RESEARCH LETTER

Evidence for non-uniform dispersal in the biological invasions of two naturalized North American bird species

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ABSTRACT

Most previous attempts to model the geographical range expansion of an invading species assume random dispersal of organisms through a homogeneous environment. These models result in a series of uniformly increasing circles radiating out from the centre of origin over time. Although these models often give reasonable fits to available data, they do not typically include mechanisms of dispersal. Alternatively, models that include assumptions of non-random dispersal and a heterogeneous environment inevitably result in an anisotropic or jagged invasion front. This front will include propagules of pioneer individuals for the expanding species. Existing data from biological invasions reveal that the spatial structure of an invading species usually exhibits these propagules. Using population data gathered from the past century, we investigated the propagules of two North American invading bird species: the European starling (*Sturnus vulgaris* Linnaeus), and the house finch (*Carpodacus mexicanus* Müller), and found a correlation between propagule location and habitat quality. These results suggest that dispersing individuals seek out favourable habitat and remain there, thus introducing a possible mechanism for explaining non-uniform dispersal during invasions. When combined with results from other studies, our results suggest that propagules provide starting points for future population expansion of an invading species.

Key words abundance, biological invasion, birds, dispersal, European starling, house finch, invasion front, models, North America, propagule.

INTRODUCTION

Understanding the spread of an exotic species remains one of the most difficult problems faced by conservation biology. Exotic species can have profound effects on the ecosystems they invade (Singer *et al.*, 1984; King, 1985; Vitousek, 1986, 1990; Mack & D'Antonio, 1998) and often compete with indigenous species for food and other resources (e.g. Kerpez & Smith, 1990). The majority of biological invaders in recent centuries have travelled through the conscious or unconscious assistance of humans, although there have been a few notable exceptions (e.g. cattle egret, *Bubulcus ibis* Linnaeus, Handtke & Mauersberger, 1977). In addition, human presence commonly alters disturbance patterns, which may favour the expansion and persistence of exotics (Dukes & Mooney, 1999). Once introduced, the future success of the exotic species is difficult to predict even if the natural history of the invader is known (Gilpin, 1990; Williamson & Fitter, 1996).

However, several biologists have attempted to model the invasion dynamics of successful exotic species (see Hengeveld, 1989 and numerous examples therein).

A biological invasion can be thought of as consisting of several phases (Brown & Lomolino, 1998; Maurer *et al.*, 2001). While not all organisms follow the pattern described below, the description represents a typical invasion sequence. The first phase is the establishment of a founding population, which is followed by a rapid expansion of the range boundary. When the species reaches a barrier to further dispersal, populations behind the invasion front continue to increase to a level of abundance that saturates the local habitat. After saturating available habitats within the new range boundary, population abundance levels off and fluctuates around a relatively constant mean abundance.

Previous attempts to model the expansion of an invading population have assumed that diffusion is a relatively continuous process occurring within a homogeneous environment (Skellam, 1951; Lubina & Levin, 1988; Van den Bosch *et al.*, 1992; Veit & Lewis, 1996; but see Hengeveld & Van den Bosch, 1997). These models assume further that individual animals move randomly with respect to one another and the

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environment. For example, Van den Bosch *et al.* (1992) assumed that the geographical range expansion of an invading species could be viewed as a series of uniformly increasing circles from a centre of origin in which the radius of the circle increases each year at a constant rate. The assumptions of random movement and homogeneous environment are straightforward and seem to give reasonable fits to the data. It is tempting to be content with the results.

The problem with accepting models that fit data well, when the underlying processes being modelled do not correspond well to model assumptions, is that one may be tempted to make predictions or statements about the process that are ultimately unverifiable. With respect to range expansions of exotic species, it is likely that environments are almost never homogeneous, particularly when viewed at larger spatial scales, such as across continents. In addition, we lack convincing evidence that random-dispersal models account for the mechanisms of geographical range expansion. If we are to understand more fully the underlying reasons for geographical range expansion, we must test hypotheses that explain biological invasions mechanistically.

The assumption that environments are heterogeneous rather than uniform seems to be an important component of the explanations of most ecological phenomena (e.g. Botkin, 1990). If species invading a new geographical region encounter heterogeneous rather than uniform ecological conditions, the range boundary should advance at different speeds in different directions. In other words, the invasion front for a species would not be isotropic. Furthermore, if individuals disperse in groups rather than independently, any anisotropic range expansion would be exaggerated. Is there any evidence that invasions of species are anisotropic?

Anisotrophy in the spatial pattern of range expansion may arise by different mechanisms in different populations. Individuals may disperse independently of one another but encounter different ecological conditions in different directions, and thus the invasion front would be jagged based on these ecological differences. Individuals may also disperse together in groups and colonize locations far ahead of the rest of the invasion front. Hengeveld (1994) referred to these as 'propagules' and suggested that they provided starting points for population expansion.

We examine the problem of range expansion by establishing the pattern of invasion of two species of birds introduced into the eastern United States during the past century: the European starling (*Sturnus vulgaris* Linnaeus) and the house finch (*Carpodacus mexicanus* Müller). In approximately 1890 a flock of starlings was released in New York City (Cabe, 1993), and in 1940 a small number of house finches was introduced on Long Island, New York (Elliot & Arbib, 1953). For both species, human dominance of the landscape created an environment favourable to the establishment and expansion of populations, and both spread rapidly across the continent in the ensuing decades. This is due probably to the fact that nesting and foraging requirements of both species complement human-altered habitat conditions remarkably well (European starling: Tinbergen, 1981; Feare, 1984; Cabe, 1993; house finch: Hill, 1993). Range expansion in these species is non-uniform and anisotropic in its spatial pattern (see figures and descriptions in Maurer *et al.*, 2001). We examine the nature of sites where propagules are first established, and attempt to determine why dispersing propagules choose particular sites in which to settle.

MATERIALS AND METHODS

To examine the spatial patterns of range spread in North America, we obtained data from the Christmas Bird Counts (CBC) programme on the abundance of European starlings and house finches. Additional information on the house finch spread is available from other sources, but we used CBC data because it records abundance over a period of time that covers both the invasion of European starlings and the more recent invasion of house finches. The manner of data collection presents some observational errors and biases (Maurer, 1994). Despite this, it is the best available continent-wide dataset covering the past century and it, along with similar surveys, has proved useful in numerous studies (e.g. Root, 1988; Brown & Maurer, 1989; Maurer, 1994; Flather & Sauer, 1996; James *et al.*, 1996; Villard & Maurer, 1996).

Maurer *et al.* (2001) demonstrated that range expansion for the starling is anisotropic, and showed that current starling abundances are higher in places with higher human population densities. In order to test for non-uniform dispersal in the pattern of range spread, we needed first to determine how to define propagules at the invasion front. In so doing, we defined the leading edge of an expanding geographical range as the boundaries of the largest minimum convex polygon enclosing CBC locations in which the species was present. Since Christmas Bird Count data are used, the range boundary thus represents the species' winter range. Winter geographical ranges for the house finch in eastern North America were larger than the preceding summer geographical ranges (unpublished data), likely because winter range boundaries were extended during fall dispersal. We expect the same is true for starlings, although we lack the data to map out their summer ranges.

After establishing range boundaries, propagules were defined as any CBC census that met one or more of the following three criteria: (1) any census location in a given year that expanded the leading edge of the geographical range more than 10%; (2) any census location in a given year that was located on the edge of the range and had a population count that exceeded the average count for all censuses that year; and (3) any census location in a given year that had a count greater than three standard deviations above the mean
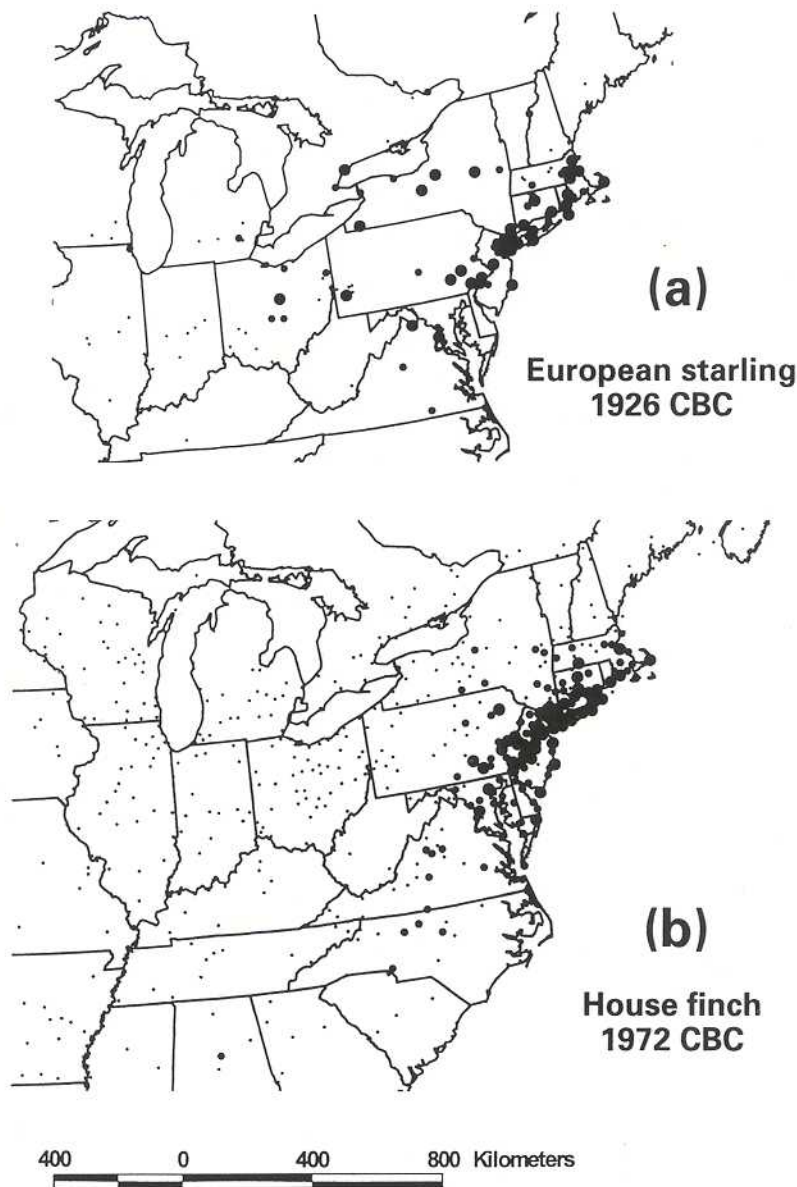
Fig. 1 Christmas bird counts for two species of birds during their biological invasion time period. The largest dots indicate high abundance at that location (> 50 birds), the next largest dots represent low abundance (50 or less), and the smallest dots indicate the absence of the species at that location. (a) 1972 CBC data for the house finch (*Carpodacus mexicanus* Müller). (b) 1926 CBC data for the European starling (*Sturnus vulgaris* Linnaeus). Notice the propagule location in Chicago, a site of future high abundance.

census count and was found nearer to the edge of the range than to the point of release (New York City). Using this definition, we systematically compiled a list of all propagule locations in different years for the European starling ($n = 29$) and house finch ($n = 33$). Figure 1 illustrates typical data from a year during which invasions were occurring for each species. Note that there are a number of localities where a significant number of birds were seen far in advance of the

invasion front. If such sites met our criteria listed above, we classified them as propagule locations. The most common criterion qualifying a location as a propagule was the first criterion (> 10% range extension, 22/29 in the starling and 30/33 in the finch). In addition, roughly half of the propagule locations for each species met more than one of the criteria listed above (13/29 in the starling and 17/33 in the house finch).

Given the set of propagule locations for the two species, it is necessary to show that these populations are a non-random set of the possible locations that the species could occupy. If propagules represent dispersing groups of individuals that locate favourable areas for future colonization, then the current abundance at a location that supported a propagule should be higher, on average, than at any randomly selected location. For the European starling, we obtained average current abundances for all CBC census locations on which the species was observed. We then ranked locations in order of their current abundance and assigned each location a percentile. For example, a location with a percentile of 0.87 means that the population abundance at that point is higher than 87% of all other census routes.

Since house finches are still in the process of spreading westward across North America (National Geographic Society, 1999) from their introduction in New York (Elliott & Arbib, 1953), their current abundance in eastern North America may not reflect their long-term abundance. Instead of determining current abundance, we assumed that locations with high human population densities will, on average, have more favourable conditions for establishment of house finch populations than locations with low human population densities. To test the validity of this assumption, we correlated data from native populations of house finches in western North America with data on human population densities. In the west, house finches are found in numerous undisturbed areas as well as in cities, while in the east house finches are found almost exclusively in settled areas (Hill, 1993). Thus the correlation between human density and house finch density in western North America would probably be lower than in the east. For the correlation, we selected randomly 96 counties in the western United States that contained a census from the North American Breeding Bird Survey (BBS), and calculated human population density from the US counties database in GIS ArcView (US Bureau of the Census, 1994). Average abundance of house finches for BBS censuses conducted between 1966 and 1998 located in these 96 counties were then correlated with human population density estimates. There was a significant positive correlation (Fig. 2, $P < 0.0001$), so we conclude that counties with high population densities in the eastern United States will provide more suitable habitat for colonization than counties with low human population densities. For each of the 33 CBC census locations identified as propagules, we obtained the percentile score for human population densities of the county containing that propagule.

In order to establish the degree of spatial autocorrelation in percentile scores, we estimated semivariance functions for each species (Maurer, 1994). Semivariance analysis for both species indicated that although there was evidence of spatial autocorrelation in percentile scores among propagule locations, it was lesser in magnitude than sampling variability among locations. This means that any statistically significant
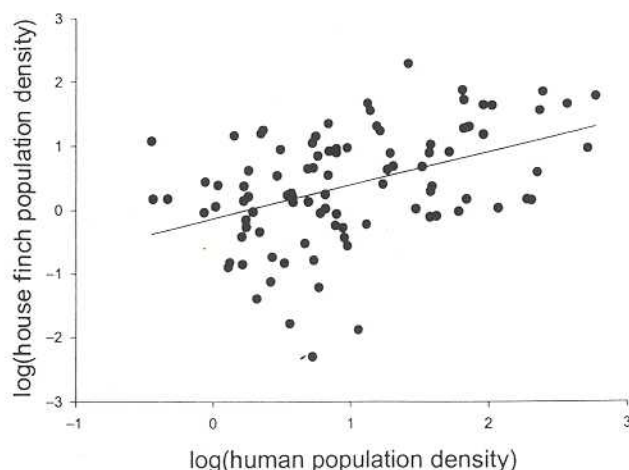

Fig. 2 Correlation between human density (individuals/km²) and house finch (*Carpodacus mexicanus* Müller) density (individuals/BBS route) for 96 randomly selected US counties ($P < 0.0001$, $R = 0.428$).

patterns in percentile scores cannot be attributed to spatial autocorrelation, since such patterns must exceed sampling variation. However, in order to be conservative, we used a rejection region for statistical tests of $P < 0.01$.

If propagule locations were random with respect to current abundance, then the frequency distribution of percentile score should be approximately uniform and symmetric about a percentile of 0.5. We tested this in two ways. First, we used a one-tailed binomial test to determine if abundance percentiles were symmetrically distributed around 0.5. The null hypothesis for this test was that the proportion of percentiles less than 0.5 was equal to $1/2$. Secondly, we used a one-sample Student's t-test to test the null hypothesis that the average arcsine of the square root of percentiles for each species was less than $arcsin [(0.5)^{1/2}]$ against the one-sided alternative that the average was greater than this value. One-sided tests are appropriate here since we expect a priori that propagule locations have higher abundances or habitat favourability than non-propagule locations.

RESULTS

Locations that were identified as receiving propagules of European starlings during the expansion of this species westward across North America now harbour populations significantly larger than the median population for the species (Fig. 3a). Only six of the 29 propagule sites for this species had abundance percentiles less than 0.5 (proportion of sites with percentiles < 0.5 = 0.21, $n = 29$, $P < 0.01$). Most propagule sites ranked considerably higher than the median abundance (average percentile = 0.70, average arcsin square root transformed percentile = 1.13, d.f. = 28, $t = 4.9$, SE = 0.05, $P < 0.01$).
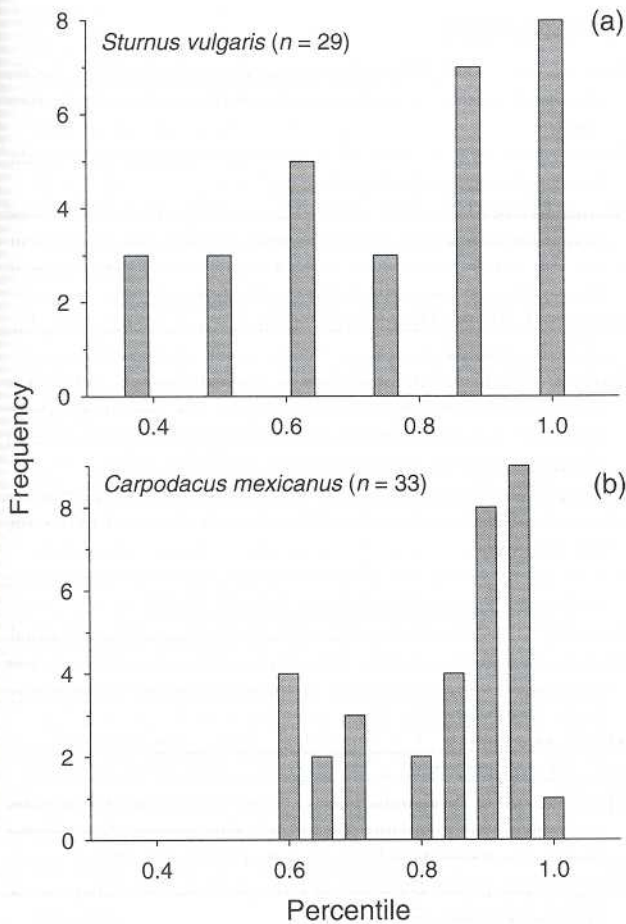
Fig. 3 Histograms showing the frequency distribution of percentile scores for human population densities for propagule locations. Higher percentile scores indicate better habitat. (a) European starling (*Sturnus vulgaris* Linnaeus). (b) House finch (*Carpodacus mexicanus* Müller).

Similarly, locations that were identified as receiving propagules of house finches during the current expansion of this species westward across North America have human populations significantly larger than the median population (Fig. 3b). Only a single propagule site had a human population percentile score less than 0.5 (proportion of sites with percentiles $< 0.05 = 0.03$, $n = 33$, $P < 0.01$). Most propagule sites for house finches ranked considerably higher than the median human abundance percentile (average percentile = 0.81, average arcsin square root transformed percentile = 1.14, d.f. = 32, $t = 11.6$, SE = 0.03, $P < 0.01$).

We conclude, therefore, that locations receiving propagules during the range expansion of these two species provided significantly better ecological conditions for the establishment and subsequent maintenance of persistent populations than sites not receiving propagules. Thus, the spread of these

species in North America was neither uniform nor random. Rather, population expansion followed a consistent pattern of propagules establishing themselves in locations that provided better than average ecological conditions.

DISCUSSION

We have shown that for the biological invasions of the European starling and house finch, contrary to an assumption made by most models (e.g. Skellam, 1951; Van den Bosch *et al.*, 1992), invasion fronts did not progress uniformly or randomly. Instead, propagules of individuals moved out ahead of the rest of the invasion front into isolated habitats. We have demonstrated a significant correlation between propagule location and habitat quality, which suggests that dispersing propagule populations seek out favourable habitat and settle there rather than dispersing randomly.

The sceptic will point out that two of our criteria used in determining whether a location qualified as a propagule dealt with its abundance at the time of expansion (see criteria two and three in materials and methods section above). If the expanding species maintained high abundance simply due to early arrival at that site rather than excellent habitat quality, then current abundance at that site would simply be an artifact of the way we classified our propagules. Although we doubt that areas of poor habitat would continue to sustain high abundances in subsequent decades, we tested the potential problem by performing the same analyses as above using the propagules classified only according to the first criterion (i.e. > 10% range extension, abundance at the time of expansion not greater than average). Results show the same pattern as before, although insufficient sample sizes in the European starling prevented the achievement of statistical significance. For the starling 10 of 12 propagules classified according to criterion one alone have higher than average abundance ($P = 0.019$), and the average current abundance percentile is higher than 0.5 (average percentile = 0.69, $P = 0.028$). For the house finch, 14 of 15 propagules have higher than average abundance ($P < 0.01$), and the average current abundance percentile is significantly higher than 0.5 (average percentile = 0.83, $P < 0.01$). Thus, the correlation between propagule location and habitat quality stands even if we use only the range expansion criterion (i.e. criterion one) to classify propagules.

An alternative interpretation to this correlation is that 'choice' is not involved at all. Rather, birds dispersed more or less randomly to sites, and then differentially survived based on differences in habitat quality. However, we doubt that this is the case. First of all, it makes intuitive sense that if a particular habitat did not meet the needs of dispersing birds, the bird(s) would disperse elsewhere due to their highly mobile nature (Cody, 1985). In addition, direct experimental evidence of site choice in birds has been found in pied flycatchers

(*Ficedula hypoleuca* Pallas, Lundberg *et al.*, 1981) and prothonotary warblers (*Protonotaria citrea* Boddaert, Petit & Petit, 1996); and indirect evidence for site choice has been found in willow ptarmigan (*Lagopus lagopus* Linnaeus, Moss, 1972), yellow-headed blackbirds (*Agelaius phoeniceus* Linnaeus, Orians & Wittenberger, 1991), collared flycatchers (*Ficedula albicollis* Temminck, Doligez *et al.*, 1999), green woodpeckers (*Picus viridis* Linnaeus, Rolstad *et al.*, 2000) and sage sparrows (*Amphispiza belli* Cassin, Misenhelter & Rotenberry, 2000). We feel that it is most probable that the dispersing propagules of starlings and finches we studied indeed 'chose' their destination.

Although dispersing individuals and populations generally choose to settle in better than average habitat, it is not an entirely deterministic process; there is still some uncertainty about the quality of habitat that propagule populations will settle in. We suspect that different taxa would have varying levels of randomness in the habitat quality of their dispersal destinations based on their life history characteristics and differences in dispersing mobility (Williamson & Fitter, 1996). For example, the invasion front for a biological invasion by a dandelion would be expected to advance more randomly than a grey wolf invasion front.

In addition, Maurer *et al.* (2001) show that populations on the edges of invasion fronts have higher than average per capita rates of increase. We suspect that an invading species uses propagule locations to establish fast-growing source populations (Grinnell, 1922; Shmida & Wilson, 1985; Pulliam, 1988) from which to build up total numbers and to establish new populations in the nearby surrounding areas. The fact that propagule locations lie typically in excellent habitat supports this idea of a source population in embryo. Future investigations may reveal if this idea is indeed true. If propagules established by an invading species are shown to burgeon into source populations, we can then make reasonably accurate predictions about the future population dynamics of propagules for a species undergoing geographical range expansion. This information would especially be useful for scientists studying the dynamics of expanding, undesirable exotic species.

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BIOSKETCHES

David E. Gammon completed this research while working as an undergraduate with his adviser, Brian A. Maurer. Since then, he has taken a drastic shift in his research focus; he currently studies bird vocalizations under the tutelage of Myron C. Baker. However, in the future he is interested in using macroecological methods to compare the vocalizations of multiple bird taxa.

Brian A. Maurer is an Associate Professor in the Department of Fisheries and Wildlife, with a joint appointment in the Department of Geography, at Michigan State University. His research interests include theoretical and applied ecology, conservation biology and macroecology. He has authored two books on geographical scale ecology and serves on editorial boards for several journals in the ecological sciences.