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 (22), 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.

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

Typical of solitary anoles (13), *A. carolinensis* habitat use spans from ground to tree crown (14). However, where *A. carolinensis* and *A. sagrei* (or their close relatives) co-occur elsewhere, *A. carolinensis* perch heights higher than *A. sagrei* (13–16). Thus, we used an introduction experiment to test Collette’s prediction (16) 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
and table S4; (22)), 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, (22)). 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; (22)) or with distance between islands (Mantel test; P = 0.15, \(t_{9} = 2.7\), \(P = 0.012\); table S7, (22)). 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 to 1995 are still extant (Fig. 4). Moreover, when they co-occur, the two species interact agonistically (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 hypotheses 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 (12–16); 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 (17). Evolutionary divergence may also arise, however, from selection to reduce
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 (23), 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 brought 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.

**REFERENCES AND NOTES**

12. Information on materials and methods is available on Science Online.

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**SUPPLEMENTARY MATERIALS**

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Materials and Methods

Supplementary Acknowledgments

Figs. S1 and S2

Tables S1 to S7

References (29–43)

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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.

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pecially 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 O2 partial pressure less than 60% that at sea level (J). 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 (9–12) 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 currently 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