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URBAN EVOLUTION

Global urban environmental change drives adaptation in white clover

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Urbanization transforms environments in ways that alter biological evolution. We examined whether urban environmental change drives parallel evolution by sampling 110,019 white clover plants from 6169 populations in 160 cities globally. Plants were assayed for a Mendelian antiherbivore defense that also affects tolerance to abiotic stressors. Urban-rural gradients were associated with the evolution of clines in defense in 47% of cities throughout the world. Variation in the strength of clines was explained by environmental changes in drought stress and vegetation cover that varied among cities. Sequencing 2074 genomes from 26 cities revealed that the evolution of urban-rural clines was best explained by adaptive evolution, but the degree of parallel adaptation varied among cities. Our results demonstrate that urbanization leads to adaptation at a global scale.

Urbanization is a driver of both environmental and evolutionary change. Towns and cities are rapidly expanding throughout the world to accommodate human population growth. These urban areas represent novel ecosystems, in which urban development alters multiple environmental factors (1). Recent research

shows that urban environmental change can influence four evolutionary processes: mutation, genetic drift, gene flow, and adaptation due to natural selection (2, 3). Despite numerous examples of how urbanization affects genetic drift and gene flow (4, 5), the effects of urbanization on adaptive evolution have received less attention (6–8). Adaptation to

urban environments can affect species' conservation (9), the spread of pests and disease (2), and eco-evolutionary feedbacks (10), as well as urban planning and human society (11). However, the few examples of adaptation to urban environments focus on just one or a small number of cities in a single region (2). It is therefore unclear whether populations can adapt to urban habitats in similar ways across cities throughout the world.

Parallel adaptive evolution is most likely when populations experience similar environmental selective pressures on the same genes or phenotypes (12, 13). For urbanization to drive parallel evolution, urban areas must converge in environmental features that affect

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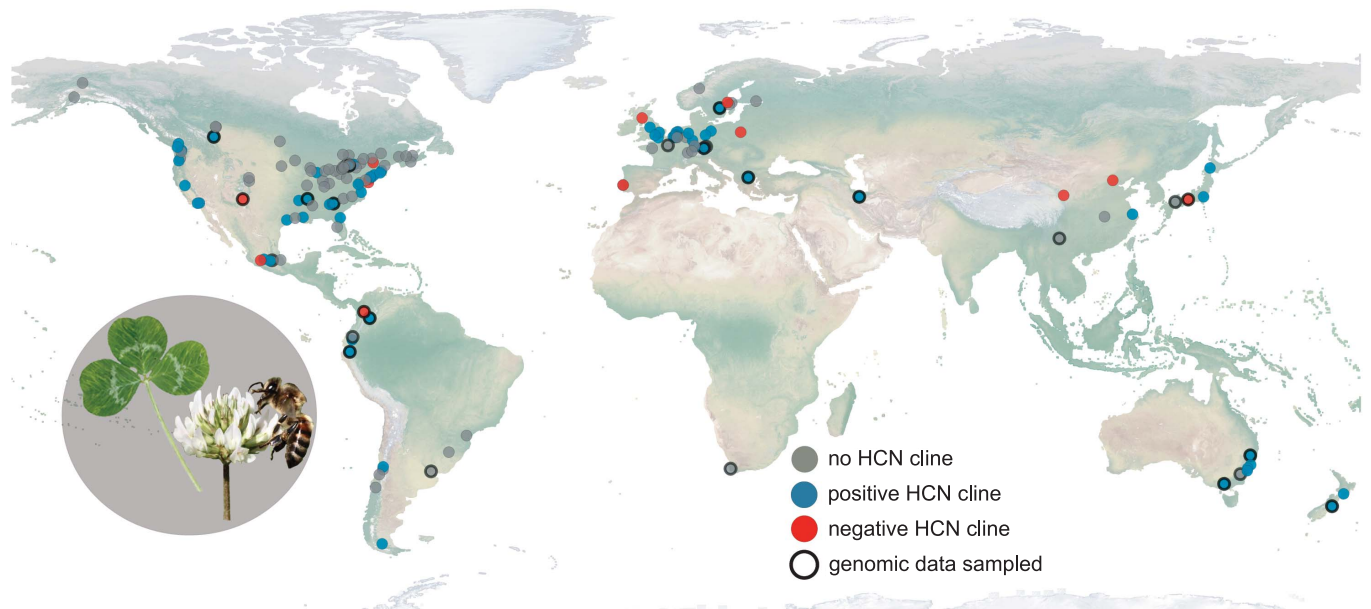


Fig. 1. Cities sampled for urban environmental and evolutionary change. Blue dots indicate cities with positive clines for hydrogen cyanide (HCN) production along urban-rural gradients ($HCN_{urban} < HCN_{rural}$). Red dots show negative clines ($HCN_{urban} > HCN_{rural}$). Gray dots indicate cities without a cline. Plants from the 26 cities outlined in black underwent whole-genome sequencing. Inset: White clover and a honey bee.

an organism's fitness. Urbanization can lead to similar environmental changes across cities (14), but whether urban environmental convergence causes parallel evolution has never been examined at a global scale.

Here we test how global urbanization affects environmental change and evolution in a cosmopolitan plant species, white clover (*Trifolium repens* L., Fabaceae). White clover populations are polymorphic for the production of hydrogen cyanide (HCN), an antiherbivore chemical defense controlled by two genes (15). At least one functional allele at each of two unlinked loci (*Ac* and *Li*) is required to produce HCN following tissue damage, whereas plants that are homozygous for gene deletions (*ac* and *li* alleles) at either locus lack HCN (16, 17). Notably, these deletions occur throughout the world, resulting in standing genetic variation on which selection can act (18). Previous work showed that herbivores select for the production of HCN, and abiotic stressors (e.g., freezing and drought) influence the costs and benefits of the metabolic components underlying the defense (19, 20). Variation in these environmental factors is credited with driving the evolution of clines in HCN production at continental and regional scales (21, 22), including in response to urban environments (23–25). Thus, HCN production could evolve in response to urbanization if there are urban-rural gradients in herbivory, winter temperature, or drought.

We examined global urban environmental and evolutionary change across the diverse climates that white clover inhabits. To this end, we created the Global Urban Evolution Project

to test for parallel evolution and urban adaptation in natural populations across white clover's worldwide range. The present study builds on our previous work on white clover (23–25) by sampling cities globally across diverse climates in both the native (Europe and western Asia) and introduced ranges, by quantifying many environmental factors from each population and by integrating evolutionary genomic analyses using whole-genome sequence data. This project spanned 160 cities across 26 countries (Fig. 1) (15) in white clover's native and introduced ranges (Fig. 1 and fig. S1). From these cities, we phenotyped 110,019 plants from 6169 sampling sites (hereafter “populations,” table S1). Populations within each city were sampled along an urban-rural transect, with half of each transect in urban and suburban areas (i.e., areas with high building density) and the other half in rural areas (Fig. 2, E to G) (15).

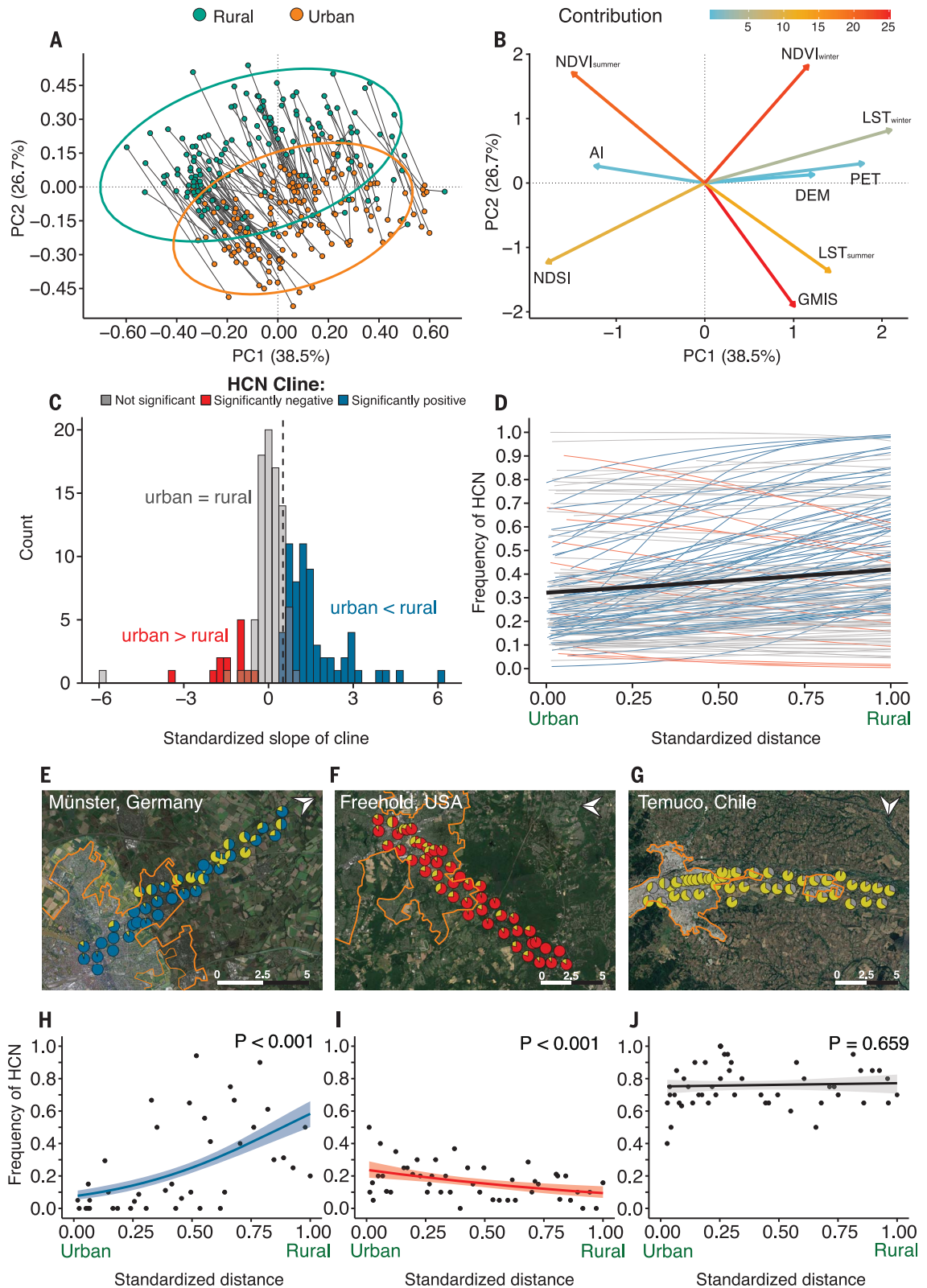
Across 160 cities, we tested whether urban white clover habitats converged to be more similar among cities and less variable within cities in their environmental characteristics compared to rural habitats (15). Urban and rural habitats significantly diverged (MANOVA H_0 : $urban_{mean} = rural_{mean}$, $P_{bootstrapped} < 0.01$, Fig. 2A) along two principal-component axes that accounted for 65% of the variation in the multivariate environments between the two habitats across cities. Urban locations consistently had more impervious surface, higher summer temperatures, and less vegetation than rural populations (Fig. 2B and fig. S2). The remaining environmental variables changed along urban-rural gradients in many cities, but

these changes were less consistent in direction among cities (fig. S2 and table S2). Although urban and rural environments diverged on average, urban-rural changes in the environment were not always parallel (MANOVA H_0 : parallel urban-rural changes among cities, $P_{bootstrapped} < 0.01$, Fig. 2A). Additionally, environmental variance among urban populations within a city was lower than the environmental variance among rural populations ($F_{9,1570} = 31.76$, $P < 0.001$, fig. S3). Together these results show that on average, urbanization leads to similar and less-variable environmental conditions in some factors (e.g., impervious surface, summer temperature, summer vegetation) but not in others (e.g., potential evapotranspiration, snow cover, winter vegetation), which could lead to variation in the degree of parallel evolution.

We next tested whether convergent urban environmental change causes parallel evolution in an ecologically important trait of white clover. We examined evolution in response to urbanization by testing for a relationship between HCN production and distance to the urban center (i.e., an “HCN cline”), as well as other metrics of urbanization (15). Our model explained 28% of the variation in the frequency of HCN production within populations (table S3). Across 160 cities, distance from the city center was positively related to the frequency of HCN-producing plants (distance: $\chi^2_{df=1} = 12.35$, $P < 0.001$). The probability that a plant produced HCN increased by 44% on average from the center of an urban area to the furthest rural population (Fig. 2C, D). However, cities varied in the strength and direction

Fig. 2. Urban environmental and evolutionary change across cities. (A) Principal component analysis showing environmental differences between urban (orange dots) and rural (green dots) habitats; ovals represent 95% confidence interval (CI). Lines connect urban and rural habitats from the same city. (B) The eigenvectors for environmental variables, colored according to their contribution to PC2. The environmental variables included vegetation in winter (NDVI_{winter}) and summer (NDVI_{summer}), snow accumulation (NDSI), surface temperature in winter (LST_{winter}) and summer (LST_{summer}), aridity index (AI), potential evapotranspiration (PET), impervious surface (GMIS), and elevation (DEM).

(C) Histogram of the slopes from binomial regressions of the relationship between HCN production within populations and distance from the city center. Distance was standardized to vary between 0 (urban center) and 1 (furthest rural population) in each city, so that cities that varied in size were compared on the same scale. The dashed vertical line corresponds to the mean slope across cities, and overlap between bars showing cities with significant (blue and red) and nonsignificant (grey) is shown as muted colors. (D) The relationship between HCN production within populations and distance for each city; colors correspond to those in (C). The black line shows the positive main effect of distance across cities ($P < 0.001$). (E to G) Examples of transects, with the orange lines showing the urban boundary, and pie charts (jittered to reduce overlap) showing the proportion of HCN+ plants colored in yellow. (H to J) Frequency of HCN production versus distance for the cities shown in (E) to (G). The line shows the regression line \pm 95% CI.



of clines (distance \times city interaction: $\chi^2_{df=1} = 1001$, $P < 0.001$; Fig. 2, C and D). Overall, 47% of cities exhibited a significant ($P < 0.05$) cline (15), with 39% of cities (62 of 160) showing a

positive cline in which HCN production was less common in urban than rural populations, and 8% of cities (13 of 160) had negative clines (Fig. 2 and table S4). Positive and negative

clines occurred in both the native and introduced ranges, with the former being more prevalent among continents and across diverse climates (Fig. 1).

Given the prevalence of HCN clines at a global scale, we sought to identify the evolutionary processes driving variation in the strength and direction of clines. In addition to natural selection, nonadaptive evolution can lead to the evolution of clines (26). Notably, the epistatic genetic architecture of HCN

production makes the loss of the trait more likely with increased genetic drift (26). Therefore, the prevalence of positive clines could reflect stronger drift in urban populations (4, 5). To examine whether urban populations exhibited stronger drift, we estimated pairwise nucleotide diversity (π) of putatively neutral sites

using whole-genome sequence data from ~80 individuals per city, with samples equally split between urban and rural habitats across 26 cities ($N = 2,074$) (15). These cities were selected to capture variation in the strength and direction of clines, geography, and climate (Fig. 1) (15).

Genetic diversity was not consistently different between urban and rural habitats and did not explain variation in the slope of HCN clines along urban-rural gradients. On average, urban and rural habitats did not differ in neutral genetic diversity ($F_{1, 25} = 0.028$, $P = 0.87$; Fig. 3A). Furthermore, the difference in π between urban and rural habitats within a city was not strongly related to the slope of HCN clines ($F_{1, 24} = 0.25$, $P = 0.62$; Fig. 3B and fig. S4), and urban-rural differences in genetic diversity were similar between cities with and without clines ($F_{1, 24} = 0.017$, $P = 0.90$).

Variation in the strength of genetic differentiation and gene flow between urban and rural habitats can influence the ability of populations to adapt to urban environments (27). To test the association between genetic differentiation and the evolution of HCN clines, we estimated population genetic differentiation between urban and rural populations using both F_{ST} and principal components analysis (PCA) (fig. S5), in addition to urban-rural admixture (fig. S6) (15). Urban-rural F_{ST} was low [mean = 0.012 ± 0.002 (SE)] and did not differ significantly between cities with and without clines ($F_{1, 24} = 1.47$, $P = 0.24$; Fig. 3C and fig. S4). Neither F_{ST} ($F_{1, 24} = 1.42$, $P = 0.25$; Fig. 3D) nor urban-rural differentiation measured using PCA ($F_{1, 24} = 1.10$, $P = 0.31$, fig. S5) predicted the strength of clines in HCN production. The absence of strong differentiation was associated with extensive admixture between urban and rural populations (fig. S6). Because genetic differentiation is consistently low and gene flow appears to be high among urban and rural populations, the repeated evolution of clines suggests strong selection on HCN production along urban-rural gradients. This conclusion is further supported by direct tests of selection on the *Ac* and *Li* loci, as well as HCN production, in which differentiation (using a statistic equivalent to F_{ST}) between urban and rural populations was stronger than expected under neutral evolution in cities with HCN clines compared to cities without clines (Fig. 3, E and F) (15).

Multiple environmental stressors are known to influence the evolution of HCN production at continental scales (20–22, 28), so we asked: What environmental factors explain variation in the evolution of HCN production along urban-rural gradients? Environmental factors related to drought and vegetation cover were the strongest predictors of variation in HCN clines, accounting for 11.3% of the variation in the strength of clines (tables S5 and S6). Change in potential evapotranspiration (PET) along urban-rural gradients was one of the

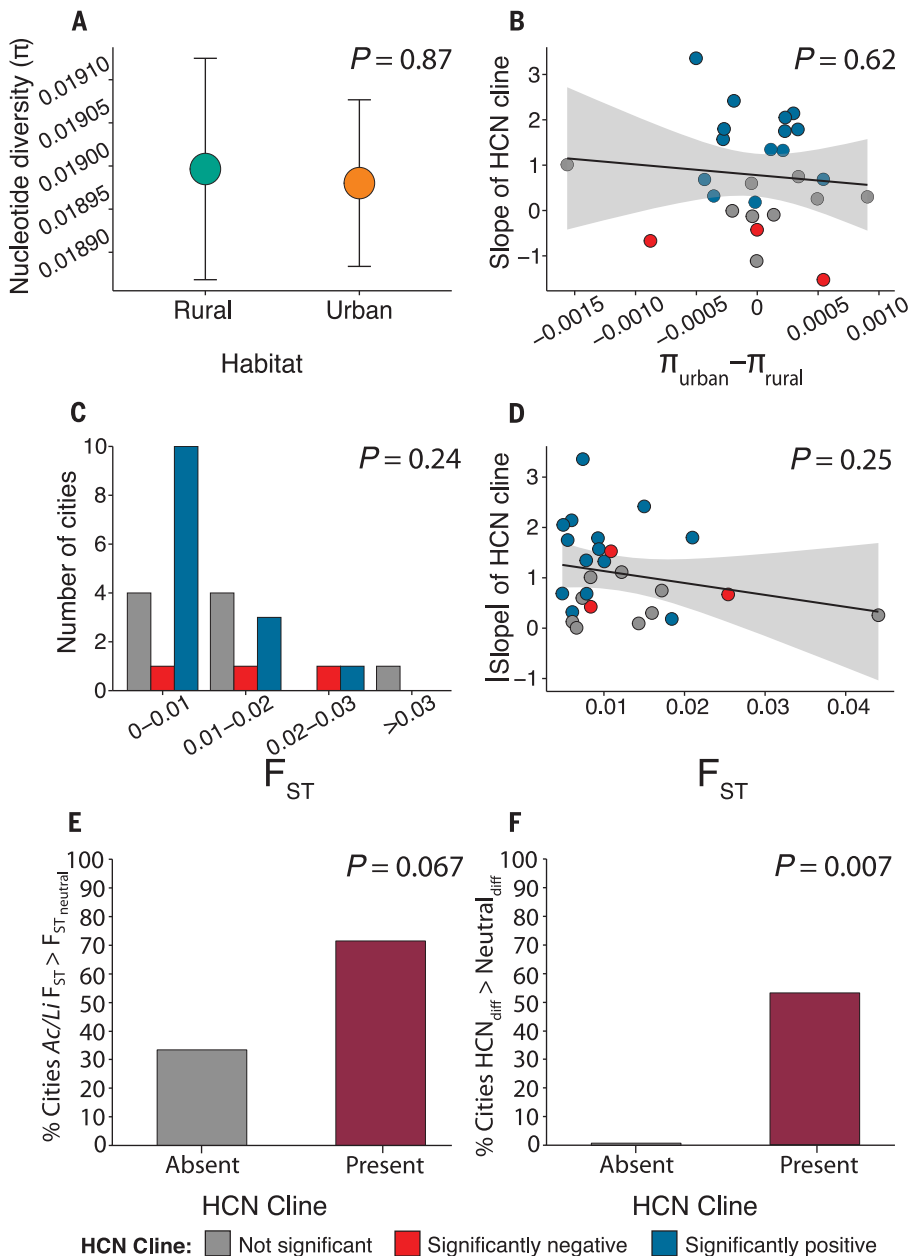


Fig. 3. Genetic diversity and differentiation within and between urban and rural habitats. (A) Mean (\pm SE) pairwise nucleotide diversity (π) for urban (orange) and rural (green) plants across cities. (B) The relationship between the slope of HCN clines versus the difference in nucleotide diversity between habitats, where each point is a city. (C) Histogram showing the distribution of genetic differentiation (F_{ST}) between urban and rural habitats for each city, colored by respect to the significance of HCN clines. (D) Relationship between the absolute value of the slope of HCN clines versus F_{ST} . (E) Percentage of cities in which differentiation between urban and rural habitats at *Ac* or *Li* exceeds neutral expectation in cities with or without significant HCN clines (15). (F) Percentage of cities with differentiation in HCN production between urban and rural habitats that exceeds neutral expectation in cities with or without significant HCN clines (15). P values in (E) and (F) correspond to χ^2 test for independence.

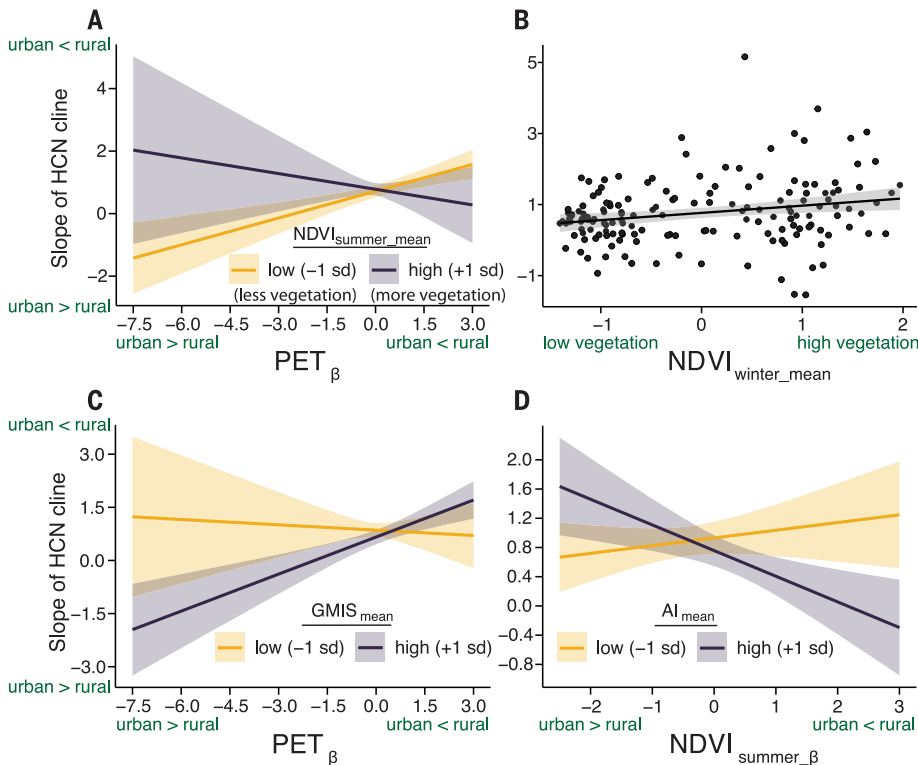


Fig. 4. Environmental predictors of urban-rural clines in HCN production. (A) Change in potential evapotranspiration along urban-rural gradients (PET_{β}) interacts with the regional amount of summer vegetation (i.e., $NDVI_{summer_mean}$) to explain variation in the slopes of HCN clines. (B) The relationship between the slopes of HCN clines and the regional amount of winter vegetation ($NDVI_{winter_mean}$). (C) PET_{β} interacts with the regional amounts of impervious surface ($GMIS_{mean}$) to predict the slope of HCN clines. (D) Change in summer vegetation along urban-rural gradients ($NDVI_{summer_beta}$) interacts with regional aridity (AI_{mean}) to explain variation in the slope of HCN clines. Acronyms as in Fig. 2.

most consistent predictors of evolution in HCN production (table S5); the frequency of HCN production tended to be higher in rural than urban populations in cities where PET was also greater in rural habitats (Fig. 4, A and C, and fig. S7). Because high PET can lead to plant water stress under low soil moisture, this result is consistent with drought selecting for higher HCN production, a pattern also observed at continental scales (27). However, the effect of PET on the evolution of HCN production only occurs when the amount of vegetation in and around cities is low (Fig. 4A). When vegetation cover is relatively high (and impervious surface is low) along the whole urban-rural transect, HCN clines tend to be positive regardless of variation in PET (Fig. 4, A to C). Notably, the amount of vegetation is positively correlated with invertebrate herbivore biomass and diversity (29), which can select for increased HCN production (20). When combined with the observation that herbivores are often less abundant in urban habitats (30), our evidence suggests that herbivores are selecting for greater HCN production in rural than urban areas. The positive association between urban-rural changes in vegetation and the positive slope of HCN clines

in some cities further supports this interpretation (Fig. 4D). Put simply, herbivory seems to select for higher HCN production in rural areas, but in the absence of strong herbivore pressure (i.e., when there is less vegetation across the whole gradient), drought is the main selective agent. Contrary to previous findings, urban-rural changes in temperature and snow cover did not explain changes in HCN production (24), suggesting that urban-rural changes in these abiotic factors are not a general explanation for the evolution of clines at a global scale.

Our results have general implications for understanding how environmental change affects adaptation in widespread species. Parallel evolution is a hallmark of natural selection because it suggests that adaptation proceeds in a repeatable way when populations face similar environments (12, 13). However, departures from parallel evolution are common, and a major goal of recent research involves quantifying how ecological and evolutionary factors interact to influence variation in adaptive responses to similar environments (12). Our results show that white clover rapidly adapts to urban environments on a global scale, but there is considerable variation in the strength

and direction of HCN clines that is driven by variation in particular biotic and abiotic factors that differ in how they change along urban-rural gradients among cities. Variation in additional unmeasured factors (e.g., gene flow from agricultural varieties, pollution, etc.) might further explain variation in the strength of clines, and future work will seek to explore such mechanisms.

Urbanization is increasingly transforming rural and natural environments into unique ecosystems that Earth's biodiversity has never experienced, and these changes are altering the evolution of life. If adaptation to urban environments is common, then this could have cascading effects on populations and ecosystems. This knowledge could help conserve some of Earth's most vulnerable species (9), mitigate the impacts of pests (2), improve human well-being (8, 11), and contribute to understanding fundamental eco-evolutionary processes (10).

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SUPPLEMENTARY MATERIALS

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Material and Methods

Supplementary Text

Figs. S1 to S16

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