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Range structure analysis: unveiling the internal structure of species' ranges

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Abstract Assessing risks of local extinction and shifts in species ranges are fundamental tasks in ecology and conservation. Most studies have focused either on the border of species' range or on complex spatiotemporal dynamics of populations within the spatial distribution of species. The internal properties of species ranges, however, have received less attention due to a general lack of simple tools. We propose a novel approach within a metapopulation framework to study species ranges based on simple mathematical rules. We formulate and test a model of population fluctuations through space to identify key factors that regulate population density. We propose that spatial variability in species abundance reflects the interaction between temporal variability in population dynamics and the spatial variability of population parameters. This approach, that we call range structure analysis, integrates temporal and spatial properties to diagnose how each parameter contributes to species occupancy throughout its geographic range.

Keywords Range dynamics · Population biology · Species distribution · Species' border · Metapopulation

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Introduction

Ever since the study of MacArthur and Wilson, extinction–colonization dynamics have been regarded as fundamental processes to understand persistence, composition, and diversity of species from local to global scales (MacArthur 1960; MacArthur and Levins 1964) . Extinction and colonization rates vary across the geographic range of species as a consequence of changes in habitat size, connectivity, and suitability, as well as due to local demographic processes and metapopulation dynamics (Carter and Prince 1981; Holt 1983; Holt et al. 1997; Maurer and Brown 1989; Morlon et al. 2009; Holt et al. 2005). The relative contribution of extinction and colonization processes underlie the emergence of patterns in the internal structure of geographic ranges (Brown et al. 1996; Gaston 2003; Hengeveld and Haeck 1982), such as range boundaries (Case and Taper 2000; Holt and Keitt 2000, 2005), range expansion (Arim et al. 2006; Holt 2003), and density variation across the range (Brown et al. 1995; Hengeveld and Haeck 1982). Notwithstanding their importance, to our knowledge, extinction and colonization process has not been mapped within the range of species.

In the case of range boundaries, Holt and Keitt (2000) used the well-known metapopulation model proposed by Levins (1970) to suggest that the emergence of range boundaries can be explained by changes in the relative importance of extinction (e), colonization (c), and amount of suitable habitat (k) at a given position (x) in the context of the following model:

$$\frac{dp(x)}{dt} = p(x)c(x)\Big\{k(x) - p(x)\Big\} - e(x)p(x), \qquad (1)$$

Fig. 1 Temporal (*left panel*) and spatial (*right panel*) variability in parameters. Inverse distance weight interpolation was applied after calculating parameters for each route independently

(a) habitat suitability (k)

(b) $dk/d(x, y)$

(c) colonization (c)

(d) $dc/d(x, y)$

(e) extinction (e)

(f) $de/d(x, y)$
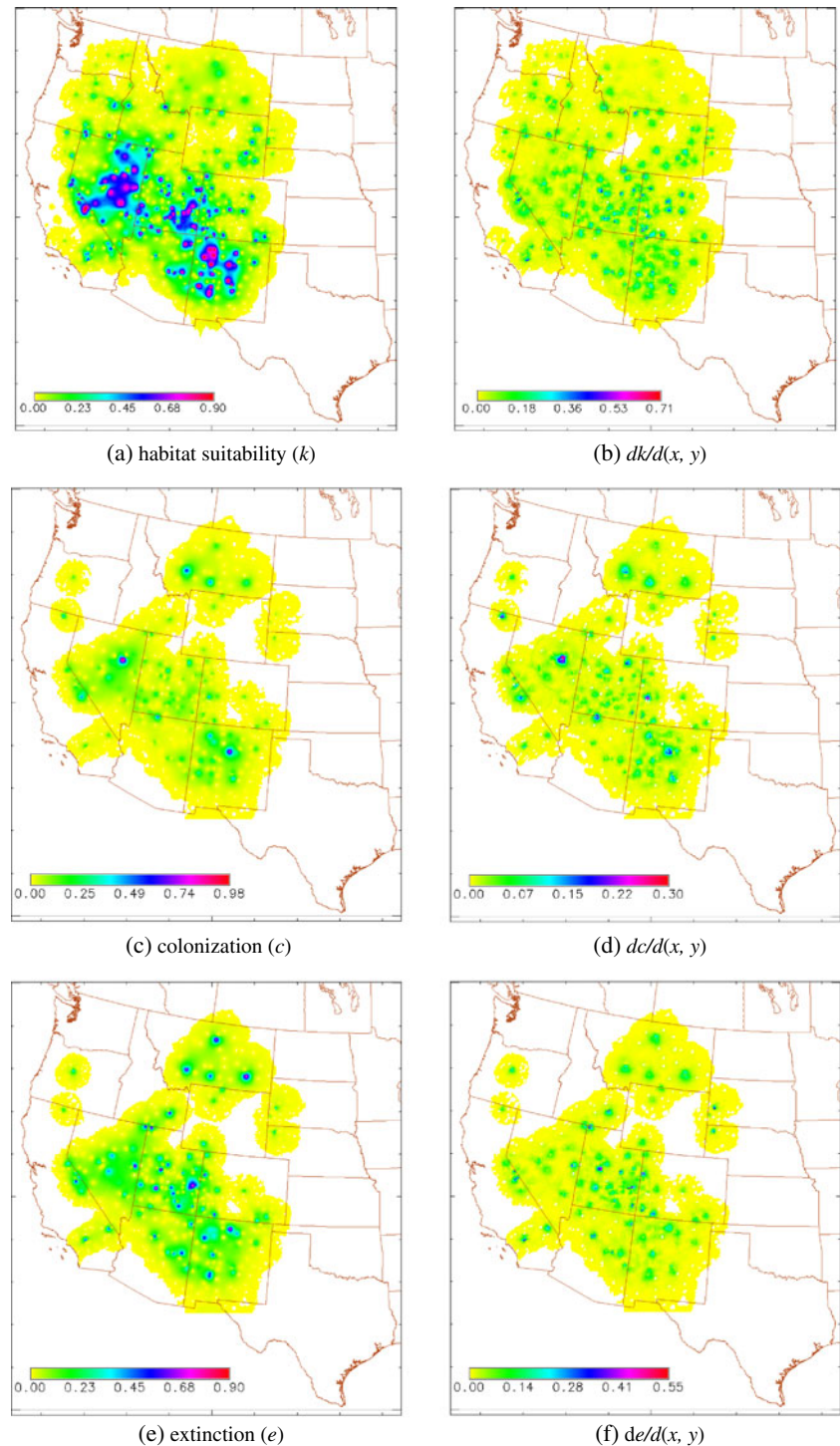
where $p(x)$ is the probability of occupancy at position x. This model, while providing insights into the nature of range boundaries along one dimensional gradients, has a limited ability to deal with the spatial complexity of range boundaries and internal structure.

In this paper, we expand the model proposed by Holt and Keitt (2000) to account for the variability of extinction and colonization rates across the geographic range of species. We show that the emergence of patterns in the internal structure, as well as in the boundary of ranges can be fruitfully understood as resulting from the interaction between temporal variability in population dynamics and the spatial variability of population parameters (Fig. 1) .

Our goal is to formulate a diagnostic approach, that we call range structure analysis (RSA), to elucidate the internal structure of a species' geographic range. We integrate temporal and spatial dimensions in a concrete and simple expression to assess the spatial variability in the relative contribution of extinction and colonization rates within the geographic range of species. We illustrate RSA and its implications for conservation and management with the empirical example of the range of Piñon jays, *Gymnorhinus cyanocephalus*.

Range structure analysis

Our goal is to assess the relative contribution of extinction and colonization processes to the persistence of a species within its range. In principle, we would like to assess how these two rates vary at any single location (x, y). To do this, we can modify (1) to:

$$\frac{dp(x, y)}{dt} = p(x, y)c(x, y)\Big\{k(x, y) - p(x, y)\Big\} - e(x, y)p(x, y). \quad (2)$$

Notice that now, p should be regarded as the proportion of time that the habitat patch centered at coordinates x, y stays occupied, which we model as a function of its quality (k) and the value taken by local extinction (e) and colonization (c) processes.

The effect of each parameter $(\cdot)$ on p is given by how its variability across space affects changes in the probability of occupancy. One way to account for this effect is by computing the spatial derivative of each parameter when the system is at equilibrium p^*. This leads us to propose the following model:

$$\frac{dp^*}{d(x, y)} = \frac{\partial p^*}{\partial e}\frac{de}{d(x, y)} + \frac{\partial p^*}{\partial c}\frac{dc}{d(x, y)} + \frac{\partial p^*}{\partial k}\frac{dk}{d(x, y)}. \quad (3)$$

The partial contributions of c, e, and k, (3) may be obtained analytically from the equilibrium state of Eq. 2

$(p^* = k - e/c)$, then: $\partial p^*/\partial e = -c^{-1}$, $\partial p^*/\partial c = ec^{-2}$, and $\partial p^*/\partial k = 1$.

Expression 3 defines a gradient in a three dimensional parameter space which permits to evaluate the contribution of each parameter to population persistence across the spatial gradient. This is what we call a RSA. Under such framework, RSA entails the following three steps: (1) Obtain independent estimates of the parameters k, e, and c at each spatial location (x,y). (2) Compute their spatial derivatives (i.e., $\frac{d\cdot}{d(x,y)}$), 3) compute the partial derivatives of the equilibrium values associated to the dynamic model represented by (2) (e.g., $\partial p^*/\partial c = ec^{-2}$ for colonization), 4) multiply the spatial derivatives obtained in step two by the partial derivatives of step 3, which represents the contribution of each parameter (i.e., c,e,k) to the equilibrium persistence at any one particular location (x,y). Once this procedure is carried out, one can identify the parameter that dominates the dynamics at a particular location by finding the term $\left(\frac{\partial p^*}{\partial \cdot}\frac{d\cdot}{d(x,y)}\right)$ with the highest value for each position (x,y) within the range.

Application

Dataset

RSA requires to assess the frequency of occupation throughout the species range. We illustrate the model using Piñon jays (PIJA; *G. cyanocephalus*) from the North American Breeding Bird Survey (BBS, Sauer et al. 2005) dataset. While other datasets are certainly relevant to assess spatial changes in occupancy dynamics (e.g., Christmas Bird Count), the large scale and large time span of the BBS, makes it an ideal census that explicitly depict demographic features of species (e.g., birth, emigration) relevant to occupation dynamics. The BBS consists of yearly censuses conducted in June across North America spanning from 1966 to the present. Each route consists of a 40-km transect. An observer travels by vehicle along each transect and stops every 0.8 km and counts all birds detected by sight or sound within a 0.4-km radius during a 3-min period.

PIJA are highly social, non-territorial birds, with a lifespan of roughly 11 years, that depend heavily on piñon seed (Balda et al. 1997; Klimkiewicz and Futcher 1989). Dispersal occurs in the fall, mostly by females going to adjacent flocks in search of males (Marzluff and Balda 1989). Occasionally, young PIJA males wander to maximize their reproductive output (Marzluff and Balda 1992), thereby minimizing fluctuations in population sizes during the summer. Overall, the individual home ranges of PIJA are remarkably stable through the year and remain mostly

limited to the home range boundaries of the flock (circa. 20 km^2; Balda and Bateman 1971; Marzluff and Balda 1992). This makes PIJA a good candidate to illustrate the model presented here.

PIJA has been recorded in a total of 244 routes between 1968 and 2005. To assure adequate sampling and to minimize the effect of stochasticity upon occupancy, only those routes that recorded PIJA in 10 or more years, which occurred in 106 routes, were analyzed. PIJA reach their highest abundances in Arizona and New Mexico (Balda and Bateman 1971; Marzluff and Balda 1992). The BBS shows that persistent populations have been recorded every year as far north as southern Oregon and Montana (Sauer et al. 2005).

Parameter estimation

Because RSA concerns the estimation of the relative contribution of parameter values at each spatial location within the range, we calculated k, e, and c for each route located at coordinates x, y, when the above requirements were met. These values were used to generate continuous maps for each parameter using inverse distance weight interpolation (Fortin and Dale 2005). The grain for such interpolated maps was set to the minimum distance between sample locations (8 km), thereby assuring that no two routes were found within one map cell.

To estimate k, a generalized linear model with logistic link (Venables and Ripley 2002; Hosmer et al. 2011) was used to model the probability of bird habitat being present.

To balance this statistical analysis, we incorporated routes with known PIJA absences, by including 106 randomly selected routes within the spatial extent of the species range where PIJA have not been recorded in the 38 year span considered in this study. A training dataset of 25 % of the total routes was used to generate the model, and validation was done using a χ^2−test on a confusion table on the remaining 75 % of the routes. Predictors were chosen to describe the most relevant environmental factors of PIJA survival and reproduction (Marzluff and Balda 1989). We estimated habitat suitability (k) for each route from the median date of last snowfall for years 1961–1990 (CLIMAPS, National Climatic Data Center), elevation, forest density, and forest types (Zhu and Evans 1994). The estimated error for habitat suitability was set to two standard deviations from the predicted value for each route. The variables that contribute the most to habitat suitability are in decreasing order: elevation, forest density, date of last snowfall, and forest type (Table 1) all of which may be related to food availability (i.e., pinyon nut crop) and roosting and nesting habitat quality. Even though neither of the individual categories of forest types are significant, the inclusion of forest types as a variable to model habitat suitability is justified because together they contribute significantly to explain PIJA presence. This is further evident by looking at the analysis of deviance table (Table 2).

Colonization and extinction were estimated using the standard procedure outlined in Clark and Rosenzweig (1994); (see also Diamond and May 1977; Samaniego et al. 2012). However, counts, and thus metapopulation

Table 1 Logistic regression model to estimate habitat suitability, k

	Estimate	Std. Error	z value	$Pr(> |z|)$
(Intercept)	−19.493	2585.101	−0.01	0.994
Elevation	0.003	0.001	4.92	0.000
Forest Density	−0.0310	0.011	−2.93	0.003
Date of Last Snowfall	−0.277	0.147	−1.88	0.061
Forest Type: Douglas-fir	16.262	2585.101	0.01	0.995
Forest Type: Elm-ash-cottonwood	0.036	4725.898	0.00	1.000
Forest Type: Fir-spruce	−2.375	2991.797	−0.00	0.999
Forest Type: Lodgepole pine	15.172	2585.101	0.01	0.995
Forest Type: Oak-hickory	−0.337	3791.811	−0.00	0.999
Forest Type: Piñon-juniper	17.763	2585.100	0.01	0.995
Forest Type: Ponderosa pine	17.836	2585.100	0.01	0.995
Forest Type: Western hardwoods	13.700	2585.101	0.01	0.996
Null deviance: 277.24 df: 199				
Residual deviance: 185.51 df: 188				

Note that in spite of none of the forest types showing significant z values, the inclusion of Forest Type has a significant effect on the presence of PIJA per route (See Table 2).

Table 2 Analysis of deviances table shows the changes in the fit of all possible models by adding and subtracting one parameter at the time

Variable	df	Deviance	AIC	$Pr(\chi^2)$
Elevation	1	190.66	224.66	2×10^{-6}
Forest Type	8	202.45	222.45	3×10^{-5}
Forest Density	1	176.93	210.93	2×10^{-3}
Date of Last Snowfall	7	192.39	214.39	9×10^{-4}

parameters, are subject to detection errors where observers fail to report birds that are present. We therefore, performed an explicit error assessment by considering a Hidden Markov Model in this particular implementation of RSA (see Supporting Information for further details).

Error may affect either the temporal ($\frac{\partial p^*}{\partial \cdot}$) or spatial factor ($\frac{d \cdot}{d(x,y)}$); we consider only errors in the spatial gradients, because the system is assumed to be at steady state, p^*. We performed an RSA in which each term, $\frac{\partial p^*}{\partial \cdot}\frac{d \cdot}{d(x,y)}$, was calculated as its expected value plus or minus error of omission. This gave four possible ways to calculate an error-gradient map.

We studied the worse case, where adjacent cells have error values of opposite sign. Thus, we assessed the effect of error on the final RSA map by generating a map for each parameter with its maximum error while holding the other two at their expected value (i.e., with no error). The sensitivity of RSA to errors was evaluated, by cross-tabulating maps with and without errors for each parameter, and differences were assessed using a χ^2-test (see SI Table S.1).

Unveiling the internal structure of the range

For each parameter ($\cdot$), absolute values for the spatial gradient ($\frac{d \cdot}{d(x,y)}$) on the continuous maps were calculated as $\sqrt{(x_j - x_{j-1})^2 + (y_j - y_{j-1})^2}$, where each quadratic term represents the difference between locations (j and $j-1$) in the given direction (x and y). We calculated each component ($\frac{\partial p}{\partial \cdot}\frac{d \cdot}{d(x,y)}$) of the gradient and identified, for each cell in the map, the term with the largest relative value in Eq. 3, thereby depicting the internal structure of the range.

Results

RSA allows to identify specific locations, within the geographic range of a species, where a given parameter is most important in driving spatial variation in occupancy dynamics (Fig. 2). In this particular example, extinction and colonization are the most important parameters driving PIJA persistence throughout its range and dominate in a similar proportion of sites (49.4 and 49.8 % respectively), while habitat suitability dominates in only 0.8 % of the sites and is restricted to well-defined areas within the range where abundance is high. Our results point out that the way colonization and extinction vary in importance across the geographic range of a species is much more complex and richer in spatial structure than previously thought (Fig. 2). Even though our analyses shows that extinctions dominate over colonization on range margins for PIJA (Fig. 2b), as expected (e.g., Holt and Keitt 2000), it does so in many other areas of the
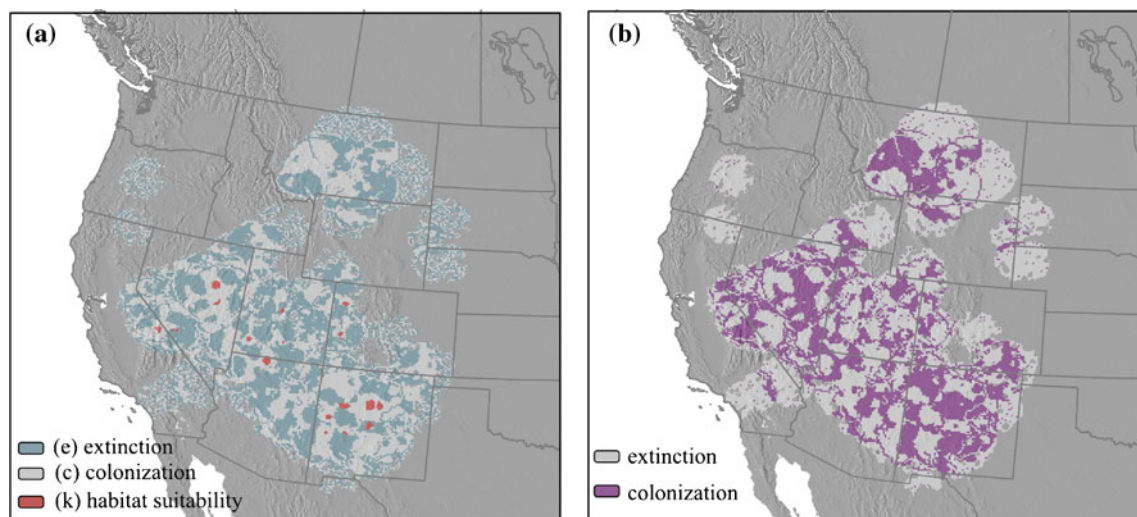

Fig. 2 **a** Spatial distribution of most important parameters for population persistence across the geographic range of Piñon jays. **b** Distribution of areas where colonization exceed extinction. Note that colonization dominates extinction in those areas where the total contribution of colonization exceeds the total contribution of extinction, which denotes source and sink areas respectively

range and not only in the boundaries, forming pockets of extinction-dominated areas interspersed by colonization dominated ones. The ecological and evolutionary consequences of this spatial mosaic in colonization and extinction dynamics should be the subject of further study (as shown by Curnutt et al. 1996; Guo et al. 2005; Holt et al. 2005; Holt and Pickering 1985; Pulliam 1988). Interestingly, this pattern is apparent for PIJA not only in isolated populations (e.g., northern California and Oregon on the western margin of the range and Nebraska and South Dakota on the eastern flank) but also in more connected but still marginal populations in southern California, central Colorado, eastern Idaho, and northern and eastern Montana (Fig. 2). A more informative representation of the same information can be achieved by plotting a binary map of those places where colonization exceed extinction (i.e., the ratio between the contributions of colonization and extinction to $p(x, y)$, Fig. 2b), which in the case of our example shows that source patches, where colonization exceed extinction, are mostly located to the interior of the border of species range. These sites should be particularly important from a conservation perspective as they are responsible for the overall cohesion of the species range.

Discussion

The dynamics of species populations are highly variable throughout the species range (Brown et al. 1995, 1996) as a consequence of the temporal and spatial variability in important demographic processes that affect growth rates and hence population persistence (Jansen and Yoshimura 1998; Keymer et al. 2000; Kawecki and Holt 2002; Gonzalez and Holt 2002; Ronce 2007). The prevailing view is that there is a gradient of population dynamics extending radially from the center of abundance and shifting from populations with net positive growth to populations that would not persist without immigration on the periphery (Brown et al. 1995; McGill and Collins 2003; Williams et al. 2003). This results in dispersal and source-sink dynamics that are ultimately responsible for setting the range boundary (Holt and Pickering 1985; Pulliam 1988; Dias 1996; Kirkpatrick and Barton 1997; Holt 2003). RSA show that complex spatial patterns in colonization, extinction, and habitat suitability exist within the species ranges. These spatial patterns could serve as a rough guide to inform conservation actions and planning within the range of species.

RSA effectively partitions the range to estimate the differential contributions of population parameters to species persistence. This approach is not limited to metapopulation dynamics as in the example presented here. RSA may be applied to any population model, as long as parameters relevant to the temporal trajectory of populations can

be used in Eq. 3. Our approximation assumes a particular type of population dynamics (i.e., metapopulation model) for the entire range, which seems to be a safe assumption in many cases (Liebhold et al. 1993; Bjørnstad et al. 1998; Hanski 1999; Williams et al. 2003; Cabral and Schurr 2010). The same as similar approaches (e.g., landscape capacity; Hanski and Ovaskainen 2000), we assume that populations have reached steady state, thereby making this approach most suitable to equilibrial situations. More research is necessary to assess how sensitive are RSA results to departures from equilibrium conditions.

RSA is a first-order approximation to understand the relative contribution of different processes to population dynamics in heterogeneous landscapes. As such, it can be improved in several ways. Our model (the same as the original model upon which ours is based, proposed by Holt and Keitt (2000) does not include dispersal explicitly in the dynamics, although it is implicitly included in the estimation of colonization and extinction rates, and this could be a way of adding complexity and realism to the model. This may be an important next step for RSA since dispersal, and the particular form of a dispersal kernel, may play a critical role in affecting colonization and extinction rates and thus local and regional persistence (e.g., Hanski 1999; Labra et al. 2003; Holland and Hastings 2008). Similarly, our formulation assumes that extinction and colonization do not interact; however, we know that they do, for example, through "rescue effects" (Brown and Kodric-Brown 1977). This could be easily incorporated through the explicit consideration of the interaction between colonization and extinction processes as in the generalized metapopulation model proposed by Harding and McNamara (2002). Finally, an interesting new venue for developing RSA may consider comparisons with current niche modeling techniques (Peterson et al. 2011) since both can generate a prediction of the spatial occupancy of species. However, RSA do this by including demographic-level information in addition to environmental data, which may complement niche modeling exercises.

RSA can be a valuable tool to inform management and conservation decisions. In Piñon Jays, for example, where habitat suitability is an important parameter, special care should be taken to preserve the piñon-juniper woodland habitat. Where colonization governs the dynamics, management should concentrate on preserving the connectivity between habitats and populations (Keitt et al. 1997). However, parameter estimation should be done carefully, as it constitutes a crucial step in RAS. In the Piñon Jay example, two main sources of errors are possible. The first source of error is associated to the choice of the spatial grain of analysis and the spatial interpolation process itself (i.e., Inverse Distance Weight). In this respect, interpolation methods not only provide simple—and

biologically deprived—approximations to the spatial variability of species, but also minimize the influence of routes with very low occupancy, and presumably subjected to large stochasticity, not considered in this analysis. However, such interpolation methods are known to be unbiased descriptors that often outperform other distribution modeling techniques (Bahn and McGill 2007). A second source of errors is associated with the estimation of parameters in populations that fluctuate in abundance over time, which for conspicuous species like PIJA, likely translates into false absences (i.e., recording an absence when in fact the species is present; MacKenzie et al. 2005; Royle and Link 2006; Wintle et al. 2004). To assess the importance of different sources of error in affecting the results herein reported, we applied a hidden Markov chain model to the PIJA dataset to simulate errors in population size estimation (see Supporting Information). The results of this analysis show that RSA is robust to errors in parameter estimation.

Several additional testable hypotheses arise from the approach proposed here. Particularly relevant to the emerging field of landscape genetics (Manel et al. 2003; McRae and Beier 2007) is the ability to identify areas containing populations governed by different parameters, which are expected to exhibit variable degree of evolutionary divergence and genetic variability dependent on the relationship between colonization and extinction processes (Turelli et al. 2001; Brooks 2006). RSA could help identifying areas within the range where adaptive potential to track changes in the environment, as expected under climate change scenarios, is higher and thus essential for species persistence. This highlights the importance of landscape-level assessment of occupancy, such as RSA, to understand how landscape structures provide the spatial template for adaptation (Hanski 1999; Brooks 2006; McRae et al. 2008; Pearman et al. 2008; Kearney and Porter 2009).

Finally, it is worth to mention that while RSA introduces what we think it is a promising approach to understanding the internal dynamic of geographic ranges and a way to undertake population management at regional scales, its application requires large spanned datasets in time and space. We have illustrated RSA using one of the most extensive one, the North American Breeding Bird Survey. Acknowledging that such information on species occurrence remains scarce, there is no reason to believe that such information will become more readily available as field information is gathered by the different agencies in charge of wildlife monitoring. Our intention here is to provide a modeling approach to assess occupancy at large spatial scale posing an old known trade-off between explanation and prediction power, where the possibilities to provide large-scale predictions as tools for management at state or even country level is clearly limited by the availability of high-quantity datasets. However, we believe that the approach is worthwhile and provides additional information on the internal dynamics of species range by merging space and time in a succinct model.

In conclusion, RSA quantifies and makes explicit relationships between spatial gradients of population parameters and temporal fluctuations in abundances. This synthetic approach should be directly applicable in management and conservation biology. Most importantly, we believe that it provides a concrete basis to understand the spatial dimensions of species ecology and demography, as well as their evolutionary consequences.

References

Arim M, Abades S, Neill P, Lima M, Marquet P (2006) Spread dynamics of invasive species. Proc Natl Acad Sci USA 103:374–378. doi:10.1073/pnas.0504272102

Bahn V, McGill BJ (2007) Can niche-based distribution models outperform spatial interpolation? Global Ecol Biogeogr 6:733–742. doi:10.1111/j.1466-8238.2007.00331.x

Balda RP, Bateman GC (1971) Flocking and annual cycle of the pion jay, *Gymnorhinus cyanocephalus*. Condor 73:287–302

Balda R, Kamil A, Bednekoff P (1997) Predicting cognitive capacities from natural histories: examples from four corvid species. Curr Ornithol 13:33–66

Bjørnstad ON, Stenseth NC, Saitoh T, Lindgjærde OC (1998) Mapping the regional transition to cyclicity in *Clethrionomys rufocanus*: spectral densities and functional data analysis. Res Popul Ecol 40:77–84

Brooks C (2006) Quantifying population substructure: extending the graph-theoretic approach. Ecology 87:864–872

Brown JH, Kodric-Brown A (1977) Turnover rates in insular biogeography—effect of immigration on extinction. Ecology 58:445–449

Brown JH, Mehlman DW, Stevens GC (1995) Spatial variation in abundance. Ecology 76:2028–243

Brown JH, Stevens GC, Kaufman DM (1996) The geographic range: size, shape, boundaries, and internal structure. Annu Rev Ecol Syst 27:597–623

Cabral JS, Schurr FM (2010) Estimating demographic models for the range dynamics of plant species. Global Ecol Biogeogr 19:85–97. doi:10.1111/j.1466-8238.2009.00492.x

Carter RN, Prince SD (1981) Epidemic models used to explain biogeographical distribution limits. Nature 293:644–645

Case TJ, Taper ML (2000) Interspecific competition, environmental gradient, gene flow, and the coevolution of species' border. Am Nat 155:582–605

Clark CW, Rosenzweig ML (1994) Extinction and colonization processes: parameters estimates from sporadic surveys. Am Nat 143:583–596

Curnutt JL, Pimm SL, Maurer BA (1996) Population variability of sparrows in space and time. Oikos 76:131–144

Diamond JM, May RM (1977) Species turnover rates on islands: dependence on census interval. Science 197:266–270

Dias PC (1996) Sources and sinks in population biology. Trends Ecol Evol 11:326–330

Fortin M, Dale M (2005) Spatial analysis: a guide for ecologists. Cambridge University Press, Cambridge

Gaston KJ (2003) The structure and dynamics of geographic ranges. Oxford series in ecology and evolution. Oxford University Press, New York

Gonzalez A, Holt RD (2002) The inflationary effects of environmental fluctuations in source-sink systems. Proc Natl Acad Sci USA 99:14872–14877

Guo Q, Taper M, Schoenberger M, Brandle J (2005) Spatial-temporal population dynamics across species range: from centre to margin. Oikos 108:47–57

Harding KC, McNamara JM (2002) A unifying framework for metapopulation dynamics. Am Nat 160:173–85

Hanski I (1999) Metapopulation ecology. Oxford University Press

Hanski I, Ovaskainen O (2000) The metapopulation capacity of a fragmented landscape. Nature 404:755–758. doi:10.1038/35008063

Hengeveld R, Haeck J (1982) The distribution of abundance. I. measurements. J Biogeogr 9:303–316

Holland MD, Hastings A (2008) Strong effect of dispersal network structure on ecological dynamics. Nature 456:792–795. doi:10.1038/nature07395

Holt RD (1983) Lecture notes in biomathematics, chap. Models for peripheral populations: the role of immigration. Springer-Verlag, Berlin, pp 25–32

Holt RD (2003) On the evolutionary ecology of species' range. Evol Ecol Res 5:159–178

Holt RD, Keitt TH (2000) Alternative causes for range limits: a metapopulation perspective. Ecol Lett 3:41–47

Holt RD, Keitt TH (2005) Species' borders: a unifying theme in ecology. Oikos 108:3–6

Holt RD, Pickering J (1985) Infectious disease and species coexistence: a model of lotka-volterra form. Am Nat 126:196–211

Holt RD, Lawton JH, Gaston KJ, Blackburn TM (1997) On the relationship between range size and local abundance: back to basics. Oikos 78:183–190

Holt RD, Keitt TH, Lewis MA, Maurer BA, Taper ML (2005) Theoretical models of species? Borders: single species approaches. Oikos 108:18–27

Hosmer DW, Lemeshow S, May S (2011) Applied survival analysis: regression modeling of time to event data. Wiley, Hoboken

Jansen VAA, Yoshimura J (1998) Populations can persist in an environment consisting of sink habitats only. Proc Natl Acad Sci USA 95:3696–3698

Kawecki TJ, Holt RD (2002) Evolutionary consequences of asymmetric dispersal rates. Am Nat 160:333–347

Kearney M, Porter W (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecol Lett 12:334–350. doi:10.1111/j.1461-0248.2008.01277.x

Keitt TH, Urban DL, Milne BT (1997) Detecting critical scales in fragmentes landscapes. Conserv Ecol 1:4

Keymer JE, Marquet PA, Velasco-Hernández JX, Levin SA (2000) Extinction thresholds and metapopulation persistence in dynamic landscapes. Am Nat 156:478–494

Kirkpatrick M, Barton NH (1997) Evolution of a species range. Am Nat 150:1–23

Klimkiewicz MK, Futcher AG (1989) Longevity records of North American birds: supplement 1. J Field Ornithol 60:469–494

Labra F, Lagos NA, Marquet PA (2003) Dispersal and transient dynamics in metapopulations. Ecol Let 6:197–204. doi:10.1046/j.1461-0248.2003.00413.x

Levins R (1970) Some mathematical questions in biology, chap. Extinction, 77–107. American Mathematical Society, Providence

Liebhold AM, Rossi RE, Kemp WP (1993) Geostatistics and geographic information systems in applied insect ecology. Annu Rev Entomol 38:303–327. doi:10.1146/annurev.en.38.010193.001511

MacArthur RH (1960) On the relative abundance of species. Am Nat 94:25–37

MacArthur RH, Levins R (1964) Competition, habitat selection, and character displacement in a patchy environment. Proc Natl Acad Sci USA 51:1207–1210

MacKenzie D, Nichols JD, Royle JA, Pollock KH, Bailey LL, Hines JE (2005) Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic, San Diego

Manel S, Schwartz MK, Luikart G, Taberlet P (2003) Landscape genetics: combining landscape ecology and population genetics. Trends Ecol Evol 18:189–197

Marzluff JM, Balda RP (1989) Causes and consequences of female-based dispersal in a flock-living bird, the Piñon jay. Ecology 70:316–328

Marzluff JM, Balda RP (1992) The Pinyon jay: behavioral ecology of a colonial and cooperative corvid. T. & A.D. Poyser, London

Maurer B, Brown J (1989) Distributional consequences of spatial variation in local demographic processes. Ann Zool Fenn 26:121–131

McGill B, Collins C (2003) A unified theory for macroecology based on spatial patterns of abundance. Evol Ecol Res 5:469–492

McRae BH, Beier P (2007) Circuit theory predicts gene flow in plant and animal populations. Proc Natl Acad Sci USA 104:19885–19890. doi:10.1073/pnas.0706568104

McRae BH, Dickson BG, Keitt TH, Shah VB (2008) Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89:2712–2724. doi:10.1890/07-1861.1

Morlon H, White EP, Etienne RS, Green JL, Ostling A, Alonso D, Enquist BJ, He F, Hurlbert A, Magurran AE, Maurer BA, McGill BJ, Olff H, Storch D, Zillio T (2009) Taking species abundance distributions beyond individuals. Ecol Lett 12:488–501. doi:10.1111/j.1461-0248.2009.01318.x

Pearman PB, Guisan A, Broennimann O, Randin CF (2008) Niche dynamics in space and time. Trends Ecol Evol 23:149–158. doi:10.1016/j.tree.2007.11.005

Peterson AT, Soberón J, Pearson RG, Anderson RP, Martinez-Meyer E, Nakamura M, Araùjo MB (2011) Ecological niches and geographic distributions. Princeton University Press, Princeton

Pulliam RH (1988) Sources, sinks, and population regulation. Am Nat 132:652–661

Ronce O (2007) How does it feel to be like a rolling stone? Ten questions about dispersal evolution. Annu Rev Ecol Syst 38:231–253. doi:10.1146/annurev.ecolsys.38.091206.095611

Royle JA, Link WA (2006) Generalized site occupancy models allowing for false positive and false negative errors. Ecology 87:835–841

Samaniego H, Srandour G, Milne BT (2012) Analyzing Taylors Scaling Law: qualitative differences of social and territorial behavior on colonization/extinction dynamics. Popul Ecol 54:213–223. doi:10.1007/s10144-011-0287-0

Sauer JR, Hines JE, Fallon J (2005) The north american breeding bird survey, results and analysis 1966–2005. Version 6.2.2006, Tech. rep. USGS Patuxent Wildlife Research Center, Laurel

Turelli M, Barton N, Coyne J (2001) Theory and speciation. Trends Ecol Evol 16:330–343

Venables WN, Ripley BD (2002) Modern applied statistics with S-PLUS, 3rd edn. Springer, New York

Williams CK, Ives AR, Applegate RD (2003) Population dynamics across geographical ranges: time-series analyses of three small game species. Ecology 84:2654–2667

Wintle BA, McCarthy MA, Parris KM, Burgman MA (2004) Precision and bias of methods for estimating point survey detection probabilities. Ecol Appl 14:703–712

Zhu Z, Evans D (1994) United states forest types and predicted percent cover from AVHRR data. Photogramm Eng Rem S 60:525–531