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Original article

A successful avian invasion occupies a marginal ecological niche

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ABSTRACT

Biological invasions often threaten biodiversity, yet their ecological effects are unpredictable and in some cases may be neutral. Assessing potential interactions between invasive and native species is thus important to understand community functioning and prioritize conservation efforts. With this purpose, we compared the ecological niche and occurrence of a successful avian invader in SW Europe, the common waxbill (Estrildidae: *Estrilda astrild*), with those of co-occurring native passerine species. We found that common waxbills occupy a marginal niche relative to the community of native passerines, with a larger average ecological distance to the remaining species in the community compared to the native species amongst themselves, and a nearest-neighbour ecological distance identical to those of native species. Furthermore, ecological similarity did not predict co-occurrence of waxbills with other bird species. This is consistent with the invasion using a vacant niche in unsaturated communities, which is likely related to invading waxbills occupying partly human-modified habitats. Similar explanations may apply to other biological invasions of human-modified environments. Results also suggest that detrimental ecological effects due to interspecific competition with native passerines are unlikely. Notwithstanding, the ecological nearest-neighbour of common waxbills was the reed bunting (*Emberiza schoeniclus*), whose SW European subspecies are endangered, and may justify conservation attention regarding possible interactions between these two species.

1. Introduction

Biological invasions, defined here as the unaided geographic spread of an exotic species beyond its introduction sites (rather than the conservationist usage for when there is a negative impact on local ecosystem), can bring negative consequences for ecosystems and biodiversity, but ecologically detrimental invasions may not represent the majority of invasion events (Blackburn et al., 2009; Goodenough, 2010). Species extinctions attributed to invasive species have been mostly linked to invasions by predators, parasites or diseases, particularly in island or lake environments (Mooney and Cleland, 2001; Davis, 2003; Sax et al., 2007), whereas evidence is less abundant for the same processes occurring at a continental scale (Mooney and Cleland, 2001; Bauer and Woog, 2011) or for extinction of native species caused by direct competition with invaders (Davis, 2003). For example, invasive birds can compete strongly with native cavity-nesting species for nesting sites (e.g. Koenig, 2003), but competition for other resources is generally not found to have major effects on native avifauna (reviewed in Blackburn et al., 2009; Bauer and Woog, 2011; but see also Freed and Cann, 2009).

If competition between exotic and native species is important, more diverse communities are predicted to make invasions more difficult, a concept referred to as biotic resistance (Elton, 1958). Some experimental studies finding a negative relationship between numbers of introduced and native species at local scales support this idea (reviewed in Shea and Chesson, 2002; Bruno et al., 2003), and suggest that local species richness can be limited by interspecific competition for resources. But the relation between numbers of native and invasive species is often the opposite at larger spatial scales (Shea and Chesson, 2002; Friedley et al., 2007; Bulleri et al., 2008). Thus, it may often be the case that natural ecosystems are not saturated with species and structured primarily by competition, but instead communities are unsaturated and structured also by stochastic influences (Cornell and Lawton, 1992). Consistent with this, in some ecological systems there is no evidence for invasion resistance (Cornell, 1999; Blackburn and Duncan, 2001) or species saturation (Shea and Chesson, 2002; Friedley et al., 2007; Sax et al., 2007), and there are even examples of positive correlations between local abundance of invasive species and the diversity or abundance of natives (e.g. Davies et al., 2005; Altieri et al., 2010; Bonter et al., 2010).

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Nonequilibrium conditions may characterize most communities, meaning that niche space is not saturated and thus invasive species may establish interrelationships with the biotic and abiotic environment that are vacant (Rohde, 2005). Within this reasoning invasive species may be established without detrimental ecological effects. A way to assess whether biological invasions involve competition with natives is to compare the ecological niches of invasive and native species in the invasion range, since increased niche similarity can indicate occurrence of interspecific competition (Cornell and Lawton, 1992; Schoener, 1982). If communities are saturated, native species would have been shaped to partition niche space efficiently, and an invasive species could only establish by using a niche similar to an existing native species, thus competing for resources. In the other extreme case, if communities are unsaturated, exotic species may successfully invade by occupying vacant ecological niches, and detrimental ecological effects would be less likely.

To assess those scenarios, we compared the ecology of a very successful invasive bird species, the common waxbill (*Estrilda astrild*), with the native community of passerines it encountered in the ongoing invasion of SW Europe. The common waxbill is a small granivorous passerine in the Estrildidae family, native to sub-Saharan Africa. It has been widely transported by humans and introduced to several parts of the world (Stiels et al., 2011). In Europe, the largest invasion by common waxbills started in the 1960s with introductions at several locations near the Portuguese coastline; the species now covers practically the entire territory of Portugal with suitable habitat, and also adjacent parts of Spain (Reino and Silva, 1998; Sullivan et al., 2012). Common waxbills were mostly associated with wetland edges in the early stages of the invasion, and expanded into other types of habitat, including irrigated farmland and riparian areas (Reino and Silva, 1998).

To evaluate the potential for competition by invading waxbills, we characterized multiple ecological traits of common waxbills and sympatric native passerines in Portugal, and compared them in multidimensional niche space to estimate niche similarity among species. At the broad multi-species level of this analysis it is not feasible to estimate niche overlap (e.g. Poling and Hayslette, 2006; Brazill-Boast et al., 2010). Instead, we infer potentially detrimental competition between waxbills and natives from niche distances, using niche distances amongst native species as a control, representing ecologically stable communities. We also assessed co-occurrence of waxbills with native species based on ecological similarity or dissimilarity. If native communities do not possess vacant niches and waxbills invaded by being strong competitors, we expect that niche distances between the common waxbill and native species are inferior to the distances within the community of native species. In addition, spatial co-occurrence between common waxbills and ecologically similar species could potentiate competition. In contrast, if the common waxbill invasion used vacant niche space, we would expect that niche distances to common waxbills are larger than within the native community, and would not expect spatial co-occurrence of species based on ecological similarity.

2. Materials and methods

2.1. Ecological niche similarity

We collected information on various aspects of the ecological niche of the common waxbill and native passerines of Portugal, using literature and field data. We considered native resident or regularly breeding passerines from wetland, farmland or mixed habitats with open areas, which are the broad habitats of waxbills (Cramp and Perrins, 1994a; Reino and Silva, 1998), and did not include birds of other guilds (e.g. aerial birds such as swallows or swifts) or specialists of other types of habitat (e.g. forest birds such as treecreepers). Species larger than 30 g were also not considered, as competition between waxbills (7–8 g) and much larger birds is implausible. Appendix Table A.1 lists the 26 species that met these criteria.

Ecological traits included information on habitat, time of breeding, nesting and foraging preferences, size, diet, and bill shape, in a total of 15 variables. Literature-based information was collected from The Complete Birds of the Western Palearctic (Cramp, 1988, 1992; Cramp and Perrins, 1993, 1994a, 1994b) and complemented with information from Catry et al. (2010), when the former was insufficient in detail, or did not contain data relative to the Iberian Peninsula. Data from the Iberian Peninsula were preferentially used, since some ecological traits, such as time of breeding, can differ between the southern and northern latitudes of the Western Palearctic (Cramp, 1988, 1992; Cramp and Perrins, 1993, 1994a, 1994b). In addition to this, we used morphological measurements from passerines captured in mist-nets at places where common waxbills had been observed, throughout the invasion range (Fig. 1). The ecological traits are summarized in Table 1. Their detailed descriptions are given in Appendix A, and the values for each species are in the Appendix Table A.1.

We used two methods to compare the ecological niche of common waxbills and the other species in multidimensional space. In the first approach we used Non-metric Multidimensional Scaling

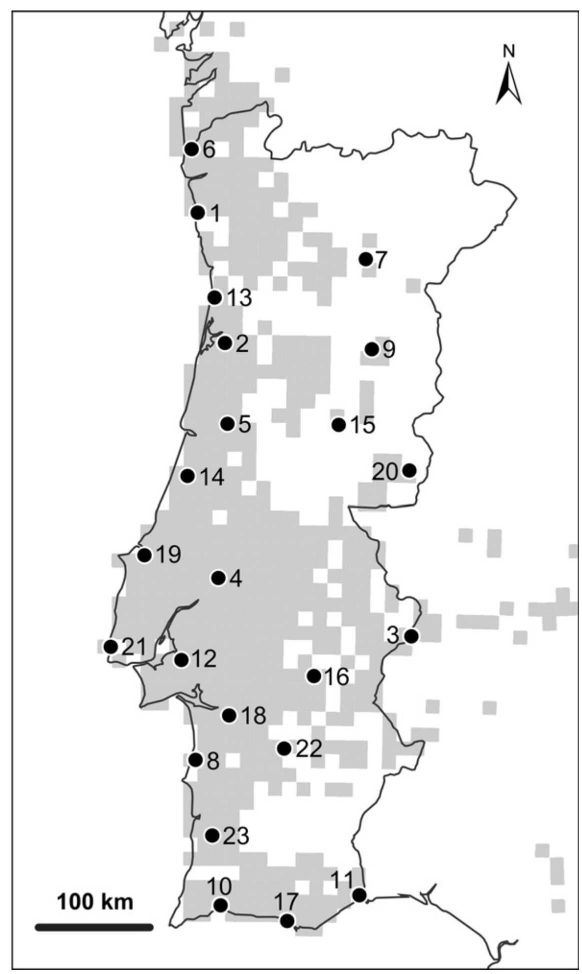

Fig. 1. Distribution of common waxbills in the western Iberian Peninsula (grey squares; data from Equipa Atlas, 2008; Rodríguez, 2003), and location of the 23 study sites (black dots) with numbers indicating visit order.