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More and more generalists: two decades of changes in the European avifauna

Isabelle Le Viol[1,2,*], Frédéric Jiguet[1],
Lluis Brotons[3,4], Sergi Herrando[3], Åke Lindström[5],
James W. Pearce-Higgins[6], Jiří Reif[7],
Chris Van Turnhout[8] and Vincent Devictor[9]

[1]*National Museum of Natural History, UMR7204-MNHN-CNRS-UPMC, 55 Rue Buffon, 75005 Paris, France*
[2]*ETC-BD, 57 Rue Cuvier, 75005 Paris, France*
[3]*European Bird Census Council and Institut Català d'Ornitologia, Museu de Ciències Naturals, Barcelona, Catalonia, Spain*
[4]*Centre Tecnològic Forestal de Catalunya, Solsona, Catalonia, Spain*
[5]*Department of Biology, Biodiversity Unit, Lund University, 223 62 Lund, Sweden*
[6]*UK British Trust for Ornithology, Thetford, Norfolk IP24 2PU, UK*
[7]*Laboratory of Ornithology, Palacký University, Olomouc, Czech Republic*
[8]*SOVON Dutch Centre for Field Ornithology, PO Box 6521, 6503 GA Nijmegen, The Netherlands*
[9]*Institut des Sciences de l'Evolution, UMR-CNRS-UM2-5554, Université de Montpellier 2, 34095 Montpellier, France*
*Author for correspondence (ileviol@mnhn.fr).

Biotic homogenization (BH) is a process whereby some species (losers) are systematically replaced by others (winners). While this process has been related to the effects of anthropogenic activities, whether and how BH is occurring across regions and the role of native species as a driver of BH has hardly been investigated. Here, we examine the trend in the community specialization index (CSI) for 234 native species of breeding birds at 10 111 sites in six European countries from 1990 to 2008. Unlike many BH studies, CSI uses abundance information to estimate the balance between generalist and specialist species in local assemblages. We show that bird communities are more and more composed of native generalist species across regions, revealing a strong, ongoing BH process. Our result suggests a rapid and non-random change in community composition at a continental scale is occurring, most likely driven by anthropogenic activities.

1. INTRODUCTION

Biotic homogenization (BH), a process that causes ecological communities to become increasingly similar to each other as some species (losers) are systematically replaced by others (winners) [1–3], is suggested to affect biodiversity at different spatial scales [4–6]. It may have severe consequences on community and ecosystem functioning [7]. Gains in similarity among local assemblages, which have been widely observed across differing continents, habitats and taxa, can be caused by both native and exotic species [8–10]. However,

the extent to which these changes are caused by variation in native species abundance or by the expansion of exotic species in local assemblages is still unclear.

The dynamics of BH can be conceptualized using predictions from ecological niche theory. Specialist species should be favoured in rather stable environments, whereas generalists should be more able to thrive in disturbed habitats [11]. Environmental change should therefore result in a non-random filtering of species within assemblages resulting in more similar communities. Measuring the relative occurrence [6] or abundance [4] of specialist species in local assemblages (the so-called community specialization index, CSI; [12]) can therefore reflect community response to large-scale disturbance [13] related to anthropogenic activities [4,14] and to climate change [15]. However, whether the cumulated responses of native species populations to environmental changes, measured at local (site) scales, can drive consistent trends in BH at national or continental scales remains unclear.

Here, we assess whether variation in the abundance of native species alone may drive BH. In particular, we use data from local sites to test whether BH has occurred during the period 1990–2008 at national and European scales by calculating the temporal trend in the average specialization of local bird communities (CSI), which reflects the dynamics of specialists versus generalists in species assemblages. We also assess the concurring change in community richness and diversity.

2. MATERIAL AND METHODS

(a) Bird monitoring

We used high-resolution data of the yearly composition of bird communities in sites monitored from 1990 to 2008 in six European countries: Sweden, United Kingdom, France, The Netherlands, the Czech Republic and Catalonia (Spain). The database contained more than 13 900 000 detected birds, belonging to 234 species surveyed in more than 10 111 sites from 1990 to 2008 (see the electronic supplementary material, appendix S1: details on distribution of sampling effort). Each monitoring scheme has specific methodologies to ensure national standardization. Although the precise methods vary between schemes, combined, they provide high-quality data for building pan-European biodiversity indicators based on trends in population abundance [16]. In brief, observers monitor fixed study plots or transects or points yearly in which each individual seen or heard is counted. The date, duration (plots, transects) and lengths (transects) of the surveys are standardized, and the same observer monitors the same site across years. A given site is generally surveyed at least twice during the breeding season to ensure the sampling of both early and late breeders. For a given species in a given site, the maximum abundance recorded during the breeding season is retained.

(b) Trends in community specialization index

The trend in CSI was calculated in three steps. First, for each of the 234 studied species, we calculated a species specialization index (SSI) [5]. Here, the SSI is simply given by the variation in species preference for different habitat types. Habitat preference was provided by the Bird EUNIS database (ETC-DB; [17]) that describes a species affinity level for nesting and foraging per EUNIS habitat ($n = 98$, electronic supplementary material, appendix S2), per biogeographical region ($n = 11$). Levels of affinity are coded from 1 to 3 by experts to describe increasing habitat preference (code 3: primary habitats; 2: secondary; 1: others). We retained the higher level per species for each habitat and calculated SSI values as the coefficient of variation of species affinity across the range of habitat classes (see the electronic supplementary material, appendix S3 and S4). Note that several approaches can be used to estimate species' specialization [18]. Here, we searched for a relevant, ordered classification of species along a habitat specialist–generalist gradient rather than for a real measure of niche position and breadth. In this context, expert knowledge was shown to be efficient in providing relevant estimates of SSI [19] (see the electronic supplementary material, appendix S4).
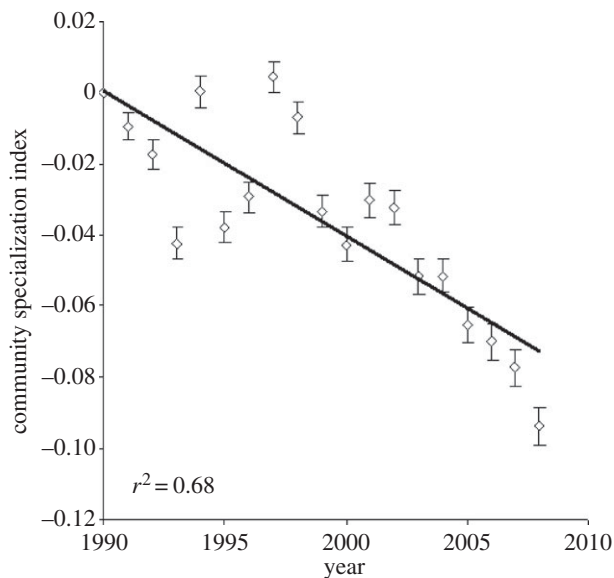
Figure 1. A significant decrease of community specialization index reflecting the relative increase of generalist species in local assemblages of breeding birds in Europe from 1990 to 2008 as a driver of the ongoing BH process across the continent. Changes in CSI were calculated from the yearly changes in 234 species' abundance at local sites (10 111) from standardized national breeding bird surveys across six European countries. The significance of the trend in CSI, the estimates and the standard errors were obtained using longitudinal spatial analysis (year effect on CSI: slope $b = -0.0042 \pm 0.0005$; $p < 0.001$).

Second, we calculated a CSI for each site and for each year as the average SSI of detected species weighted by local species abundance as follows: $CSI = sum(a_i \times SSI_i)/sum(a_i)$, where a_i is the abundance of species i [4]. The CSI reflects the relative abundance of more- or less-specialized species in local assemblages, and is therefore expected to decrease following the relative declines of specialists (species with high SSI).

Third, we performed longitudinal spatial analysis of CSI trend (http://lme4.r-forge.r-project.org/book/): we modelled yearly change in CSI across the studied sites by using mixed-models (R package nlme) with year as the explanatory covariate, country as a covariate, site as a random factor (nested within country), the number of sampled sites per year per country as weight and an exponential spatial autocorrelation structure. Year was used as a fixed factor, so that this first model provided us with an estimate of CSI for each year and its corresponding standard error (figure 1) accounting for spatial autocorrelation, for variations in sampling effort, and for variations between country and sites in the level of CSI.

Then, we tested the significance of this trend in CSI accounting for temporal autocorrelation: a generalized least-squares model summarized the overall trend in CSI using the estimates of CSI per year from the first model as the dependent variable and year as a continuous explanatory covariate. This model was weighted by the error associated to each yearly estimate (weight = $1/\text{s.e.}^2$) and included a first-order temporal autocorrelation structure. The slope of this last regression is an estimate of the average trend in CSI from 1990 to 2008. Note that we obtained similar qualitative results when using different weights in the first model (see the electronic supplementary material, appendix S5). Similar models (without country as controlling factor) were conducted to estimate the trend in CSI within each country separately. Similar analyses were also performed for species richness and Simpson diversity index. We also used an alternative statistical framework (generalized additive mixed-models; [20]) to account for both spatial and temporal autocorrelation in a single model. This generated similar qualitative results although failed to converge for some indices.

3. RESULTS

At the multi-national scale, the CSI strongly decreased over the past two decades (figure 1; year effect, slope

$b = -0.0042 \pm 0.0004$; $p < 0.001$), the trend in Simpson diversity was positive ($b = 0.0002 \pm <0.00001$; $p = 0.023$), whereas species richness showed no significant trend (see the electronic supplementary material, appendix S6). The CSI decreased significantly in Sweden ($b = -0.0075 \pm 0.0008$; $p < 0.001$, $n = 5239$), France ($b = -0.0021 \pm 0.0007$; $p = 0.002$, $n = 7530$) and the United Kingdom ($b = -0.0030 \pm 0.0003$; $p < 0.001$, $n = 33937$). It showed a negative non-significant trend in the Czech Republic ($b = -0.0011 \pm 0.001$; $p = 0.29$, $n = 801$) and in the Netherlands ($b = -0.0007 \pm 0.0006$, $p = 0.29$, $n = 15002$), and a positive non-significant trend in Catalonia ($b = 0.0040 \pm 0.0024$; $p = 0.08$, $n = 1499$; electronic supplementary material, appendix S7).

4. DISCUSSION

Overall, our result reveal that local species assemblages are increasingly composed of habitat generalists. Importantly, the decrease in the CSI did not result from the colonization of exotic species (no exotic species were included in the dataset analysed: see the electronic supplementary material, appendix S3). However, the positive trend in Simpson diversity index and the stable species richness suggest that some species have become more abundant in local assemblages. There has been a strong ongoing BH process affecting breeding birds across Europe during the past two decades, consistent with preceding temporal studies on BH at smaller spatial resolutions [6,14]. This general pattern is also supported by population declines in particular specialized species or groups (e.g. farmland and woodland birds) and/or as a consequence of more positive trends of some habitat generalists (e.g. European wild bird indicators; [16]). It is also in accordance with the decrease in taxonomic beta diversity detected in Europe at different spatial resolutions for different taxa [8–9,21].

Our results further reveal that beyond this European trend, the trend in CSI varied within Europe, as did its temporal pattern (see the electronic supplementary material, appendix S7). The decrease in CSI probably results from different sources of environmental changes. For instance, while some studies have shown that land-use changes were probably a major driver of the decrease in CSI [4,6,14], others have shown that climate change was also contributing to this decrease [15]. As climatic and habitat niche are correlated to some extent [22], the observed changes in community composition probably integrate different sources of environmental changes that are difficult to separate. Besides, the relative importance of different drivers of change in CSI probably differs according to the region considered, as hinted by the variation in temporal patterns in CSI between countries. For example, recent land-use patterns vary across Europe from 1990 to 2000, urbanization was most conspicuous in the Netherlands, agricultural extensification in the Czech Republic, changes in forest land cover in France and the UK and agricultural intensification in France [23].

In this context, relating the dynamics of CSI to land-use and climate changes in different areas may offer a promising venue for future research. This

approach could also be applied to taxonomic groups other than birds. In particular, the CSI approach may reveal whether areas of conservation interest (e.g. Natura 2000-sites) are sufficient to maintain high levels of CSI for different groups in the long run.

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