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during the learning phase exhibited higher decoding power for odor samples than in the well-trained phase (fig. S33), which critically depended on the neurons with significant delay-period activity (fig. S34).

We then analyzed whether the delay-period odor selectivity of neurons is correlated with the behavioral performance of mice. The Euclidean distance between delay-period activity after different odor samples was calculated for a given neuron and then averaged for all neurons simultaneously recorded to represent neuronal selectivity for each mouse in one day. Although only 2 to 13 neurons (median of 8) were simultaneously recorded each day from a mouse, significant correlation between behavioral performance and neuronal selectivity was observed during the learning (days 2 to 5) but not well-trained phase (Fig. 4H and fig. S35).

The importance of mPFC delay-period activity in the learning phase of a WM task is consistent with its central role in flexible cognitive control in changing environments (2, 3, 12). However, the DL-PFC activity in primates is important in WM tasks after subjects are well trained (3, 12). Because mPFC appeared earlier than DL-PFC during evolution (12), the functional difference between mPFC and DL-PFC suggests that memory retention in novel situations may represent an evolutionarily more primitive function. It is not clear which brain region in rodents is homologous or analogous to DL-PFC in primates (3, 12), but delay-period activity in brain regions other than mPFC (3, 5, 19, 27–30) could mediate WM in well-trained mice. Activity of mPFC in other periods during the behavioral task may underlie inhibitory control (14), decision-making (15), and motor selection (16). Nevertheless, the present finding underscores the notion that properly regulated delay-period activity of mPFC is critical for memory retention in attention-demanding WM tasks in novel situations.

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EVOLUTIONARY BIOLOGY

Rapid evolution of a native species following invasion by a congener

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In recent years, biologists have increasingly recognized that evolutionary change can occur rapidly when natural selection is strong; thus, real-time studies of evolution can be used to test classic evolutionary hypotheses directly. One such hypothesis is that negative interactions between closely related species can drive phenotypic divergence. Such divergence is thought to be ubiquitous, though well-documented cases are surprisingly rare. On small islands in Florida, we found that the lizard *Anolis carolinensis* moved to higher perches following invasion by *Anolis sagrei* and, in response, adaptively evolved larger toepads after only 20 generations. These results illustrate that interspecific interactions between closely related species can drive evolutionary change on observable time scales.

In their classic paper, Brown and Wilson (1) proposed that mutually negative interactions between closely related species could lead to evolutionary divergence when those species co-occurred. In the six decades since, this idea has been debated vigorously, with support that has vacillated, depending on the latest set of theoretical treatments and comparative studies [reviewed in (2–5)]. However, tests of interaction-driven evolutionary divergence have been slow to capitalize on the growing recognition that evolutionary change can occur rapidly

in response to strong divergent natural selection [but see (6–9)]; thus, evolutionary hypotheses about phenomena once thought to transpire on time scales too long for direct observation can be tested in real time while using replicated statistical designs.

An opportunity to study such real-time divergence between negatively interacting species has been provided by the recent invasion of the Cuban brown anole lizard, *Anolis sagrei*, into the southeastern United States, where *Anolis carolinensis* is the sole native anole. These species have potential to interact strongly [e.g., (10)], being very similar in habitat use and ecology (11). We investigated the eco-evolutionary consequences of this interaction on islands in Florida (12) using an *A. sagrei* introduction experiment, well-documented natural invasions by *A. sagrei*, genomic analyses of population structure, and a common garden experiment. This multifaceted approach can rule against several of the most

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difficult alternative hypotheses [e.g., plasticity, ecological sorting, environmental gradients (*2*, *5*)] while directly testing two predictions for how *A. carolinensis* responds to its congeneric competitor.

Typical of solitary anoles (*13*), *A. carolinensis* habitat use spans ground to tree crown (*14*). However, where *A. carolinensis* and *A. sagrei* (or their close relatives) co-occur elsewhere, *A. carolinensis* perches higher than *A. sagrei* (*13–16*). Thus, we used an introduction experiment to test Collette's prediction (*14*) that competitive interactions with *A. sagrei* should drive an increase in *A. carolinensis* perch height. In early May 1995, we chose six islands that contained resident populations of *A. carolinensis* and collected pre-introduction perch height data from undisturbed lizards (*12*). Later that month, we introduced small populations of *A. sagrei* to three treatment islands, leaving three control islands containing only *A. carolinensis* (*12*). From May to August 1995–1998, we measured perch heights for both species. The *A. sagrei* populations grew rapidly [table S1; (*17*)], and by August 1995, *A. carolinensis* on treatment islands already showed a significant perch height increase relative to controls, which was maintained through the study [Fig. 1, fig. S1, and table S2; (*12*)].

We next predicted, following (*14*), that this arboreal shift by *A. carolinensis* would drive the evolution of larger toepads with more lamellae (adhesive, setae-laden, subdigital scales). Toepad area and lamella number (body-size corrected) correlate positively with perch height among anole species (*14*, *18–20*), and larger and better-developed toepads improve clinging ability (*20*), permitting anoles to better grasp unstable, narrow, and smooth arboreal perches. We tested the prediction in 2010 on a set of islands partially overlapping those used in 1995–1998 (*12*). We surveyed 30 islands and found that *A. sagrei* had colonized all but five (*12*). We compared *A. carolinensis* populations on these five islands without the invader (hereafter "un-invaded") to *A. carolinensis* populations on six islands that, on the basis of 1994 surveys, were colonized by *A. sagrei* sometime between 1995 and 2010 (hereafter "invaded") [Fig. 2; (*12*)].

From May to August 2010, we measured perch height for undisturbed lizards and found that, as in the 1995 introduction experiment, *A. carolinensis* perch height was significantly higher on invaded islands [fig. S2 and table S3; (*12*)]. We then tested whether the perch height shift had driven toepad evolution by measuring toepad area and lamella number of the fourth toe of each hindleg for every *A. carolinensis* captured (*12*). We found that *A. carolinensis* on invaded islands indeed had larger toepads and more lamellae [traits corrected for body size; Fig. 3, A and C, and table S3; (*12*)].

This morphological change occurred quickly. Assuming, conservatively, that *A. sagrei* reached all six invaded islands in 1995, *A. carolinensis* populations on invaded and un-invaded islands have diverged at mean rates of 0.091 (toepad area) and 0.077 (lamellae) standard deviations per generation [haldanes (*21*); rates > zero, each

one-tailed *P* < 0.02; (*12*)], comparable to other examples of rapid evolution (*21*) such as soapberry bug beak length (*22*) or guppy life history (*23*).

We tested several alternative processes that could have generated the observed divergence. First, we used a common garden experiment to investigate possible posthatching, developmental responses to physical challenges imposed

by arboreality during growth (i.e., phenotypic plasticity). We took gravid *A. carolinensis* females from four invaded and four un-invaded islands in July 2011, collected their eggs in the laboratory, and raised the offspring in identical conditions (*12*). The effect of *A. sagrei* invasion on *A. carolinensis* toepad characteristics persisted in the common garden [Fig. 3, B and D,
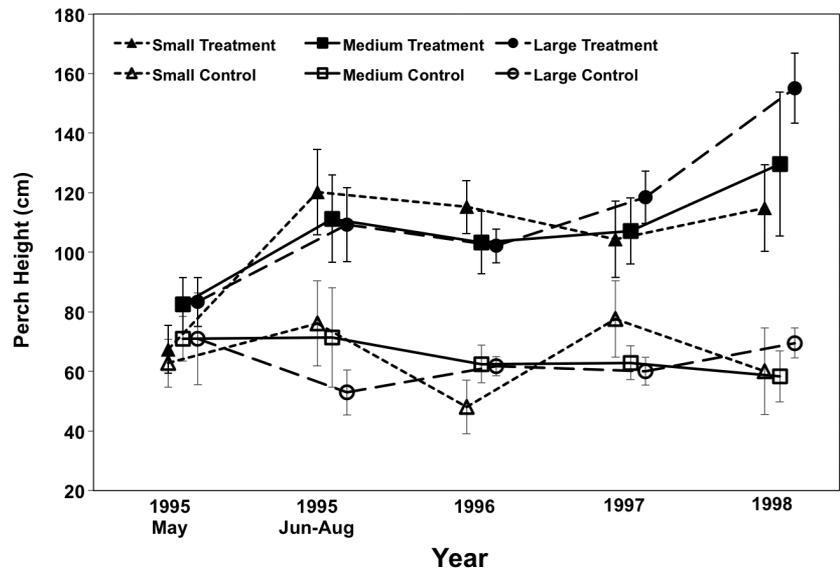

Fig. 1. Perch height shift by *A. carolinensis* after the experimental introduction of *A. sagrei*. We introduced *A. sagrei* to one small, one medium, and one large island (treatment; closed symbols) in 1995, keeping three similarly sized control islands (open symbols). Island means (±1 SE) are shown for perch height. *Anolis sagrei* introduction corresponds with a significant perch height increase by *A. carolinensis* (linear mixed models: treatment × time interactions, all *P* < 0.001 [(*12*)]; tables S1 and S2].

Fig. 2. 2010 study islands along the Intracoastal Waterway. *Anolis carolinensis* inhabits all study islands. Six study islands were invaded by *A. sagrei* sometime between 1995 and 2010 (closed circles), and five study islands remain un-invaded today (open circles). Nineteen additional non–study islands were surveyed ["x"; (*12*)]; 17 of these contained *A. carolinensis* and were invaded by *A. sagrei*; and two were empty of both species.
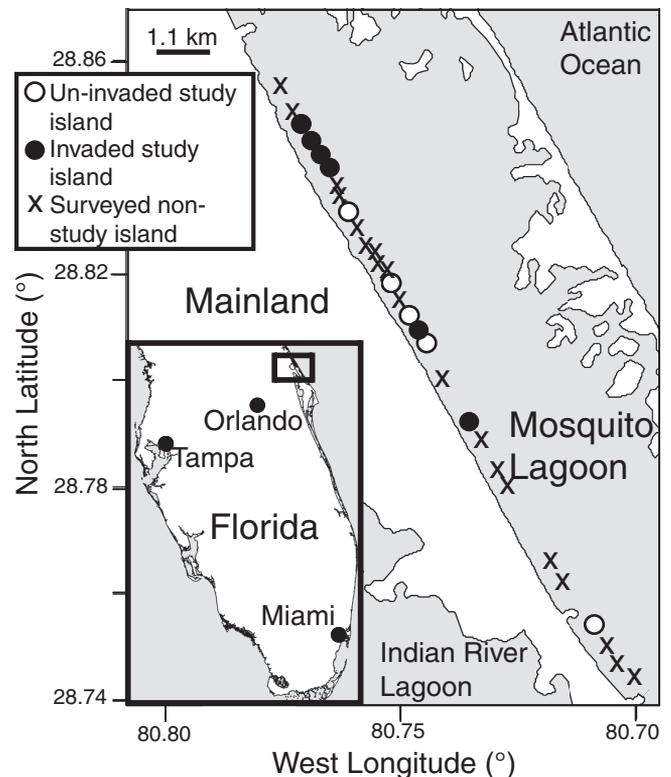
and table S4; (12)], suggesting genetically based divergence in nature (though we cannot rule out transgenerational plasticity).

Second, observed divergence in *A. carolinensis* could have arisen through nonrandom migration of individuals with large toepads among invaded islands, instead of arising independently on each island. Thus, we tested whether relatedness among *A. carolinensis* populations is independent of *A. sagrei* invasion. In 379 *A. carolinensis* individuals from four un-invaded and five invaded islands, we genotyped 121,973 single-nucleotide polymorphisms across the genome [table S5, (12)]. Individuals from the same island were closely related, and islands were largely genetically independent (pairwise-F_{ST} 0.09–0.16; table S6). We found no evidence that population relatedness in *A. carolinensis* was correlated with whether an island had been colonized by *A. sagrei* [Fig. 4; (12)] or with distance between islands (Mantel test; $P >$ 0.25), suggesting that gene flow is relatively limited
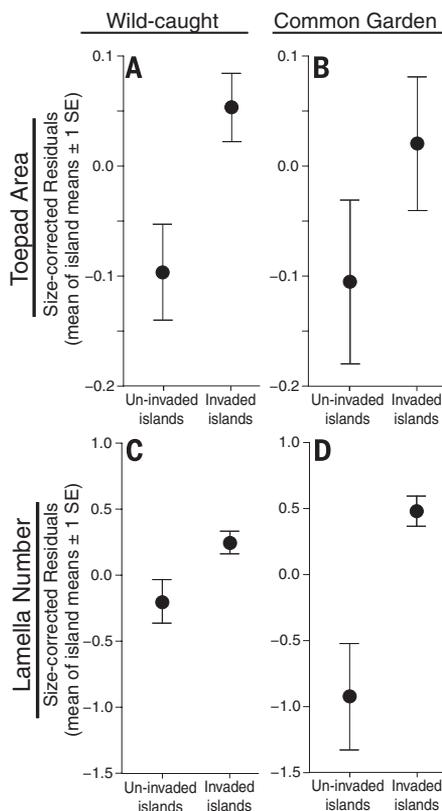
among islands and that island populations were independently founded from the mainland.

Third, toepad changes could have been generated by adaptation to environmental differences among islands that are confounded with the presence of *A. sagrei* [e.g., (24)]. However, invaded and un-invaded islands do not differ in characteristics important to perching or arboreal locomotion [e.g., vegetated area, plant species richness, or available tree heights; table S7; (12)]. Fourth, toepad changes could have arisen through ecological sorting, wherein *A. sagrei* was only able to colonize those islands on which the existing *A. carolinensis* population was already sufficiently different. However, *A. sagrei* seems capable of successfully colonizing every island it reaches, regardless of resident *A. carolinensis* ecology or morphology: All 10 *A. sagrei* populations introduced in 1994–1995 are still extant (12), and *A. sagrei* inhabits nearly every other island surveyed in the lagoon (Fig. 2). Finally, toepad changes observed in *A. carolinensis* in 2010 could be unrelated to interactions with *A. sagrei* if the latter's invasion merely missed the five islands with the lowest *A. carolinensis* perch heights (fig. S2) by chance; however, this would occur only one time in 462. In sum, alternative hy-

potheses of phenotypic plasticity, environmental heterogeneity, ecological sorting, nonrandom migration, and chance are not supported; our data suggest strongly that interactions with *A. sagrei* have led to evolution of adaptive toepad divergence in *A. carolinensis*.

Brown and Wilson called evolutionary divergence between closely related, sympatric species "character displacement" (1), and our data constitute a clear example of this. Resource competition has been the interaction suggested most often as the source of divergent selection during character displacement [sometimes specifically called "ecological character displacement" (1–3)]. For *A. carolinensis* and *A. sagrei*, resource competition for space likely is important: Allopatric *A. carolinensis* and *A. sagrei* overlap in their use of the habitat (12–14, 16); moreover, when they co-occur, the two species interact agonistically (10), and our experimental data show a rapid spatial shift by *A. carolinensis* following *A. sagrei* introduction. The two species also overlap in diet and thus may compete for food (17). Competition for food is strong among co-occurring *Anolis* and has been shown to be mitigated by differences in perch height (11). Evolutionary divergence may also arise, however, from selection to reduce
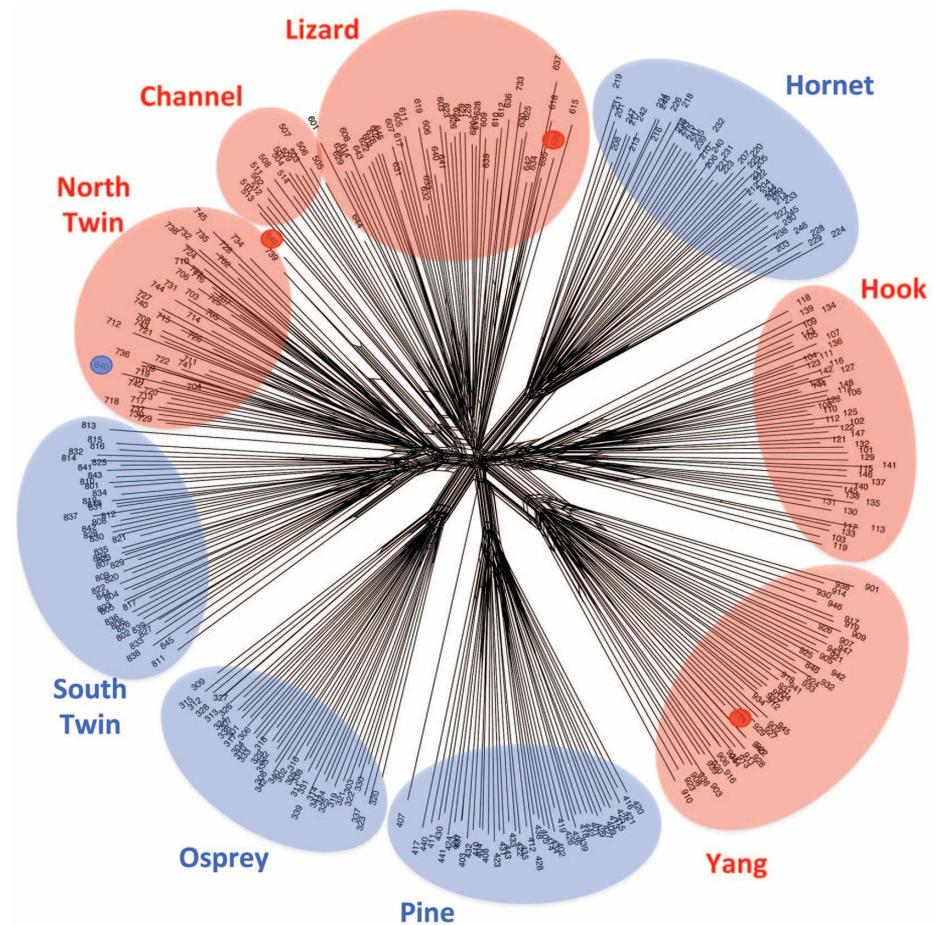

Fig. 3. Divergence in wild-caught and common garden *A. carolinensis*. Mean-of-island-means size-corrected residuals (±1 SE) are shown. The invasion of *A. sagrei* corresponds to a significant increase in both traits for wild-caught lizards (**A** and **C**) in 2010 [five islands un-invaded, six invaded; linear mixed models (LMM); (A) toepad area, $\beta_{invaded} =$ 0.15, $t_9 = 2.7$, $P = 0.012$; (C) lamella number, $\beta_{invaded} =$ 0.54, $t_9 = 3.1$, $P = 0.009$]. (**B** and **D**) Common garden offspring from invaded islands had significantly larger toepad characteristics [four un-invaded islands; four invaded; LMM; (B) toepad area, $\beta_{invaded} = 0.14$, $t_6 =$ 2.1, $P = 0.043$; (D) lamella number, $\beta_{invaded} = 1.45$, $t_6 =$ 3.6, $P = 0.006$]. All P values are one-tailed.

Fig. 4. Neighbor-net analysis of genetic distance for *A. carolinensis* individuals from invaded (red) and un-invaded (blue) islands (12). Small shaded areas enclose individuals that do not cluster with their own island; the color of these areas represents invasion status of their home islands.

interspecific hybridization; yet, such "reproductive character displacement" (*4*) seems an unlikely explanation for our results, as *A. carolinensis* and *A. sagrei* already differ markedly in species-recognition characteristics, males of both species nearly exclusively ignore heterospecific females in staged encounters (*25*), and the species have never been reported to successfully produce hybrids. We note, finally, that other mutually negative interactions such as apparent competition (*26*) and intraguild predation (*27*) could also produce divergence among overlapping species. These remain to be explored in this system, though some evidence exists for at least the latter (*17*).

Here, we have provided evidence from a replicated, natural system to support the long-held idea (*4*) that interspecific interactions between closely related species are an important force for evolutionary diversification (*2*). Moreover, we show that evolutionary hypotheses such as character displacement can be rigorously tested in real time following human-caused environmental change. Our results also demonstrate that native species may be able to respond evolutionarily to strong selective forces wrought by invaders. The extent to which the costs of invasions can be mitigated by evolutionary response remains to be determined (*28*), but studies such as this demonstrate the ongoing relevance of evolutionary biology to contemporary environmental issues.

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NEW WORLD ARCHAEOLOGY

Paleoindian settlement of the high-altitude Peruvian Andes

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Study of human adaptation to extreme environments is important for understanding our cultural and genetic capacity for survival. The Pucuncho Basin in the southern Peruvian Andes contains the highest-altitude Pleistocene archaeological sites yet identified in the world, about 900 meters above confidently dated contemporary sites. The Pucuncho workshop site [4355 meters above sea level (masl)] includes two fishtail projectile points, which date to about 12.8 to 11.5 thousand years ago (ka). Cuncaicha rock shelter (4480 masl) has a robust, well-preserved, and well-dated occupation sequence spanning the past 12.4 thousand years (ky), with 21 dates older than 11.5 ka. Our results demonstrate that despite cold temperatures and low-oxygen conditions, hunter-gatherers colonized extreme high-altitude Andean environments in the Terminal Pleistocene, within about 2 ky of the initial entry of humans to South America.

Human settlement of high-altitude mountains and plateaus is among the most recent of our species' biogeographic expansions. Earth's highest-altitude lands, located in the Tibetan and Andean regions, pose numerous physiological challenges, including hypoxia (low-oxygen conditions), high solar radiation, cold temperatures, and high energetic costs of subsistence (*1*). These conditions are especially prevalent in the treeless landscapes higher than 4000 meters above sea level (masl), with little fuel for campfires, twice the sea-level caloric intake needed to maintain normal metabolic function (*2*), and O$_2$ partial pressure less than 60% that at sea level (*1*). Current archaeological models (*3*) emphasize these challenges to explain a lack of pre-Holocene [>11.5 thousand years ago (ka)] (*4*) archaeological evidence above 4000 masl on the Tibetan (*5*) and Andean (*6*) Plateaus.

In the Andes, human biogeographic expansion to high-altitude lands likely stemmed from adjacent areas in Peru (*6*), Chile (*7*), and Argentina (*8*) (Fig. 1A). By ~13.5 to 12.1 ka or earlier, foragers had settled the Pacific Coast (*9*–*13*) and the Southern Cone (*14*), and by ~12.7 to 11.3 ka groups occupied caves at ~2600 masl in central Peru (*15*, *16*) and up to 3300 masl in the Atacama Desert of northern Chile (*17*, *18*). In northwest Argentina, multiple sites at 3400 to 3800 masl date to ~12.0 ka, possibly as early as ~12.8 ka (*8*), although most pre-Holocene occupations have only single, unreplicated radiocarbon ages. Above 4000 masl, the earliest known Andean sites (table S1) date from the first millennium of the Holocene (*19*), with widespread occupation after ~9 ka (*6*–*8*) and earliest year-round settlement after ~7.1 ka (*20*).

Whether genetic adaptations or environmental amelioration were necessary for high-altitude

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