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Local extinction and turnover rates at the edge and interior of species' ranges

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One hypothesis for the maintenance of the edge of a species' range suggests that more central (and abundant) populations are relatively stable and edge populations are less stable with increased local extinction and turnover rates. To date, estimates of such metrics are equivocal due to design and analysis flaws. Apparent increased estimates of extinction and turnover rates at the edge of range, versus the interior, could be a function of decreased detection probabilities alone, and not of a biological process. We estimated extinction and turnover rates for species at the interiors and edges of their ranges using an approach which incorporates potential heterogeneity in species detection probabilities. Extinction rates were higher at the edges (0.17 ± 0.03 [$\widehat{SE}$]) than in the interiors (0.04 ± 0.01), as was turnover. Without taking the probability of detection into account these differences would be artificially magnified. Knowledge of extinction and turnover rates is essential in furthering our understanding of range dynamics, and in directing conservation efforts. This study further illustrates the practical application of methods proposed recently for estimating extinction rates and other community dynamic parameters.

Introduction

Macroecological studies, studies directed at understanding the division of food and space among species at large spatial and temporal scales (Brown & Mauer 1989, Brown 1995), have received much attention in recent years (*see* Brown 1999, Gaston & Blackburn 1999 for most recent reviews), with one focus being on patterns of abundance across species' ranges (Brown 1984, Brown *et al.* 1995). One generality resulting from pattern analyses performed to date is that abundance is highest at the center of a species range and declines gradually towards the boundaries, with the edge, or limit of a species range being defined where abundance declines to zero (Brown 1984, Brown *et al.* 1995). Brown (1984) suggests that this smooth transition is seen in plants and invertebrates, as well as in vertebrates (Whittaker 1956, 1960, Bystrak 1981, Brown 1995). Brown (1984) recognized multimodal patterns of abundance resulting from environmental patchiness as an exception to the classic pattern of a unimodal distribution and further suggested that, in some cases, a more complex 'internal structure' of high and low abundances could exist in some species' ranges (Brown *et al.* 1995, 1996). More recently, additional calls have been made to further develop theory that links abundance and range (Ney-Nifle & Mangel 2000).

One theoretical construct that has been invoked to understand mechanisms that lead to the observed general pattern of lower abundances at the edge as opposed to the interior of a species' range is source-sink dynamics (Pulliam 1988). Smaller populations at the edge of range can be considered sink populations (where deaths exceed births) being maintained by immigrants from, usually more central, source populations (where births exceed deaths) and that these states are relatively stable (Wiens & Rotenberry 1981). This framework leads to the prediction that smaller, peripheral populations are more likely to undergo turnover events (i.e. extinction and colonization) than larger, more centrally located populations (Curnutt *et al.* 1996).

In further investigating population dynamics at the edge and interior of species' ranges, Mehlman (1997) found increased extinctions during severe weather events and increased colonization when weather patterns ameliorated at the edge as compared with more central regions of a species' range. This finding supports the assertion that turnover rates are higher at locations with low abundances, particularly at the edge of a species' range.

However, using marine fish spawning stock and recruitment data, Leggett and Frank (1997) did not find support for the 'species range hypothesis' as proposed by Miller *et al.* (1991), which suggests that recruitment variation in flatfishes should be more variable at the edge than in the interior of a species range.

One reason for conflicting and meager evidence in support of the hypothesis of greater extinction and turnover rates at the edge of range, as well as for potential problems with the overall pattern analyses of abundance variation across species ranges, is that estimates used in these investigations are based on ad-hoc abundance estimators in which probabilities of detection are not taken into account (Brown 1984, Brown *et al.* 1995, Curnutt *et al.* 1996, Leggett & Frank 1997, Mehlman 1997, *see* Blackburn *et al.* 1999 for further examples). Individuals and species may be present, but not detected. Detection probabilities for species are a function of both abundance (number of individuals in the sampled area) and the various factors (size, behavior, activity, etc.) that make individuals of some species more or less detectable than individuals of another (*see* Nichols *et al.* 1998a). Thus, we expect detection probabilities for species to be lower in areas of low abundance. Now assume that populations at the edge of a range really do have lower abundances than populations at more central locations in the range. The lower detection probabilities associated with these low abundances could lead to the apparent increased rates of local extinction, colonization and turnover if these community-dynamic rate parameters are estimated using methods that do not account properly for detection probability. Thus, the potential positive relationship between abundance and detection probability would produce a negative relationship between abundance and ad hoc estimates of both local extinction and turnover, even when there is no relationship between abundance and the true, underlying rate parameters. In general, probabilities of detection are important nuisance factors that can affect parameter estimates and can generate 'patterns' in data (Williams *et al.* 2002). In particular, it may be a mistake to assume that detection probabilities simply reflect 'random noise', an assumption underlying many investigations (e.g., Brown 1984, Mehlman 1997). Fortunately, methodologies are available to estimate probabilities of detection and to incorporate these parameters in models that permit estimation of other parameters.

Methodologies for estimating probabilities of detection of individual animals for the purpose of estimating animal abundance have been developed in the past century (*see* Seber 1982, White *et al.* 1982, Pollock *et al.* 1990, Nichols 1992, Williams *et al.* 2002). These methods have been extended to the problem of incorporating species-level detection probabilities to estimate such community-level parameters as species richness (number of species), extinction, and turnover (Burnham & Overton 1979, Bunge & Fitzpatrick 1993, Boulinier *et al.* 1998a, Nichols *et al.* 1998a, 1998b, Hines *et al.* 1999).

Unfortunately, in testing the above patterns and process, there are few, if any, properly designed studies that would allow for reliable abundance and turnover rate estimation for a single species at many points in space across its range. The approach we take here is to focus on groups of species defined as being either at the edge or in the interior of their ranges at single locations in space rather than trying to focus on a single species across the whole of its range (Curnutt *et al.* 1996, Mehlman 1997). This approach also controls for potentially confounding landscape differences because the two defined groups occur at the same locations in space and can be compared using a paired design. We take this approach because methodologies have recently been developed to estimate species richness (number of species), local extinction, local turnover, and probabilities of detection within this community-level framework (Boulinier *et al.* 1998a, Nichols *et al.* 1998a, 1998b, Hines *et al.* 1999). These methodologies require only species presence/absence data, and not abundance estimates.

One data set that can be reasonably analyzed using these methodologies is the U.S. Breeding Bird Survey (BBS), a continent-wide survey of breeding birds (Peterjohn & Sauer 1993). Although individual species abundance estimates from these data may be questionable due to the inability to estimate probabilities of detection of individual birds (Thompson *et al.* 1998), species-level probabilities of detection, and the community-level quantities species richness, extinction and turnover can be estimated. We estimate these parameters using data from individual BBS route locations for two groups of birds, those at the edge and interior of their range. We tested three predictions. Based on the empirical evidence of low abundance near the edge of a species' range and on the necessary relationship between species-level detection probability and abundance, we predicted (1) lower probabilities of detection for species at the edge of their range than those more interior. Because populations at the edge of the species range are expected to be less stable and to depend on immigrants from more stable, central populations for persistence, we predicted that species at the edge of their range would have (2) higher extinction, and (3) higher turnover rates than those in more central locations.

Material and methods

Data

Presence/absence data were obtained from the BBS, a continent-wide survey of breeding birds coordinated by the U.S. Geological Service and the Canadian Wildlife Service (Bystrak 1981, Robbins *et al.* 1986, Peterjohn & Sauer 1993). Each BBS route consists of 50 stops 0.8 km apart along secondary roads. At each stop one observer counts all birds seen or heard within three min during one morning of each breeding season (typically late in May to late June). Data were summarized for each ten consecutive stops as a list of species detected (five lists per route). We focused on routes in Ohio during 1982–1987 due to the availability of a breeding bird atlas for the delineation of species' ranges during this time period (*see* below). We also focused only on daytime passerines and "near-passerines" (Columbiformes, Cuculiformes, Apodiformes, Coraciiformes, Piciformes) because these species are what the BBS is designed to detect most reliably.

Range boundaries

We felt it was important to estimate range boundaries from a data source that was independent of the BBS data, as did Mehlman (1997). We focused on Ohio for which coarse range maps in field guides (Peterson 1980, Sibley 2000) exist, but also for which a breeding bird atlas was constructed during the years 1982–1987 (Peterjohn & Rice 1991). This atlas project consisted of a series of breeding season surveys for birds in stratified, randomly chosen 7-minute degree blocks (*see* Peterjohn & Rice 1991 for details). It should be noted that this atlas provides a minimum estimate of extent of range, since undetected occurrences lead to underestimates of the extent of a range. In our analysis this would lead us towards possibly misclassifying some species-locations as 'edge' when in fact they were 'interior.' This would conservatively bias us towards not detecting differences in the parameters in which we were interested. We first examined coarse range maps in field guides (Peterson 1980, Sibley 2000) and determined whether a species range had an edge limit in Ohio. We then used a more detailed Ohio breeding bird atlas (Peterjohn & Rice 1991) to delineate each BBS route location with respect to this edge limit.

Ohio has five physiogeographic regions ranging from unglaciated mountains to flat plains (Lafferty 1979, Peterjohn & Rice 1991), and often the edge of a species' range was associated with a boundary between two of these physiogeographic regions. If there appeared to be such an association for a species, we delineated each Ohio BBS route as being located in a county within the species range ('interior') or in a county outside the preferred physiogeographic range, or through which the physiogeographic boarder was located ('edge').

There were a few species (e.g. Carolina chickadee (*Poecile carolinensis*) for which a species range limit did not conform to a physiogeographic boundary, and for these, we focused on the five nearest surveyed blocks to each route. If ≥ three of these blocks contained confirmed breeders, we classified the route as 'interior' and if < three of these blocks contained confirmed breeders we classified the route as 'edge' of range for that species. This classification using the five nearest blocks also matched well with those range limits coinciding with a physiogeographic boundary.

It was clear during our classification of routes that even though some species occurred in all states and provinces surrounding Ohio, these species did not occur in all of Ohio. This 'internal structure' to a species' range, in which large internal areas of a range may contain no individuals, has been recognized by others (i.e. Brown *et al.* 1996), and we decided to recognize these 'edges' also. Often there was a clear boundary associated with a physiogeographic region between presence and absence of these species within Ohio. For example, many warblers breed in the wooded hills of southeastern Ohio but not in the flat prairie of northwestern Ohio, even though these same species will breed in parts of all states/provinces surrounding Ohio. Field guide maps (Peterson 1980, Sibley 2000) were too coarse to delineate these boundaries, but the *Ohio Breeding Bird Atlas* (Peterjohn & Rice 1991) did. When there was a clear 'edge' delineated on the range maps, we categorized routes as 'edge' and 'interior' as previously described. We would have preferred to estimate parameters for these 'internal edges' separately from other edges, but a lack of data prevented us from doing so. Because we hypothesized that source-sink dynamics would be acting similarly for peripheral and internal edges, we felt comfortable categorizing both types as 'edge'. For our estimation methods to perform adequately we felt we needed to have at least eight edge and eight interior species at each route, and this combining of both peripheral and internal edges helped to increase our sample sizes of 'edge' species. We also felt this was a conservative classification, because if local populations associated with 'interior edges' of a species range functioned more similarly to interior populations than to 'peripheral edge' populations, we would be biased towards not finding any differences in the parameter estimates of edge and interior species.

From other work with closed population capture-recapture models (Otis *et al.* 1978, Menkens & Anderson 1988), it has been shown that in cases with small sample sizes and low probabilities of detection, estimates of abundance (or in our case, number of species instead of number of individuals) can be poor. We nevertheless thought our probabilities of detection would be high, as recently found in other studies (i.e. Boulinier *et al.* 2001), helping to ameliorate our small sample size problems. Winkler and Kampichler (2000) also successfully used a jackknife estimator (*see* below), similar to the one we used, to estimate species richness in a community with as few as eight species.

Parameter estimation

The five aggregate groups of stops within each BBS route were considered sampling replicates of the bird community associated with each route. For each group (interior and edge) on each route, the average probability of detection, species richness, extinction and turnover rates were estimated. We first estimated probabilities of detection and species richness for the two groups using the jackknife estimator of species richness proposed by Burnham and Overton (1979). For estimating extinction and turnover rates we used the estimators proposed by Nichols *et al.* (1998a). Specifically, to estimate probability of extinction we used eq. 4 of Nichols *et al.* (1998a)

$$1-\hat{\phi}_{ij}=1-\frac{\hat{M}_j^{R_i}}{R_i} \tag{1}$$

where $\hat{\phi}_{ij}$ is the complement of extinction probability, R_i is the number of species observed in period *i*, and $\hat{M}_j^{R_i}$ is the estimated number of species still present at time *j* of those observed in period *i*. The extinction rate of Eq. 1, can be defined as the proportion of species becoming locally extinct between two successive sampling years, *i* and *j*, among species present the first year, *i*.

To estimate turnover we used eq. 7 of Nichols *et al.* (1998a)

$$1-\hat{\phi}_{ji}=1-\frac{\hat{M}_i^{R_j}}{R_j} \tag{2}$$

which is the extinction probability estimator with data placed in reversed time order and defines turnover rate as the proportion of new species (not present the previous sampling year) among species present in a particular year.

We use this capture-recapture approach because some species are likely to be missed in sampling efforts. This methodology takes into account heterogeneity in detectability among species and survey routes, a problem that certainly can confound analyses such as these. If detection probabilities of these two groups differ, then extinction and turnover rates for 'edge' species could be higher due to lower detection probabilities alone, and not for any ecological reason.

Boulinier *et al.* (1998a) explain and justify using this approach for the analysis of BBS data, and further details of these estimators can be found in Nichols *et al.* (1998b). We used COMDYN (Hines *et al.* 1999), which was developed specifically for the study of community dynamics, to estimate parameters in which we were interested as well as their associated variances. Other examples of this approach can be found in recent papers by Cam *et al.* (2000) and Boulinier *et al.* (2001). We applied this methodology to routes at which ≥ eight edge and interior species were detected during the years 1982–1987, the years in which the Ohio Breeding Bird Atlas was conducted. We averaged species richness estimates and estimated extinction and turnover rates over available years for each route and compared estimates from edge and interior routes using paired *t*-tests. We present our estimates as means ± $\widehat{\text{SE}}$.

Results

Detection probabilities and species richness

Using our strict delineation of edge of range and our criteria of having at least 8 species in both edge and interior groups at each route, we were able to utilize data from 6 routes in Ohio. Average probabilities of detection were significantly lower for species at the edge of their range (0.78 ± 0.04) than for those in the interior of their range (0.92 ± 0.01; $t = -3.84$, df = 5, $P = 0.01$). For these six locations the average estimated number of species at the edge of their range was 11.02 ± 1.56 and 53.61 ± 1.69 species in the interior of their range.

Extinction and turnover rates

Average estimated annual probability of extinction was higher in the group of species at the edge of their range (0.17 ± 0.03) than for the group in the interior of their range (0.04 ± 0.01; $t = -3.56$, df = 5, $P = 0.01$). Average estimated turnover rates were also greater for the group of species at the edge of their range (0.21 ± 0.03), than for the species in the interior of their range (0.05 ± 0.01; $t = -5.27$, df = 5, $P < 0.01$). The estimated average number of local colonizing species per year for each route was similar for the edge and interior groups, 3.61 ± 0.81 and 3.70 ± 0.69 respectively. However since there were overall fewer species in the edge group, this similarity in number of colonists reflects greater colonization rates for the edge species.

Discussion

Results of these analyses supported our predictions that species at the edge of their range would have higher extinction and turnover rates and lower probabilities of detection than those species in the interior of their range. Our study focused on a community-level perspective and used novel estimation methods, which we feel allowed us to better estimate the parameters of interest than has been previously done (Curnutt *et al.* 1996, Leggett & Frank 1997, Mehlman 1997). Specifically, we were able to estimate the community-level parameters of interest in such a manner that these estimates were not confounded with detection probabilities. We will first discuss detection probabilities and then extinction and turnover rates.

Detection probabilities

Detection probabilities were clearly lower for species at the edges (0.78) of their range than in the interior (0.92) of their range in Ohio. This finding is consistent with (1) the empirical generalization of low abundances at the edge of a species' range and (2) the likely relationship between abundance and species-level detection probability. If these differences in detection probabilities had not been taken into account, extinction rates may have been overestimated for species at the edge of their range, indicating a stronger pattern than exists. More importantly, our data-analytic methods preclude the possibility that differences in detection probabilities were responsible for the estimated differences in quantities of interest. Besides spatial variation in detection probabilities, our modeling also took into account heterogeneity in detection probabilities among species within each group. This was important as previous analyses with BBS data provided substantial evidence of heterogeneous detection probabilities among species (Boulinier *et al.* 1998a). Brown (1984) recognized that considerable sampling error can occur over space, but he assumed that this sampling error would reflect random 'noise' and would only make it harder to detect a 'true' pattern resulting from an ecological process. However we believe that in some cases, such as in our investigation, failure to deal with a 'nuisance' parameter such as the probability of detection, can give rise to patterns and may not be solely random noise.

Extinction and turnover rates

Extinction and turnover rates for species at the edge of their range were four times greater than those of species located at the interior of their range. The increased community dynamics at the edge of range are consistent with the suggestion that populations located there are less stable than those considered to be interior. Interior populations may be the source for new individuals to colonize locations left empty by local extinction events (Boulinier *et al.* 1998b). Our analysis supports this prevailing view (Curnutt *et al.* 1996). However, much stronger support for this assertion would come from banding studies in which movements of individual animals could be tracked. The feasibility of a program of such scale is questionable, but large-scale bird banding programs have been developed and may provide some utility and guidance (Tautin *et al.* 1999). Monitoring programs that are developing for other taxa may also be able to be designed to provide important data for such questions (Oostermeijer & Van Swaay 1998, Smith & Petranka 2000).

What role abundance plays at the edge of range is unknown due to our inability to estimate abundances well across a species range, although theoretical developments have taken place (Brown 1984). It may be that increased turnover dynamics associated with edge populations are a result of stochasticity associated with small population sizes, or it may be that population sizes actually change very little at some range edges and variation in certain abiotic or biotic factors of a species niche (Hutchinson 1957, Root 1988, Brown *et al.* 1996, Mehlman 1997) are the sole cause of turnover events. Most likely, there is an interaction between population size and such factors.

To separate these possibilities and to further develop theory linking abundance and range, abundance estimates will need to be made across a species' range and well-designed programs will need to be established for this purpose. Large-scale survey programs are in place (i.e. BBS) but such programs may need to adjust their methodologies to provide appropriate data for abundance estimation (e.g., *see* Yoccoz *et al*. 2001). Fortunately such methodologies have recently been developed to estimate probabilities of detection as well as abundance, such as distance sampling (Burnham *et al*. 1980, Buckland *et al*. 2001), double-observer methods (Nichols *et al*. 2000) and auditory removal methods (Farnsworth *et al*. 2002). A proper spatial sampling design (e.g., in the case of the BBS, one not based solely on secondary roads) is also very important to reasonable inference. With the current increased interest in conservation, particularly avian conservation (Marzluff & Sallabanks 1998), and the need for reliable information and parameter estimates, improvements such as these seem warranted.

Our results suggest that species on the edge of their range are more likely to undergo extinction events. This result would suggest superficially that conservation efforts should be focused on core areas of ranges, especially if these core areas always maintain edge areas. However, in some instances, edge populations may contain unique local adaptations, or be evolutionary significant units that may be worth the focus of conservation efforts. Also, factors that cause extinction events may not act equally across a species range. If habitat destruction is most likely to take place in central, core areas, then edge populations may be the only populations left to preserve (Channel & Lomolino 2000).

During the time period of our study (1982–1987) the extinction and turnover rates appeared to be consistent with a local dynamic equilibrium, suggesting the collective ranges of species classified as edge species were neither expanding, nor contracting. However over a longer time frame methodologies such as this could be used to address expanding and contracting ranges as suggested in Boulinier *et al*. (2001). For example, we could compute estimates of community-level rates of increase in species richness ($\hat{\lambda}$ of Nichols *et al*. 1998a) for species at the edge and interior of their range. If we hypothesize that changes will occur as a result of global warming, then we should be able to predict that groups of species will expand ($\lambda > 1$) and contract ($\lambda < 1$) in certain parts of their range (Davis *et al*. 1998). Using the above-mentioned methodologies we could test these predictions.

Finally, although our estimates of extinction and turnover are general with respect to residency status, direction of edge of range, habitat preference and many other factors, we did limit ourselves to BBS routes in Ohio, due to our familiarity with the region and the availability of a detailed Breeding Bird Atlas to help us delineate where a BBS route was located with respect to species' range. Our results are specific to birds that have a range limit in Ohio and we have no statistical inference to other range limits or to other species. Similar analyses in other locations and with other taxa would be useful in testing the generality of our results. Our results illustrate the wide potential applications of the approach used to address questions regarding factors affecting local extinction rates and community dynamics in general.

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