Article

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Shifts in Winter Distribution in Birds: Effects of Global Warming and Local Habitat Change

As global warming intensified toward the end of the 20th century, there was a northward shift in winter ranges of bird species in Cape Cod, Massachusetts, USA. These pole-ward shifts were correlated to local increases in minimum winter temperatures and global temperature anomalies. This evidence, plus other recent results, suggests that during the last two decades global warming has led to massive and widespread biogeographic shifts with potentially major ecological and human consequences. Local habitat changes associated with urban sprawl affected mainly forest birds with more northern winter distributions. In Cape Cod, the effects of warming on bird distributions are more substantial at the start of the 21st century, than those of habitat alteration, but as urban sprawl continues its importance may rival that of global warming.

INTRODUCTION

It has become evident that much of the surface of the globe has become human-dominated (1). Major agents of ecological change include atmospheric warming at global spatial scales (2, 3), and extensive but local-scale conversion of natural habitats to land covers such as suburban sprawl (4-6). The evidence for such global and local-scale changes is compelling, raising the question whether these changes are sufficient to affect organisms (7, 8), and whether globally-driven changes can overwhelm local changes from other sources (9-11). In this paper, we use long-term bird censuses to evaluate the relative effects of globally-driven increases in winter temperatures, and of local changes in habitats, on assemblages of birds overwintering on Cape Cod, Massachusetts, USA.

METHODS

The Cape Cod Christmas Bird Count of overwintering birds, currently run under the sponsorship of the National Audubon Society, spans a relatively long period (70 years). This count is the oldest of the censuses that are done every December within 15-mile diameter geographical areas throughout the Commonwealth of Massachusetts. For many of the initial years the census in the Cape Cod circle (Fig. 1, inset map) were directed by Dr. L. Griscom of Harvard University, one of the founders of American ornithology. His successors in managing and performing the counts include some of the elite within the Massachusetts birding community. The well-honed identification ability of these skilled observers guarantees that species counts are a robust aspect of these censuses. The censuses also report numbers of each species, but these values are not as consistently taken as the species identification.

To evaluate the relative effect of global warming trends, we hypothesized, based on previous results, that the winter distribution ranges may be controlled by the cold extremes of temperature regimes (12, 13). Thus, we obtained data on the mean minimum temperature that occurred annually from October to February from the National Weather Service (http://www.nws.noaa.gov/information_center.html). If warming was biologically meaningful we would find that southern species sensitive to cold winters would extend their winter-range pole-ward during the warming period, and that species with more northern ranges might be able to survive winter farther north. The net result would be a shift in the ratio of southern to northern species. To assess this possibility, we used maps of winter geographical range (14, 15) for each bird species recorded in the censuses. We examined the range between northern and southern extremes of the distribution relative to Cape Cod, and classified each species as of northern or southern winter distribution depending on whether the wintering range was mostly north or south of Cape Cod.

Across the decades, the Christmas Bird Counts have included different numbers of observers and kilometers driven and walked, differed in distances traveled by boat, and changes in routes taken within the count circles; for example, counts during World War II (1941-1945) were significantly undermanned. Normalizing for all these variables would yield data that were, in our view, too distant from real bird species numbers. Instead, we compensated for such methodological differences by focusing on internal comparisons within the data sets, such as the number of species with southern winter distribution (S) relative to the number of northern species (N), rather than on total numbers of species. Increases in S/N would suggest that overwintering ranges have extended northward. This would be evidence that climate-related changes were making it possible for species to survive winters at more northerly latitudes than in previous decades.

There is an additional feature that simultaneously complicates the interpretation of the census data, but also makes for a more interesting comparison. In Cape Cod, as in virtually all the shorelines of the world, there have been remarkable changes in land use during recent decades (6, 16, 17). In the first half of the 1900s, the Cape Cod area recovered its forested cover from the near complete pasture it was during the mid 1800s. During the second half of the 20th century, the landscape of Cape Cod, as elsewhere, has undergone a marked shift away from forests and agriculture to urban land uses (Fig. 1, 16-18). Thus, within the Christmas Count census circles urbanization has reduced forested area, increased edge habitats associated with residential land-use habitats and natural and man-made turf and agricultural land covers, but left aquatic and grassland areas largely unchanged (Fig. 1, inset graph). These changes in land covers mean that the assemblage of overwintering birds – particularly those species preferring forest and edge habitats – might not only be responding to global-scale temperature-related changes, but also to local changes in the mosaic of habitats they find available for winter use (19).

To assess the relative effects of local changes in habitats for overwintering birds, *vis a vis* the global climate-related changes, we compared the number of southern and northern species of birds that prefer habitats (aquatic, grasslands) that

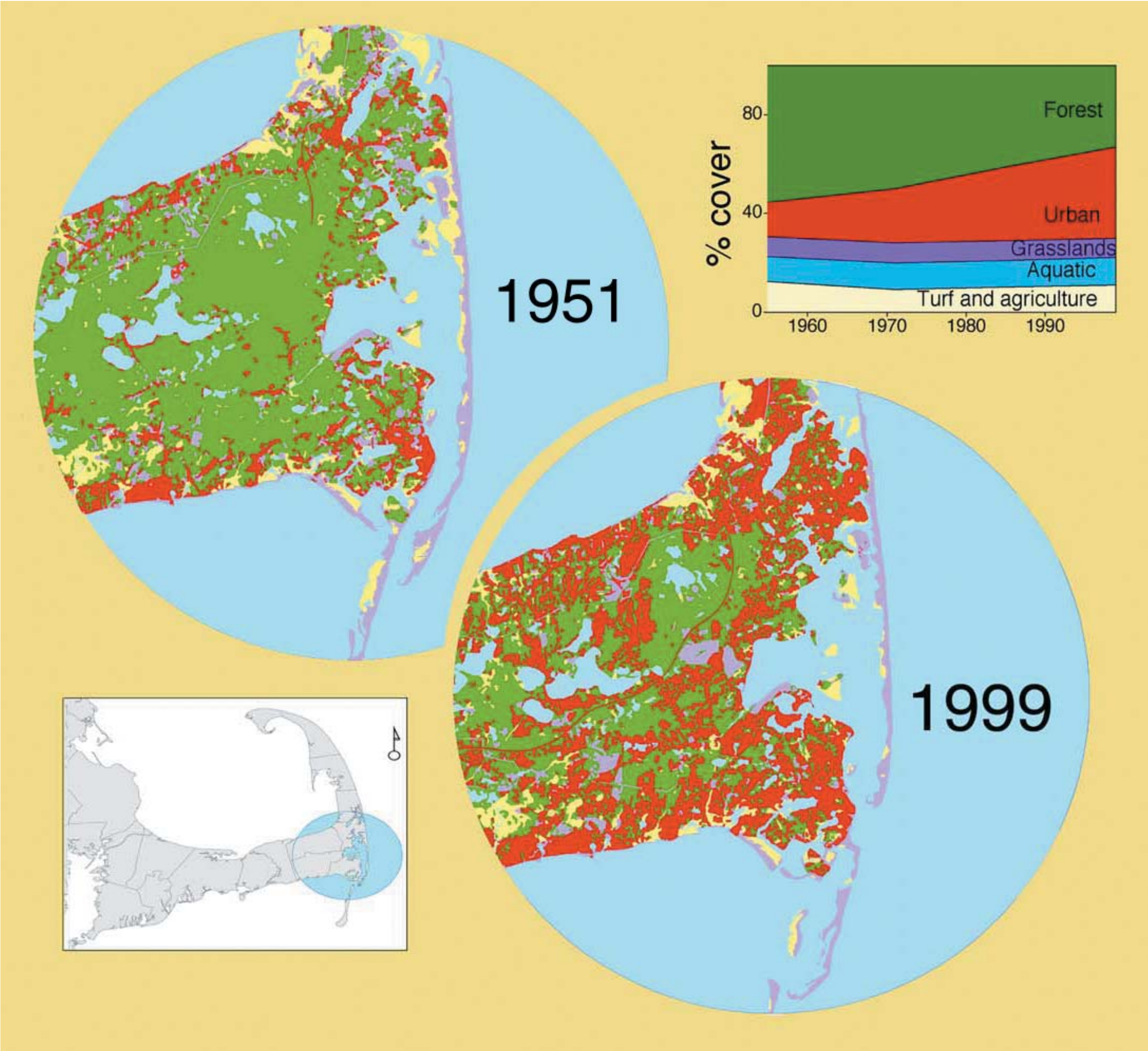

Figure 1. Changes in land-cover type, 1951 and 1999 (maps in circles), on the Christmas Census Circle. Color code: green = forest, red = urban, purple = grasslands, blue = aquatic, and yellow = turf and agriculture. Cartography for the maps and data by T. Stone and G. Fiske of the Woods Hole Research Center, Woods Hole, MA, from data provided by MassGIS. The location of the Cape Cod circle within Cape Cod is shown in the inset on lower left. The % of the area within the circle covered by each land-cover type (data available from 1951, 1971, 1985, and 1999), is shown in the inset on upper right.

did not change in recent decades, with birds that preferred habitats (forests, edge) whose areas changed significantly (Fig. 1, inset). To carry out this comparison, we used our own field experience, as well as Peterson (14) and Sibley (15) to assign each species found in the censuses into groups with given habitat preferences: edge (including shrub-woodlands, suburban developments, parklands), grassland (including wetlands, dunes, old fields), forest, and aquatic (including ponds, lakes, estuaries, and open sea) (Table 1). These classifications are certainly over-simple, but do provide general guidelines while being few enough that there were enough species in each category for meaningful patterns to emerge. In a minority of cases, species habitat preferences – for example, edge *versus* forest – were not clear cut; in such instances we applied our field experience to assign the species to one habitat or another. We would conclude that changes in habitat significantly alter distributions if changes in the number of overwintering species that prefer a specific habitat parallel changes in the area of that habitat.

RESULTS AND DISCUSSION

The number of bird species found in the Cape Cod census increased from the 1930s through the century (Fig. 2A). Some of the increase must be a result of changes in observation procedures, some might be owing to global atmospheric changes, and some to local habitat changes. There were always more species with southern winter distributions, probably simply a reflection of greater species richness at lower latitudes (Fig. 2A).

To sort out effects of climatic warming from effects of differences in census procedures, we used the internal comparison, calculating numbers of species with southern distributions relative to those with northern distribution for each year of the record (S/N, Fig. 2B). S/N varied from 1930 to about 1970; after 1970 there was a clear increase in S/N, from about 2.5 to 5 (Fig. 2B).

Bird assemblages found during any one winter at a site are likely to be affected by local as well as by global temperature regimes, since species need to survive at a local site, but many species do migrate across a broad latitudinal range from south and

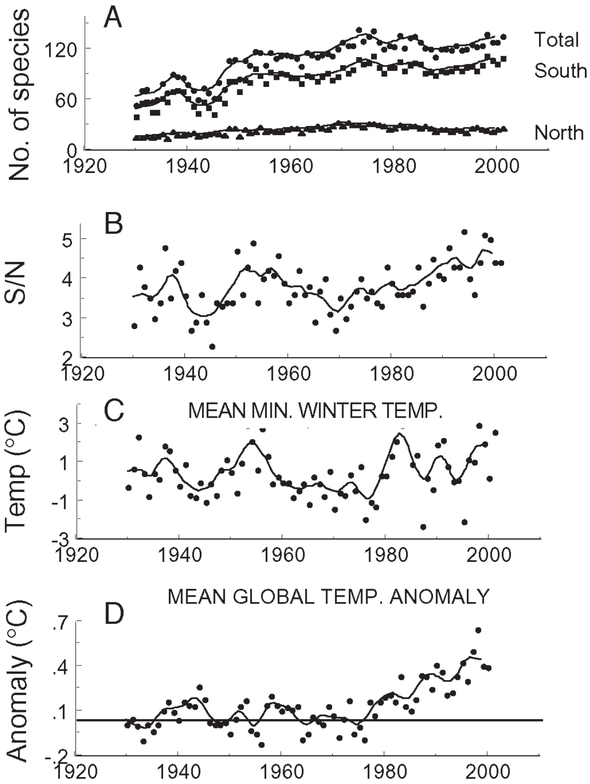

Figure 2. A: Time course of the total number of wintering bird species, and number of species with southern and northern winter distributions (relative to the latitude of Cape Cod), recorded in the Cape Cod Christmas Count survey from 1930 to 2001. Points represent each year, trends are lowest fits calculated with a decadal tension. Data for this figure compiled from the National Audubon Society (http://www.audubon.org/bird/cbc/).
B: Ratio of number of bird species with southern distributions to those with northern distributions in the Cape Cod Christmas Counts, 1930-2001. Points represent each year, trends are lowest fits calculated with a decadal tension.
C: Mean minimum winter temperature recorded in Provincetown, Cape Cod, Massachusetts, 1930-2001. This Cape Cod site is 45 km from the Cape Cod Christmas Count circle.
D: Mean global temperature anomaly, calculated as the difference between a year's mean global temperature relative to the mean for all years in the record. Data from the National Climate Center, NESDIS, National Oceanic and Atmospheric Administration.

central North America (7). Accordingly, we compared the time course of S/N to contemporaneous changes in local (Fig. 2C) and global (Fig. 2D) temperature regimes. Local mean minimum winter temperatures were highly variable, but there was a suggestion that in the last two decades of the 20th century, local temperatures were not as cold as earlier in the century. This warming trend was much clearer in the global temperature anomalies (Fig. 2D).

The ratio of southern to northern species in the Cape Cod censuses was well-correlated to local and global temperature regimes (Fig. 3A). Increases in local mean minimum winter temperatures during 1930-1990 were accompanied by increases in S/N (Fig. 3). The ratio also increased during the 1990s, with a similar slope, but that relationship was offset upwards. The upwards offset is unexplained, but may be related to recent short-term but large-scale regional warming, allowing significantly more species from additional southern areas to move northward. S/N also responded to global temperature anomalies (Fig. 3B). During decades when the anomaly remained low (< 0.1°C, 1930-1970), the ratio varied with no evident pattern; after the onset of heat forcing following the 1970s (global temperature anomalies > 0.1°C), the values of the ratio emerge from the cluster of points, and clearly increase as global-scale forcing increased the temperature anomaly (Fig. 3B). These results suggest that local amelioration of winters, as well as global-scale warming, have been followed by clear shifts in the winter avifauna of Cape Cod, with southern species becoming relatively more common, and northern species less so. This is consistent with the notion (20-22) that as the world warms, we will find a poleward shift of species ranges.

The number of southern and northern species associated with aquatic, edge, grassland, and forest habitats changed across the decades (Fig. 4). The number of species with southern affinities increased across all habitat preferences, presumably largely as a result of global warming. The increases in southern species among habitat types were not contemporaneous, suggesting the influence of other unidentified mechanisms (Fig. 4). Changes in the number of southern species, however, seemed unrelated to changes in local habitats, since the increase took place even in the case of aquatic species whose preferred habitats did not change materially in area. The number of northern species increased somewhat from 1920-1970, and decreased after the 1970s. Forest birds increased up to the 1970s, perhaps a reflection of the recovery of forests from earlier pastureland, but the post-1970 decrease was particularly evident in the case of forest-dwelling birds (Fig. 4). Surprisingly, the edge species showed increases similar to those affecting species preferring other habitats, even though urbanized areas have increased significantly, forming more edge habitat (Fig. 1). Thus the comparisons across habitats suggest that the local land-cover changes (for example, loss of about 20% of forest area (Fig. 1, inset) may have mainly affected northern forest-loving species after the 1970s.

On the whole, the pattern across the decades of the 20th century suggests that the numbers of species preferring different habitats showed similar time courses, with changes more closely linked to warmer temperature anomalies (Fig. 3) than to changes in areas of the different habitats (Fig. 4), except for northern species associated with forest habitats. Even though the landscape of Cape Cod has changed materially during the 20th century (Fig. 1), the resulting habitat changes on Cape Cod seem not to have been large enough as yet to match the larger impact of global warming trends, at least insofar as the composition of the overall wintering avifauna is concerned (23). Of course, greater urban sprawl will have proportionately larger effects, and at some point may have effects that match or even overwhelm those of global warming.

The results of this report make evident that temperature-related forcing, as well as local changes in habitat distribution created by urban sprawl, have altered the composition of winter bird assemblages on Cape Cod. While this report was in review, Parmesan and Yohe (24) published evidence that although local influences were important, a globally-coherent fingerprint of northward shifts in distributions for 219 species of a remarkably widespread range of organisms. Similar changes were reported for other organisms (20-22, 24-26). Our data, and these recent results, inevitably lead to the conclusion that we might be witnessing a phenomenon that is affecting not only birds, but a wide variety of other organisms – viruses, bacteria, invertebrates, fish, agricultural crop species, and many other taxa. If this pattern is general, we might expect to find a massive poleward shift of species across the world. These results suggest that we might be in the midst of massive global-scale biological changes, changes that are not only relevant to those interested in species distributions, but could have major consequences for many other aspects, including fisheries, agriculture, and public health.

Table 1. Species of birds identified in the Cape Cod Christmas Bird Counts (1930-2001), with our assignation as to geographical winter ranges with southern (S) and northern (N) affinities, and habitat preferences (A: aquatic, E: edge, W: woods, and G: grassland). Scientific names for the species can be found in Sibley (15).

Species	Geographical affinity	Habitat preference	Species	Geographical affinity	Habitat preference	Species	Geographical affinity	Habitat preference
Common Loon	N	A	Purple Sandpiper	N	A	Carolina Wren	S	E
Pacific/Arctic Loon	S	A	Red Knot	S	A	Marsh Wren	S	G
Red-throated Loon	S	A	Dunlin	S	A	Sedge Wren	S	G
Red-necked Grebe	N	A	Sanderling	S	A	Golden-crowned Kinglet	S	W
Horned Grebe	S	A	Semipalmated Sandpiper	S	A	Ruby-crowned Kinglet	S	W
Pied-billed Grebe	S	A	Western Sandpiper	S	A	Blue-gray Gnatcatcher	S	E
Northern Fulmar	N	A	Least Sandpiper	S	A	Eastern Bluebird	S	E
Sooty Shearwater	N	A	Pomarine Jaeger	S	A	Hermit Thrush	S	W
Cory's Shearwater	N	A	Parasitic Jaeger	S	A	American Robin	S	E
Greater Shearwater	S	A	Long-tailed Jaeger	N	A	Loggerhead Shrike	S	E
Leach's Storm-Petrel	N	A	Laughing Gull	S	A	Northern Shrike	N	E
Northern Gannet	S	A	Bonaparte's Gull	S	A	Gray Catbird	S	E
Great Cormorant	N	A	Common Black-headed Gull	N	A	Northern Mockingbird	S	E
Double-crested Cormorant	S	A	Ring-billed Gull	S	A	Brown Thrasher	S	E
American Bittern	S	G	Herring Gull	S	A	Water Pipit	S	G
Black-crowned Night-Heron	S	A	Glaucous Gull	N	A	Bohemian Waxwing	N	W
Yellow-crowned Night-Heron	S	A	Iceland Gull	N	A	Cedar Waxwing	N	E
Green-backed Heron	S	A	Lesser Black-backed Gull	S	A	European Starling	S	E
Little Blue Heron	S	A	Great Black-backed Gull	N	A	Orange-crowned Warbler	S	E
Snowy Egret	S	A	Black-legged Kittiwake	N	A	Nashville Warbler	S	E
Great Egret	S	A	Common Tern	S	A	Black-and-White Warbler	S	W
Great Blue Heron	S	A	Razorbill	N	A	Cape May Warbler	S	E
Mute Swan	S	A	Common Murre	N	A	Yellow-rumped Warbler	S	E
Snow Goose	S	A	Thick-billed Murre	N	A	Yellow-throated Warbler	S	W
Canada Goose	S	A	Dovekie	N	A	Prairie Warbler	S	E
Brant	S	A	Black Guillemot	N	A	Blackpoll Warbler	S	W
Mallard	S	A	Atlantic Puffin	N	A	Pine Warbler	S	W
American Black Duck	S	A	Turkey Vulture	S	E	Palm Warbler	S	E
Gadwall	S	A	Bald Eagle	S	A	Ovenbird	S	W
Green-winged Teal	S	A	Northern Harrier	S	W	Northern Waterthrush	S	W
American Wigeon	S	A	Sharp-shinned Hawk	S	E	Common Yellowthroat	S	E
Northern Pintail	S	A	Cooper's Hawk	S	W	Yellow-breasted Chat	S	E
Northern Shoveler	S	A	Northern Goshawk	N	W	Rose-breasted Grosbeak	N	W
Blue-winged Teal	S	A	Red-shouldered Hawk	S	W	Northern Cardinal	S	E
Ruddy Duck	S	A	Red-tailed Hawk	S	E	Painted Bunting	S	E
Wood Duck	S	A	Rough-legged Hawk	N	G	Rufous-sided Towhee	S	E
Canvasback	S	A	American Kestrel	S	E	Grasshopper Sparrow	S	G
Redhead	S	A	Merlin	S	E	LeConte's Sparrow	S	G
Ring-necked Duck	S	A	Peregrine Falcon	S	G	Sharp-tailed Sparrow	S	A
Greater Scaup	N	A	Gyrfalcon	N	G	Seaside Sparrow	S	G
Lesser Scaup	S	A	Ruffed grouse	N	W	Vesper Sparrow	S	G
King Eider	N	A	Northern Bobwhite	S	E	Savannah Sparrow	S	G
Common Eider	N	A	Ring-necked Pheasant	N	E	Song Sparrow	S	E
Black Scoter	N	A	Rock Dove	S	E	American Tree Sparrow	S	E
White-winged Scoter	N	A	Mourning Dove	S	E	Field Sparrow	S	E
Surf Scoter	N	A	Common Barn Owl	S	E	Chipping Sparrow	S	E
Harlequin Duck	N	A	Short-eared Owl	S	G	Dark-eyed Junco	S	E
Oldsquaw	N	A	Long-eared Owl	S	E	White-throated Sparrow	S	E
Barrow's Goldeneye	N	A	Great Horned Owl	S	W	White-crowned Sparrow	S	E
Common Goldeneye	S	A	Barred Owl	S	W	Fox Sparrow	S	E
Bufflehead	S	A	Snowy Owl	N	G	Lincoln's Sparrow	S	G
Common Merganser	S	A	Eastern Screech-Owl	S	W	Swamp Sparrow	S	G
Red-breasted Merganser	S	A	Northern Saw-whet Owl	N	W	"Ipswich" Sparrow	S	G
Hooded Merganser	S	A	Belted Kingfisher	S	A	Lapland Longspur	N	G
King Rail	S	G	Red-bellied Woodpecker	S	E	Snow Bunting	N	G
Clapper Rail	S	G	Northern Flicker	S	E	Eastern Meadowlark	S	G
Virginia Rail	S	G	Red-headed Woodpecker	S	E	Red-winged Blackbird	S	G
Sora	S	G	Yellow-bellied Sapsucker	S	W	Rusty Blackbird	S	E
Yellow Rail	S	G	Downy Woodpecker	S	E	Brown-headed Cowbird	S	E
American Coot	S	A	Hairy Woodpecker	S	W	Common Grackle	S	E
American Oystercatcher	S	A	Western Kingbird	S	E	Northern Oriole	S	E
Semipalmated Plover	S	A	Eastern Phoebe	S	E	Baltimore Oriole	S	E
Piping Plover	S	A	Horned Lark	S	G	House Sparrow	S	E
Black-bellied Plover	S	A	Tree Swallow	S	E	Pine Siskin	N	W
Killdeer	S	G	Blue Jay	S	E	American Goldfinch	S	E
Marbled Godwit	S	A	American Crow	S	E	Red Crossbill	N	W
Willet	S	A	Tufted Titmouse	S	E	White-winged Crossbill	N	W
Greater Yellowlegs	S	A	Black-capped Chickadee	N	E	Pine Grosbeak	N	W
Lesser Yellowlegs	S	A	Boreal Chickadee	N	W	Common Redpoll	N	E
Red Phalarope	S	A	Brown Creeper	S	W	Purple Finch	S	E
Long-billed Dowitcher	S	A	White-breasted Nuthatch	S	E	House Finch	N	E
Common Snipe	S	G	Red-breasted Nuthatch	S	W	Evening Grosbeak	N	W
American Woodcock	S	E	House Wren	S	E			
Ruddy Turnstone	S	A	Winter Wren	S	W			

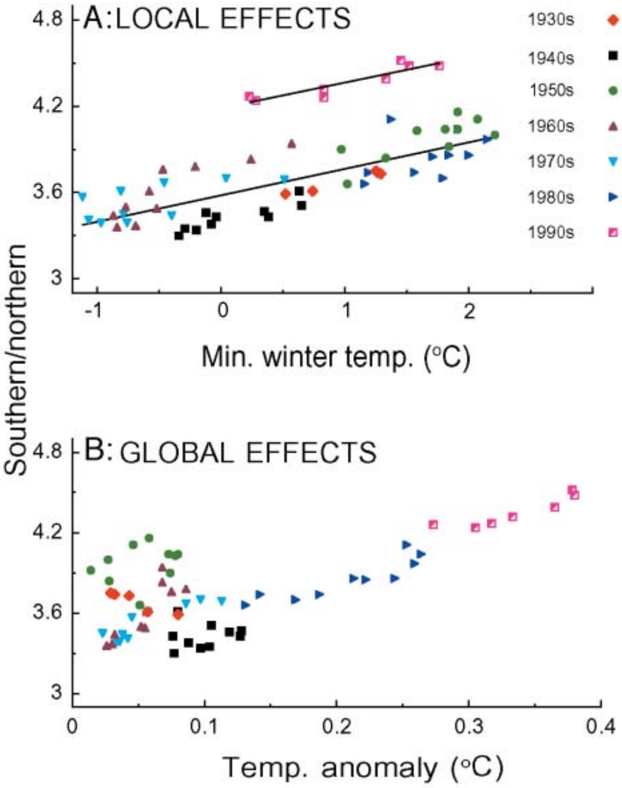

Figure 3. Ratio of number of bird species with southern to northern winter distributions in the Cape Cod Christmas Counts (Fig. 2B), plotted *versus* mean winter temperatures (Fig. 2C) to examine effects of local temperature changes (Fig 2A), and *versus* global temperature anomalies (Fig. 2D), to assess effects of global temperature changes (bottom panel). Regressions for top panel are $y = 0.18x - 2.29$, $F = 98.3^{**}$, $R^2 = 0.65$, for 1930-1980 and $y = 0.18x - 1.5$, $F = 28.9^{**}$, $R^2 = 0.83$ for 1990s.

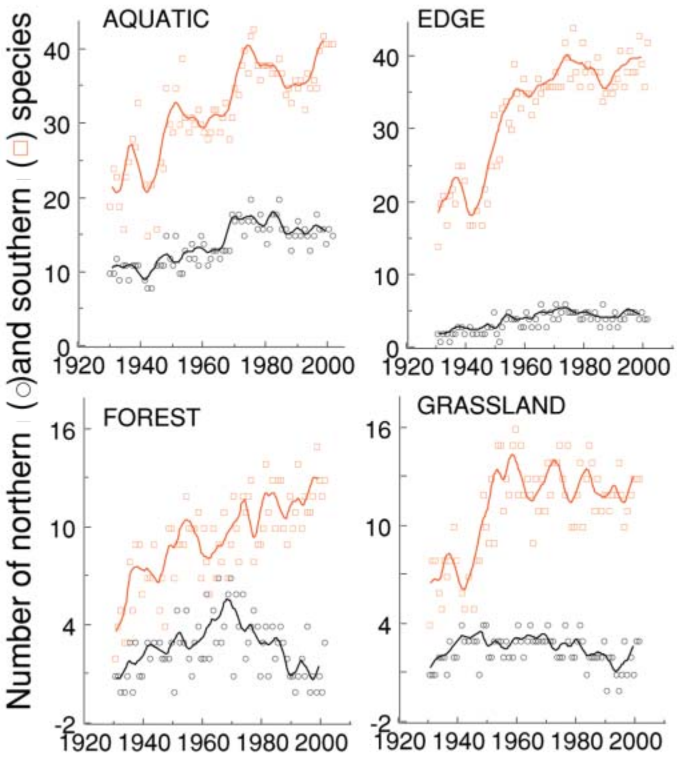

Figure 4. Time course of the number of bird species preferring aquatic (ponds, lakes, estuaries, open ocean), edge (shrub-woodlands, suburban residential areas, parklands), forest, and grassland (wetlands, dunes, old fields) habitats in the Cape Cod Christmas Counts, 1930-2001. The number of species with southern and northern winter ranges are shown to allow internal comparisons within the counts. Points represent each year, trends are lowest fits calculated with a decadal tension.

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23. The scope of work reported here could be readily enlarged by examination of censuses recorded from different latitudes, such as Maine to Florida, to see if the species shifts demonstrated by the Cape Cod data are seen latitudinally, and comparing coastal *versus* continental sites. This extensive examination would also test the robustness of the links of global and local forcing to the biological effects.

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