To predict the niche, model colonization and extinction

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Abstract. Ecologists frequently try to predict the future geographic distributions of species. Most studies assume that the current distribution of a species reflects its environmental requirements (i.e., the species' niche). However, the current distributions of many species are unlikely to be at equilibrium with the current distribution of environmental conditions, both because of ongoing invasions and because the distribution of suitable environmental conditions is always changing. This mismatch between the equilibrium assumptions inherent in many analyses and the disequilibrium conditions in the real world leads to inaccurate predictions of species' geographic distributions and suggests the need for theory and analytical tools that avoid equilibrium assumptions. Here, we develop a general theory of environmental associations during periods of transient dynamics. We show that time-invariant relationships between environmental conditions and rates of local colonization and extinction can produce substantial temporal variation in occupancy–environment relationships. We then estimate occupancy–environment relationships during three avian invasions. Changes in occupancy–environment relationships over time differ among species but are predicted by dynamic occupancy models. Since estimates of the occupancy–environment relationships themselves are frequently poor predictors of future occupancy patterns, research should increasingly focus on characterizing how rates of local colonization and extinction vary with environmental conditions.

Key words: dynamic occupancy; environmental associations; geographic range dynamics; habitat selection; invasions; metapopulation; process models; species distribution models.

Introduction

Predicting the future geographic ranges of species is a critical need in a rapidly changing world. Most studies in this field are pattern based and rely on statistical models or machine learning algorithms to characterize the likelihood that a site is occupied by a given species based on the environmental characteristics of that site (hereafter occupancy–environment relationships). These studies then use these relationships to predict occupancy under a different set of environmental conditions assuming the same occupancy–environment relationships (Guisan and Thuiller 2005). Implicitly, these studies assume that current distribution of a species reflects its environmental requirements or niche. Studies using taxon-specific process models have shown that this assumption often leads to overestimation of both range losses and gains in response to environmental change (Iverson et al. 2004, Morin and Thuiller 2009). However, these process models are typically highly parameterized and include taxon-specific structures that can make it difficult to assess the generality of these findings.

We develop a general theory of the transient dynamics of occupancy–environment relationships using simple metapopulation models. Occupancy–environment relationships can, and often are, described in terms of continuous functions; however, for clarity and without any loss in generality, we focus on the case in which there are two discrete types of environments. We characterize environmental associations both in terms of the difference in occupancy between these two environments (*A*) and in terms of the ratios of the occupancies in these two environments (*R*). We show that during range expansion, early estimates of occupancy–environment relationships are rarely good predictors of future occupancy–environment relationships. We then present three case studies of occupancy–environment relationships during actual avian invasions. Changes in estimated occupancy–environment relationships over the course of all three invasions are consistent with theoretical predictions.

To illustrate our underlying argument, as well as clarify the meaning of the quantities *A* and *R,* we begin with a simple thought experiment (Fig. 1). Consider a species invading two environments in which colonization, the rate at which unoccupied patches become occupied, and extinction, the rate at which occupied patches become unoccupied, differ. Early in an invasion, differences in occupancy between environments are determined mostly

Step 1: Assume a relatively simple metapopulation process with colonization and extinction rates that do not vary with time (time-invariant), but are specific to each environment. For example:

Environment 1: colonization (γ_1) = 0.5; extinction (ε_1) = 0.3
Environment 2: colonization (γ_2) = 0.4; extinction (ε_2) = 0.1

Step 2: Imagine a set of patches in each environment that are unoccupied to begin with and then are independently invaded. (Environment 1, green. Environment 2, purple. Boxes with hatching are occupied by the invading species.)
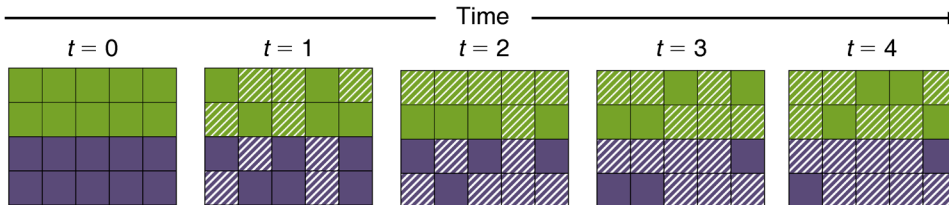
Step 3: For each time step, analyze the occupancy–environment pattern and graph results.

Quantities measured in occupancy–environment studies, typically at a single time, and often assumed to predict values at future times	Time			
	$t = 1$	$t = 2$	$t = 3$	$t = 4$
Proportion of patches occupied in environment 1 (p_1)	5/10	6/10	6/10	6/10
Proportion of patches occupied in environment 2 (p_2)	4/10	6/10	7/10	8/10
Difference in occupancy between two environments (A): $A = p_1 - p_2$	0.1	0	−0.1	−0.2
Ratio of occupancies between two environments (R): $R = p_1/p_2$	1.25	1	0.86	0.75
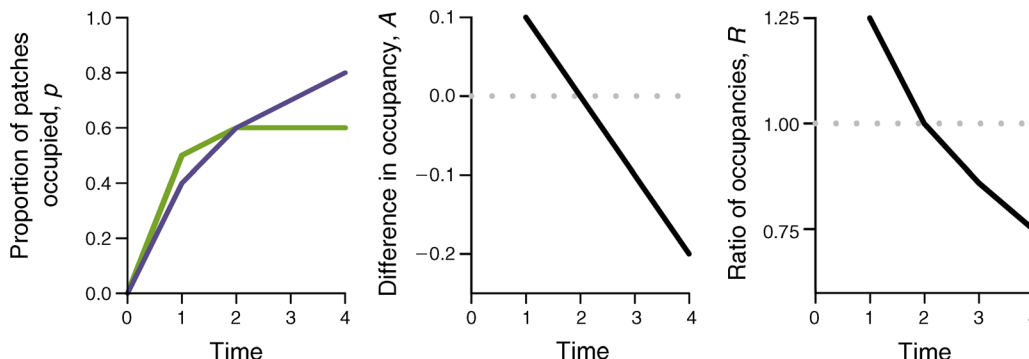
Conclusion: Two measures of environmental selection (A and R) vary over time when a system is not at equilibrium.

Fig. 1. A thought experiment: a species invading two environments.

by colonization. (At time step 1 in a discrete case, such as Fig. 1, differences are determined entirely by colonization, hence the higher occupancy in habitat 1 in this example). However, as the number of occupied patches increases, differences between environments in extinction rates begin to play a more important role. In the example in Fig. 1, the differences between environments in terms of extinction rate are greater than the differences in terms of colonization rates, so environment 2 eventually has a higher occupancy, even though environment 1 has the higher colonization rate and initially had a higher occupancy. Ecologists typically observe occupancies over a narrow range of time, finding larger probabilities of

occupancy in one environment than the other, and assume that these values are predictive of the future. For the example in Fig. 1, a pattern-based, or static, analysis at time step 1 would actually misidentify the eventual direction of environmental selection. In the next section, we more thoroughly consider the metapopulation dynamics implicit in this thought experiment.

Extending metapopulation theory to address transient occupancy–environment relationships

While metapopulation models can take many different forms (Levins 1969, Hanski 1982, Gotelli 1991), most variations can be reparameterized into the following form

$$\frac{dp}{dt} = ap^2 + bp + c \qquad (1)$$

where a, b, and c are constants that are functions of the underlying colonization and extinction rates, p is the regional occupancy (the proportion of patches occupied within some area), and dp/dt is the derivative of p with respect to time, t. In one of the simplest versions of Eq. 1, colonization (γ) and extinction (ε) are independent of regional occupancy (i.e., $a = 0$, $b = -(\gamma + \varepsilon)$, and $c = \gamma$). As in the thought experiment, we consider two sets of patches representing different environments, with occupancies p_1 and p_2, following this simple version of Eq. 1, but differing in colonization and/or extinction rates. We define environment 1 as having a colonization rate greater than or equal to the colonization rate in environment 2 ($\gamma_1 \geq \gamma_2$). Under these conditions, both A and R have straightforward equilibrium values

$$A_{eq} = \frac{\gamma_1}{\gamma_1 + \varepsilon_1} - \frac{\gamma_2}{\gamma_2 + \varepsilon_2} \qquad (2)$$

$$R_{eq} = \frac{\gamma_1(\gamma_2 + \varepsilon_2)}{\gamma_2(\gamma_1 + \varepsilon_1)}. \qquad (3)$$

In the simplest case of a system near equilibrium, an examination of static species–environment relationships (i.e., estimating A_{eq} or R_{eq}) provides information about environment-specific differences in these functions (Eqs. 2 and 3) of colonization and extinction rates. But inferences about the relationships between the environment and either extinction or colonization are not readily obtained without additional information or structural assumptions (e.g., Hanski 1994), because an infinite number of values of γ_1, γ_2, ε_1, and ε_1 can lead to the same values for A_{eq} or R_{eq}. This difficulty in discerning processes from patterns is not surprising (Tyre et al. 2001) and perhaps could be ignored by pragmatists, so long as systems are near equilibrium when observed and we only wish to make predictions about future equilibrium conditions. On the other hand, many systems are not at equilibrium and may not reach equilibrium in a reasonable time. Moreover, in many circumstances, we are concerned with the transient dynamics that occur when a system is far from equilibrium (Hastings 2004).

To study how A and R may vary at the edge of an expanding geographic range over time under this model, we assume that $p(0) = 0$, which means Eq. 1 can be solved (see Appendix A for details of solution) to yield the following expression for time-specific occupancy, $p(t)$

$$p(t) = \frac{\gamma(1 - e^{-(\gamma + \varepsilon)t})}{\gamma + \varepsilon} \qquad (4)$$

where e is the base of the natural logarithm. Eq. 4 suggests the potential for time-varying values of A and R. Focusing first on A, we consider its first derivative

$$\frac{dA}{dt} = \gamma_1 e^{-(\gamma_1 + \varepsilon_1)t} - \gamma_2 e^{-(\gamma_2 + \varepsilon_2)t}. \qquad (5)$$

Expression 5 suggests three scenarios (in addition to the trivial example where $\gamma_1 = \gamma_2$ and $\varepsilon_1 = \varepsilon_2$). If $\gamma_1 + \varepsilon_1 < \gamma_2 + \varepsilon_2$, then dA/dt is decreasing over time, but is always positive, so A is positive and increases asymptotically toward its equilibrium (curve i in Fig. 2A). Under this same scenario, R starts at γ_1/γ_2 and increases asymptotically towards its equilibrium value (curve i in Fig. 2B). The implication is that early measurements of A or R will systematically underestimate later values. In the second scenario ($\gamma_1 + \varepsilon_1 = \gamma_2 + \varepsilon_2$), A is positive and increases asymptotically to its equilibrium (curve ii in Fig. 2A), similarly to scenario 1, however $R = \gamma_1/\gamma_2$ for all t (curve ii in Fig. 2B). This is the only case in which early measurement of environmental selection, via R, accurately predicts future conditions. In the third and final scenario, $\gamma_1 + \varepsilon_1 > \gamma_2 + \varepsilon_2$, the value of A is positive and increasing until time, t^*, given by

$$t^* = \frac{\ln \gamma_1 - \ln \gamma_2}{\gamma_1 + \varepsilon_1 - \gamma_2 - \varepsilon_2} \qquad (6)$$

after which, A decreases to its equilibrium value (curves iii–v in Fig. 2A). As in the first two scenarios, R starts at γ_1/γ_2; however, under this scenario R decreases asymptotically to its equilibrium value (curves iii–v in Fig. 2B). Under this third scenario, researchers would find early evidence for habitat selection in the form of A or R that later declines in strength and can potentially reverse itself (i.e., different habitats appear to be selected for, depending on the timing of the static assessment; curve v in Fig. 2A and 2B). Early estimates of A, in particular, can be uninformative, as future values of A may be higher and then lower.

We were interested in how the above predictions would change if we considered more realistic models in which colonization and extinction vary as a function of regional occupancy. Therefore, we considered a different version of Eq. 1 where a is negative and both b and c are positive. Provided that $b < |a|$ and c is not too large, this model behaves very similarly to that of Levins (1969), with $|a|$ equal to the colonization rate and $|a| - b$ equal to the extinction rate. This model can be interpreted ecologically as a situation where there is a constant supply of colonists from outside the region (c), which is augmented by an internal source of colonists that increases as occupancy increases. Under these constraints, Eq. 1 can be solved to yield

$$p(t) = \frac{|\lambda_{''}|\left(1 - e^{a(\lambda_{''} - \lambda_{'})t}\right)}{1 + \left|\lambda_{''}/\lambda_{'}\right| e^{a(\lambda_{''} - \lambda_{'})t}} \qquad (7)$$

where $\lambda_{'} = -b/2a - \sqrt{b^2/4a^2 - c/a}$, $\lambda_{''} = -b/2a + \sqrt{b^2/4a^2 - c/a}$, and the equilibrium value is $\lambda_{''}$ (Appendix A). If we assume that c, the supply of colonists from outside the region, is small (e.g., $c = 0.01$), then $\lambda_{'}$ is a negative value
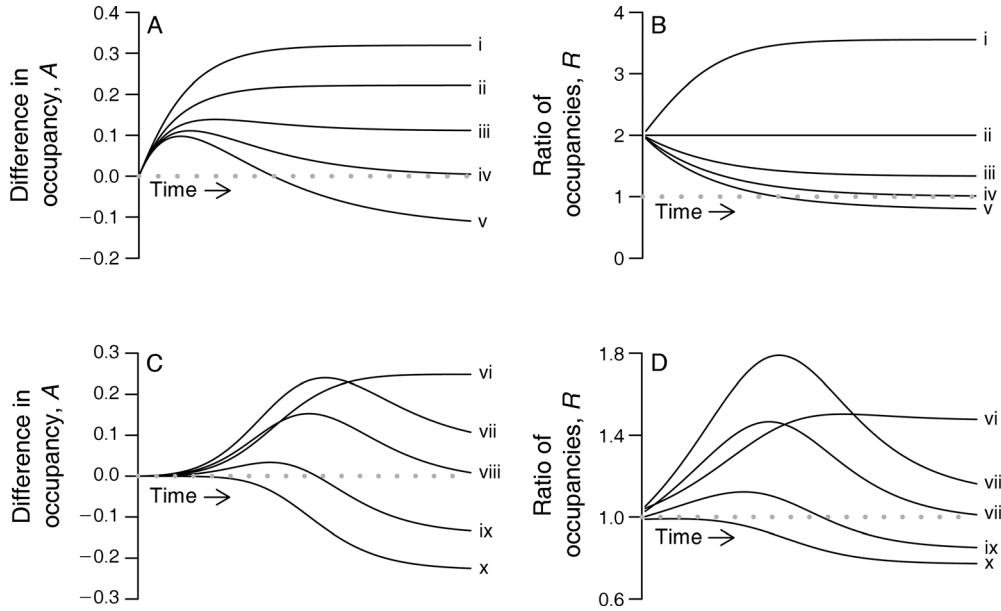
FIG. 2. Selection for one environment over another at the edge of an expanding range depends on whether (A, B) colonization and extinction are unaffected by regional occupancy or (C, D) depend on regional occupancy, and (A, C) whether selection is measured as the difference in the occupancy rate of two environments or (B, D) the ratio of occupancy rates between two environments, and the parameter values. Curves i–v share the same values for colonization (γ) and extinction (ε) in environment 1 and for colonization in environment 2 ($\gamma_1 = 0.2$, $\varepsilon_1 = 0.25$, and $\gamma_2 = 0.1$). The extinction rate in environment 2 distinguishes curves i–v ($\varepsilon_2 = 0.7$ [i]; 0.35 [ii]; 0.2 [iii]; 0.125 [iv]; 0.075 [v]). Curves vi–x share the same values for four of six parameters ($a_1 = -0.6$, $b_1 = 0.45$, $c_1 = c_2 = 0.01$) and differ in terms of two parameters ($a_2 = -0.8$[vi]; -0.45[vii – x] and $b_2 = 0.4$ [vi]; 0.3 [vii]; 0.34[viii]; 0.4 [ix]; 0.44 [x]).

very close to zero, $\lambda_{\prime\prime} \cong {}^{b}/_{|a|}$, and Eq. 7 can be approximated as

$$p(t) \cong \frac{|\lambda_{\prime\prime}|(1 - e^{-bt})}{1 + \left|{}^{\lambda_{\prime\prime}}/_{\lambda_{\prime}}\right| e^{-bt}}. \quad (8)$$

Under this scenario, the absolute and relative differences between two environments with different a and b tend toward

$$A_{eq} \cong \frac{b_1}{|a_1|} - \frac{b_2}{|a_2|} \quad (9)$$

$$R_{eq} \cong \frac{b_1|a_2|}{b_2|a_1|}. \quad (10)$$

For clarity, we define environment 1 to have a b greater than or equal to b in environment 2 (i.e., $b_1 \geq b_2$). Dynamics under this model are highly variable, and for many parameter combinations, A and R reach their highest (or lowest) values during the middle of the invasion (curves vii–ix in Fig. 2C–D). The only conditions under which the static pattern of selection increases or decreases monotonically are when $b_1 = b_2$ or b_1 is only slightly larger than b_2, and the difference between $|a_2|$ and $|a_1|$ is sufficiently large (curves vi and x in Fig. 2C–D). The ecological implication from these models is that as long as colonization is dependent on regional occupancy, early estimates of A and R may

provide very little information about either future values of these quantities or how colonization and extinction rates differ between habitats.

The relatively simple theory developed here suggests a variety of ways that A and R can vary over time, even when the environment–process relationship is time-invariant. Available studies suggest that occupancy–environment relationships do in fact change over time (Johnson and Krohn 2002, Václavík and Meentemeyer 2011), but do not provide sufficient information to determine whether empirical relationships are similar to examples in Fig. 2. Therefore, we conducted analyses for three case studies of environment–occupancy relationships during avian invasions.

METHODS

For each case study, we fit independent single season (i.e., static) occupancy models for each year that had sufficient data using a habitat covariate to predict occupancy. The case studies differ from the theoretical models in that the habitat covariate (environmental condition) in each example is continuous, so we define p_1 and p_2 as the expected occupancies in patches whose habitat covariates are in the 95% and 5% percentiles, respectively, of the continuous distributions of the habitat covariates (in all case studies, higher values of the habitat covariate correspond to expected higher quality). We estimated A and R based on the maximum
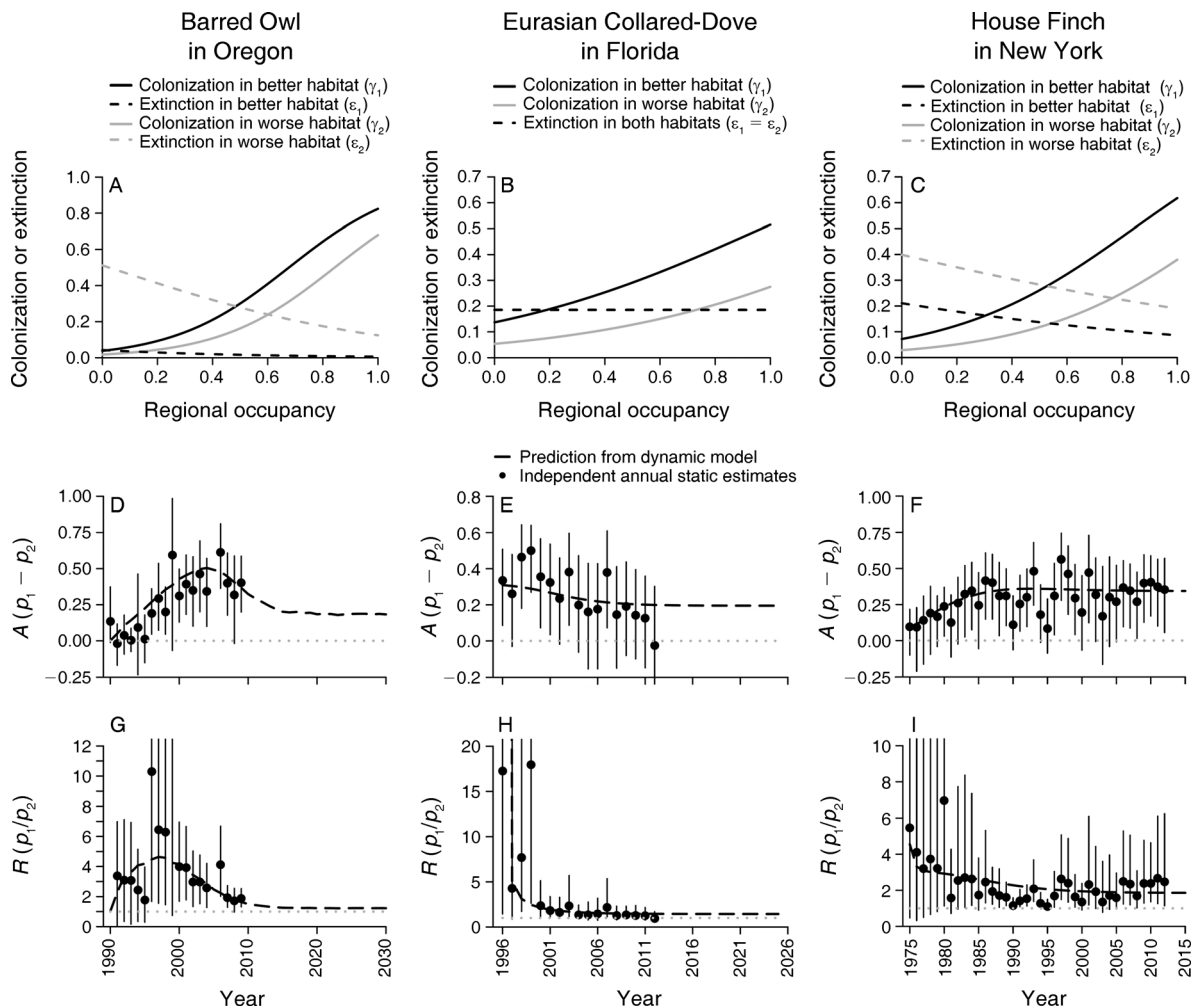
FIG. 3. Colonization and extinction rates as a function of environmental conditions and regional occupancy according to the best dynamic model for (A) Barred Owls, (B) Eurasian Collared-Dove, and (C) House Finch. For all three species, predictions of (D–F) A and (G–I) R based on a dynamic model (lines) are similar to estimates based on static analyses based on each year's data. Estimates (solid circles) are shown with 95% confidence intervals (whiskers). Note that some confidence intervals extend past the upper end of the y-axis in panels (G–I) and the prediction for 1956 in panel (H) is also greater than the y-axis upper limit.

likelihood estimates of occupancy and the associated covariance matrix.

We compare these estimates to predictions of A and R from a dynamic model fit to the same data. For the Barred Owl, we relied on the best model identified through past work (Yackulic et al. 2012). For the other two case studies, we identified the best model according to Akaike's information criterion (AIC) through an iterative process in which we first chose the best of four potential structures for detection probability: (1) constant, (2) varying by stop (early stops are hypothesized to have higher detection probability a priori), (3) varying by year, and (4) varying by year and stop. Next, we considered models that added an autologistic covariate (calculated over the whole study area) to colonization only, extinction only, and both colonization and extinction. Lastly, we added the habitat

covariate to colonization only, extinction only, and both colonization and extinction and chose the best structure. We also included the habitat covariate to predict initial occupancy. This best structure was then used to predict expected occupancy for all sites in the data set over time. Predicted A and R were then calculated based on sites with covariates responding to 5% and 95% of the distribution of the covariates. Both static and dynamic models were fit in PRESENCE version 6.4 (Hines 2006).

Barred Owl case study

Data come from incidental Barred Owl detections during Northern Spotted Owl surveys at the Tyee Density Study Area in Roseburg, Oregon, USA. Previous analyses have characterized the Barred Owl invasion at the Tyee site using dynamic occupancy

models in which colonization and extinction were dependent on both regional occupancy and a habitat covariate, the amount of riparian forest in each survey polygon in a given year (Yackulic et al. 2012; Fig. 3A). We used the same covariate here in the single-season analyses.

Eurasian Collared-Dove and House Finch case studies

Both species have been analyzed previously using specialized forms of dynamic occupancy models, however these analyses did not include environmental conditions as covariates (Wikle 2003, Bled et al. 2011). Eurasian Collared-Dove and House Finches are both thought to be associated with human development in their introduced range. Therefore we used the human influence index, an index of development that has been used in past studies of species distributions (e.g., Yackulic et al. 2011), as our habitat covariate. For both case studies, we downloaded North American Breeding Bird Survey (BBS) data for the state in which the species was first introduced: Florida and New York, respectively (*available online*).[6] We defined occupancy at the route level and considered each group of 10 stops as an opportunity for detection. Geographic coordinates for each route were downloaded, and the human influence index was calculated based on the midpoint of the route.

RESULTS

Barred Owls and riparian forest between 1990 and 2009

Annual estimates of A increased throughout the late 1990s and 2000s before leveling off and declining slightly in the last few years (Fig. 3D, G). Estimates of R were very high in the late 1990s and early 2000s and have declined in recent years as Barred Owls became ubiquitous in the study site. The patterns in annual estimates of A and R are consistent with simulated expectations based on previous analysis of colonization and extinction rates and appear similar to some of the predictions from the general theory (e.g., curve vii in Fig. 2C–D). In contrast to apparent changes in occupancy–environment relationships, dynamic models of time-invariant relationships between amount of riparian forest and both local colonization and extinction probabilities fit the data well.

Eurasian Collared-Dove and the human influence index between 1996 and 2012

During the period for which A and R are estimable, they both declined (Fig. 3E, H). However, Eurasian Collared-Doves were present for at least a decade prior to 1996. From 1996–2003, the 95% confidence intervals of A and R are greater than 0 and 1, respectively, in six years. Qualitatively these patterns appear consistent with the latter halves of Fig. 2A–B (curve iii) and Fig. 2C–D (curve vii). The dynamic modeling suggested that

[6] https://www.pwrc.usgs.gov/bbs

colonization depended on regional occupancy and the amount of human development (Fig. 3B; Appendix B), so patterns prior to 1996 were likely more similar qualitatively to Fig. 2C–D (curve vii). Predictions of A and R from the dynamic model correspond well with the actual annual estimates.

House Finch and the human influence index between 1975 and 2012

Dynamic modeling suggests that rates of both local colonization and extinction of House Finches are dependent on regional occupancy and the amount of human development (Fig. 3C; Appendix B). We were unable to estimate A and R until 1975 because of an insufficient number of detections in the BBS. From 1975 to 1985, A increases, after which it remains fairly steady around a value of 0.35 for the rest of the time series, agreeing with predictions from the dynamic model (Fig. 3F). As predicted by the dynamic model, R begins at high values and declines to a value of ~2 (Fig. 3I). Estimates of A and R decline during the early to mid-1990s, coincident with outbreaks of *Mycoplasma gallisepticum*, an infectious disease that caused widespread declines. Qualitatively, with the exception of the 1990s, these patterns are consistent with Fig. 2A–B (curve iii) and Fig. 2C–D (curve vii).

DISCUSSION

We have shown that temporal variation in occupancy–environment relationships is expected when a species' distribution is not at equilibrium, even when process–environment relationships remain constant. In our view, it is these latter relationships between the environment and rates of extinction and colonization that should be of primary interest, rather than the changing occupancy–environment patterns that they produce. The theory we developed produces a variety of trajectories, some of which occurred in the case studies (Figs. 2 and 3). Disequilibrium is likely to be common at the edges of many species' ranges, where local populations will often either be declining or increasing in response to recent changes in environmental conditions. In rapidly spreading organisms, such as the species considered in our case studies, the edge of the range is constantly being redefined. In the case of the Eurasian Collared-Dove, A and R show patterns in Louisiana (not presented) similar to those in Florida, but with an approximately four-year lag. As a consequence, estimates of A and R varied over time, but also across space during much of the 1990s and 2000s. Whereas the three species considered in our case studies appear to be at or nearing equilibrium approximately two decades after first arriving at a location, disequilibrium conditions could persist for much shorter or longer periods of time depending on the rates of population processes, especially dispersal, relative to the rate at which environmental conditions are changing. In some tree species, for example, disequilibrium could persist for

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hundreds to thousands of years and vary spatially (Saltré et al. 2013).

While it may seem odd that researchers have frequently relied on analyses and theory that assume equilibrium conditions to predict dynamics (i.e., range shifts), such mismatches are common in ecology (Hastings 2004). Whereas there are increasing numbers of researchers using various types of process based models to predict range change, we have sought a very general approach to illustrate how occupancy–environment relationships can change in complex ways over time (and space) even when the underlying governing equations are time-invariant and relatively simple. In the absence of the arguments we have made here, the natural tendency might be to interpret changes in occupancy–environment relationships over time as the result of shifts in a species' niche (Guisan et al. 2014). In the light of our theoretical arguments and case studies, however, we would argue that researchers should minimally first determine that species are at equilibrium in both time periods and geographic areas being compared before arguing for a shift in equilibrium conditions. Of course, our preference would be to focus on the relationships between environmental conditions and both local extinction and colonization, as changes in these relationships are the basis for changes in equilibrium occupancy.

Both the theory we have developed here and our case studies suggest that characterizing current occupancy–environment relationships to predict future occupancy patterns under different distributions of habitat or climatic conditions can be misleading. The substantial variation in the occupancy–environment relationship that was easily generated by simple models of constant environment–process relationships and that was also evident in all three case studies has nontrivial implications for the substantial resources currently directed at characterizing static patterns. In the case of Barred Owls, which are implicated in the decline of the endangered Northern Spotted Owl (Dugger et al. 2011, Yackulic et al. 2014), an occupancy–environment analysis conducted a decade ago might have led to the incorrect conclusion that Barred Owls would continue to be found mostly in riparian forest, with significant (and incorrect) implications for management. In contrast, an analysis of the relationship between riparian forest and probabilities of patch extinction and colonization likely would have led to appropriate predictions. More broadly, hundreds of published papers each year seek to address important issues, such as biological response to changing climate and ongoing invasions, by characterizing occupancy–environment relationships. Interestingly, much of the methodological research in this area currently focuses on fitting nonlinear relationships between occupancy and environmental covariates, with far less attention on characterizing either the ecological or the observation processes that produce these patterns (Yackulic et al. 2013).

Our focus has been on biological invasions, as we were initially motivated by the Barred Owl invasion of the Pacific Northwest in the United States and associated consequences for the endangered Northern Spotted Owl (Yackulic et al. 2012, 2014). However, the likelihood of being misled by time-specific analyses of pattern is very general and extends far beyond the context of invasions (e.g., see Appendix A). Our simple examples focused on time-invariant relationships between vital rates and a single source of variation, one environmental covariate. Relationships between the environment and either colonization or extinction could themselves exhibit temporal variation, further reducing the utility of static occupancy–environment relationships for any purpose other than time-specific description. It is also unlikely that single covariates will be solely responsible for all spatial and temporal variation in vital rates. Instead, we would expect multiple habitat features, as well as factors such as interspecific interactions and climate, to be important sources of variation in the vital rates underlying occupancy dynamics. Perhaps most importantly, we would expect global change to be characterized by space–time changes in these covariates themselves. Nonstationary dynamics of covariate drivers of vital rates provide strong arguments not only for dynamic modeling, but for joint modeling of occupancy dynamics and dynamics of the drivers themselves (see Nichols et al. [2011] for climate change, Yackulic et al. [2014] for interspecific interactions, and Miller et al. [2012] for habitat dynamics). Finally, we note the necessity of making strong assumptions about species dispersal abilities when attempting to predict future species distribution patterns from static habitat–occupancy relationships. The direct incorporation into dynamic modeling of autologistic neighborhood effects on rates of colonization and extinction (Bled et al. 2011, Yackulic et al. 2012, Eaton et al. 2014) is one promising approach to dealing with this issue directly.

Process models developed to date have been extremely informative, but also very taxon-specific, limiting their widespread application (Anderson et al. 2009, Morin and Thuiller 2009). The work we present suggests that modeling general metapopulation processes (colonization and extinction) holds promise as a way forward in both understanding and predicting range dynamics (Buckland and Elston 1993, MacKenzie et al. 2003, Miller et al. 2012).

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendicies A and B are available online: http://dx.doi.org/10.1890/14-1361.1.sm

Reports