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the coseismic mean stress change. For a homogeneous half-space we have

$$\frac{\partial g_i^k(x,\xi)}{\partial \xi_k} = \frac{(1-2\nu)}{2\pi\mu}\frac{x_i-\xi_i}{R^3} \quad (2)$$

where μ is shear modulus, and R is the euclidean distance between x and ξ. Therefore, equation (1) can be written as:

$$u_i(x) = \frac{(\nu_u-\nu)}{2\pi\mu(1+\nu_u)}\int \Delta\sigma_{kk}(\xi)\frac{x_i-\xi_i}{R^3}dV_\xi. \quad (3)$$

To determine surface displacements due to complete draining of a permeable surface layer with thickness D, overlying impermeable rocks, we integrate equation (3) from the surface to depth D. Note that equation (3) scales with $(\nu_u - \nu)$.

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Correspondence and requests for materials should be addressed to S.J. (sj@eps.harvard.edu).

Urbanization effects on tree growth in the vicinity of New York City

Jillian W. Gregg*‡†, Clive G. Jones† & Todd E. Dawson*‡

* *Ecology and Evolutionary Biology, Cornell University, Ithaca, New York 14853, USA*

† *Institute of Ecosystem Studies, Millbrook, New York 12545, USA*

Plants in urban ecosystems are exposed to many pollutants and higher temperatures, CO_2 and nitrogen deposition than plants in rural areas[1–5]. Although each factor has a detrimental or beneficial influence on plant growth[6], the net effect of all factors and the key driving variables are unknown. We grew the same cottonwood clone in urban and rural sites and found that urban plant biomass was double that of rural sites. Using soil transplants, nutrient budgets, chamber experiments and multiple regression analyses, we show that soils, temperature, CO_2, nutrient deposition, urban air pollutants and microclimatic variables could not account for increased growth in the city. Rather, higher rural ozone (O_3) exposures reduced growth at rural sites. Urban precursors fuel the reactions of O_3 formation, but NO_x scavenging reactions[7] resulted in lower cumulative urban O_3 exposures compared to agricultural and forested sites throughout the northeastern USA. Our study shows the overriding effect of O_3 despite a diversity of altered environmental factors, reveals 'footprints' of lower cumulative urban O_3 exposures amidst a background of higher regional exposures, and shows a greater adverse effect of urban pollutant emissions beyond the urban core.

Urbanization of the globe is accelerating, with potentially large impacts on vegetation in cities and surrounding areas[8]. Urban air contains high concentrations of many gaseous, particulate and photochemical pollutants (such as NO_x, HNO_3, SO_2, H_2SO_4, O_3 and volatile organic compounds)[1,5,6]; and urban soils are high in heavy metals and can be more hydrophobic and acidic than surrounding rural environments[2]. Although many of these contaminants have detrimental effects on plant growth, urban environments also have higher rates of nutrient and base-cation deposition[1,5], warmer temperatures (urban 'heat-island' effect)[3] and increased CO_2 concentrations[4]—factors that often, but not invariably, enhance plant growth. Given the potential for interactions among all factors[9] and the relative absence of studies examining more than two or three factors in combination, understanding the net effect of multiple anthropogenic environmental changes in an urban environment and the relative importance of the individual factors remains a major challenge.

We used an inherently fast-growing clone of Eastern cottonwood (*Populus deltoides*) as a 'phytometer'[10] to integrate the net growth response to multiple anthropogenic environmental changes in New York City compared to surrounding rural environments. Rapid growth rates, continuous growth throughout the season, and responsiveness to a range of climatic and pollutant variables[11–15] make this widespread riparian and early successional tree species a suitable indicator. Soil transplants, nutrient budgets, chamber replication of field conditions and multiple regression approaches were then used to determine the key driving variables. Urban and rural site comparisons were selected from known steep pollution gradients[1,16] across relatively short spatial scales (~100 km). Local variation in light and precipitation was minimized by growing plants in open fields with drip irrigation. Temperature effects on season length were controlled by synchronizing transplant and

‡ Present addresses: US EPA Western Ecology Division, Corvallis, Oregon 97333, USA (J.W.G.); Department of Integrative Biology, University of California, Berkeley, California 94720, USA (T.E.D.).

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Table 1 **Urban and rural atmospheric pollutants near New York City.**

	Urban	Rural
Atmospheric gases (p.p.b.): $\bar{x}$ annual mean (±s.e.)		
SO_2	**18.7 (0.3)**	2.3 (0.0)
NO	**39.3 (3.5)**	*0.5 (0.06)*
NO_2	**37.7 (0.7)**	*6.2 (0.25)*
O_3*	16.0 (1.5)	**28.0 (0.6)**
CO_2†	***408 (0.2)***	*358 (0.4)*
Suspended particulates (>10 μg, μg m^{-3}): $\bar{x}$ annual mean (±s.e.)		
Pb	**0.09 (0.00)**	0.04 (0.00)
NO_3^-	**5.47 (0.4)**	0.44 (0.04)
SO_4^{2-}	**12.4 (0.8)**	4.3 (0.2)
Total	**57.3 (5.2)**	19.4 (2.3)
Wet deposition (mg m^{-2}): $\bar{x}$ third quarter total (±s.e.)		
SO_4^{2-}	913.8 (151.2)	725.6 (65.9)
NO_3^-	519.9 (74.4)	465.7 (31.6)
NH_4^+	**142.2 (10.0)**	60.7 (6.9)
PO_4^{3-}	*0.6 (0.01)*	0.8 (0.1)
K^+	2.5 (1.4)	2.8 (0.6)
Ca^{2+}	59.5 (31.9)	17.0 (4.0)
Mg^{2+}	14.8 (8.8)	5.1 (1.0)
Na^+	**72.9 (36.3)**	14.4 (2.1)
Cl^-	**133.7 (17.3)**	41.3 (4.4)
H^+	18.0 (4.9)	19.0 (1.1)
pH‡	4.3 (0.1)	4.2 (0.1)

Atmospheric pollutant concentrations at urban and rural sites over the three years of experiments. Urban atmospheric gases, suspended particulates and wet deposition data were monitored at the New York State Department of Environmental Conservation's Morrisania, Green Point and Eisenhower Park air monitoring stations[16], respectively (adjacent to sites $NY_{1,3+4}$, locations in Methods and Fig. 3b). Rural data are from HV_1[29], with the exception of SO_2, Pb and CO_2 which were available from Belleayre[16] (~70 km northwest of HV_1), Wallkill[16] (~70 km southwest of HV_1) and LI_1[17]. Bold values show exposures that were significantly higher (paired *t*-tests, $P < 0.05$). Italics indicate data available in only one year in which case statistics represent intra-annual comparisons. Rural NO_x and urban/rural CO_2 concentrations were collected in years subsequent to field experiments, but follow well-documented urban–rural patterns[4,5]. *May–September; †14 h, p.p.m., August 1996[17]. ‡Precipitation weighted mean.

harvest dates within each growing season. The remaining microclimatic and pollutant differences were monitored at adjacent climate and air quality monitoring stations (http://climod.nrcc.cornell.edu, http://www.dec.state.ny.us, and http://www.ecostudies.org).

The relative importance of atmospheric (that is, pollutants and residual microclimatic variation) versus soil effects was determined by growing cottonwoods in soils reciprocally transplanted from remnant urban and rural primary forest stands previously shown to differ in pH, hydrophobicity, conductivity, heavy metals (including Pb, Ni, S, Zn, Cu, Al and Mn) and base cation concentrations (Ca^{2+} and Mg^{2+})[2,17]. Potting soil with slow-release fertilizer was also used to estimate maximum growth potential at all sites independent of soil transplants. Given the net growth responses to site and soil treatments, we used the nutrient budgets to assess effects of wet and dry deposition; the chamber experiments to simulate urban and rural thermal, CO_2 and O_3 environments; and multiple regression analyses to relate final season biomass from field experiments to the remaining variables potentially responsible for observed growth differences.

Contrary to expectations, cottonwoods grew twice as large amid the high concentration of multiple pollutants in New York City compared to rural sites (Fig. 1). Greater urban plant biomass was found for all urban–rural site comparisons, two separate planting dates in the first year and two further consecutive growing seasons. Urban–rural growth differences occurred for the faster-growing trees in the fertilized potting soils and the slower-growing trees in the forest soil treatments, but there was no significant effect of soils transplanted from urban versus rural forests ($F_{1,263} = 2.4$, $P = 0.124$). The consistently greater urban plant biomass, independent of soil type, indicated that growth differences between urban and rural sites were due to atmospheric rather than soil alterations.

The beneficial effects of increased nutrient deposition or higher urban temperatures and CO_2 concentrations were primary factors potentially responsible for an increase in plant growth in the urban atmosphere (Table 1). However, the twofold growth differences between urban and rural sites occurred for the fertilized potting soil treatments where cottonwoods had access to three to five orders of magnitude more N, P, K^+, Ca^{2+} and Mg^{2+} in fertilizer than from atmospheric deposition (11.1, 4.8, 9.2, 3.2 and 0.2 g respectively in fertilizer, compared to 28.1, 0.07, 0.31, 7.3 and 1.8 mg deposited to urban plants, respectively). Furthermore, atmospheric nutrient inputs were highest in year 2 when saplings grew the least (for example 2.2, 2.7 and 2.0 kg N ha^{-1} per season via wet deposition at study site NY_4 for years 1, 2 and 3 respectively), and PO_4^{3-} showed a trend toward higher deposition at the rural sites (Table 1). The fertilization effects of nutrient deposition therefore did not appear to account for greater urban cottonwood biomass.

While temperature effects on season length were controlled via simultaneous transplant and harvest dates, a greater increase in C gain relative to respiratory C losses at the warmer daily temperatures (+1.8 °C mean growing period temperatures[17]) could have enhanced cottonwood growth in the urban environment [18]. Because the relationship between C fixation and CO_2 concentration

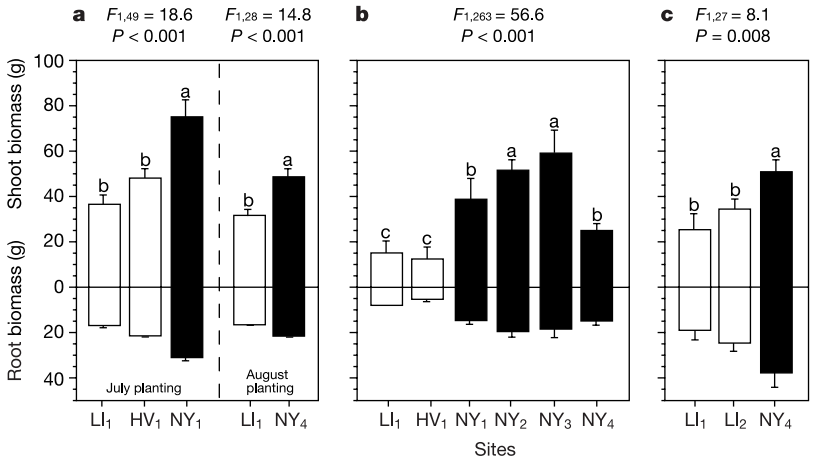

Figure 1 Cottonwood growth in urban and rural sites. Final season shoot and root biomass (mean ± s.e., potting soils) for cottonwoods grown in urban (filled, NY_{1-4}) and rural (open; HV_1, LI_{1-2}) sites in the vicinity of New York City for three consecutive growing seasons (**a**–**c**). Site locations in Methods and Fig. 3b. Values that fall below the zero line are for belowground biomass. *F* and *P* statistics are for linear contrasts of analyses of variance comparing total biomass for urban versus rural sites. Independent comparisons for above- and belowground biomass gave the same result. Bars with different letters indicate values significantly different using the Tukey–Kramer HSD.

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increases most with the initial rise in CO_2 above ambient conditions[18], incrementally elevated urban CO_2 concentrations (+50 p.p.m.) could also have increased growth in urban sites. However, a series of chamber experiments simulating urban and rural thermal and CO_2 environments failed to reveal individual or combined effects of elevated urban temperatures and CO_2 concentrations on total ($F_{1,1-Temp} = 0.74$, $P = 0.55$; $F_{1,1-CO2} = 0.67$, $P = 0.56$; $F_{1,1-Temp + CO2} = 1.55$, $P = 0.43$), above- or below-ground biomass. The absence of a CO_2 effect is in agreement with other studies on this clone at higher CO_2 concentrations[13]. Multiple regression analysis also failed to reveal any relationship between final season biomass in urban and rural field sites and ambient temperature regimes whether the data were summarized as the maximum, minimum or mean of the daily temperature profiles or as cumulative growing degree-days (base 15 °C; $P = 0.882$, 0.895, 0.226 and 0.160, respectively; forward stepwise regression analysis).

The urban pollution haze can reduce maximum incoming radiation (1,800 $\mu mol\, m^{-2}\, s^{-1}$ photosynthetically active radiation) by up to 18%[19], but light levels remained far above photosynthetic saturation for this species (700 $\mu mol\, m^{-2}\, s^{-1}$)[12]. High concentrations of condensation nuclei can also increase precipitation in urban centres[3], but irrigation waters were supplied at a rate far in excess of precipitation (6.2 cm H_2O d^{-1}) and there were no consistent differences in precipitation between our urban and rural sites ($F_{1,10} = 0.85$, $P = 0.36$). Whereas lower relative humidity[3] (−10.3% mean growing period comparisons[17]), increased CO_2 concentrations and even the pollutants themselves could all have reduced stomatal conductance in the urban sites, thereby minimizing pollutant impacts[18], the offset of detrimental impacts could not account for a relative increase in plant growth in urban compared to rural sites.

Overall, then, the collective results of all experiments and environmental comparisons provided no evidence that greater urban cottonwood biomass was due to enhanced growth in the urban atmosphere. Yet the same pattern could have arisen if detrimental effects reduced growth in the country. Because nutrient budgets, temperature and CO_2 experiments, temperature regressions and microclimatic comparisons could not account for an increase in plant growth in the city, clearly these factors also could not account for reduced growth in the country. As expected, most atmospheric gases, suspended particulates and wet deposition components that could reduce plant growth were either higher in New York City or did not differ between urban and rural sites (Table 1). However, O_3 was significantly higher at rural sites, and thus could have reduced growth in the country. Primary O_3 precursors are emitted in cities, but must react in sunlight to form O_3 as air masses move to rural environments[20]. Ozone exposures were therefore consistently higher for rural sites both to the north and the east of the city in all consecutive growing seasons (paired t-tests, $P < 0.001$).

An open-top chamber experiment exposing cottonwood to ambient and greater O_3 exposures representative of those at the urban and rural sites (33 versus 59 p.p.b. growing period mean

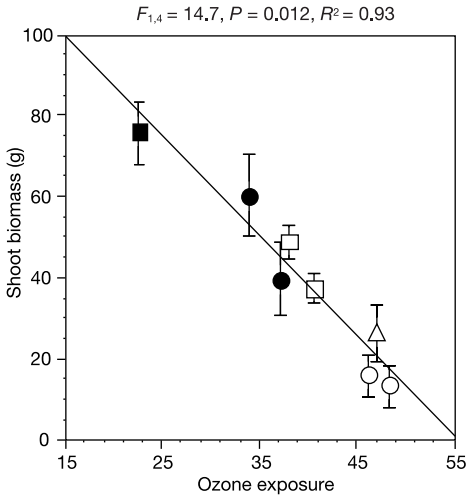

Figure 2 Cottonwood biomass related to O_3 exposure. Final season cottonwood shoot biomass (mean ± s.e., potting soils) at urban (filled) and rural (open) field sites versus ambient O_3 exposure (growing period 12-hour mean, p.p.b.; data available for NY_1, NY_3, HV_1 and LI_1; ref. 16). Squares, circles and triangles represent years 1, 2 and 3, respectively. F and P statistics show significance of O_3 effects from a multiple regression analysis with growing degree-days (base 15 °C; $F_{1,4} = 0.2$, $P = 0.685$) and urban versus rural sites ($F_{1,4} = 0.04$, $P = 0.866$) as additional independent variables. Variance inflation factors <10 demonstrated the lack of collinearity.

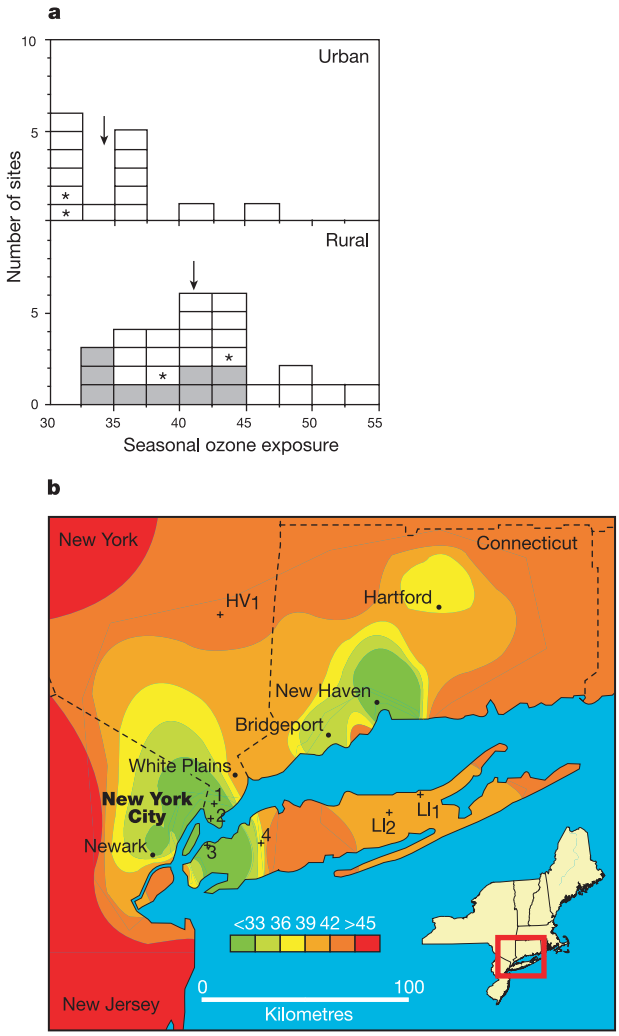

Figure 3 Urban and rural O_3 exposures in the northeastern USA. **a**, Histograms of O_3 exposures (12-hour mean p.p.b., May–September, year 2) for all urban and rural sites in the US EPA AIRS database for the northeastern USA (excluding Maine and Pennsylvania; rural grey: forested; rural white: agricultural). Exposures were significantly lower in urban compared to rural sites ($t_{41} = 4.1$, $P < 0.001$). Arrows show mean exposures. Asterisks show exposures at sites used in this study. Results were consistent for mean and cumulative peak O_3 (AOT40 or SUM06[7]) comparisons. **b**, Inverse distance weighted interpolation of O_3 exposure (units as above) for all US EPA AIRS sites in the New York/New Jersey/Connecticut region in year 2. The lower cumulative urban exposures appear as the green-yellow 'footprints' up to 500 km^2 in size. Note that footprints of lower urban O_3 appear only for areas with extensive urban, suburban and rural monitoring stations. Urban (NY_{1-4}), Hudson Valley (HV_1) and Long Island (LI_{1-2}) site locations are also shown.

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concentrations, respectively) showed a 50% reduction in cottonwood biomass at the greater O_3 exposures ($F_{1,7} = 10.0$, $P = 0.016$)—an effect magnitude comparable to that found between urban and rural field sites. Multiple regression analysis showed that final season biomass was significantly inversely related to ambient O_3 exposures across all field sites and years of experiments, accounting for 93% of variation (Fig. 2). Within-season comparisons also showed that incremental changes in leaf area production were inversely related to cumulative O_3 exposures ($F_{1,289\,Yr1} = 8.2$, $P = 0.004$; $F_{1,188\,Yr2} = 11.5$, $P < 0.001$) independent of effects due to site, soil, time through the season or growing degree-days. Less leaf area was produced in the sites with the highest O_3 exposures and this pattern held, despite the switch in sites with the highest exposures between measurement intervals.

Analysis of the US Environmental Protection Agency's Alliance of Information and Referral Systems (AIRS) database (http://www.airs.org) showed that O_3 exposures at our rural sites were representative of mean non-urban agricultural and forested exposures throughout the northeastern USA (Fig. 3a). Consequently, the detrimental effect of higher rural than urban O_3 exposures was not due to extreme high exposures downwind of an urban centre[20]. Instead, urban exposures were significantly lower than non-urban sites throughout the region. Spatial interpolation of the O_3 data for the New York/New Jersey/Connecticut region revealed footprints consisting of relatively low cumulative O_3 exposures in urban areas with a background of higher regional exposures (Fig. 3b). While NO_x titration reactions have been shown to reduce O_3 within the urban core[7], regional interpolations specifically omit the urban data[21], so the footprints of lower cumulative urban O_3 exposures have not previously been documented.

Of the many factors that could affect plant growth in urban environments, soil factors, nutrient deposition, temperature, CO_2, urban air pollutants and microclimatic variables could not account for the greater urban plant biomass. Rather, all evidence indicated that the greatest effect of the multiple anthropogenic environmental changes was the secondary reactions: these produced the higher rural O_3 exposures that reduced growth in the country. Because cottonwood is mid-range in O_3 sensitivity, with many species showing greater responses to ambient O_3 exposures[22–24], reduced growth in response to higher rural O_3 exposures is unlikely to be restricted to this cottonwood clone. These results do not negate the known detrimental effects of multiple urban pollutants, but show the greater effect of secondary reactions that create higher cumulative O_3 exposures beyond the urban core. Although individual 1-hour peak concentrations are typically higher in urban centres[7], our data indicate that the higher cumulative exposures at rural sites had the greatest impact.

Our research thus determines the relative importance of multiple anthropogenic environmental changes under current field conditions, and reveals a number of counter-intuitive results. (1) There was greater plant growth amid multiple pollutants in urban compared to rural environments. (2) Higher urban temperatures, CO_2 concentrations and N deposition could not account for increased growth in the city. (3) Ozone was the single overriding factor accounting for observed growth differences among multiple anthropogenic environmental changes. (4) The most detrimental effects of multiple urban pollutant emissions occurred in rural environments, with (5) footprints of reduced impact of lower cumulative urban O_3 exposures on a background of higher regional exposures.

These findings are in contrast to the extensive monitoring, warning and effects research within city centres, suggestions that ecological differences between urban and rural environments could be due to higher urban than rural O_3 exposures[25], and the pervasive perception that rural environments are safe havens from urban pollutant emissions. As such, our work highlights the need to reconsider relative pollutant impacts in urban and rural environments as air sheds merge throughout the globe. Although extensive global change research has studied potential impacts of temperature, CO_2 and N deposition, this study shows overriding O_3 impacts amid these other factors. □

Methods

Field comparisons

Cottonwood growth in New York City was compared to a northern rural site in the Hudson Valley (HV) and eastern rural sites on Long Island (LI) for three consecutive growing seasons (1992–1994). Rooted cuttings (Clone ST109; initial height 10–25 cm; 5–12 leaves) were transplanted to the field on 4–7 July, drip irrigated (3.8 litres day^{-1} in four intervals at 06:00, 10:00, 14:00 and 18:00 hours) and harvested before bud set and leaf senescence on 13–15 September. A second planting was also made on 6 August in year 1. Final season biomass comparisons were supplemented with measurements of total leaf area (area $= 3.772 - 1.611 \times$ length $+ 0.745 \times$ length^2, $r^2 = 0.976$, $P < 0.001$) measured biweekly on all plants in year 1 and tri-weekly on three plants per soil treatment in year 2. Urban and rural sites (locations shown in Fig. 3b) were located at The New York Botanical Garden, Bronx (NY_1); Hunts Point Water Works, Bronx (NY_2); Con Edison Fuel Depot, Austoria (NY_3); Eisenhower Park, Hempsted (NY_4); The Institute of Ecosystem Studies, Millbrook (HV_1); Cornell University Horticultural Research Laboratory, Riverhead (LI_1); and Brookhaven National Laboratory, Upton (LI_2). Herbivory was negligible (<1% total leaf area) and did not vary between urban/rural site and soil treatments (ANOVA, $P > 0.5$).

Soils were collected from the organic and top soil horizons of remnant oak-dominated urban and rural forest stands and transplanted to urban and rural sites. Soils were transplanted from one urban and one rural forest to all sites in year 1 (five plants per soil origin), and from two urban and two rural forests from each of the HV and LI comparisons to all respective HV and LI sites in year 2 (four forest soils per site, ten plants per soil origin, eight forest soils in total). All soils were fine sandy loam: Charlton and Hollis series for the urban–rural HV comparisons and Montauk series for LI comparisons. Soils were sieved (1-cm mesh), mixed thoroughly, placed in 19-litre pots, transported to each site, and buried on 1-m centres. Holes were dug 50% below pot depth and backfilled with gravel and sand for drainage. HV soils were collected from Van Cortland and Pelham Bay Parks, Bronx, and Housetonic and Mohawk State Forests, northwestern Connecticut. LI soils were collected from Cunningham and Alley Pond Parks, Queens, The David Weld Preserve, Nissequogue, and Edward Stevenson's woods, Mt Sinai. The potting soil treatment, also used at all sites and all years of experiments (ten plants per site; 15 plants per site for the second planting of year 1), was perlite:topsoil:peat (1:2:1 v/v), with limestone (10.2 g per pot), 5N-10P-5K fertilizer (13.6 g per pot), phosphate (20%, 10.2 g per pot) and slow-release fertilizer (Osmocote 14N-14P-14K, Scotts-Sierra Co.; 113.4 g per pot). Site, soil and site × soil were the main effects in analyses for the first planting of year 1 and these factors were nested within HV and LI comparisons in year 2. Collinearity between time and growing degree-days for intra-annual foliar comparisons forced removal of the non-significant temperature effect from the regression model ($F_{1,286\,Yr1} = 0.00$, $P = 0.988$; $F_{1,187\,Yr2} = 1.4$, $P = 0.232$).

Nutrient budgets

N, P, K^+ and base-cation deposition were calculated from NH_4^+–N, NO_3^--N, PO_4^{3-}–P, K^+, Ca^{2+} and Mg^{2+} concentrations in precipitation[16] with dry deposition assumed to equal that in rainfall[26]. Nutrient comparisons in otherwise clear and odourless irrigation waters showed that $As^{3+,5+}$, Ba^{2+}, Cd^{2+}, $Cr^{2+,3+}$, Cu^{2+}, F^-, $Pb^{2+,3+,4+}$, $Se^{+,2+}$, Ag^+ and Zn^{2+} were all below detection limits. The remaining detectable constituents (NH_3, NO_3^-, Ca^{2+}, $Fe^{2+,3+}$, K^+, Mg^{2+}, $Mn^{2+,3+}$, Na^{2+}, SO_4^{2-}, Cl^-, alkalinity, hardness, total solids, pH, anion-cation balance, conductivity and turbidity) were not different between urban and rural sites (*t*-tests, $P > 0.05$), and were not related with phytometer biomass (forward stepwise regression analysis, $P > 0.25$).

Chamber experiments

Field conditions were simulated as closely as possible by transplanting cottonwoods into the same 19-litre pots with fertilized potting soils and providing full sun and an ample water supply (biweekly irrigation to field capacity for open-top chambers and the same drip irrigation for chamber experiments). The open-top chamber O_3 experiment was performed at the Boyce Thompson Institute Field Facility in Ithaca, New York, from 7 July to 21 September 1996, in conjunction with an experiment that included four chambers per treatment but showed no significant chamber effects ($N = 5$ plants per chamber)[27]. Temperature and CO_2 growth chamber experiments (Conviron PGW36, Controlled Environments, Inc.) simulated the temperatures and CO_2 concentrations of the NY_1 and LI_1 sites in year 2. Since cottonwoods showed twofold growth differences between sites in the first three weeks of the field experiments[17], chamber conditions were set to the average conditions of the first 21 days and experiments lasted three weeks. Control conditions were: min. 18.8 °C/ max. 30.3 °C temperatures (ramped linearly between 6:00 and 15:00), and 350 ± 3 p.p.m. CO_2 concentrations. Treatments were asymmetrically elevated temperatures (min. 21.1 °C/ max. 31.9 °C) and elevated CO_2 concentration (400 ± 3 p.p.m.). Days were set to 14.5 hours, relative humidity was 50%, and light was maintained above 900 $\mu mol^{-1}\,m^{-2}\,s^{-1}$ with dawn and dusk simulated by ramping chamber lights in 25% increments at 15-min intervals. Each experiment was repeated twice, switching the treatments between chambers ($N = 7$ plants per chamber) with treatment effects tested against the treatment by replicate interaction[28]. Further analyses using individual plants as the experimental unit confirmed the absence of temperature and CO_2 effects.

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Correspondence and requests for materials should be addressed to J.W.G. (jwg1@cornell.edu).

Strong population substructure is correlated with morphology and ecology in a migratory bat

Cassandra M. Miller-Butterworth*†‡, David S. Jacobs* & Eric H. Harley†

** Department of Zoology, University of Cape Town, Private Bag, Rondebosch, 7701, South Africa*
† Wildlife Genetics Unit, Division of Chemical Pathology, University of Cape Town, Observatory, 7925, South Africa

Examining patterns of inter-population genetic diversity can provide valuable information about both historical and current evolutionary processes affecting a species. Population genetic studies of flying and migratory species such as bats and birds have traditionally shown minimal population substructure, characterized by high levels of gene flow between populations[1,2]. In general, strongly substructured mammalian populations either are separated by non-traversable barriers or belong to terrestrial species with low dispersal abilities[3]. Species with female philopatry (the tendency to remain in or consistently return to the natal territory) might show strong substructure when examined with maternally inherited mitochondrial DNA, but this substructure generally disappears when biparentally inherited markers are used, owing to male-mediated gene flow[4]. Male-biased dispersal is considered typical for mammals[5], and philopatry in both sexes is rare. Here we show strong population substructure in a migratory bat species, and philopatry in both sexes, as indicated by concordance of nuclear and mtDNA findings. Furthermore, the genetic structure correlates with local biomes and differentiation in wing morphology. There is therefore a close correlation of genetic and morphological differentiation in sympatric subspecific populations of this mammalian species.

Schreibers' long-fingered bat, *Miniopterus schreibersii natalensis* (Chiroptera, Verspertilionidae), migrates seasonally between wintering roosts (hibernacula) and summer maternity colonies in South Africa. Ringing studies[6] indicate that fidelity to both roost types is well developed. *Miniopterus schreibersii natalensis* were sampled (Fig. 1, Supplementary Table S1) from four South African maternity roosts (Die Hel (DHL), Jozini Dam (JD), Peppercorn (PC) and Sudwala (SW)), one hibernaculum (Steenkampskraal (SKK)), four roosts that are occupied all year round but are used primarily as summer roosts (De Hoop (DHP), Koegelbeen (KB), Grahamstown (G) and Maitland Mines (MM)) and one transient pre-maternity roost (Shongweni Dam (SHD)). An analysis of six dinucleotide microsatellite loci indicated that the *M. s. natalensis* population was genetically substructured into three major subpopulations, occurring in the south (DHL and DHP), west (SKK and KB) and northeast (G, MM, SHD, JD, PC and SW) regions of the country (Fig. 2, Supplementary Table S2). Colonies within each subpopulation were genetically similar and thus poorly differentiated: ρ values ranged between -0.005 and 0.068 ($P > 0.05$ for all comparisons). Genetic distances between these colonies were also low: $(\delta\mu)^2$ ranged between 0.084 and 0.446. However, colonies from different subpopulations were strongly differentiated, both when examined individually through pairwise comparisons (range of ρ values 0.152–0.686, $P < 0.01$ for all comparisons; range of $(\delta\mu)^2$ values 1.033–5.286) and when pooled into the three subpopulations (range of ρ values 0.351–0.623, $P \leq 0.0001$ for all comparisons; range of $(\delta\mu)^2$ values 2.037–4.550). Each colony had sufficiently

‡ Present address: Laboratory of Genomic Diversity, National Cancer Institute, PO Box B, Frederick, Maryland 21702, USA.

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