus*) in a suburban area. *Journal of Mammalogy* **84**, 615–626.
- \*HOFFMANN, I. E., MILLES, E., PIETA, K. & DITTAMI, J. P. (2003b). Anthropogenic effects on the population ecology of European ground squirrels (*Spermophilus citellus*) at the periphery of their geographic range. *Mammalian Biology* **68**, 205–213.
- HOLT, R. D. (1984). Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *American Naturalist* **124**, 377–406.
- HOLT, R. D. (1985). Population-dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. *Theoretical Population Biology* **28**, 181–208.
- HOLT, R. D. (2011). Evolution in source–sink environments: implications for niche conservatism. In *Sources, Sinks and Sustainability* (eds J. LIU, V. HULL, A. T. MORZILLO and J. A. WIENS), pp. 23–57. Cambridge University Press, Cambridge.
- DEL HOYO, J., ELLIOTT, A. & CHRISTIE, D. (2007). *Handbook of the Birds of the World*. Lynx Edicions, Barcelona.
- HULL, V., MORZILLO, A. T. & LIU, J. (2011). Impact of a classic paper by H. Ronald Pulliam: the first 20 years. In *Sources, Sinks and Sustainability* (eds J. LIU, V. HULL, A. T. MORZILLO and J. A. WIENS), pp. 3–22. Cambridge University Press, Cambridge.
- JEHLE, R. & SINSCH, U. (2007). Migration and orientation in amphibians: an overview. *Zeitschrift für Feldherpetologie* **14**, 137–152.
- JOHNSON, D. M. (2004). Source–sink dynamics in a temporally heterogeneous environment. *Ecology* **85**, 2037–2045.
- \*JOHNSON, R. C., WEBER, P. K., WIKERT, J. D., WORKMAN, M. L., MACFARLANE, R. B., GROVE, M. J. & SCHMITT, A. K. (2012). Managed metapopulations: do salmon hatchery 'sources' lead to in-river 'sinks' in conservation? *PLoS One* **7**, e28880.
- \*KEAGY, J. C., SCHREIBER, S. J. & CRISTOL, D. A. (2005). Replacing sources with sinks: when do populations go down the drain? *Restoration Ecology* **13**, 529–535.
- \*KELLER, D., BRODBECK, S., FLOSS, I., VONWIL, G. & HOLDEREGGER, R. (2010). Ecological and genetic measurements of dispersal in a threatened dragonfly. *Biological Conservation* **143**, 2658–2663.
- \*KERBIRIOU, C., LE VIOL, I., BONNET, X. & ROBERT, A. (2012). Dynamics of a northern fulmar (*Fulmarus glacialis*) population at the southern limit of its range in Europe. *Population Ecology* **54**, 295–304.
- \*KERLEY, L. L., GOODRICH, J. M., MIQUELLE, D. G., SMIRNOV, E. N., QUIGLEY, H. B. & HORNOCKER, M. G. (2002). Effects of roads and human disturbance on Amur tigers. *Conservation Biology* **16**, 97–108.
- \*KOIVULA, M. J. (2005). Effects of forest roads on spatial distribution of boreal carabid beetles (Coleoptera: Carabidae). *Coleopterists Bulletin* **59**, 465–487.
- KREBS, J. R. & DAVIES, N. B. (1993). *An Introduction to Behavioural Ecology*. Wiley-Blackwell, Oxford.
- KRITZER, J. P. & SALE, P. F. (2006). *Marine Metapopulations*. Academic Press, New York.
- \*KRUCHEK, B. L. (2004). Use of tidal marsh and upland habitats by the marsh rice rat (*Oryzomys palustris*). *Journal of Mammalogy* **85**, 569–575.
- \*LAMPILA, S., WISTBACKA, R., MAKELA, A. & ORELL, M. (2009). Survival and population growth rate of the threatened Siberian flying squirrel (*Pteromys volans*) in a fragmented forest landscape. *Ecoscience* **16**, 66–74.
- \*LEE, P. F., SHEN, S. F., DING, T. S., CHIOU, C. R. & YUAN, H. W. (2005). Habitat selection of the cooperative breeding Taiwan Yuhina (*Yuhina brunneiceps*) in a fragmented forest habitat. *Zoological Studies* **44**, 497–504.
- LEVINS, R. (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* **15**, 237–240.
- LIU, J., HULL, V., MORZILLO, A. T. & WIENS, J. A. (2011). *Sources, Sinks and Sustainability*. Cambridge University Press, Cambridge.
- LOREAU, M., DAUFRESNE, T., GONZALEZ, A., GRAVEL, D., GUICHARD, F., LEROUX, S. J., LOEUILLE, N., MASSOL, F. & MOUQUET, N. (2013). Unifying sources and sinks in ecology and earth sciences. *Biological Reviews* **88**, 365–379.
- LUCK, G. W. (2003). Differences in the reproductive success and survival of the rufous tree creeper (*Climacteris rufa*) between a fragmented and unfragmented landscape. *Biological Conservation* **109**, 1–14.
- MACARTHUR, R. H. & WILSON, E. O. (1967). *The Theory of Island Biogeography*. Princeton University Press, Princeton.
- \*MAES, J., MUSTERS, C. J. M. & DE SNOO, G. R. (2008). The effect of agri-environment schemes on amphibian diversity and abundance. *Biological Conservation* **141**, 635–645.
- \*MANOLIS, J. C., ANDERSEN, D. E. & CUTHBERT, F. J. (2002). Edge effect on nesting success of ground nesting birds near regenerating clearcuts in a forest-dominated landscape. *Auk* **119**, 955–970.
- \*MAYER, C., SCHIEGG, K. & PASINELLI, G. (2009). Patchy population structure in a short-distance migrant: evidence from genetic and demographic data. *Molecular Ecology* **18**, 2353–2364.
- MAZGAJSKI, T. D. & REJT, L. (2006). The effect of forest patch size on the breeding biology of the great spotted woodpecker *Dendrocopos major*. *Annales Zoologici Fennici* **43**, 211–220.
- \*MCCLEERY, R. A. (2009). Reproduction, juvenile survival and retention in an urban fox squirrel population. *Urban Ecosystems* **12**, 177–184.
- MILLS, L. S. (2013). *Conservation of Wildlife Populations: Demography, Genetics, and Management*. Wiley-Blackwell, Chichester.



- MIMS, M., OLDEN, J., SHATTUCK, Z. & POFF, N. (2010). Life history trait diversity of native freshwater fishes in North America. *Ecology of Freshwater Fish* **19**, 390–400.
- \*MIOTTO, R. A., CERVINI, M., BEGOTTI, R. A. & GALETTI, J. (2012). Monitoring a Puma (*Puma concolor*) population in a fragmented landscape in southeast Brazil. *Biotropica* **44**, 98–104.
- MORRIS, D. W. (2011). Source–sink dynamics emerging from unstable ideal free habitat selection. In *Sources, Sinks and Sustainability* (eds J. LIU, V. HULL, A. T. MORZILLO and J. A. WIENS), pp. 58–81. Cambridge University Press, Cambridge.
- MORRIS, D. W. & DIFFENDORFER, J. E. (2004). Reciprocating dispersal by habitat-selecting white-footed mice. *Oikos* **107**, 549–558.
- MORRIS, D. W., LUNDBERG, P. & RIPA, J. (2001). Hamilton's rule confronts ideal free habitat selection. *Proceedings of the Royal Society B: Biological Sciences* **268**, 921–924.
- \*MÜLLER, M., SPAAR, R., SCHIFFERLI, L. & JENNI, L. (2005). Effects of changes in farming of subalpine meadows on a grassland bird, the whinchat (*Saxicola rubetra*). *Journal of Ornithology* **146**, 14–23.
- \*NAGY, L. R. & HOLMES, R. T. (2004). Factors influencing fecundity in migratory songbirds: is nest predation the most important? *Journal of Avian Biology* **35**, 487–491.
- \*NAPPI, A. & DRAPEAU, P. (2009). Reproductive success of the black-backed woodpecker (*Picoides arcticus*) in burned boreal forests: are burns source habitats? *Biological Conservation* **142**, 1381–1391.
- \*NARANJO, E. J. & BODMER, R. E. (2007). Source–sink systems and conservation of hunted ungulates in the Lacandon Forest, Mexico. *Biological Conservation* **138**, 412–420.
- NEWBY, J. R., MILLS, L. S., RUTH, T. K., PLETSCHER, D. H., MITCHELL, M. S., QUIGLEY, H. B., MURPHY, K. M. & DESIMONE, R. (2013). Human-caused mortality influences spatial population dynamics: pumas in landscapes with varying mortality risks. *Biological Conservation* **159**, 230–239.
- NEWMARK, W. D. (1995). Extinction of mammal populations in western North American national parks. *Conservation Biology* **9**, 512–526.
- \*NOVARO, A. J., FUNES, M. C. & WALKER, R. S. (2005). An empirical test of source–sink dynamics induced by hunting. *Journal of Applied Ecology* **42**, 910–920.
- \*NYSTRAND, M., GRIESSER, M., EGGERS, S. & EKMAN, J. (2010). Habitat-specific demography and source–sink dynamics in a population of Siberian jays. *Journal of Animal Ecology* **79**, 266–274.
- \*ORTEGA, C. P. & ORTEGA, J. C. (2003). Brown-headed Cowbird (*Molothrus ater*) parasitism on Warbling Vireos (*Vireo gilvus*) in southwest Colorado. *Auk* **120**, 759–764.
- \*PAKANEN, V. M., RONKA, A., BELDA, E. J., LUUKKONEN, A., KVIST, L. & KOIVULA, K. (2010). Impact of dispersal status on estimates of local population growth rates in a Temminck's stint *Calidris temminckii* population. *Oikos* **119**, 1493–1503.
- \*PALSTRA, F. P., O'CONNELL, M. F. & RUZZANTE, D. E. (2007). Population structure and gene flow reversals in Atlantic salmon (*Salmo salar*) over contemporary and long-term temporal scales: effects of population size and life history. *Molecular Ecology* **16**, 4504–4522.
- PARKS, S. A. & HARCOURT, A. H. (2002). Reserve size, local human density, and mammalian extinctions in the US protected areas. *Conservation Biology* **16**, 800–808.
- PASINELLI, G., RUNGE, J. P. & SCHIEGG, K. (2011). Source–sink status of small and large wetland fragments and growth rate of a population network. In *Sources, Sinks and Sustainability* (eds J. LIU, V. HULL, A. T. MORZILLO and J. A. WIENS), pp. 216–238. Cambridge University Press, Cambridge.
- PEARSON, S. M. & FRATERIGO, J. M. (2011). Habitat quality, niche breadth, temporal stochasticity, and the persistence of populations in heterogeneous landscapes. In *Sources, Sinks and Sustainability* (eds J. LIU, V. HULL, A. T. MORZILLO and J. A. WIENS), pp. 115–139. Cambridge University Press, Cambridge.
- \*PEERY, M. Z., BECKER, B. H. & BEISSINGER, S. R. (2006). Combining demographic and count-based approaches to identify source–sink dynamics of a threatened seabird. *Ecological Applications* **16**, 1516–1528.
- \*PENNUTO, C. M., KRAKOWIAK, P. J. & JANIK, C. E. (2010). Seasonal abundance, diet, and energy consumption of round gobies (*Neogobius melanostomus*) in Lake Erie tributary streams. *Ecology of Freshwater Fish* **19**, 206–215.
- PERLUT, N. G., STRONG, A. M., DONOVAN, T. M. & BUCKLEY, N. J. (2008). Grassland songbird survival and recruitment in agricultural landscapes: implications for source–sink demography. *Ecology* **89**, 1941–1952.
- \*PETERSON, D. P., FAUSCH, K. D. & WHITE, G. C. (2004). Population ecology of an invasion: effects of brook trout on native cutthroat trout. *Ecological Applications* **14**, 754–772.
- PINHEIRO, J., BATES, D., DEBROY, S., SARKAR, D. & the R Development Core Team. (2012). nlme: linear and nonlinear mixed effects models. R package, version 3.1–103.
- POSSINGHAM, H. P., WILSON, K. A., ALDEMAN, S. J. & VYNNE, C. H. (2006). Protected areas: goals, limitations, and design. In *Principles of Conservation Biology* (eds M. J. GROOM, G. K. MEFFE and C. R. CARROLL), pp. 509–591. Sinauer Associates, Sunderland.
- POWELL, L. A., CONROY, M. J., HINES, J. E., NICHOLS, J. D. & KREMENTZ, D. G. (2000). Simultaneous use of mark-recapture and radiotelemetry to estimate survival, movement, and capture rates. *Journal of Wildlife Management* **64**, 302–313.
- PULLIAM, H. R. (1988). Sources, sinks, and population regulation. *American Naturalist* **132**, 652–661.
- PULLIAM, H. R. & DANIELSON, B. J. (1991). Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *American Naturalist* **137**, 50–66.
- PULLIN, A. S. & STEWART, G. B. (2006). Guidelines for systematic review in conservation and environmental management. *Conservation Biology* **20**, 1647–1656.
- \*PURCELL, K. L. (2006). Abundance and productivity of Warbling Vireos across an elevational gradient in the Sierra Nevada. *Condor* **108**, 315–325.
- \*RANGEL-SALAZAR, J. L., MARTIN, K., MARSHALL, P. & ELNER, R. W. (2008). Population dynamics of the ruddy-capped nightingale thrush (*Catharus frantzii*) in Chiapas, Mexico: influences of density, productivity and survival. *Journal of Tropical Ecology* **24**, 583–593.
- REAL, L. A. & BROWN, J. H. (1991). *Foundations of Ecology: Classic Papers with Commentaries*. University of Chicago Press, Chicago.
- \*REYNOLDS, M. H., SEAVY, N. E., VEKASY, M. S., KLAUITTER, J. L. & LANIAWE, L. P. (2008). Translocation and early post-release demography of endangered Laysan teal. *Animal Conservation* **11**, 160–168.
- \*RINTALA, J. & TIAINEN, J. (2008). A model incorporating a reduction in carrying capacity translates brood size trends into a population decline: the case of Finnish starlings, 1951–2005. *Oikos* **117**, 47–59.
- RITCHIE, L. E., BETTS, M. G., FORBES, G. & VERNES, K. (2009). Effects of landscape composition and configuration on northern flying squirrels in a forest mosaic. *Forest Ecology and Management* **257**, 1920–1929.
- RIVARD, D. H., POITEVIN, D., PLASSE, D., CARLETON, M. & CURRIE, D. J. (2000). Changing species richness and composition in Canadian National Parks. *Conservation Biology* **14**, 1099–1109.
- \*ROBINSON, H. S., WIELGUS, R. B., COOLEY, H. S. & COOLEY, S. W. (2008). Sink populations in carnivore management: cougar demography and immigration in a hunted population. *Ecological Applications* **18**, 1028–1037.
- \*ROSHIER, D. A., HEINSOHN, R., ADCOCK, G. J., BEERLI, P. & JOSEPH, L. (2012). Biogeographic models of gene flow in two waterfowl of the Australo-Papuan tropics. *Ecology and Evolution* **2**, 2803–2814.
- RUNGE, J. P., RUNGE, M. C. & NICHOLS, J. D. (2006). The role of local populations within a landscape context: defining and classifying sources and sinks. *American Naturalist* **167**, 925–938.
- SCHAUB, M., AEBISCHER, A., GIMENEZ, O., BERGER, S. & ARLETTAZ, R. (2010). Massive immigration balances high anthropogenic mortality in a stable eagle owl population: lessons for conservation. *Biological Conservation* **143**, 1911–1918.
- SCHAUB, M., JAKOBER, H. & STAUBER, W. (2013). Strong contribution of immigration to local population regulation: evidence from a migratory passerine. *Ecology* **94**, 1828–1838.
- SCHAUB, M. & ROYLE, J. A. (2014). Estimating true instead of apparent survival using spatial Cormack-Jolly-Seber. *Methods in Ecology & Evolution* **5**, 1316–1326.
- SCHAUB, M., ULLRICH, B., KNÖTZSCH, G., ALBRECHT, P. & MEISSER, C. (2006). Local population dynamics and the impact of scale and isolation: a study on different little owl populations. *Oikos* **115**, 389–400.
- \*SCHMIDT, D. J., CROOK, D. A., O'CONNOR, J. P. & HUGHES, J. M. (2011). Genetic analysis of threatened Australian grayling *Prototroctes maraena* suggests recruitment to coastal rivers from an unstructured marine larval source population. *Journal of Fish Biology* **78**, 98–111.
- \*SCHMITZ, H. J., HOFMANN, P. R. P. & VALENTE, V. L. S. (2010). Assemblages of drosophilids (Diptera, Drosophilidae) in mangrove forests: community ecology and species diversity. *Iheringia Série Zoológica* **100**, 133–140.
- \*SCHWARTZ, C. C., HAROLDSON, M. A., WHITE, G. C., HARRIS, R. B., CHERRY, S., KEATING, K. A., MOODY, D. & SERVHEEN, C. (2006). Temporal, spatial, and environmental influences on the demographics of grizzly bears in the greater Yellowstone ecosystem. *Wildlife Monographs* **161**, 1–8.
- SEMLITSCH, R. D. (2000). Principles for management of aquatic-breeding amphibians. *Journal of Wildlife Management* **64**, 615–631.
- SHMIDA, A. & ELLNER, S. (1984). Coexistence of plant species with similar niches. *Vegetatio* **58**, 29–55.
- \*SMITH, W. P. & PERSON, D. K. (2007). Estimated persistence of northern flying squirrel populations in temperate rain forest fragments of Southeast Alaska. *Biological Conservation* **137**, 626–636.
- \*SMITH, W. P., PERSON, D. K. & PYARE, S. (2011). Source-sinks, metapopulations, and forest reserves: conserving northern flying squirrels in the temperate rainforests of Southeast Alaska. In *Sources, sinks and sustainability* (eds J. LIU, V. HULL, A. T. MORZILLO and J. A. WIENS), pp. 399–422. Cambridge University Press, Cambridge.
- STACEY, P. B. & TAPER, M. (1992). Environmental variation and the persistence of small populations. *Ecological Applications* **2**, 18–29.
- \*STOUT, W. E., TEMPLE, S. A. & PAPP, J. M. (2006). Landscape correlates of reproductive success for an urban-suburban red-tailed hawk population. *Journal of Wildlife Management* **70**, 989–997.
- \*TAKADA, M. B., YOSHIOKA, A., TAKAGI, S., IWABUCHI, S. & WASHITANI, I. (2012). Multiple spatial scale factors affecting mirid bug abundance and damage level in organic rice paddies. *Biological Control* **60**, 169–174.

- \*TURGEON, K. & KRAMER, D. L. (2012). Compensatory immigration depends on adjacent population size and habitat quality but not on landscape connectivity. *Journal of Animal Ecology* **81**, 1161–1170.
- WATKINSON, A. R. & SUTHERLAND, W. J. (1995). Sources, sinks and pseudo-sinks. *Journal of Animal Ecology* **64**, 126–130.
- WEATHERHEAD, P. J. & FORBES, M. R. L. (1994). Natal philopatry in passerine birds: genetic or ecological influences? *Behavioral Ecology* **5**, 426–433.
- WELLS, K. D. (2010). *The Ecology and Behavior of Amphibians*. University of Chicago Press, Chicago.
- \*WERNER, E. E., RELYEA, R. A., YUREWICZ, K. L., SKELLY, D. K. & DAVIS, C. J. (2009). Comparative landscape dynamics of two anuran species: climate-driven interaction of local and regional processes. *Ecological Monographs* **79**, 503–521.
- WILLIAMS, B. K., NICHOLS, J. D. & CONROY, M. J. (2002). *Analysis and Management of Animal Populations*. Academic Press, San Diego.

## VIII. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

**Appendix S1.** Parameter values extracted from the 96 assessments found in 79 studies that provided evidence for either source or sink populations.

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