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Using demographic attributes from long-term monitoring data to delineate natural population structure

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Summary

1. The concept of 'natural' populations is a foundation of modern ecology and conservation, with a large body of theoretical literature using these discrete demographic units to understand population dynamics and prioritize conservation strategies. To date, there are currently no objective methods for empirically delineating large-scale population boundaries using demographic data.

2. We present a novel approach for using large-scale, citizen-science monitoring data to quantify geographic structure in trend and abundance and identify distinct natural populations. We demonstrate this approach by delineating populations of eight passerine species using data collected as part of the North American Breeding Bird Survey.

3. Our approach was able to identify geographic structure in both trend and abundance and to delineate distinct populations for all eight species. An independent validation of three species indicated this demographic variation was reflected in underlying vital rates.

4. *Synthesis and applications*. Natural populations are biologically based alternatives to the traditional geographically defined units that can improve the ability of researchers and managers to quantify spatial variation in population dynamics. Our analysis of natural population structure in breeding songbirds demonstrates that species can show substantial geographic variation in population attributes and underlying demography. We recommend managers define spatial units using natural populations when setting regional population objectives for both single and multispecies conservation plans.

Key-words: Andrewartha & Birch, Breeding Bird Survey, conservation planning, demography, hierarchical clustering, local population, monitoring, natural population, population dynamics

Introduction

In one of the seminal contributions to modern ecological theory, Andrewartha & Birch (1954) formalized the concept of ecological populations by recognizing that the dynamics shaping the distribution and abundance of species operate at two spatial scales: 'local' populations and 'natural' populations. At the local scale, immigration and emigration are the primary drivers of population dynamics, making local populations vulnerable to extinction/recolonization over short time-scales (Camus & Lima 2002). The local population concept has subsequently played a central role in modern population ecology and conservation by providing the foundation for metapopulation theory (Camus & Lima 2002). At larger spatial scales, however, immigration and emigration simply reshuffle individuals among local populations and therefore do not contribute to changes in the overall number of individuals over time. Thus, natural population (Andrewartha & Birch 1954) dynamics are governed primarily by birth and death processes rather than redistribution processes (Berryman 2002). On contemporary time-scales, natural populations form a fundamental unit

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for understanding ecological processes (i.e. spatial and temporal variation in demographic rates). Additionally, because natural populations act as distinct demographic units, they form the foundation for understanding the causes of species' declines and for prioritizing conservation strategies (Hughes, Daily & Ehrlich 1997; Ceballos & Ehrlich 2002). However, despite the central importance of natural populations in ecology and conservation, objective methods to delineate demographic populations at large spatial scales remain unavailable (Camus & Lima 2002; Jones, Doran & Holmes 2007).

To date, the most progress on delineating large-scale population structure has occurred in the field of population genetics. Within the genetic population paradigm (Waples & Gaggiotti 2006), the processes that structure populations, such as mating, gene flow and genetic drift, are well studied (Slatkin 1987; Hartl & Clark 1997) and researchers have developed a host of empirical approaches to delineate populations and identify genetic structure. For example, genetic markers (allele frequencies) and model-based clustering methods are often used to probabilistically assign individuals to populations or to define the number of genetically distinct populations in a host of vertebrate taxa (Falush, Stephens & Pritchard 2007). Likewise, the causes and consequences of genetic divergence have been used to define geographic structure in a number of animal taxa, including amphibians (Newman & Squire 2001), birds (Zink *et al.* 2000) and mammals (Rosenberg *et al.* 2002). These methods, combined with the large amount of published genetic and phenotypic data, have allowed researchers to make substantial progress in assessing the geographic structure of evolutionary processes and delineating genetic populations at appropriate biological scales. Although the methods available for delineating genetic populations are increasingly powerful, the results largely reflect the evolutionary population paradigm where populations are defined by the ability of individuals to mate or share genes (Waples & Gaggiotti 2006). In contrast, these approaches may not reflect the ecological population paradigm proposed by Andrewartha & Birch (1954), in which populations are defined by shared demographic rates (Waples & Gaggiotti 2006).

Unfortunately, there are currently no objective, quantitative approaches for using demographic data to delineate the boundaries of natural populations. Although some progress has been made in delineating demographic populations for species that occur in discrete breeding habitats (Ruckelshaus *et al.* 2006), most techniques currently used to delineate populations in ecological or management contexts are largely independent of the demographic processes that structure populations. Most commonly, populations are defined using study area borders (Berryman 2002), range limits (Ceballos & Ehrlich 2002), geographic isolation (Atwood 1991) or habitat limits (Sauer, Fallon & Johnson 2003). Although these methods are undoubtedly useful in certain contexts (Vucetich, Nelson & Phillips 2006), they are largely arbitrary with regard to demographic processes and therefore provide little insight into the structure or scale of natural populations. Furthermore, because these methodologies do not account for the demographic attributes of populations that are most immediately relevant to conservation, management strategies often proceed in the absence of the critical information about demographic population structure (Rodrigues & Gaston 2002). Such shortcomings are likely to be most pronounced in species that inhabit large geographic areas that span political or habitat boundaries and display heterogeneous demographic trends across their range. Given the global decline of many such plant and animal species (Ceballos & Ehrlich 2002; Inger *et al.* 2015), there is a critical need for analytical methods that integrate demographic information to understand the geographic structure of natural populations.

In this paper, we develop an analytical approach that uses count data from a large-scale monitoring program to delineate natural populations. Our approach takes site-level estimates of trend and abundance and uses a spatially explicit clustering technique to hierarchically group sites based on shared demographic attributes. The resulting cluster tree can then be used to determine the number of natural populations and delineate population boundaries. We use this approach to delineate the natural populations of eight species of breeding songbirds using data collected from the North American Breeding Bird Survey (BBS). To test whether our approach identified distinct populations, we used an independent demographic data set to test whether the trend and/or abundance differences among populations of three species were associated with differences in adult apparent survival and/or productivity. By quantifying spatial variation in demographic attributes (i.e. trend and abundance), our approach advances the natural population concept proposed by Andrewartha & Birch (1954) and provides a framework for understanding large-scale population processes and for conducting more efficient and effective conservation.

Materials and methods

FOCAL SPECIES AND MONITORING DATA

To develop our approach, we selected eight species of North American songbirds (four eastern and four western) that have been identified as conservation priorities based on either large rangewide declines or small geographic ranges (Table 1). The four species within each region were selected because they share similar habitat requirements, exhibit variation in breeding and non-breeding geographic range size and display a variety of movement strategies (migratory vs. resident). Abundance data used for our analysis were obtained from the North American BBS (https://www.pwrc.usgs.gov/bbs/RawData/), which provides reliable annual monitoring for all of the species included in our analysis.

We considered two time-scales for our analysis. First, we quantified contemporary population structure by limiting our analysis

Table 1. Focal species summary: rangewide population statuses of the eight focal species included in our analysis. For trend estimates, values within parentheses are the 95% Bayesian credible interval

Species	Global population size*	Rangewide percentage annual decline[†]	Breeding range size (km^2)[‡]	Long-distance migrant?
Eastern				
Wood Thrush[§] (*Hylocichla mustelina*)	11 000 000	−2·1 (−2·3, −2·0)	6 025 794	Y
Eastern Wood-Pewee (*Contopus virens*)	5 500 00	−1·4 (−1·6, −1·3)	7 070 129	Y
Kentucky Warbler[§] (*Geothlypis formosa*)	2 800 000	−1·1 (−1·5, −0·6)	3 035 602	Y
Eastern Towhee (*Pipilo erythrophthalmus*)	28 000 000	−1·4 (−1·6, −1·3)	5 303 850	N
Western				
Hermit Warbler[§] (*Setophaga occidentalis*)	2 500 000	−0·1 (−0·8, 0·6)	612 936	Y
Western Wood-Pewee (*Contopus sordidulus*)	9 200 000	−1·6 (−2·3, −1·1)	15 621 570	Y
Chestnut-backed Chickadee (*Poecile rufescens*)	9 700 000	−1·6 (−2·5, −0·7)	2 361 011	N
Black-throated Gray Warbler (*Setophaga nigrescens*)	2 400 000	−1·5 (−2·3, −0·7)	3 094 380	Y

[*] http://rmbo.org/pifdb/.
[†] http://www.mbr-pwrc.usgs.gov/bbs/.
[‡] http://explorer.natureserve.org/.
[§] Species included on the 2012 Partner's in Flight Watchlist.

to BBS data collected between 2000 and 2013. Given that passerines have brief life spans and early sexual maturity, population dynamics operate over short time-scales (Sæther *et al.* 2005) and therefore this recent period is expected to provide information about current demographic processes. Furthermore, because management efforts typically focus on contemporary rather than past threats, we also expect this time-scale to be of most immediate relevance to conservation and management. Because understanding how abundance changes over longer time-scales can be relevant to conservation, we also conducted a second analysis based on the full (1966–2013) BBS data. Here, we focus our analysis, results and discussion of population structure on the contemporary time-scale and use the long-term analysis as a means to quantify the degree to which geographic variation in trend and abundance contribute to the observed population structure.

DELINEATING POPULATIONS

For each species, we first estimated the relative abundance and percentage annual change (i.e. trend) for each BBS route where the species was detected during the two periods. At each route, abundance was estimated as the mean of the annual counts, after correcting for route and observer effects (Link & Sauer 2002). Abundance estimates were then scaled to fall between 0 and 1 by dividing by the maximum abundance of each species. Route-level trends were estimated using a Poisson regression with the corrected annual counts as the response variable and year as a continuous predictor. See Appendix S1 in Supporting information for further details regarding estimation of route-level demographic rates.

Next, we used the trend, relative abundance, latitude and longitude of each BBS route to calculate a multivariate Euclidean distance matrix for all routes for each of the eight species. Because the raw latitude and longitude values are numerically larger than the trend and abundance estimates, the multivariate distances were weighted by geographic distance. This weighting has the desirable property of ensuring that routes that are separated by large distances are less likely to be clustered together than routes that are close together and thereby provides a spatial constraint on population delineation. In contrast, we had no *a priori* reason to weight trend or abundance and since these attributes were similar in magnitude, we included the raw values in the distance matrix calculations.

For each species, the distance matrix was then used to perform a hierarchical agglomerative clustering analysis using the 'hclust' function in R (R Core Team 2013) and Ward's method to estimate the distance between clusters (Appendix S1). Hierarchical clustering begins with each of the n routes as a separate group and then uses the distance matrix to cluster routes, producing a hierarchical tree with $n - 1$ levels (Figs 1b and 2b). Once the BBS routes were clustered, the resulting hierarchical tree can be used to classify distinct geographic populations. To determine the number of populations for each of the eight species, we used the Kelley–Gardner–Sutcliffe (KGS) penalty function (Kelley, Gardner & Sutcliffe 1996) implemented using the 'kgs' function in the R package MAPTREE v1.4-7 (White & Gramacy 2012). The level of the tree with the minimum penalty represents the optimal number of groups (Carvalho *et al.* 2011; Appendix S1).

Although weighting geographic distance more heavily than demographic attributes is desirable for creating spatially contiguous populations, one potential side effect is that the observed clustering structure may simply reflect geographic sampling location rather than variation in trend or abundance. We therefore used two methods to determine the degree to which population structure was influenced by the demographic data. First, we quantitatively assessed the relative contribution of the trend/abundance estimates to the observed clustering structure by comparing the topology of three trees built with identical geographic data, but different demographic data. The three trees used for this comparison were two demographic trees based on the contemporary (2000–2013) and long-term (1966–2013) BBS data plus a third tree based only on geographic distance between BBS routes (hereafter the 'geographic' tree). These comparisons are important because the geographic data in each tree are identical and as such any changes in topology are strictly the result of changes in the trend and/or abundance of BBS routes. We quantified changes in tree topology using the Robinson–Foulds distance metric (abbreviated dT; Robinson & Foulds 1981), which measures the number of internal branches found on one tree that are not found on the other (Kuhner & Felsenstein 1994). Because there is no direct statistical interpretation of dT values (Kuhner & Felsenstein 1994), we report all distances as a proportion of

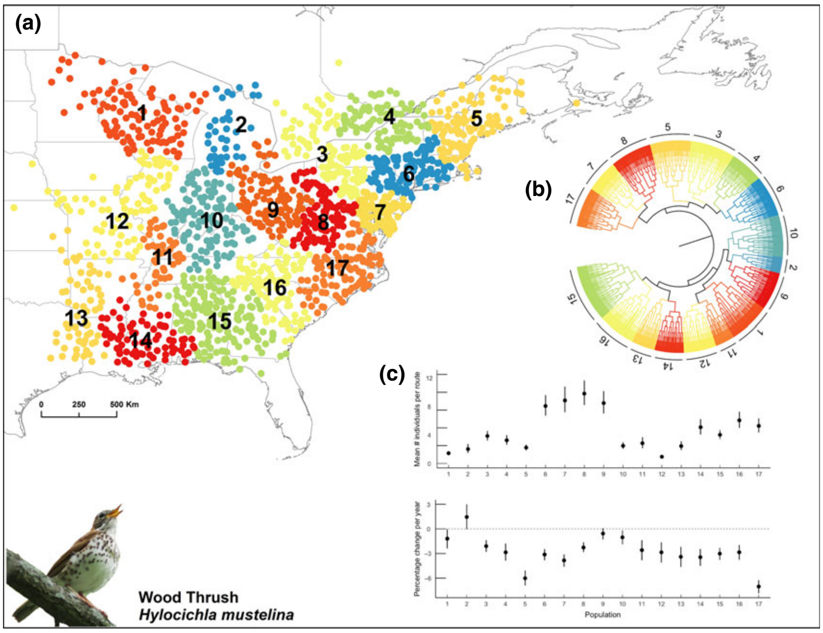

Fig. 1. Results of the population grouping for Wood Thrush. (a) Breeding range (in grey) and geographic structure of the 17 populations identified by clustering routes based on trend, abundance and spatial proximity. Each point shows the location of Breeding Bird Survey routes that detected Wood Thrush between 2000 and 2013. (b) The hierarchical tree produced by the clustering algorithm. Nodes and branches are coloured based on population membership. (c) Population-level estimates of abundance (top) and trend (bottom) for each population. Bars show 95% Bayesian credible intervals.

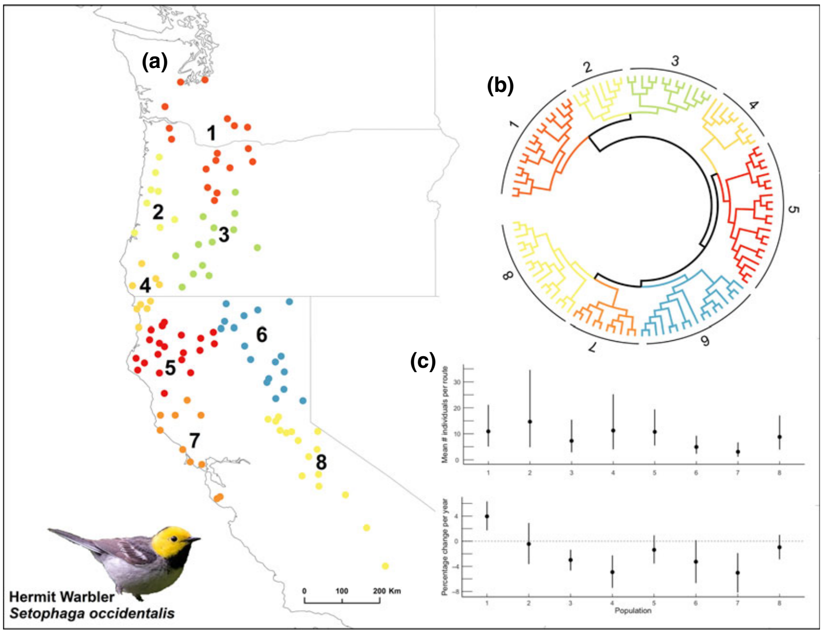

Fig. 2. Results of the population grouping for Hermit Warbler. (a) Breeding range (in grey) and geographic structure of the eight populations identified by clustering routes based on trend, abundance and spatial proximity. Each point shows the location of Breeding Bird Survey routes that detected Hermit Warbler between 2000 and 2013. (b) The hierarchical tree produced by the clustering algorithm. Nodes and branches are coloured based on population membership. (c) Population-level estimates of abundance (top) and trend (bottom) for each population. Bars show 95% Bayesian credible intervals.

their theoretical maximum, which is $2n - 6$ for two trees fit to the same n BBS routes. If clustering is driven solely by geographic distance, the trees will be identical and the dT value will equal 0. In contrast, dT values greater than 0 indicate that the inclusion or modification of trend/abundance data influenced tree topology. We note, however, that because all three trees in our analysis use identical geographic data, the topologies will be correlated and the actual maximum will be less than the theoretical maximum. All dT values were estimated using the R package PHANGORN v1.99-13 (Schliep 2011).

Secondly, we used the KGS penalty method to compare the number of populations classified by each of the three trees and mapped their geographic boundaries to visually assess the role of trend/abundance data. If population structure is driven solely by geographic structure, we expected the three trees to produce the same number of populations and for population boundaries to remain unchanged when trend/abundance data are added or modified.

ASSESSING POPULATION STRUCTURE

Once the structure and number of contemporary populations was determined for each species, we used five additional methods to assess the effectiveness of our method for delineating ecological populations. First, we used 'coef.hclust' function in the R package CLUSTER to estimate the agglomerative/divisive coefficient for each species' tree (Maechler *et al.* 2014). The divisive coefficient varies between 0 and 1, with values close to 1 indicating that well-defined clusters have been identified. Secondly, we conducted a non-metric multidimensional scaling (NMDS) with the 'metaMDS' function in the R package VEGAN (Oksanen *et al.* 2014) to visualize the multivariate structure and place 95% confidence ellipses on the KGS defined populations. Thirdly, we used the 'adonis' function in the R package VEGAN to examine the proportion of variance in the route-level trend and abundance distance matrices that was explained by the groupings from the KGS defined populations. Adonis is a permutation based ANOVA that can partition variance explained in a distance matrix using pseudo *F*-statistics. Because the groupings implicitly account for spatial proximity, this method allowed us to examine the contribution of route-level trend and abundance after controlling for geographic proximity.

Fourthly, we calculated population-level estimates of both trend and abundance and then tested whether each population differed significantly from adjacent populations in these attributes. For both metrics, we used a hierarchical model developed to estimate regional trends and abundances from BBS data (Link & Sauer 1998, 2002). For each population, we estimated abundance as the mean of the expected counts across years for all routes in the population. Trend was estimated as the geometric mean of the proportional changes in abundance (Link & Sauer 2002; Appendix S1). To determine whether adjacent populations differed in either trend or mean abundance, we derived posterior distributions for the difference in trend/abundance for all adjacent populations and considered any posterior with >95% of the posterior density above or below zero to be evidence of significant differences in demographic attributes, though we also considered posteriors with >90% of the density above or below zero as strong support for population differences.

INDEPENDENT VALIDATION OF POPULATION STRUCTURE

We independently validated the geographic structure of our contemporary natural populations using data from Monitoring Avian Productivity and Survivorship (MAPS) banding stations (DeSante, O'Grady & Pyle 1999) between 2000 and 2008 (data from years after 2008 were not available at the time of our analysis). Because MAPS stations do not sample canopy-dwelling species, we restricted our analysis to the three ground foraging species (Kentucky Warbler, Wood Thrush and Eastern Towhee; Fig. S1).

We assigned MAPS stations to population clusters by creating convex hulls around the BBS routes within each population and indexing each station by the population in which it is located. To assess variation in productivity among population clusters, we modelled the probability of a captured bird being a young bird as a logit-linear function of fixed population cluster effects and random station and year effects (Appendix S1). We assessed variation in adult apparent survival probability among population clusters using ad hoc robust design Cormack–Jolly–Seber models (Hines, Kendall & Nichols 2003).

To validate the results of our clustering analysis, we first correlated the trend and abundance estimates for each population with the corresponding productivity and survival estimates. For each of the three species, if the trend or abundance estimates were strongly ($r \geq 0{\cdot}7$) or moderately ($0{\cdot}4 \leq r < 0{\cdot}7$) correlated with the MAPS vital rates, we further tested whether adjacent populations that differed significantly in trend/abundance also differed with regards to productivity or survival. We did this by subsetting the MAPS stations to include only stations within the adjacent populations of interest and then fitting the productivity and survival models with and without population cluster as a fixed effect. The two models were then compared using a likelihood ratio test (LRT), with a significant LRT indicating that the populations differ with regards to the vital rate of interest. Because this test was carried out independently for each population pair, we applied a Bonferroni correction to each individual test to ensure that the overall type I error rate did not exceed 0·05 for each species. Finally, for population pairs with significant LRT results, we checked whether the direction of the differences in productivity and/or survival were consistent with the differences in trend and/or abundance.

Results

Using the contemporary BBS data set, our method was able to delineate spatially distinct populations that varied in both trend and abundance for each species (Figs 1, 2 and S2–S8). On average, each species was divided into 13·25 populations (range 8–20; Table 2). When all eight species were considered, the number of populations was not significantly correlated with range size (Spearman's $r = 0{\cdot}486$, $P = 0{\cdot}22$). However, the number of populations was significantly correlated with range size when Western Wood-Pewee, the species with the largest range, was not considered ($r = 0{\cdot}941$, $P = 0{\cdot}001$). After accounting for range size, eastern species averaged more populations than western species (estimate ± SE = −7·03 ± 1·32, $P = 0{\cdot}006$).

Comparisons of trees with different trend/abundance data indicate that variation in these attributes played a substantial role in shaping tree topology, and therefore population structure. When compared to trees built only with geographic data, the addition of contemporary trend/abundance data altered tree topologies by an average of 34% per species (range 23–43%; Table 2). When the contemporary demographic trees were compared to the long-term demographic trees, tree topologies changed by an average of 29% per species (range 17–40%; Table 2). Visual comparison of the population boundaries also indicated that adding or altering trend/abundance data had a large influence of the number and geographic configuration of populations (Figs S9 and S10).

Across all eight species, the mean geographic area of the contemporary populations was 149 904 km^2 (Table 2). The geographic size of the populations was significantly correlated with the total geographic size of the breeding range ($r = 0{\cdot}966$, $P < 0{\cdot}001$), but did not differ between regions (estimate ± SE = −31 890 ± 147 700, $t = -2{\cdot}16$, $P = 0{\cdot}097$) or based on migratory status (estimate ± SE = −12 640 ± 1·7780, $t = 3{\cdot}94$, $P = 0{\cdot}51$).

All four of our assessment methods indicated that the clustering analysis was able to identify and delineate regional populations that differed in demographic attributes. The agglomerative coefficients were >0·99 for all species, indicating strong grouping structure for all eight

Table 2. Population grouping results: for each species, the number of demographic populations, as determined using the Kelley–Gardner–Sutcliffe (KGS) penalty function, mean population area, results of the *adonis* tests for trend and abundance (see text for details), and the Robinson–Foulds distance metric comparing the topology of the contemporary (2000–2013) hierarchical clustering tree to trees based on geographic distance only and on long-term (1966–2013) monitoring data

			Trend[1]		Abundance*		Robinson–Foulds distance†	
Species	Number of populations	Mean population area (km^2)	R^2	P	R^2	P	vs. geographic tree	vs. long-term tree
Eastern								
Wood Thrush	17	187 036	0·017	0·048	0·26	<0·001	0·36 (1128/3102)	0·35 (1100/3102)
Eastern Wood-Pewee	20	199 567	0·017	0·029	0·24	<0·001	0·41 (1594/3738)	0·33 (1244/3738)
Kentucky Warbler	13	99 152	0·033	0·11	0·16	<0·001	0·43 (468/1110)	0·40 (440/1110)
Eastern Towhee	17	175 161	0·077	<0·001	0·31	<0·001	0·23 (676/2960)	0·21 (628/2960)
Western								
Hermit Warbler	8	18 350	0·10	0·099	0·11	0·089	0·36 (78/216)	0·17 (36/216)
Western Wood-Pewee	14	322 328	0·044	<0·001	0·11	<0·001	0·28 (495/1748)	0·28 (482/1748)
Chestnut-backed Chickadee	8	82 740	0·026	0·633	0·10	0·004	0·26 (102/394)	0·34 (134/394)
Black-throated Gray Warbler	9	114 901	0·028	0·58	0·12	<0·001	0·39 (192/488)	0·37 (182/488)

*For trend and abundance, R^2 and P-values are based on the results of the *adonis* permutation test using the route-level trend/abundance matrix as the predictor and the population groupings as the fixed response variable.

†Robinson–Foulds distances (dT) are based on comparing the contemporary (2000–2013) demographic tree to either the geographic distance tree (left column) or the long-term (1966–2013) demographic tree (right column) and are expressed as the observed dT divided by the maximum possible dT (shown in parentheses).

species. Visual inspection of NMDS plots indicated that the groupings identified by the agglomerative clustering were largely distinct in ordination space (Figs S11 and S12).

Results from the *adonis* models indicate that, for most species, the groupings identified by the agglomerative clustering explained a significant proportion of the variance in route-level trend and/or abundance (Table 2). For seven of the eight species, R^2 values for the variance in abundance explained by our groupings were significant at the $\alpha = 0{\cdot}05$ level and all species had significant R^2 values at the $\alpha = 0{\cdot}1$ level. R^2 values for the variance in trend explained by our groupings were significant at the $\alpha = 0{\cdot}05$ level for half of the species (4/8) and were significant at the $\alpha = 0{\cdot}1$ level for five of the eight species. For all eight species, the R^2 values were smaller for trend than abundance. Furthermore, all R^2 values were <0·26, indicating that spatial constraints likely played a large role in grouping populations, especially for western species, which on average had lower R^2 values and dT values than eastern species.

Analysis of population-level trend and abundance provided strong evidence that our method was successful at identifying populations that were distinct with regards to trend and/or abundance (Tables S1–S8). Overall, 81% (135/166) of adjacent populations differed in trend and/or abundance with probability >0·95 and 85% (142/166) differed with probability >0·90. However, the proportion of populations that differed in demographic attributes was higher for eastern populations (92%; 112/122) than for western populations (68%; 30/44; $\chi^2 = 15{\cdot}15$, $P < 0{\cdot}001$). As with the results from the *adonis* models, this suggests that spatial constraints may have played a more important role in delineating populations of western species than of eastern species.

Overall, the comparison of vital rate estimates among adjacent populations provided independent support for the clustering results. For all three species with adequate MAPS sampling, trend estimates were moderately correlated with productivity estimates (Fig. 3). The MAPS analysis also indicated that Eastern Towhee populations with higher productivity tended to have higher abundance ($r = 0{\cdot}603$, $P = 0{\cdot}013$). Comparison of productivity models with and without population as a fixed effect indicated that the vast majority of adjacent populations that differed significantly in trend also differed significantly in productivity, even after controlling for multiple comparisons [Wood Thrush: 88·2% (15/17) of population pairs; Kentucky Warbler: 100% (4/4) of population pairs; Eastern Towhee: 73·3% (11/15) of population pairs]. Of the population pairs with significantly different productivity, the majority differed in the direction predicted based on their trend estimates [Wood Thrush: 93·3% (14/15); Kentucky Warbler: 100% (4/4); Eastern Towhee: 63·6% (7/11)]. For Eastern Towhee, 93·3% (14/15) population pairs that differed significantly in abundance also differed in productivity and 64·3% (9/14) of those populations differed in the direction predicted based on the differences in abundance. No relationship was found between productivity and abundance in Wood Thrush ($r = 0{\cdot}414$, $P = 0{\cdot}21$) or Kentucky Warbler ($r = 0{\cdot}16$, $P = 0{\cdot}52$) populations and neither trend nor abundance was correlated with apparent survival for any of the three species.

Discussion

Ecologists have long acknowledged that advancing ecological theory and managing declining species requires an operational definition of what constitutes a population

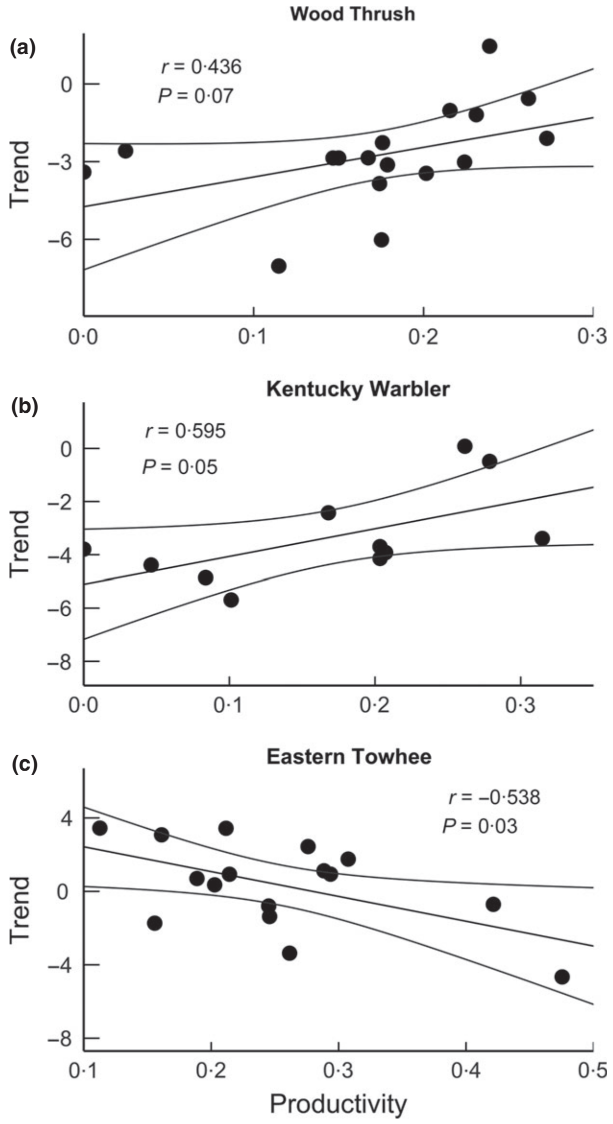

Fig. 3. Correlation between trend estimates based on Breeding Bird Survey data and productivity estimates based on Monitoring Avian Productivity and Survivorship data for populations of three North American bird species. Note different axis limits on each plot.

(Andrewartha & Birch 1954; Berryman 2002). Despite this recognition, there are surprisingly few methods available for quantifying geographic structure in demographic attributes and delineating ecological populations in an objective manner (Camus & Lima 2002). In this paper, we have proposed one such approach and demonstrate the application of our method using continental-scale count data for eight North American songbird species. For all eight species, our approach was able to identify geographic structure in trend and abundance and to delineate populations that show variation in these attributes. Comparisons of population structure across different periods and to purely geographic structure indicate that these patterns were shaped by spatial variation in population attributes and independent data collected via the MAPS banding program corroborate the regional demographic patterns obtained from the BBS data.

Pairwise comparison of adjacent population attributes confirmed that the vast majority (~85%) of adjacent populations differed significantly in either trend and/or abundance. In cases where adjacent populations did not differ in at least one attribute, visual inspection of the population maps suggest that spatial constraints may have been the primary cause of population delineation. For example, Kentucky Warbler populations 12 and 13 did not differ significantly in either trend or abundance (Table S3), but further inspection reveals that these populations share only a small portion of their borders (Fig. S3). These spatial constraints appear to have been particularly important for western species, as indicated by the lower proportion of adjacent populations that differed in population attributes and the smaller dT values for the demographic vs. the geographic trees. The importance of spatial constraints for western species may result from the fact that these species occur in patchier habitats than the habitats used by the eastern species (Tewksbury, Hejl & Martin 1998).

Demographic data collected through the MAPS banding program provided an independent validation of the results obtained using BBS data. For the three species with adequate MAPS sampling, the demographic data provide evidence that the geographic structure in population trends was reflected in underlying vital rates, particularly productivity. Interestingly, productivity was positively correlated with trend for the two obligate long-distance migrants (Wood Thrush and Kentucky Warbler), but negatively correlated for the partial migrant/resident Eastern Towhee, possibly resulting from differences in density dependence between these migratory strategies (Both 2000). Productivity was also positively correlated with abundance for Eastern Towhees. In general, both abundance and productivity tended to be higher in southern populations than in northern populations (Fig. S4), indicating that our clustering approach may have captured a latitudinal gradient in the number of broods per season (Greenlaw 1996). Assuming that abundance at BBS routes is an index of breeding density within each population, the lack of correlation between productivity and abundance in the two long-distance migrants again suggests that the abundance of obligate migrants and partial migrants may be controlled by different demographic factors. Alternatively, differences in abundance may be driven by variation in habitat quality, which may not be reflected in productivity rates if reproductive success is density-dependent. Regardless of the biological mechanisms, the MAPS data provide an independent validation that clustering local sites based on count data was able to quantify geographic structure in demographic rates. Furthermore, the scale of the populations identified by our approach is far larger than the typical dispersal distance of most songbirds (Tittler, Villard & Fahrig 2009), suggesting the movement dynamics likely played a negligible role in the observed geographic structure of these populations. As a result, the method we propose provides an operational approach that can link empirical studies to the theoretical framework proposed by Andrewartha & Birch (1954) over sixty years ago, explicitly linking local populations that share underlying vital rates.

Given the central importance of identifying demographic population structure to ecology and conservation, it is important that any approach for delineating populations is broadly applicable to many species. Conventionally, demographic rates have been collected by tracking individual organisms using labour-intensive and costly mark–recapture methods (White & Burnham 1999). Although these methods can provide reliable estimates of vital rates within the sampling area and time frame, implementing them over larger spatial and temporal scales is generally cost-prohibitive (Zipkin *et al.* 2014). As such, the scale of most vital rate data is of limited value for identifying rangewide population geographic structure. In contrast, count data are relatively easy to collect over large spatial and temporal scales and a large number of standardized monitoring programs already collect these types of data for many species (Smit, Zuiderwijk & Groenveld 1999; Weir & Mossman 2005; Roy, Rothery & Brereton 2007). Thus, the approach that we have outlined provides a robust and objective method for quantifying geographic structure in demographic attributes that is widely applicable to many existing monitoring programs. Furthermore, our approach could be refined to utilize less standardized types of count data, such as presence-only data or opportunistically collected citizen-science data. Given the growing number and availability of citizen-science data sets (Sullivan *et al.* 2009) and analytical tools to estimate demographic rates from these data (Zipkin *et al.* 2014), we expect that our approach will be applicable to a large number of plant and animal species.

Although assessing population structure is important to advancing ecological theory, we expect that our approach will be particularly valuable for scientists and managers tasked with mitigating the widespread declines observed in many species (Pimm *et al.* 2014). At present, conservation work is often conducted without regard to population structure (Hughes, Daily & Ehrlich 1997) or on populations that are delineated by geopolitical or geophysiographic boundaries (Vazquez, Rodríguez & Arita 2008). Such arbitrary populations may not be useful for identifying the causal factors that are driving declines (Rodrigues & Gaston 2002) or for conservation of diversity at the population scale (Hughes, Daily & Ehrlich 1997). For example, bird conservation in North America is conducted within Bird Conservation Regions (BCRs) that share similar bird communities, habitat, and resource management issues (Commission for Environmental Cooperation, 1998). Although BCRs may be appropriate for regional coordination of bird conservation and management, it is unlikely their boundaries coincide with the boundaries of the natural populations of the species of concern. For the eight species included in our analysis, BCRs within each species range contained, on average, portions of 3·75 (±0·97) different natural populations. This overlap indicates that each BCR contained, on average, only 26% of each natural population, underscoring the limitations of using BCR boundaries to assess demographic population structure.

In contrast to BCRs, our approach inherently captures the demographic and spatial attributes that are most directly relevant to population processes and subsequent conservation action. Moreover, our approach is scalable and can be tailored to match the temporal scale over which the ecological factors of interest operate. For example, comparing population structure across the contemporary and long-term data sets indicated that geographic patterns in trend and abundance have changed considerably for Kentucky Warblers and Wood Thrush, but have remained virtually unchanged for Hermit Warblers (Table 2). Additional comparisons of this nature could provide a powerful tool to understand how environmental factors have shaped contemporary population dynamics. Using our approach, it is also possible for managers to compare the tree topology and demographic population structure across multiple species, providing a rigorous method to quantify geographic regions that may be important for multispecies conservation planning.

Additionally, by combining monitoring data with information about population-specific abundance data, it may be possible to conduct viability analyses for each population and in this way determine the persistence of populations under future land-use and climate scenarios. For example, regional monitoring data within each population could be combined with remote-sensing data to quantify how land use and climate have influenced population dynamics. Moreover, by quantifying the drivers of population change within and among natural populations, conservation practitioners can differentiate and proactively manage for rangewide vs. region-specific threats and prioritize limited conservation resources among regions. The hierarchical nature of our classifications also allows managers to focus on more fine-scale geographic structure within regional populations to mitigate threats that are more local in nature. Regardless of how the population structure is used, our approach provides an alternative to using arbitrary boundaries to define populations and therefore increases the likelihood that population analyses will capture the underlying ecological dynamics that form the basis for conservation and management decisions.

Many conservation biologists argue that we have entered the sixth extinction characterized by the rapid decline of many populations (Hughes, Daily & Ehrlich 1997) and species (Pimm *et al.* 2014). Mitigating these declines will require the ability to delineate natural populations to understand the spatial scales at which demographic processes operate. Ecological dynamics do not take place in isolation from evolutionary dynamics or vice versa (Wiens & Graham 2005), and delineation of populations should ultimately account for both processes. As such, the development of effective conservation strategies in the face of rapidly changing global climate and land use will require the unification of the evolutionary and ecological population paradigms to consider both demographic vulnerability and genetic uniqueness (Crandall *et al.* 2000). Although both demographic and genetic data are rarely available for the same spatial and temporal scales, our approach could easily be expanded to incorporate both types of data to quantify biologically realistic population structure across space and time.

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Data accessibility

Breeding Bird Survey: All BBS data used in this analysis are available at https://www.pwrc.usgs.gov/bbs/RawData/.

Monitoring Avian Survival and Productivity: All MAPS data used in the analysis are available through the Smithsonian Digital Repository http://dx.doi.org/10.5479/data.nzp.2015.1109 (Rushing *et al.* 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Additional methods and materials.

Appendix S2. Additional summary figures and tables.