

Old-Growth Forests Can Accumulate Carbon in Soils

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Old-growth forests have traditionally been considered negligible as carbon sinks because carbon uptake has been thought to be balanced by respiration (1). We show that soils in the top 20-cm soil layer in preserved old-growth forests in southern China accumulated atmospheric carbon at an unexpectedly high rate from 1979 to 2003. This phenomenon indicates the need for future research on the complex responses and adaptation of belowground processes to global environmental change.

Understanding the locations and driving forces of carbon sources and sinks at plot-to-global scales is critical for the prediction and management of the global carbon cycle and ultimately the behavior of the Earth's climate system (2). Major uncertainties remain in the geospatial distribution of terrestrial carbon sources and sinks and the mechanisms that drive the distribution and its change. Research efforts have largely been focused on the investigation and quantification of the impacts of climate variability and land use activities on the carbon cycle at various spatial and temporal scales. The soil carbon balance of old-growth forests has received little attention. It is generally accepted that soil organic carbon (SOC) levels in old-growth forests are in a steady state (1). To our knowledge, the long-term dynamics of SOC in old-growth forests and the validity of the above perception have not been tested.

We conducted a study to measure the long-term dynamics (1979 to 2003) of SOC stock in old-growth forests [age > 400 years (3)] at the Dinghushan Biosphere Reserve (23°09'21"N to 23°11'30"N and 112°30'39"E to 112°33'41"E) in Guangdong Province, China. The estimation of SOC stock change requires a series of measurements of SOC concentration, bulk density, and soil thickness taken at different points in time (4, 5). In this study, we observed long-term changes in SOC concentration and bulk density but did not measure changes in soil thickness in the old-growth forests. Although soil thickness dynamics were not monitored, their possible contribution to the uncertainty in the results was analyzed and quantified by using upper and lower bounds of possible SOC change (Materials and Methods).

Results show that SOC concentration in the top 20-cm soil layer increased between 1979 and 2003 from about 1.4% to 2.35% at an average rate of 0.035% each year, which was significantly different from 0 at $\alpha = 0.05$. At the same time, the mean bulk density of the top 20-cm soil layer decreased significantly ($\alpha = 0.05$), with an average rate of 0.0032 g cm⁻³ year⁻¹. Measurements on a total of 230 composite soil samples collected between 1979 and 2003 suggested that SOC stock in the top 20-cm soil layer increased significantly during that time ($P < 0.0001$), with an average rate of 0.61 Mg C ha⁻¹ year⁻¹ (Fig. 1). The lower and upper bounds of this average rate

were 0.54 and 0.68 Mg C ha⁻¹ year⁻¹, after considering the uncertainty introduced by the lack of thickness-change monitoring. We took more than enough samples to detect the observed SOC change. In fact, statistical analysis shows that 20 samples taken every 8 to 10 years of sampling interval (or 100 samples every 5 years) would be sufficient to detect the observed SOC change rate in these forests at a 95% confidence level. More samples would be required at shorter sampling intervals to detect the observed change, given the observed spatial variability of SOC concentration and bulk density.

The driving forces for this observed high rate of SOC increase in the old-growth forests are not clear at present and deserve further study. This study suggests that the carbon cycle processes in the belowground system of these forests are changing in response to the changing environment. This result directly challenges the prevailing belief in ecosystem ecology regarding carbon budget in old-growth forests (1) and supports the establishment of a new, non-equilibrium conceptual framework to study soil carbon dynamics. Our study further highlights the need to focus on the complexity of the belowground processes, as advocated in previous research (6, 7), and the importance of establishing long-term observation studies on the responses of belowground processes to global change.

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References

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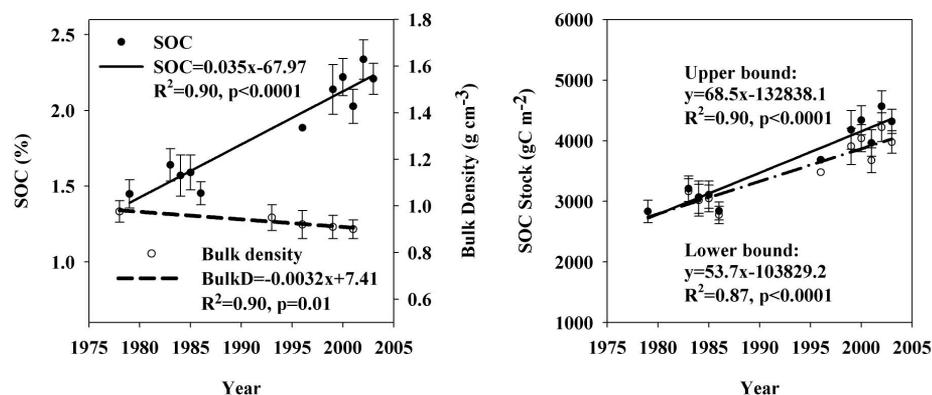


Fig. 1. Temporal changes of (left) soil organic carbon concentration, bulk density, and (right) soil organic carbon stock in the top 20-cm soil layer in broadleaved old-growth forests in Dinghushan Nature Reserve. Upper and lower bounds contain the uncertainty introduced by the lack of monitoring of soil thickness during the study period. Error bars indicate standard deviation.

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Species Interactions Reverse Grassland Responses to Changing Climate

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Species Interactions Reverse Grassland Responses to Changing Climate

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Predictions of ecological response to climate change are based largely on direct climatic effects on species. We show that, in a California grassland, species interactions strongly influence responses to changing climate, overturning direct climatic effects within 5 years. We manipulated the seasonality and intensity of rainfall over large, replicate plots in accordance with projections of leading climate models and examined responses across several trophic levels. Changes in seasonal water availability had pronounced effects on individual species, but as precipitation regimes were sustained across years, feedbacks and species interactions overrode autecological responses to water and reversed community trajectories. Conditions that sharply increased production and diversity through 2 years caused simplification of the food web and deep reductions in consumer abundance after 5 years. Changes in these natural grassland communities suggest a prominent role for species interactions in ecosystem response to climate change.

Impacts of recent climate change on plants and animals are already evident, as geographic distributions shift poleward (1, 2) and toward higher elevations (3, 4), phenological events advance in time (5–7), and some species disappear altogether (8). With further climate change still expected, prediction of future impacts has become critical to conservation planning and management. To forecast ecological change under continued climate warming, how-

ever, we need a better understanding of the relative importance of direct responses by individual species to climate versus responses mediated by changing interactions with resources, competitors, pathogens, or consumers (9–14). We imposed projected future precipitation regimes over grassland in northern California to evaluate the importance to ecosystem response of direct effects on grassland species versus indirect effects arising from species interactions.

Much of the California coastal region experiences a Mediterranean climate, characterized by wet winters and long summer droughts. Ecological responses to climate change in regions with Mediterranean climate regimes may be strongly driven by the redistribution of water in time and space (15). Changes in seasonal water

availability that affect plant phenology, for example, could lead to temporal mismatch between resource availability and consumer demand (16), which can have important effects on resource flow and ecosystem function (17). General circulation models developed at the Hadley Centre for Climate Prediction and Research (HadCM2) and the Canadian Centre for Climate Modeling and Analysis (CCM1) (18) predict substantial increases in precipitation over most of California but differ in the projected seasonality of these increases. The Hadley model calls for all additional rain to fall during the current winter rainy season, whereas the Canadian model projects increased rainfall extending into the current summer drought. The discrepancy between the two scenarios may be critical to the fate of grassland ecosystems in California, where summer drought severely constrains plant growth and the timing of rainfall is more important to annual production and species composition than the amount (19–22).

In 2001, we began a large-scale rainfall manipulation in a northern California grassland to examine the consequences of these two projected regimes for production and diversity of grassland plants and invertebrates. In a grassland at the Angelo Coast Range Reserve in Mendocino County, California (39° 44' 17.7" N, 123° 37' 48.4" W), 18 circular 70-m² plots were subjected to one of three watering treatments: a winter addition of water (January through March), a spring addition of water (April through June), and an unmanipulated ambient control (Fig. 1). Each watered plot received about 44 cm of supplementary water over ambient rainfall per year, roughly a 20% increase over mean annual precipitation but within natural variability in both amount and timing at the study site (fig. S1). We

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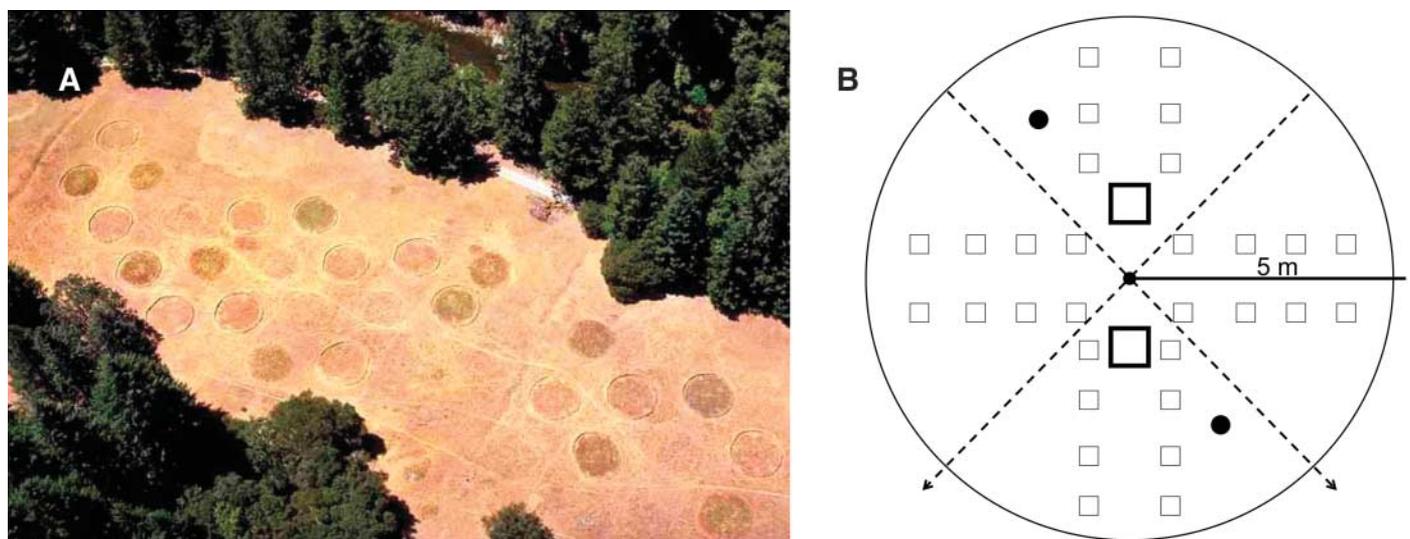


Fig. 1. (A) Bird's-eye view of experimental communities in July 2002. A nearby road is visible as a gray strip, top right. Research described here is from 18 open-grassland plots (18 additional plots were used in separate research). (B) Schematic representation of an experimental plot, shown as partitioned for measurement of plant biomass (30 900-cm²

subplots, small squares), plant species richness (two 2500-cm² subplots, large squares), foliar and flying invertebrates (two perpendicular sweep-net transects, dashed arrows), and ground-dwelling invertebrates (two pitfall traps, circles) (not to scale). Detailed methods are available online (23).

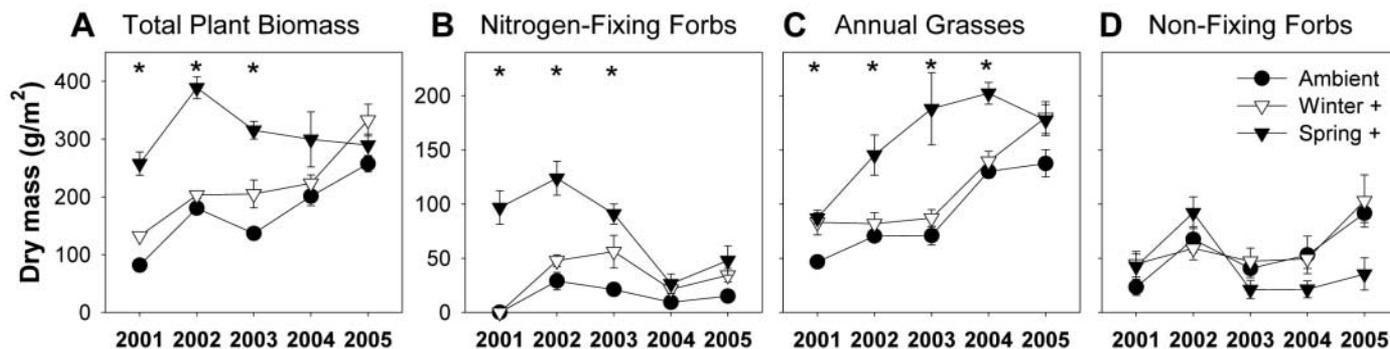


Fig. 2. Watering treatment effects on (A) total plant biomass and (B to D) biomass of individual plant groups (note difference in scales). Data represent treatment means \pm 1 SE. An asterisk denotes a statistically significant treatment difference after Bonferroni correction for multiple comparisons. See table S1 for factor significance.

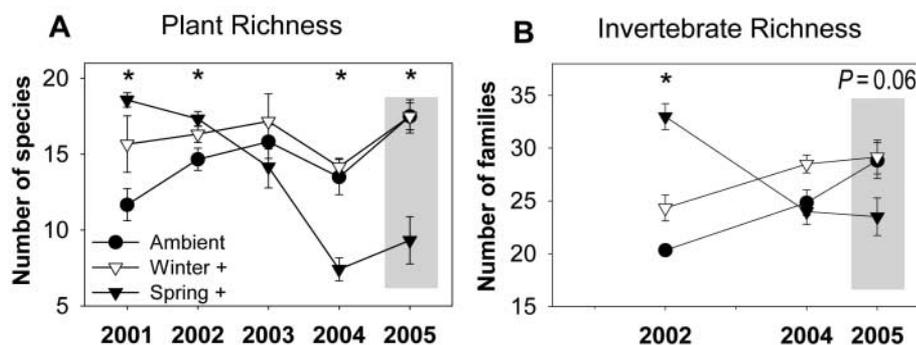


Fig. 3. Watering treatment effects on (A) plant species richness and (B) invertebrate family richness. Data represent treatment means \pm 1 SE. Gray shading highlights the year that late natural rainfall mirrored the spring-addition watering treatment. See tables S2 and S3 for taxonomic listings of plant species and invertebrate families, respectively.

examined treatment effects on plant production and species composition over 5 consecutive years and quantified responses of invertebrate herbivores and their natural enemies over 3 years (23).

Effects of increased rainfall depended critically on the seasonality of the increase. Supplemental water addition during the wet winter period produced moderate increases in plant production in some years of the study (Fig. 2), but effects did not extend to higher trophic levels (Figs. 3 and 4). In general, communities in winter-addition and ambient rainfall plots responded similarly across years to annual variation in rainfall.

Extending the rainy season via spring water addition produced much more dramatic changes in the grassland community. Plant production more than tripled in the first year and more than doubled in the second compared with the control (Fig. 2A). The strongest initial response was by nitrogen-fixing forbs, whose production increased by nearly two orders of magnitude with extended spring rainfall (Fig. 2B). Exotic annual grasses showed a weaker response to the first year of spring water addition, but after the proliferation of nitrogen-fixing forbs that year, annual grass production rose dramatically (Fig. 2C). These grasses, so-called winter annuals because they are the first plants to germinate

each year and are among the earliest to complete their life cycle and senesce, generally do not respond to extensions of the rainy season beyond April (22, 24). Early phenology thus limited the direct response of annual grasses to extended rainfall but allowed these plants to benefit in the subsequent growing season from a fertilization effect after decomposition of abundant N-fixer litter (25–27). As this process was repeated year after year, the accumulation of annual grass litter suppressed germination and regrowth of leafy forbs (Fig. 2D), as has often been seen in California annual grasslands (26, 28–30), and drove steep declines in plant species richness (Fig. 3A).

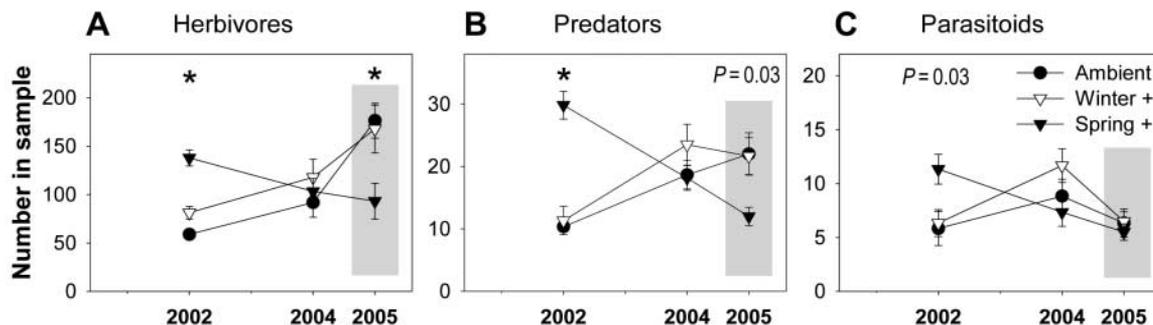
Shifts in plant composition in spring-addition plots had important consequences for biodiversity and food web structure. Initially, extended rainfall promoted increased plant species richness (Fig. 3A), and this increase, coupled with greater primary production and water availability, supported greater diversity and abundance of invertebrate herbivores, predators, and parasitoids (Figs. 3B and 4). As forbs were eliminated from spring-addition plots by annual grasses, however, plant species richness collapsed to nearly half that in control plots. With early-senescing annual grasses increasingly dominating the resource base, food availability and habitat quality for higher trophic levels dimin-

ished. This was especially true during summer, when late-blooming forbs provide a critical food resource for invertebrate herbivores (fig. S2). In contrast, annual grass litter has low nutritional value, and monocultures of these plants offer less structural complexity than mixed grass-forb assemblages.

By the fifth year of the study, when heavy rains continued into summer in a naturally extended rainy season throughout northern California, spring-addition plots stood out as islands of low biodiversity and reduced consumer abundances (Fig. 3B and 4). In addition to the nearly 50% reduction in plant species richness in spring-addition relative to control plots, invertebrate richness was 20% lower, and herbivore and predator abundances were each nearly 50% lower than ambient values measured in control plots. This simplification of the grassland community did not result from climatic conditions that were inherently unfavorable to production and diversity. Species at every trophic level benefited strongly from experimental extension of the rainy season in spring-addition plots early in the study, just as they did from a natural extension of the rainy season in winter-addition and control plots late in the study. But as altered environmental conditions persisted across years, individualistic responses by species to climate were overshadowed by the lagged effects of altered community-level interactions. The congruence between initial responses to artificial extension in spring-addition plots and responses in the grassland as a whole to naturally late rainfall in year 5 provides compelling evidence that these mechanisms are real rather than experimental artifacts.

Uncertainty remains in the projections of global climate models; indeed, the next-generation Hadley model (HadCM3) forecasts decreased rainfall over much of California (31). Yet under any scenario of future climate change, prediction of ecological effects will require understanding the web of interactions that mediate species-through ecosystem-level responses (14). To date, forecasts of range shifts and extinction probabilities are based largely on species-climate envelope models (32–34). These models are powerful initial tools

Fig. 4. Watering treatment effects on abundances (mean \pm SE) of (A) invertebrate herbivores, (B) predators, and (C) parasitoids, as measured in sweep net and pitfall trap collections. Gray shading highlights responses in the final year of the study, when late natural rainfall mirrored the spring-addition watering treatment.



with which to explore consequences of alternative climate scenarios, but they cannot forecast lagged impacts of altered higher-order interactions that will govern the trajectories of ecosystems under sustained climatic change. Nonlinearities are expected from the assembly of new combinations of species brought together by climate-induced range shifts, but these can also arise from environmental effects on the strength and direction of interspecific interactions without any change in species composition (35, 36). The nature and scales of these effects are best revealed by long-term experiments in natural field settings that improve understanding of how climate change impacts propagate through ecological communities. Indirect effects of climate on species will commonly lag behind direct effects, but their importance makes system-level interactions crucial to climate change forecasting even at subdecadal time scales.

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An X Chromosome Gene, *WTX*, Is Commonly Inactivated in Wilms Tumor

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Wilms tumor is a pediatric kidney cancer associated with inactivation of the *WT1* tumor-suppressor gene in 5 to 10% of cases. Using a high-resolution screen for DNA copy-number alterations in Wilms tumor, we identified somatic deletions targeting a previously uncharacterized gene on the X chromosome. This gene, which we call *WTX*, is inactivated in approximately one-third of Wilms tumors (15 of 51 tumors). Tumors with mutations in *WTX* lack *WT1* mutations, and both genes share a restricted temporal and spatial expression pattern in normal renal precursors. In contrast to biallelic inactivation of autosomal tumor-suppressor genes, *WTX* is inactivated by a monoallelic "single-hit" event targeting the single X chromosome in tumors from males and the active X chromosome in tumors from females.

Wilms tumor (nephroblastoma) is the most common pediatric kidney cancer and is derived from pluripotent renal precursors that produce undifferentiated blastemal cells, primitive epithelial structures, and stro-

mal components [reviewed in (1)]. In 1972, Knudson and Strong proposed that Wilms tumor, like retinoblastoma, may develop as a consequence of two independent rate-limiting genetic events, subsequently defined as biallelic

Distribution-wide effects of climate on population densities of a declining migratory landbird

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Summary

1. Increases in global temperatures have created concern about effects of climatic variability on populations, and climate has been shown to affect population dynamics in an increasing number of species. Testing for effects of climate on population densities across a species' distribution allows for elucidation of effects of climate that would not be apparent at smaller spatial scales.

2. Using autoregressive population models, we tested for effects of the North Atlantic Oscillation (NAO) and the El Niño Southern Oscillation (ENSO) on annual population densities of a North American migratory landbird, the yellow-billed cuckoo *Coccyzus americanus*, across the species' breeding distribution over a 37-year period (1966–2002).

3. Our results indicate that both the NAO and ENSO have affected population densities of *C. americanus* across much of the species' breeding range, with the strongest effects of climate in regions in which these climate systems have the strongest effects on local temperatures. Analyses also indicate that the strength of the effect of local temperatures on *C. americanus* populations was predictive of long-term population decline, with populations that were more negatively affected by warm temperatures experiencing steeper declines.

4. Results of this study highlight the importance of distribution-wide analyses of climatic effects and demonstrate that increases in global temperatures have the potential to lead to additional population declines.

Key-words: climate change, El Niño Southern Oscillation, migratory landbird, North Atlantic Oscillation, yellow-billed cuckoo

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Introduction

Global temperatures have increased by approximately 0.6 °C over the 21st century and are predicted to increase by an additional 2–6 °C over the next century (Houghton *et al.* 2001). Such rapid changes in global climate have spurred research on the effects of climatic variability on the phenology and population dynamics of many species of plants and animals (Walther *et al.* 2002; Root *et al.* 2003). Studies of several species of landbirds have shown effects of variation in large-scale climate and local temperatures on migration and breeding phenology (Dunn & Winkler 1999; Forchhammer, Post & Stenseth 2002; Visser *et al.* 2003; Wilson & Arcese 2003; Both *et al.* 2004) and on population

productivity and adult survival (Saether *et al.* 2000; Sillett, Holmes & Sherry 2000; Nott *et al.* 2002). However, these climatic effects have translated to changes in population densities in only a few studies (Forchhammer, Post & Stenseth 1998; Saether *et al.* 2000; Jonzen *et al.* 2002). This is perhaps not surprising, as spatial variation in biotic and abiotic factors makes it likely that ecological effects of climate are spatially heterogeneous, and most field studies are necessarily conducted at small geographical scales. Consequently, studies are needed that test for effects of climate on population densities across species' distributions.

Among North American landbirds, more than 30% of migratory species have declined significantly over the past 37 years (Robbins *et al.* 1989; Askins, Lynch & Greenberg 1990; Sauer, Hines & Fallon 2003). With species declining to this extent, research on the factors that limit populations is imperative in focusing our conservation efforts. To date, most of the research on

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factors that limit migratory birds in North America has focused on endogenous factors, including nest predation, brood parasitism and density-dependent habitat limitation (Robinson *et al.* 1995; Sherry & Holmes 1996; Porneluzi & Faaborg 1999), and these endogenous factors are now known to be important in limiting migratory populations. In contrast, there is no evidence for an effect of climate on annual population densities in these species, despite several studies that have found climatic effects on phenology, productivity and survival. Thus, the extent to which changes in climate may lead to population declines in North American landbirds has remained unclear.

Here, we quantify the relationships between large-scale climate, local temperatures and population dynamics of a North American migratory landbird, the yellow-billed cuckoo *Coccyzus americanus*, throughout its breeding distribution. Using survey data from throughout the USA and Canada over the past 37 years (Sauer *et al.* 2003), we examine the influence of annual variation in large-scale climate and local temperatures on annual *C. americanus* population densities. Much of the annual variation in temperatures across North America is attributable to two large-scale climate systems, the North Atlantic Oscillation (NAO) and the El Niño Southern Oscillation (ENSO) (Hurrell 1995; Trenberth & Caron 2000); in addition, recent evidence indicates that the NAO may be an important vehicle through which anthropogenic causes of climatic warming are manifest (Visbeck *et al.* 2001). Here, we document geographical variation in the strength of the NAO and ENSO on interannual fluctuations in population densities. We furthermore document that the strength of the effects of these climate systems on regional population dynamics is strongly correlated with the strength of the effects of these systems on local temperatures. Finally, we show that the strength of the effect of local temperatures on annual population densities is correlated with the magnitude of population decline: the more strongly any particular population has been affected by local temperatures, the more precipitous has been that population's decline over the past 37 years.

Materials and methods

SURVEY DATA

Coccyzus americanus is a Neotropical migratory landbird, breeding in the USA and Canada from May through September, and wintering from Venezuela through central Argentina from October through April (Hughes 1999). Among the 137 species of long-distance migratory birds that breed in North America, *C. americanus* ranks 14th in its rate of population decline. Although declines are most severe for this species in the western USA, it ranks 11th of 88 species in its rate of decline in the eastern USA (Sauer *et al.* 2003). As indices of annual *C. americanus* densities, we

used data from the US Geological Survey's Breeding Bird Survey (BBS) from 1966 through 2002, using data from 41 physiographic regions incorporating 43 US states and three Canadian provinces (<ftp://ftpext.usgs.gov/pub/er/md/laurel/BBS/DataFiles>). Each physiographic region was defined as a population, and annual population densities were calculated as mean number of *C. americanus* detected per survey route within a region within a year. Western cuckoo populations were excluded from analyses, as we analysed only regions in which more than 20 cuckoos were observed in total between 1966 and 2002.

CLIMATE AND LOCAL TEMPERATURE DATA

The winter NAO index (mean of monthly NAO index values from December through March; www.cgd.ucar.edu/~jhurrell/nao.stat.winter.html#winter) was used to represent annual NAO conditions from 1966 through 2002, and the mean of monthly values of the Southern Oscillation Index (SOI) from May through April was used to represent annual ENSO conditions (www.cpc.ncep.noaa.gov/data/indices). Local temperature data were obtained from the US National Climatic Data Center (NCDC; www.ncdc.noaa.gov/oa/climate/onlineprod/drought/ftppage.html) from NCDC divisions that overlapped the BBS physiographic regions used to define *C. americanus* populations. Mean monthly temperatures for all NCDC divisions within a BBS region were calculated, and we used mean of December through March temperatures within each year in our analyses, as both the NAO and ENSO show the strongest effects on temperatures in North America during these months (Hurrell 1995; Trenberth & Caron 2000).

POPULATION MODELS

To quantify the influences of the NAO, ENSO and local temperatures on changes in annual *C. americanus* population densities, we incorporated the climate indices and local temperatures into models of cuckoo population dynamics. We hypothesized that climate and local temperatures would have 1-year lagged effects on annual population densities on the breeding grounds by influencing cuckoo productivity in the previous year (separate analyses indicate unlagged effects of ENSO on *C. americanus* population densities, suggesting effects on survival on the wintering grounds independent of effects on cuckoo productivity; A.D. Anders unpublished data). We used density-dependent autoregressive population models, which allow for examination of the strength of previous population densities and other factors, such as climate or temperature, on annual population densities (Royama 1992). The general form of the model was:

$$X_t = a_0 + a_1(X_{t-1}) + a_2(X_{t-2}) + a_3(X_{t-3}) + b_1(Y_t - 1) + \epsilon_t \quad \text{eqn 1}$$

where X_t are log of population density, a_0 is the intrinsic rate of increase, a_i are estimates of the strength of statistical density dependence, b_1 quantifies the influence of climate or local temperature on population density, Y_{t-1} is the NAO index, SOI, or mean local temperature in year $t-1$, and ε_t represents the effects of other perturbations. Year was included as a covariate for all populations displaying a significant temporal trend (Post & Stenseth 1999). First-, second- and third-order models were tested to determine which best predicted log annual population density for each population. We then included in the best-fit model terms for climate or local temperature to determine whether inclusion of these parameters improved model fit. Parameter coefficients were estimated using ARIMA in SPSS (SPSS Inc., Chicago, IL), and model fit was examined using Akaike's Information Criterion (Burnham & Anderson 1998).

We next investigated whether spatial variation in the influences of the NAO and ENSO on population dynamics reflected variation in the response of local temperatures to these climate systems. We first conducted correlation analyses of the NAO index and local temperatures across the 37-year period for each of the 41 physiographic regions. Then, to test whether the strength of the NAO's effect on annual population density is predicted by the strength of the connection between the NAO and local temperatures, we conducted a correlation analysis of the Pearson's r for each region and the NAO coefficient from the cuckoo population model for each region. We then conducted these same analyses for ENSO.

Finally, we quantified the relationship between the influence of local temperature on annual cuckoo population densities and the magnitude of long-term population change. We calculated magnitude of population change as the slope of the regression of mean population density over time, scaled by population density at the midpoint of the survey period, for each population, using only those populations that exhibited a linear trend over the period 1966–2002 ($N = 31$ populations). We then conducted a linear regression analysis of the local temperature coefficients from each population model and the slopes of the regression of population density over time for each region.

POTENTIAL MECHANISMS OF CLIMATIC EFFECTS

Although extreme climatic events may directly affect landbird population dynamics by increasing mortality, limiting effects of climate are more likely mediated through effects on food availability (Sillert *et al.* 2000; Jones, Doran & Holmes 2003). Food availability has been shown to impact landbird productivity (Arcese & Smith 1988; Rodenhouse & Holmes 1992; Marshall *et al.* 2002), and both the NAO and ENSO have been shown to affect North American landbird productivity through effects on lepidopteran larvae (Sillert *et al.*

2000; Nott *et al.* 2002), the primary food resource for landbirds during the breeding season. We had thus hypothesized that the NAO and ENSO would have 1-year lagged effects on annual *C. americanus* densities by affecting productivity, through effects on lepidopteran larvae abundance, the previous breeding season (Post 2004).

To determine whether climate may potentially affect cuckoo dynamics by affecting food availability, in 2003 and 2004 we collected field data on lepidopteran larvae abundance and cuckoo productivity in the Ridge and Valley region of Pennsylvania. Using two 150-ha sites, we located and monitored cuckoo territories throughout the breeding season to quantify the number of nesting attempts by each pair. Lepidopteran larvae were surveyed along randomly located fixed transects within each cuckoo territory ($N = 18$ territories) during a 2–4-day period in mid- and late June. We counted the number of caterpillars per 1000 understory leaves and measured the length of each caterpillar to the nearest millimetre (caterpillars were not removed from the vegetation). In 2003, we surveyed a single $50 \text{ m} \times 1 \text{ m} \times 1 \text{ m}$ transect per territory, and in 2004 we surveyed four $12.5 \text{ m} \times 1 \text{ m} \times 1 \text{ m}$ transects per territory.

Results

Results of population models indicated that 31 *C. americanus* populations showed first-order density dependence, eight populations showed second-order density dependence, and two showed third-order density dependence. The lagged NAO climate parameter entered the best-fit population model for eight cuckoo populations, all in the southern and eastern USA (Fig. 1). The model coefficient quantifying the lagged effect of the NAO was positive for five of these populations and negative for three populations. The lagged ENSO parameter entered the best-fit model for five additional cuckoo populations, all in the north-central USA (Fig. 1); the model coefficient quantifying the lagged effect of ENSO was negative for all five populations.

In examining the relationship between large-scale climate, local temperatures, and population dynamics for each of the 41 *C. americanus* populations, model coefficients quantifying the lagged influences of the NAO and ENSO on annual population densities were positively related to the correlations between the NAO index and local temperatures ($r = 0.309$, $P = 0.026$; Fig. 2a) and SOI and local temperatures ($r = 0.498$, $P = 0.001$; Fig. 2b). Hence, the more strongly these large-scale climate systems affected local temperatures, the greater was their influence on *C. americanus* population dynamics. Because only positive correlations existed between the NAO index and local temperatures in all regions studied (Fig. 2a), we repeated our analysis using only those regions in which the population model NAO coefficients were positive ($N = 17$ populations). Results of this analysis also showed a significant positive

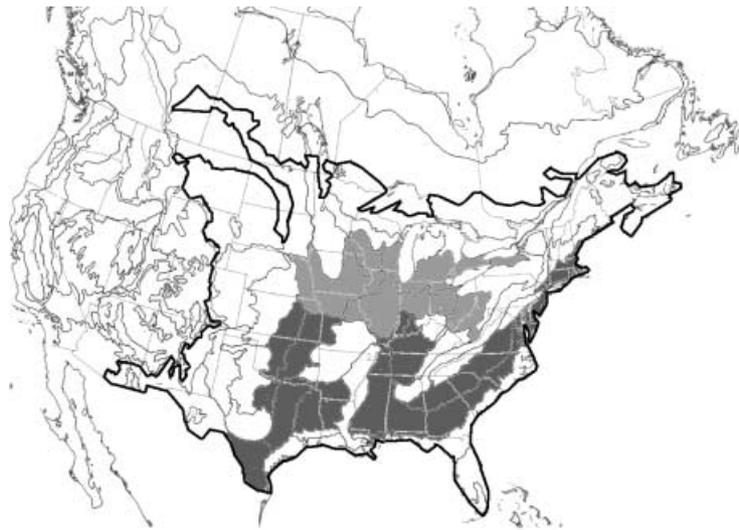


Fig. 1. Physiographic regions in which the NAO and ENSO entered the best-fit population model for *Coccyzus americanus* populations from 1966 to 2002. Black outline delineates the 41 physiographic regions analysed in this study. Dark grey indicates regions in which lagged NAO occurred in the best-fit population model; light grey indicates regions in which lagged ENSO occurred in the best-fit model (background map of BBS physiographic regions from Sauer *et al.* (2003)).

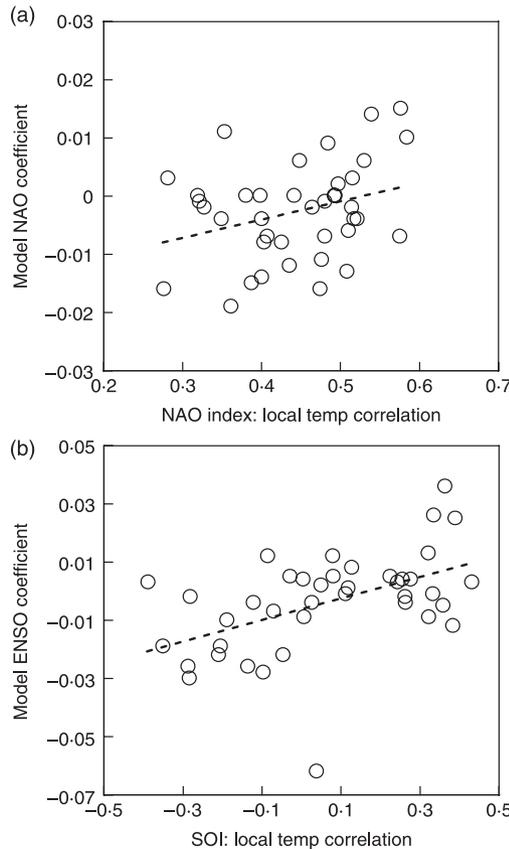


Fig. 2. Relationships between the lagged influences of the NAO and ENSO on *C. americanus* population dynamics and the strength of the correlations between these climate systems and local temperatures. (a) NAO parameter coefficient from each cuckoo population model vs. strength of the Pearson's correlation between the NAO Index and local temperature within that physiographic region. (b) ENSO parameter coefficient from each population model vs. strength of the Pearson's correlation between the Southern Oscillation Index (SOI) and local temperature within the physiographic region.

correlation between the model NAO coefficients and the Pearson's *r*'s from the NAO index and local temperature correlations ($r = 0.426$, $P = 0.044$).

Inclusion of local temperature in each population model indicated a lagged negative influence of temperature on 30 *C. americanus* populations: between 1966 and 2002, these populations experienced declines following warmer temperatures during the preceding breeding season. Linear regression analysis revealed a positive relationship between the magnitude of the influence of local temperatures on annual population densities and the magnitude of long-term population change ($t = 4.668$, $P < 0.0001$, $R^2 = 0.429$; Fig. 3). Hence, the more strongly local temperatures influenced a population's dynamics, the more precipitously that population declined.

In examining the potential of food availability as a mechanism by which climate affects annual population densities, we found that cuckoos attempted to nest on only a subset of occupied territories in 2003 and 2004, and lepidopteran larvae abundance was higher on those territories on which cuckoos nested than on occupied territories on which cuckoos did not nest (repeated measures ANOVA: $F_{1,14} = 5.28$, $P = 0.037$), with no effect of year ($F_{1,14} = 2.52$, $P = 0.135$) and no interaction between year and nesting status ($F_{1,14} = 0.47$, $P = 0.505$). Restricting the analysis to the lepidopteran survey conducted in mid-June, when cuckoos typically initiate nesting, territories on which cuckoos subsequently nested had higher lepidopteran larvae abundance (23.1 ± 6.8 SE caterpillars/1000 leaves vs. 7.0 ± 2.3 ; t -test: $t_{16} = 2.81$, $P = 0.013$) and more lepidopteran larval biomass, as indexed by summing the lengths of caterpillars per 1000 leaves (41.2 ± 13.8 mm of caterpillar/1000 leaves vs. 11.9 ± 4.5 ; $t_{16} = 2.56$, $P = 0.021$) than those territories without nests.

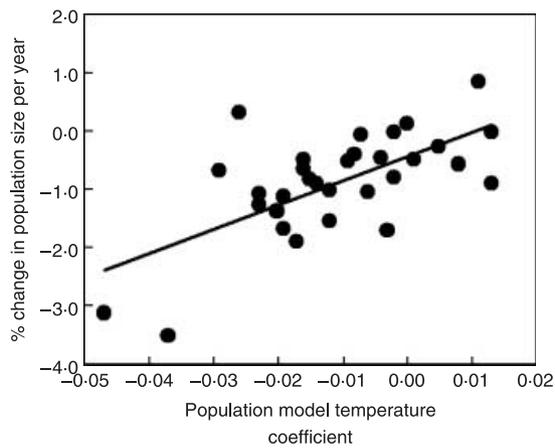


Fig. 3. Magnitude of change in *C. americanus* population density over time vs. magnitude of the lagged influence of local temperature on cuckoo population dynamics within a physiographic region.

Discussion

This study documents the spatially heterogeneous effects of large-scale climate on population densities of a North American migratory landbird across the species' breeding distribution. Our results indicate that two climate systems, the NAO and ENSO, have affected annual population densities of *C. americanus* over the past 37 years, and that the strength of the effect of climate on populations is correlated with the strength of the relationship between large-scale climate and local temperatures. In addition, the magnitude of the effect of local temperature on cuckoo populations is predictive of population decline: the more strongly and negatively any particular cuckoo population was affected by local temperatures on its breeding grounds, the more precipitous has been that population's decline over the past 37 years.

Geographic variation in the effects of the NAO and ENSO on cuckoo populations points to the importance of studying climatic effects at the scale of the species' distribution. Recent large-scale studies of the breeding phenology of European landbirds, including great tits *Parus major*, blue tits *P. caeruleus*, collared flycatchers *Ficedula albicollis*, and pied flycatchers *F. hypoleuca*, have shown geographical variation in effects of climate: in those areas of Europe that have experienced warming trends over the past one to two decades, landbird populations have displayed shifts in their breeding phenologies (Visser *et al.* 2003; Both *et al.* 2004). For the *Ficedula* species, there is a strong positive correlation between the extent of change in local temperatures and the extent of advancement of egg-laying date (Both *et al.* 2004). Field studies of North American landbirds, including black-throated blue warblers *Dendroica caerulescens* and song sparrows *Melospiza melodia*, have documented effects of

climate on productivity and adult survival at the scale of the study population (Sillett *et al.* 2000; Wilson & Arcese 2003), but those studies showed no subsequent effect on annual population densities, primarily because of recruitment of juveniles from other areas into the study populations (Sillett *et al.* 2000; Wilson & Arcese 2003). Because such field studies were necessarily conducted at relatively small geographical scales, it is possible that climatic effects on productivity or survival in these species may cause important but undetected changes in population densities at larger, regional scales.

Studies of the mechanisms by which large-scale climate could affect landbird populations have shown that the NAO and ENSO influence the abundance of lepidopteran larvae, the primary food resource for landbirds during breeding (Sillett *et al.* 2000; Nott *et al.* 2002). Research on *D. caerulescens* has shown an effect of ENSO on lepidopteran larvae abundance, and an effect of lepidopteran availability on warbler productivity (Sillett *et al.* 2000). Our field work with *C. americanus* indicates that only a subset of cuckoos attempted to breed in 2003 and 2004, and those territories on which cuckoos nested had more than three times the number and biomass of lepidopteran larvae than the occupied territories on which cuckoos did not attempt to nest. These results suggest that food availability may limit *C. americanus* productivity, as has been seen in other landbird species (Arcese & Smith 1988; Rodenhouse & Holmes 1992; Marshall *et al.* 2002).

Results of our analyses indicate that cuckoo population densities declined following warm years. There is evidence to indicate that outbreaking species of lepidopterans are more abundant in cold years: Myers (1998) found in a meta-analysis of 26 outbreaking lepidopteran species that outbreaks were more likely in cold years, and Williams & Liebhold (1995) and Miller, Mo & Wallner (1989) found higher abundances of gypsy moth *Lymantria dispar* L. larvae following cooler winter and spring temperatures. *Coccyzus americanus* is known to take advantage of outbreaking species such as gypsy moths, and warmer temperatures may act to decrease the availability of these food resources. However, it is also possible that warm winter temperatures lead to earlier spring peaks in the abundance of nonoutbreaking lepidopteran species, such that *C. americanus*, a relatively late-arriving species on the breeding grounds, misses this peak in food abundance. This type of climate-induced trophic mismatch has been seen in nonmigratory *P. major* (Visser *et al.* 1998; Stevenson & Bryant 2000) and may be even more likely in migratory species that are unable to time their spring migration in response to food availability on the breeding grounds (Both & Visser 2001).

In conclusion, we found lagged effects of two large-scale climate systems, the NAO and ENSO, on annual *C. americanus* population densities. Geographic variation in the strength of these climate systems on cuckoo

populations was underlain by geographical variation in the effects of the NAO and ENSO on local temperatures. We also found that the strength of the effect of local temperatures on populations was predictive of long-term population decline, with those populations that are more negatively affected by warm temperatures experiencing steeper declines over the past 37 years. Field data showing that cuckoo productivity is limited by lepidopteran larvae abundance point to the possibility that climate may affect *C. americanus* population densities by affecting food availability; however, data are needed to test our hypothesized mechanisms by which warm temperatures may decrease food availability. Overall, the results of this study indicate that, although endogenous factors such as nest predation, brood parasitism and habitat availability limit populations of migratory birds, exogenous factors such as large-scale climate and local temperatures also affect changes in the population densities of these species and do so in a spatially heterogeneous manner. An understanding of the limiting effects of climate on additional species, and knowledge of the mechanisms by which climate has such effects, is critical in an environment of increasing climate change.

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