BIODIVERSITY RESEARCH

More species, fewer specialists: 100 years of changes in community composition in an island biogeographical study

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ABSTRACT

Aim We measured the changes in an island avifauna over more than 100 years (1898–2006), using community indices accounting for difference in expected species sensitivity to land-use and climate changes.

Location Ouessant Island, France, Great Britain.

Methods We assessed the temporal trend of the relative proportion of generalist species breeding on Ouessant island and whether high-temperature tolerant species have replaced less tolerant species over this time period. We further tested the relationship between the observed change in the avifauna composition, and long-term population species' trends measured independently in potential source regions of colonist species (France and Great Britain).

Results During the whole study period, Ouessant island has experienced a strong increase in species richness (+41%), but a severe decline in specialist species. In contrast, we found no change in species composition in terms of their temperature-tolerance. The observed trend was highly correlated with species trends measured in the Great Britain.

Main conclusions Our results revealed an ongoing biotic homogenization process towards more generalist species, coupled with a strong local increase in species richness. The observed trend was most likely driven by a strong habitat change in the island occurring during the period considered, favouring the colonization of generalist species. Our results show that an increase in species richness can be misinterpreted as a sign of conservation improvement and that assessing change in community composition using species-specific ecological traits provides more accurate insights for conservation planning purposes.

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INTRODUCTION

The seminal work on island biogeography by MacArthur & Wilson (1967) suggested that the biota of any island is a dynamic equilibrium between the immigration of new species and extinction of species already present. The turnover of species should constantly occur, but the number of species is expected to remain unchanged. This equilibrium hypothesis has been proved insightful in interpreting many insular situations and formed a general framework for the earlier research into general laws in biogeography (Simberloff, 1974).

However, this equilibrium hypothesis should not hold if species with specific ecological traits respond faster than others to current global changes, as community composition, and species richness should be affected (Devictor & Robert, 2009). Besides, while biodiversity losses are largely documented across the globe as a result of anthropogenic pressures, species gains are also frequently observed at local scales (Sax & Gaines, 2003). But Island biogeography studies have largely focused on species number and turnover, while ecological differences between species were hardly considered explicitly.

Protected areas are currently unable to buffer against broad-scale shifts in the distribution of species or ecosystems (Lee & Jetz, 2008). In this respect, new approaches towards reserve-selection have proposed to improve traditional reserve design, taking expected changes in species distributions into account (Araújo *et al.*, 2004). Investigating which species are most likely to benefit or to suffer from current global changes is highly needed to assess the conservation success of protected areas and their potential weakness in the future. In many cases, changes in species composition are not occurring at random: the replacement of many losers by fewer winners often leads to a biased reshuffling of initial species pools towards particular species, a process termed 'biotic homogenization' (McKinney & Lockwood, 1999).

Most studies on homogenization have investigated whether and how the number of species shared by two assemblages (so called β-diversity) has increased over time and/or space. Biotic homogenization is usually assessed by calculating a similarity index (e.g. Jaccard; Bray–Curtis index), which measures the taxonomic turnover between sites (and/or time periods) using records of species presence/absence (Koleff *et al.*, 2003). However, the process of biotic homogenization can be viewed as a multifaceted, and which can alternatively be taxonomic but also functional, ecological or genetic (Olden & Rooney, 2006). An increase in taxonomic similarity (i.e. a decrease in β-diversity) would not necessarily lead to an increase in functional homogenization (which depends on the functional redundancy of the species).

Rooney *et al.* (2007) have recently highlighted the danger of uncritically applying similarity measures to derive conservation priorities as any increase in taxonomic similarity can be difficult to interpret, as either local increase or decrease in species richness may have been responsible for this increase. Moreover, beyond the number and identity of species affected by global changes, there is now growing acceptance that protected areas should not only protect but also preserve other components of diversity (e.g. functional composition) (Mouillot *et al.*, 2008). However, major changes in community functional composition have not been well-documented within protected areas over long time-periods (but see Rendón *et al.*, 2008), simply because we lack simple metrics reflecting change in community composition that are clearly linked to global changes.

Classical studies on homogenization could therefore be usefully combined with more ecological indices reflecting differences between species, *a priori* related to their sensitivity to global changes. In particular, measuring the progressive change in community composition in terms of specialist vs. generalist species should aid visualization of the impacts of habitat degradation. Indeed, the local increase in species richness was frequently observed as the result of range-expanding habitat generalists, more likely to invade disturbed ecosystems, typically at the expense of native and more specialized species (Hobbs & Mooney, 1998; Blackburn *et al.*, 2004). Moreover, niche evolution theory predicts that habitat degradation should negatively affect specialists: ecological specialists are expected to benefit from environments that are relatively homogeneous (in space and/or time), whereas generalist species should benefit from environments that are heterogeneous (Futuyma & Moreno, 1988; Kassen, 2002; Marvier *et al.*, 2004; Östergård & Ehrlén, 2005).

The decline of specialist species is also well-documented across taxa throughout the world and is generally related to land-use and land-cover alterations (e.g. plants, Fischer & Stöcklin, 1997; Rooney *et al.*, 2004; butterflies, Warren *et al.*, 2001; carabid beetles, Kotze & O'Hara, 2003; bumblebees, Goulson *et al.*, 2005; coral reef fish, Munday, 2004; birds, Julliard *et al.*, 2004; marsupials, Fisher *et al.*, 2003). Moreover, the relative composition of specialist vs. generalist species has been shown to be a robust and powerful empirical signature of global land-use changes (Devictor *et al.*, 2008a,b).

Similarly, climate warming is expected to drive changes in community composition towards more high-temperature tolerant species (Jiguet *et al.*, 2007). Measuring long time series of the relative composition of high- vs. low-temperature dwellers occurring in a given area should directly reflect the impact of climate warming (Devictor *et al.*, 2008c).

In this study, we employed a dataset spanning 108 years of bird species records in a protected area to address three principal objectives: (1) to test whether the long-term change in the bird avifauna composition over 108 years is biased towards more generalist species, as we would expect as a sign of habitat degradation, (2) to test whether the composition of the bird avifauna is increasingly dominated by warm-adapted species, as we predict that high-temperature tolerant species should benefit from climate warming, and (3) to investigate whether or not the observed trends are related to species trends occurring in major source regions for colonist species.

METHODS

Study area

Ouessant is an island located 20 km off the western coast of France (48°28′ N, 5°5′ W) and covers a surface area of 15.4 km^2 (Fig. 1). Humans exploited the whole island area until the early 20th century, either for cattle breeding or for cropping. Subsequent land-use changes occurred on the island following human departure, namely the disappearance of crop farming and a drastic decrease in grazing pressure (Gourmelon *et al.*, 2001).

Due to the presence of rare species, high biological diversity and an exceptionally preserved coastal ecosystem, this island forms part of a Regional Nature Park since 1969 and has been part of a National Park since 2007. The 40-km length of the island coastline received the status of Classified Reserve in 1979 (IUCN, 1994), which led to total protection of the island against urbanization pressure. This island was also classified as a 'Man and Biosphere Reserve' in 1988 and listed in more recent type of protected area such as International Important Bird Areas and NATURA 2000 (http://ec.europa.eu/environment/nature/natura2000/).

Figure 1 Location of Ouessant Island.

Data collection

All sources of available data (publications, reports, databases, see Appendix S1 in Supporting Information) were employed to compile breeding bird species presence or absence from 1898 to 2006. The first lists of species present on the island were mainly reported by ornithologists visiting Ouessant. Then, from 1955 to 1986, the French National Museum of Natural History carried out ornithological courses and ringing operations on the island, mainly in late summer but also in spring. Extensive annual reports of these missions have listed all species detected during these field seasons (Nicolau-Guillaumet, 1970). Since 1970, specific inventories of breeding birds were conducted for atlas construction (1970–75, 1980–85, 1985–89 and 2004–08). Finally, a permanent ornithological station was established in 1984 with two permanent observers recording all species breeding on the island every year since then.

Naturally, we acknowledge that the sampling effort may not have been constant over the entire temporal period under consideration. Nevertheless, although some species may have been present but not detected on particular years, we assume that variation in the sampling effort is unlikely to have produced consistent change in community composition (i.e. towards more generalist or more high temperature tolerant species) over 100 years. We also employed certain measures to reduce the variation in species detection in the dataset. First, we only focused on presence–absence of terrestrial breeding birds, (i.e. excluding waterbirds and seabirds) which are common in France. Then, over the 73 years of available records, we retained only the 69 years for which the taxa list was exhaustive (we excluded partial lists from 1888, 1921, 1922 and 1927). In addition, we considered only species ($n = 52$) with clearly reported breeding status (i.e. either noted as breeding or non-breeding in yearly lists) through the time investigated. Breeding status in the island is a significant distinction as this is generally easy to detect and reflects a true colonization event. We were able to exclude four species

exhibiting long periods of presence, but which possessed unknown or uncertain breeding status on the island (*Coturnix coturnix*, *Motacilla flava*, *Acrocephalus schoenobaenus* and *Sylvia communis*; see Appendix S1). Note, however, that even when we included these species in our analysis, we obtained similar results. Finally, we checked whether bird records were consistent between years (see below).

Long-term trend of avifauna composition in the island

To measure the habitat specialization level of each species, we used the species specialization index of each species (SSI) proposed by Julliard *et al.* (2006). This index is a continuous measure of habitat specialization and is calculated, for a given species, as the coefficient of variation (standard deviation/mean) of the species densities across habitats, monitored by the French Breeding Bird Survey. Values of the SSI for the species considered in this study were taken from Devictor *et al.* (2008b). Among bird species studied here, SSI ranged from 0.23 for the most generalized species (the Blackbird, *Turdus merula*) to 2.86 for the most specialized species (the Red-billed Chough, *Pyrrhocorax pyrrhocorax*). No SSI value was available for two species (the Rock Pipit, *Anthus petrosus* and the Long-eared Owl, *Asio otus*) because they were not appropriately monitored by the French Breeding Bird Survey: the Rock Pipit has a very restricted coastal distribution in France and the Long-eared Owl is a nocturnal raptor for which the Breeding Bird Survey protocol is not adequate. On this basis, we excluded these two species from our analyses. Then, a community specialization index (CSI, Devictor *et al.*, 2008a) was calculated for each of the 69 years available. For a given year, CSI was calculated as the average of all SSI values of the species reported as breeding on the island. We expect CSI to decrease if the relative composition of the species pool is increasingly biased towards generalist species through time.

We additionally estimated two measures of the climatic niche of the species considered in this study. For a given species, measures of the climatic niche were obtained using average spring/summer monthly temperature of atlas grid cells where the species is breeding in Europe (Hagemeijer & Blair, 1997): thermal optimum, defined as the mean temperature of all breeding cells in Europe, and thermal maximum, defined as the mean of the hottest 5% breeding cells. Monthly temperatures were obtained from the WORLDCLIM database (http://www.worldclim.org), as mean monthly March to August (the breeding period) temperature for the period 1950–2000. We calculated the average community value of such climatic niche metrics across bird species, to obtain a community thermal optimum index (CTO) and a community thermal maximum index (CTM). We expect CTO and CTM to increase if the relative composition of the species pool is increasingly biased towards high-temperature tolerant species (Devictor *et al.*, 2008c).

The species-specific indices developed here (SSI, and climatic niche metrics) have been estimated using recent data (post-1990s) and are considered fixed indices in time and further

applied to obtain community indices over the last 108 years. We assumed that the climatic niche metrics should not have varied greatly during the century because climate did not change greatly before the 1990s over Europe (Moisselin *et al.*, 2002). On the contrary, large habitat modifications occurred during the 20th century. These changes resulted in large modifications in habitat occurrence frequency. Yet, the SSI was shown to be robust to varying habitat frequency (Devictor *et al.*, 2008b). Moreover, if some species had adapted during the century to habitat changes in modifying their habitat specialization, this would most likely concern only a few species. We are therefore confident that using cotemporary species specialization indices does not affect our principal findings.

Finally, we further tested whether the colonization events occurring in the island were related to the long-term species trends, measured independently, in major adjacent potential source regions (Fig. 1). To do so, we used the long-term trend of each species provided by the Breeding Bird Survey in France (http://www2.mnhn.fr/vigie-nature/spip.php?rubrique11) and in Great Britain (http://www.bto.org/birdtrends2007).

Statistical analysis

Temporal variations of the different community measures considered were first calculated using linear regressions model (GLM). In these models, the time (in years) was considered as a continuous variable and the community measure (species richness, CSI, CTO, or CTM) as the dependent variable. However, any random sample of potential colonists from the continent could have produced the trend in community measures observed on Ouessant island. Therefore, we further calculated trends in each community measure obtained from the following null-model approach.

1. For each given year (where a species list in Ouessant was available during the period 1898 to 2006), a number of species (equivalent to the observed number of species occurring in the island that given year) was randomly sampled in a pool of potential colonists from the continent. The potential colonists were selected from the regional Atlas (Guermeur & Monnat, 1980; Yeatman-Berthelot & Jarry, 1995; Groupe Ornithologique Breton, 1997) covering the most likely source of colonists from the continent (i.e. from the Britain region).
2. The corresponding expected trend in CSI (and other community parameters, CTM, CTO) was calculated.
3. We estimated 1000 random trends in the expected CSI, CTM and CTO using this approach which provided the mean trend of each community parameter expected by chance. We then tested the difference between these simulated trends and the observed empirical trends. We also used a more constrained null model in which the probability of sampling a species from the continent was weighed by the species density (the density was estimated as the number of atlas cell where the species was recorded).

Additionally, we checked whether the successive inventories considered in the study were coherent between years in measuring the temporal autocorrelation between annual species lists. To do this, we performed a principal coordinates analysis of a Manhattan Similarity Matrix of yearly lists according to their species composition (Appendix S1) and further performed a Mantel test. The Manhattan Distances were chosen to limit any potential artefactual curve shape (e.g. horseshoe effect, Podani & Miklos, 2002). These lists proved to be highly temporally auto-correlated ($P < 0.001$; number of permutation = 1000).

This analysis demonstrates that bird records from successive years were highly similar and that change in species composition was gradual over the temporal period without radical changes. We are thus confident that the measured change in the bird avifauna composition is not strongly affected by drastic changes in observers' efficiency/interest for some particular groups of species (e.g. common vs. rare breeding species).

RESULTS

We found a very strong annual increase in bird species richness during the period 1898–2006 (slope of the linear regression: $+0.278 \pm 0.012$; $F_{1,67} = 553.3$; $P < 0.0001$, $R^2 = 0.90$; Fig. 2a). In contrast, during the same period, the CSI decreased steeply (slope: -0.0025 ± 0.0001 SE; $F_{1,67} = 231.8$; $P < 0.0001$, $R^2 = 0.77$; Fig. 2b). We found that the observed trend in CSI was clearly significantly more negative than simulated trends
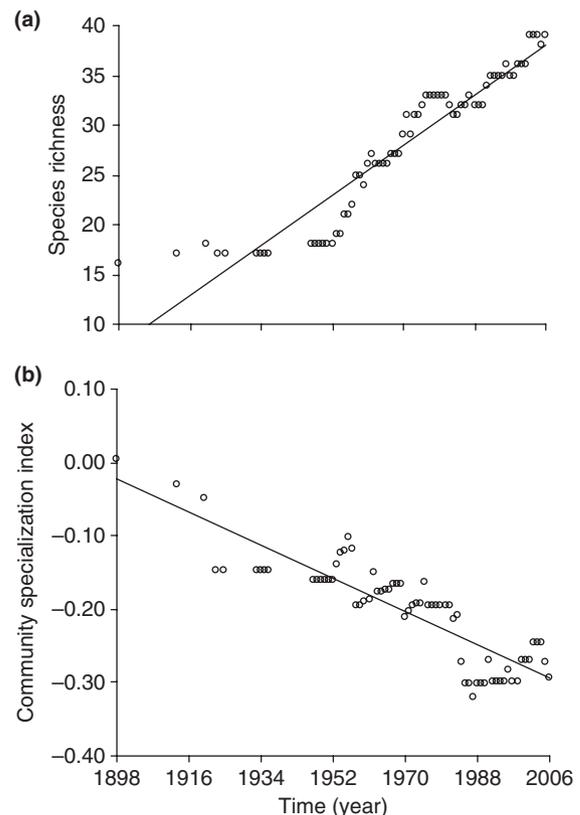

Figure 2 Temporal changes in (a) species richness and (b) community specialization index over 1898–2006 on Ouessant island.

estimated from the null model (difference of observed vs. simulated trends: -0.00251 ± 0.0001; $P < 0.001$). The observed negative trend in CSI was thus produced by colonization events positively biased towards more generalist species, and not only the result of random colonization events.

In contrast, the observed average CTO did not vary across the study period ($F_{1,67} = 0.12$, $P = 0.73$, $R^2 < 0.01$) and was not different from the simulated trends ($P = 0.52$). The observed average thermal maximum of the community (CTM) decreased significantly during the period 1898–2006 ($F_{1,67} = 81.8$, $P < 0.0001$, $R^2 = 0.55$), but at a very low rate (-0.020 ± 0.002 °C per decade; difference of observed vs. simulated trends: -0.019 ± 0.001; $P < 0.001$). Comparing the observed trends with the estimated trends from the constraint null model (in which the probability of colonization was weighed by the species density in the source) did not change the results.

We further tested whether the colonization events occurring on Ouessant island could be explained by species trends in major adjacent possible sources (France and Great Britain). The long-term trend of bird species estimated from Great Britain and from the French breeding bird survey were shown to be highly correlated (Julliard et al., 2004). More temporal data were available from the Great Britain breeding bird survey, which started in 1967 (compared to only in 1989 in France). We thus only used trends from the mainland Great Britain (which is relatively close to Ouessant: separated by a distance of 165 km, Fig. 1), available from 1967 onwards. We found that species that colonized the island (from 1967 to the present, i.e. the whole period of the Great Britain survey scheme), exhibited a positive average trend in Great Britain, whereas species that went locally extinct exhibited a negative average trend in Great Britain ($F_{1,30} = 12.1$; $P = 0.001$).

DISCUSSION

Bird species richness greatly increased over the last 100 years on the island of Ouessant. This change is likely due to many interacting process and thus we were not able to determine the exact causal ecological processes driving this pattern. Our aim was rather to find simple means to reflect whether and how local colonizations (vs. local extinctions) were the result of species a priori more likely to benefit (or to suffer) from habitat changes and climate warming. The strong decrease in the CSI identified in this study may result from three different processes: the progressive extinction of more specialized species, the colonization of more generalist species or from a combination of both. However, as only two extinctions occurred (compared with 37 colonizations), the observed change in CSI mostly resulted from the colonization by more generalist species.

Generalists were probably more likely to colonize the island as major habitat changes occurred over the temporal period considered. These include the cessation of cattle breeding and colonization of wet grasslands in small valleys by willow (Salix ssp). The drastic decrease in grazing pressure on pastures (sheep numbers decreased from 4500 in 1950 to 650 in 2003) led to

abandoned agricultural lands (Gourmelon et al., 2001), probably affecting farmland bird specialist species as well. Interestingly, we found that the colonization events of generalist species on the island were strongly related to the increasing long-term trends of these species measured independently in Great Britain. This result suggests that the success of habitat generalists on Ouessant probably mirrors the more global widespread success of generalist species occurring at larger scales.

We did not find any increase in the temporal trend of the average thermal optimum of the species (CTO), while we found a slow decline in the CTM over the century. This latter trend suggests that species that colonized the island actually breed (at a European scale) at lower maximum temperature than the initial island pool. These results suggest that change in the composition of the breeding avifauna is most likely driven by response to land-use and land-cover changes rather than a consequence of climate warming.

However, our results are based only on presence–absence data. When available, abundance should be used not only to estimate the change in species composition but also to account for the change in the number of individuals within a given species. Indeed, working solely with presence–absence data can potentially mask a great change in community composition in terms of temperature-tolerance. In addition, it is likely that, apart from the few local extinctions that had occurred in the island, a severe decrease in specialist species population sizes may have been masked. In particular, the Skylark (Alauda arvensis), (a farmland specialist species with a specific SSI = 1.2 higher than the average SSI of the species pool SSI = 0.99) has declined during the last 50 years from 350–400 breeding pairs to 15; the Chough (P. pyrrhocorax SSI = 2.9) has decreased from between 70–80 individuals to 45–55 over the same period and the Northern Wheatear (Oenanthe oenanthe, SSI = 1.7) has decreased from 34–73 breeding pairs in 1973 to only three pairs in 2006 (Nicolau-Guillaumet, 1970; Audevard, 2007). Therefore, using abundance data for this type of study would probably be a more accurate reflection of ecological homogenization and would be more powerful even over shorter time-periods than the one considered here.

The detection of global change impact on protected areas in the longer-term is essential to propose accurate conservation planning for the future. Beyond the local change of the Ouessant island avifauna described in this study, the progressive change in community composition is also occurring in landscapes at larger scales and for different taxonomic groups. For instance, biotic homogenization has changed plant community composition in Great Britain over two decades in becoming increasingly biased, towards plant species with particular successful functional traits (Smart et al., 2006). We suggest that assessing whether and how community composition of different taxonomic groups has changed regarding particular functional traits and/or ecological attributes should increase our understanding of the biotic homogenization process.

In practice, the link between conservation interest and rarity is widely used as a classical conservation tool through the

establishment of red lists of endangered species (Butchart *et al.*, 2004), but measuring the change in species conservation status was argued to be a coarse and insufficient measure of biodiversity loss (Luck *et al.*, 2003). Unfortunately, the current availability, design and assessment of protected areas are generally not conceived to deal with expected global environmental changes. Protected areas have long been rooted in the concept of durability (a protected area works best if it remains unchanged for the foreseeable future), and in the necessity to maximize species richness (Polasky *et al.*, 2000). We suggest that protected area assessment should be modified to take new symptoms of biodiversity changes into account and aim to go beyond the simplistic preservation of rare species and the maximization of species richness.

For instance, the conservation status of European bird species was assessed only twice during the period considered (respectively in 1994 and 2004, Burfield & Van Bommel, 2004). A close inspection of the data indicates that during this 10-year period, four species (The Long-tailed Tit, *Aegithalos caudatus*; the Cetti's Warbler, *Cettia cetti*; the Zitting Cisticola, *Cisticola juncidis* and the Grasshopper Warbler, *Locustella naevia*) have colonized Ouessant island. These species were all mentioned as 'secured' both in 1994 and in 2004. Yet, during the same period, five species already present on the island were newly mentioned as 'endangered' (The Linnet, *Carduelis cannabina*; the Northern House Martin, *Delichon urbicum*; the Northern Wheatear, *Oenanthe oenanthe*; the House Sparrow, *Passer domesticus* and the European Starling, *Sturnus vulgaris*). Therefore, the increase in species richness on Ouessant during 1994–2004 does not, in fact, indicate the increase in the global conservation status of the 'original' native island species pool. In this respect, our approach should be valuable as we have highlighted that avifauna composition was strongly modified at the detriment of specialist native species on the study island during the 20th century. This trend was available for the whole period and is not restricted by the time delay required to set up lists of endangered species.

Wildlife managers should concentrate on finding ways to detect meaningful long-term shifts in community composition in protected areas. Numerous studies have shown that landscape degradation can be associated (at least temporarily) with increase in species richness, abundance or diversity indices. Therefore, using changes in such non-functional metrics to create conservation guidelines can be misleading (Van Turnhout *et al.*, 2007). We suggest that, to assess protected area efficiency under global changes, working on specific characteristics such as habitat specialization or thermal optimum can be more accurate for conservation planning purposes.

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SUPPORTING INFORMATION

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

Appendix S1 Terrestrial breeding birds during the period 1898–2006 on Ouessant.

Appendix S2 Principal coordinates ordination analysis (PCoA) of years according of avifauna composition, using on Manhattan dissimilarity distance.

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