

# Convergent Phenotypic Evolution despite Contrasting Demographic Histories in the Fauna of White Sands\*

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**ABSTRACT:** When are evolutionary outcomes predictable? Cases of convergent evolution can shed light on when, why, and how different species exhibit shared evolutionary trajectories. In particular, studying diverse species in a common environment can illuminate how different factors facilitate or constrain adaptive evolution. Here we integrate studies of pattern and process in the fauna at White Sands (New Mexico) to understand the determinants of convergent evolution. Numerous animal species at White Sands exhibit phenotypic convergence in response to a novel—and shared—selective environment: geologically young gypsum dunes. We synthesize 15 years of research on White Sands lizards to assess the contribution of natural selection, genetic architecture, and population demography to patterns of phenotypic evolution. We also present new data for two species of White Sands arthropods, *Ammobaenetes arenicolus* and *Habronattus ustulatus*. Overall, we find dramatic phenotypic convergence across diverse species at White Sands. Although the direction of phenotypic response is parallel, the magnitude of phenotypic response varies among species. We also find that species exhibit strikingly different demographic patterns across the ecotone. The species with the most genetic structure between White Sands and dark-soil populations generally exhibit the least phenotypic divergence, suggesting population demography as a key modulator of adaptation. Comparative studies are particularly important for understanding the determinants of convergence in natural systems.

**Keywords:** White Sands, convergent evolution, jumping spiders, sand-treader crickets, restriction site-associated DNA sequencing.

Understanding the factors that predict evolutionary response to natural selection is a central goal of evolutionary biology. Instances of convergent evolution—the independent evolution of phenotypic similarity in different lineages—provide unparalleled opportunities to study the mechanisms of adaptive trait evolution. Ultimately, whether different species exhibit a similar evolutionary response depends critically on three interacting determinants (reviewed in Rosenblum et al. 2014): (1) natural selection (e.g., whether the mode, strength, and dimensionality of selection is similar across species), (2) genetic architecture of adaptive traits (e.g., whether heritability, mutational effect sizes, and patterns of epistasis are parallel across species), and (3) population demography (e.g., whether population size, patterns of population structure, and dynamics of gene flow are similar across species).

A key challenge for understanding evolutionary predictability—even for cases of convergent evolution—is disentangling the factors that can promote or hinder adaptive trait evolution. When different lineages in different environments are compared, patterns of phenotypic evolution can seem idiosyncratic, and it can be difficult to distinguish the contributions of selection, demography, and genomic architecture to observed patterns. In contrast, cases of repeated evolution within a single community provide exciting opportunities to differentiate among the determinants of adaptive evolution. When distantly related species exhibit similar phenotypic responses in a shared environment, we can address more nuanced hypotheses about evolutionary predictability.

Here, we integrate studies of pattern and process in the White Sands system to understand the factors that promote and hinder convergent evolution. We first synthesize what we have learned about the patterns of convergent evolution—and the mechanisms influencing that pattern—from 15 years of work on White Sands lizards. We then present new data on two invertebrate species as a next step toward a community-scale synthesis. Finally, we highlight outstanding questions about convergent evolution at White Sands, with particular attention to the interplay among natural se-

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lection, population demography, and genomic architecture. Throughout, we use a pattern-based definition of convergent evolution: the independent evolution of phenotypic similarity in different lineages. Defining convergence as a pattern—observed at the phenotypic level—allows us to be more explicit as we endeavor to link process to pattern, mechanism to outcome, and cause to consequence (reviewed in Rosenblum et al. 2014 and Stayton 2015).

### White Sands as a Stage for Convergent Evolution

White Sands is a striking and geologically recent formation in south-central New Mexico. The expansive gypsum dune system formed after the Last Glacial Maximum, with the bulk of the sedimentation deposition in the past 2,000–7,000 years (Langford 2003; Kocurek et al. 2007). At ~650 km<sup>2</sup>, White Sands is the largest gypsum dune field in the world. The gypsum sands contrast dramatically with the brown soils of the surrounding Chihuahuan Desert, creating a divergent selective environment. Many diverse animal species have colonized White Sands and have convergently evolved blanched coloration in the dune habitat (fig. 1).

The best-studied example of phenotypic convergence at White Sands is in the lizard fauna. The three lizard species that inhabit the heart of the dunes (*Sceloporus cowlesi* [Eastern fence lizard], *Holbrookia maculata* [lesser earless lizard], and *Aspidoscelis inornata* [little striped whiptail]) all exhibit dramatically blanched dorsal coloration. In contrast, populations of all three species exhibit darker dorsal coloration in the rest of their ranges, typically similar to local substrate colors (Degenhardt et al. 1996). The White Sands lizards exhibit similar general patterns of color evolution. In all three species, the change in coloration is in the same direction and is explained primarily by the brightness aspect of color (i.e., changes in brightness explain >80% of the interpopulation variation in color; Rosenblum 2006). Evolution of dorsal brightness is not only in the same direction across species but also of roughly similar magnitude across species (Rosenblum 2006; Rosenblum and Harmon 2011). While explaining less of total variation in dorsal color, changes in the hue and chroma aspects of coloration also trend in the same direction for all three species (Rosenblum 2006; Robertson and Rosenblum 2009).

In addition to dorsal color variation, sexual-signaling patches are also significantly different in color between dark and light lizards in all three species (Robertson and Rosenblum 2009). These differences are not consistent across species, which is unsurprising, given that the location, color, and use of sexual-signaling color patches vary across species (e.g., blue ventral color in male *S. cowlesi*, seasonal orange throat color in female *H. maculata*, and blue head color of male *A. inornata*;

Degenhardt et al. 1996). Differences in sexual-signaling color patches between dark and light color morphs could contribute to observed preference for local mates in White Sands *S. cowlesi* and *H. maculata* (Rosenblum 2008; Hardwick et al. 2013), but the potential for incipient speciation in White Sands lizards is outside the scope of our focus here on convergent evolution.

In addition to convergent evolution of coloration in White Sands lizards, the three lizard species also exhibit shifts in a variety of other phenotypes. Although detailed studies of heritability for these traits have not been conducted, we observe striking differences between dark-soil and White Sands populations in a myriad of traits, including morphology (e.g., body size, limb length; Rosenblum and Harmon 2011), performance (e.g., sprint speed, bite force; Des Roches et al. 2013, 2016), resource use (e.g., diet, microhabitat; Des Roches et al. 2011, 2015, 2016), and behavior (e.g., predator wariness, mate choice; Rosenblum 2008; Robertson et al. 2011; Hardwick et al. 2013). For example, in all three species, White Sands lizards tend to have relatively larger heads size than dark-soil lizards (Rosenblum and Harmon 2011; Des Roches et al. 2016). Larger head size, in turn, correlates with stronger bite force, and bite force is associated with dietary differences between light and dark populations (Des Roches et al. 2016). Specifically, for all three species, White Sands lizards consume a more varied diet than dark-soil lizards (i.e., with stronger bite and wider gape, larger and harder-bodied prey can be included in the diet; e.g., Herrel et al. 2001; Des Roches et al. 2015, 2016).

### Factors Affecting Convergence in White Sands Lizards

Despite strong evidence for convergent evolution of coloration and evidence for similar patterns of change for many other phenotypes in the three White Sands lizard species, patterns are never completely identical across species. We often find that the direction of phenotypic change is concordant but the magnitude of change is different. For example, the lesser earless lizard (*Holbrookia maculata*) often exhibits the most pronounced differences between White Sands and dark-soil habitats, while *Sceloporus cowlesi* often exhibits the least (e.g., Rosenblum and Harmon 2011 for dorsal coloration; Des Roches et al. 2015 for diet; Des Roches et al. 2013 for sprint speed).

What explains similarities and differences among species in the magnitude of divergence across the White Sands ecotone? Here we evaluate the contribution of three key determinants that can influence the direction and magnitude of phenotypic response across species: (1) natural selection, (2) genetic architecture of adaptive traits, and (3) demographic context.



**Figure 1:** Convergent evolution of blanching coloration in White Sands fauna. The top and bottom rows show representative phenotypes from White Sands and dark-soil habitats, respectively. Focal species for this study shown (from left to right): *Sceloporus cowlesi*, *Aspidoscelis inornata*, *Holbrookia maculata*, *Habronattus ustulatus*, and *Ammobaenetes arenicolus*.

*Natural Selection*

The White Sands environment clearly provides a dramatic backdrop for natural selection. Classic observational work on reptile color variation has long posited the adaptive value of substrate matching, especially for small diurnal lizards (e.g., Cott 1940; Norris and Lowe 1964). Experimental studies have also demonstrated the functional importance of substrate matching to avoid predation in a variety of taxa (e.g., Dice 1947; Reed and Janzen 1999). Several experimental studies on lizards (e.g., Luke 1989) and small mammals (e.g., Kaufman 1973) specifically used avian predators that are known to prey on lizards at White Sands, such as the loggerhead shrike and greater roadrunner (E.B.R., personal observation). Our early common-garden rearing experiments also demonstrated that color variation in the White Sands lizards was not explained by ontogenetic or physiological plasticity (Rosenblum 2005). Moreover, there is evidence that all three species experienced ecological release associated with colonizing the gypsum dunes (Des Roches et al. 2011). Specifically, fewer predators and competitors are found in White Sands, relative to dark-soil habitats, and all three focal lizard species correspondingly exhibit higher abundances in the gypsum habitat (i.e., density compensation; Des Roches et al. 2011). Thus, the context for selection at White Sands appears simple: heritable phenotypes, clear optimality criteria, an obvious agent of selection, and decreased predation and interspecific competition.

However, the dynamics of selection might be different for different species, even if they inhabit a common macroenvironment. For example, differences in microhabitat use or behavior can modulate exposure to predation and ultimately the strength of natural selection. To date, we know little about differences among species in the dynamics of selection at White Sands. However, differences among the three lizard species in foraging mode, microhabitat use, and other traits could affect dynamics of natural selection (e.g., Dixon 1967). For example, *Aspidoscelis inornata* is an active forager, while *H. maculata* and *S. cowlesi* are sit-and-wait predators (e.g., Degenhardt et al. 1996). Further, *H. maculata* typically uses open, unvegetated microhabitat, while *S. cowlesi* is more commonly found in vegetated microhabitat (e.g., Hager 2001). Thus, it is possible, for example, that selection has been stronger for optimal substrate matching in *H. maculata*, which would be consistent with the stronger phenotypic response in this species.

Explicit tests are required to understand whether dynamics of selection differ among species at White Sands. Our initial efforts to quantify selection at White Sands involved conducting large-scale enclosure experiments. We constructed replicated 100-m<sup>2</sup> enclosures in the natural gypsum habitat (Hardwick et al. 2015). We then painted dozens of White Sands *H. maculata* to match the average dorsal color of the

White Sands population and the dark-soil population. We released painted lizards into the enclosures and scored survival of substrate-matched versus that of substrate-unmatched lizards. These experiments helped confirm the activity of avian predation at White Sands but also revealed differences in lizard survival rates across relatively fine spatial and temporal scales and also different survival patterns for males and females. An alternative promising approach is the use of mark-recapture studies to assess differences in strength of selection across species. We conducted a multiyear effort to mark lizards with elastomer tags and assess traits correlated with survival in *S. cowlesi* (Des Roches et al. 2017), and comparison with a similar *H. maculata* data set (S. Des Roches and E. B. Rosenblum, unpublished data) promises to shed further light on differences in dynamics of selection among species. Ultimately, the observational and experimental approaches will complement each other in the effort to understand whether White Sands species experience different selection pressures despite sharing a common environment.

*Genetic Architecture*

Difference among species in the genetic architecture of functionally relevant traits can influence species' response to selection. Many aspects of genetic architecture can influence the probability of convergent evolution at the phenotypic level and the probability that similar genetic mechanisms underlie phenotypic convergence (reviewed in Rosenblum et al. 2014).

For White Sands lizards, convergent evolution of blanched coloration is the most obvious and tractable trait for genetic dissection. Our early candidate gene studies revealed mutations associated with blanched color in all three lizard species in the *melanocortin-1 receptor (Mcl1r)* gene (Rosenblum et al. 2004). The protein produced by *Mcl1r* is a key player in the vertebrate melanin synthesis pathway, and mutations in *Mcl1r* are known to be associated with color variation in a variety of other systems (e.g., Barsh 1996; Manceau et al. 2010). Our early work showed a strong statistical association between blanched coloration and a single *Mcl1r* mutation in each of the three White Sands lizards. All three mutations lead to amino acid substitutions, and all three substitutions occur in a transmembrane region of the protein, which is important for ligand binding, signal transduction, and structural integrity of the receptor. Our subsequent functional assays confirmed that the *Mcl1r* mutations in two of the three species (*S. cowlesi* and *A. inornata*) have important functional effects leading to decreased melanin production (i.e., by reducing receptor integration in *S. cowlesi* and reducing receptor signaling in *A. inornata*; Rosenblum et al. 2010). Although data are less conclusive for the third species (*H. maculata*), we have not ruled out a role for *Mcl1r* in color variation in this species.

The molecular signature of selection at and around the *Mcl1r* gene is also striking—and similar—for *S. cowlesi* and *A. inornata*. We recently obtained population-level sequence capture data for a ~40-kb window of the chromosomal region around the *Mcl1r* gene (the gene itself is a single exon <1 kb in length). We found no evidence for selection around *Mcl1r* in dark-soil populations of *S. cowlesi* and *A. inornata*, but we found strong evidence for selection around *Mcl1r* in White Sands populations of these species (Laurent et al. 2016). Moreover, estimates of the age of the blanched allele at White Sands were remarkably young and similar across species (i.e., 1,200 and 900 years for *S. cowlesi* and *A. inornata*, respectively; Laurent et al. 2016). Thus, there are noteworthy mechanistic similarities underlying convergent color evolution in at least two of the lizard species. Mutations at the same gene appear to have swept through the populations during a similar time period, consistent with the age of the White Sands formation itself.

In addition to similarities in genetic architecture of coloration in White Sands lizards, we find several important differences across species. One intriguing difference is the dominance of the blanched *Mcl1r* allele in *S. cowlesi* but not in *A. inornata*. Allele frequencies in natural populations, patterns of association between color phenotype and different genotypic classes, and functional studies all suggest that the blanched allele is dominant in *S. cowlesi* but recessive in *A. inornata* (Rosenblum et al. 2010). Although both dominant and recessive alleles contribute to adaptation in natural systems, allelic dominance can affect the visibility of adaptive alleles to selection, the likelihood of maladaptive gene swamping via gene flow, and ultimately the probability of fixation (e.g., Orr and Betancourt 2001; Nuismer et al. 2012). The consequences of differences in allelic dominance on the adaptive trajectories of *S. cowlesi* and *A. inornata* require further work, as does understanding other genes that contribute to convergent phenotypic evolution in the novel gypsum habitat. Variation at *Mcl1r* cannot explain all observed color variation in the White Sands system, suggesting that other genes are also involved in color variation. Moreover, we are still working to understand the molecular basis of convergent traits other than color. Ultimately, identifying the genes and gene interactions that underlie convergence at White Sands will allow us to understand how the genetic architecture of adaptive traits influences the direction and magnitude of evolutionary change across species.

### Population Demography

Differences in underlying population demography can also contribute to different evolutionary outcomes across species. A number of demographic factors—such as population size, time since colonization, and rates of gene flow—have likely influenced species response to natural selection at White

Sands. Moreover, differences among species in population demography may help explain differences among species in magnitude of evolutionary change across the ecotone.

Even our earliest molecular data suggested dramatic differences in underlying population demography among the three White Sands lizard species. Early mitochondrial data for White Sands and dark-soil populations demonstrated that patterns of population structure were different across species (Rosenblum 2006). For example, an analysis of molecular variance showed the three lizard species on a spectrum from nearly complete genetic separation between dark and light populations of *H. maculata* ( $\Phi_{ST} = 0.82$ ) to nearly complete panmixis in *A. inornata* ( $\Phi_{ST} = 0.09$ ), with intermediate structure observed for *S. cowlesi* ( $\Phi_{ST} = 0.54$ ). In the past decade, we sampled additional populations and additional regions of the genome. Our first analyses with multi-locus nuclear data (~200 single-nucleotide polymorphisms [SNPs] for *S. cowlesi* and ~50 amplified fragment length polymorphism bands for *H. maculata* and *A. inornata*) largely supported the mitochondrial patterns (Rosenblum et al. 2007; Rosenblum and Harmon 2011), again suggesting that blanched coloration could evolve under very different demographic scenarios. Our most recent data sets that rely on broader genomic sampling (i.e., >20,000 SNPs for *S. cowlesi* and >13,000 SNPs for *A. inornata*) show that adding data improves our ability to discriminate genetically among populations but that differences in underlying population demography remain among species (Laurent et al. 2016). Specifically, the inferred split time between light and dark populations was younger for *A. inornata* than for *S. cowlesi*, and there was stronger evidence for ongoing migration after colonization for *S. cowlesi* (Laurent et al. 2016).

Our data point to the possibility that gene flow may constrain local adaptation at White Sands. For example, we have the most consistent and conclusive evidence for ongoing gene flow across the White Sands ecotone in *S. cowlesi* (Rosenblum et al. 2007; Rosenblum and Harmon 2011; Laurent et al. 2016). *Sceloporus cowlesi* is also the species that tends to exhibit the least phenotypic divergence across the ecotone (e.g., for color, body size, performance, and diet; Rosenblum 2006; Rosenblum and Harmon 2011; Des Roches et al. 2013, 2015, 2016). Ultimately, understanding the relationship between gene flow and local adaptation will be facilitated by continued sampling of dark-soil populations to refine our understanding of the ancestry, time of colonization, and dynamics of ongoing gene flow for the White Sands populations.

### New Insights from New Data: White Sands Arthropods

Thus far we have focused on convergent evolution in the White Sands lizard fauna, but several additional—and more distantly related—species also exhibit blanched phenotypes

in the gypsum habitat. Here we present new data on two other dramatic examples of phenotypic convergence associated with the colonization of White Sands in the terrestrial invertebrate fauna: the sand-treader cricket *Ammobaenetes arenicolus* (Strohecker 1947) and the jumping spider *Habronattus ustulatus* (Griswold 1979). Both species are characterized by pale forms at White Sands and darker forms in the surrounding Chihuahuan Desert, convergent with the pattern observed for the lizards (fig. 1). By increasing the phylogenetic breadth of our work, we can add generality to understanding the factors that influence the direction and magnitude of evolutionary response across a shared ecotone.

We compared sand-treader crickets and jumping spiders from White Sands to those from nearby dark-soil sites. To understand phenotypic response across the ecotone in these species, we quantified coloration of the dorsal body surface, using spectrophotometry and photographic analysis. To understand the demographic history for these populations, we collected genetic data, including thousands of loci obtained with a double-digest restriction site-associated DNA sequencing (RADseq) approach and the mitochondrial *cytochrome c oxidase subunit I (COI)* gene. Sampling and methodological details are presented in appendix A, and detailed results are presented in appendix B (apps. A, B available online). Here we highlight key findings that relate to and extend our previous work on White Sands lizards.

#### *Arthropod Phenotypic Convergence*

Consistent with patterns we have previously described for White Sands lizards (Rosenblum 2006; Rosenblum and Harmon 2011), we found strong evidence for phenotypic convergence in the two lineages of terrestrial invertebrates. Populations of the sand-treader cricket *A. arenicolus* and the jumping spider *H. ustulatus* at White Sands exhibit significantly lighter dorsal body coloration than populations in the surrounding Chihuahuan Desert (fig. 2). Although both invertebrate species exhibit the same direction of phenotypic change, the magnitude of color divergence between White Sands and dark-soil individuals differs. Specifically, the spiders exhibit less divergence in dorsal coloration than the crickets in comparisons of White Sands to dark-soil populations (fig. 2). The spiders also exhibit sexual dichromatism, while the crickets do not. Specifically, both males and females are lighter in coloration at White Sands for both species, but male spiders are significantly darker than female spiders in both habitats (fig. 2).

Similar to the lizards in this system, natural selection for substrate matching is the most likely explanation for blanched coloration in White Sands invertebrates. Both *A. arenicolus* and *H. ustulatus* spend time exposed on the dunes. Jumping spiders are diurnal and active predators of other terrestrial invertebrates (Foelix 1982; Griswold 1987), and they are

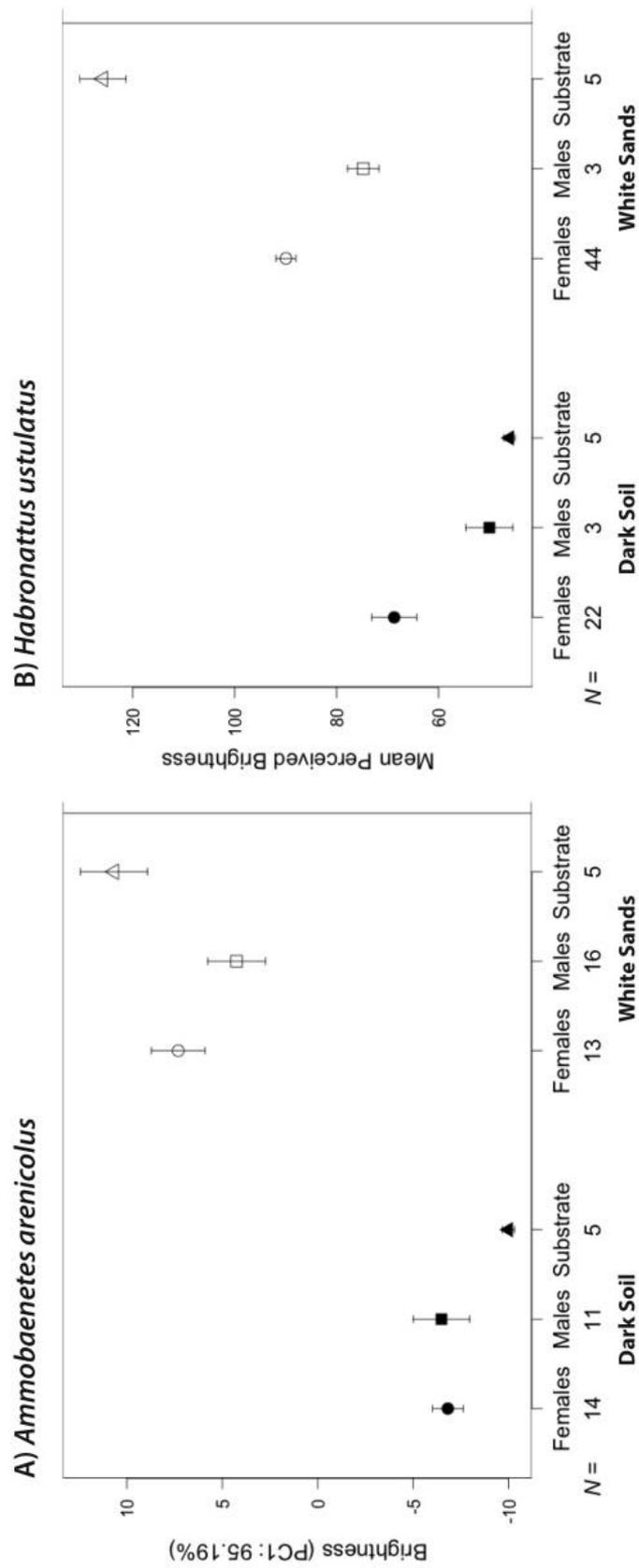
most commonly found in low vegetation or on sandy substrate near vegetative cover at White Sands. Sand-treader crickets burrow in the daytime and emerge to forage at night (Weissman 1997), and they are commonly found near their burrows at the base of the sand dunes, typically in areas with sparse vegetation cover (E.B.R. and C.E.P., personal observation). Despite differences in activity period, both species are likely targeted by a range of visually oriented predators. Therefore, dorsal color variation could be linked to selection for crypsis in *A. arenicolus* and *H. ustulatus*, as has been found in numerous other animal species (e.g., Vignieri et al. 2010). Alternatively, dorsal color variation can serve roles in thermoregulation, mate choice, aggression, and immunity (e.g., Horth 2003; Fedorka et al. 2013; Roulin 2016). However, most of these alternatives have little intuitive support (e.g., because ambient and substrate temperatures are typically lower at White Sands than in the surrounding Chihuahuan Desert [Hager 2000], a thermoregulatory hypothesis would predict the opposite patterns, where darker body color would be favored in the gypsum habitat). Although natural selection for crypsis likely explains color differences across populations, sexual selection may play a role within populations, particularly for the spiders, which—like the White Sands lizards—exhibit some sexual dichromatism.

If dynamics of selection differ between the two invertebrate species, there could be an adaptive explanation for differences in phenotypic patterns. However, additional observational and experimental studies will be required to assess whether differences between the species (or between the sexes) in habitat use, life history, and exposure to predation may have contributed to differences in phenotypic patterns across the ecotone. Experimental studies will also be particularly useful for assessing the potential for phenotypic plasticity to contribute to color variation in *A. arenicolus* and *H. ustulatus* and for identifying genes contributing to color variation in these species. Although both species are relatively difficult to breed in the lab, anecdotally we found that baby spiders born in the lab from White Sands mothers were blanched in color.

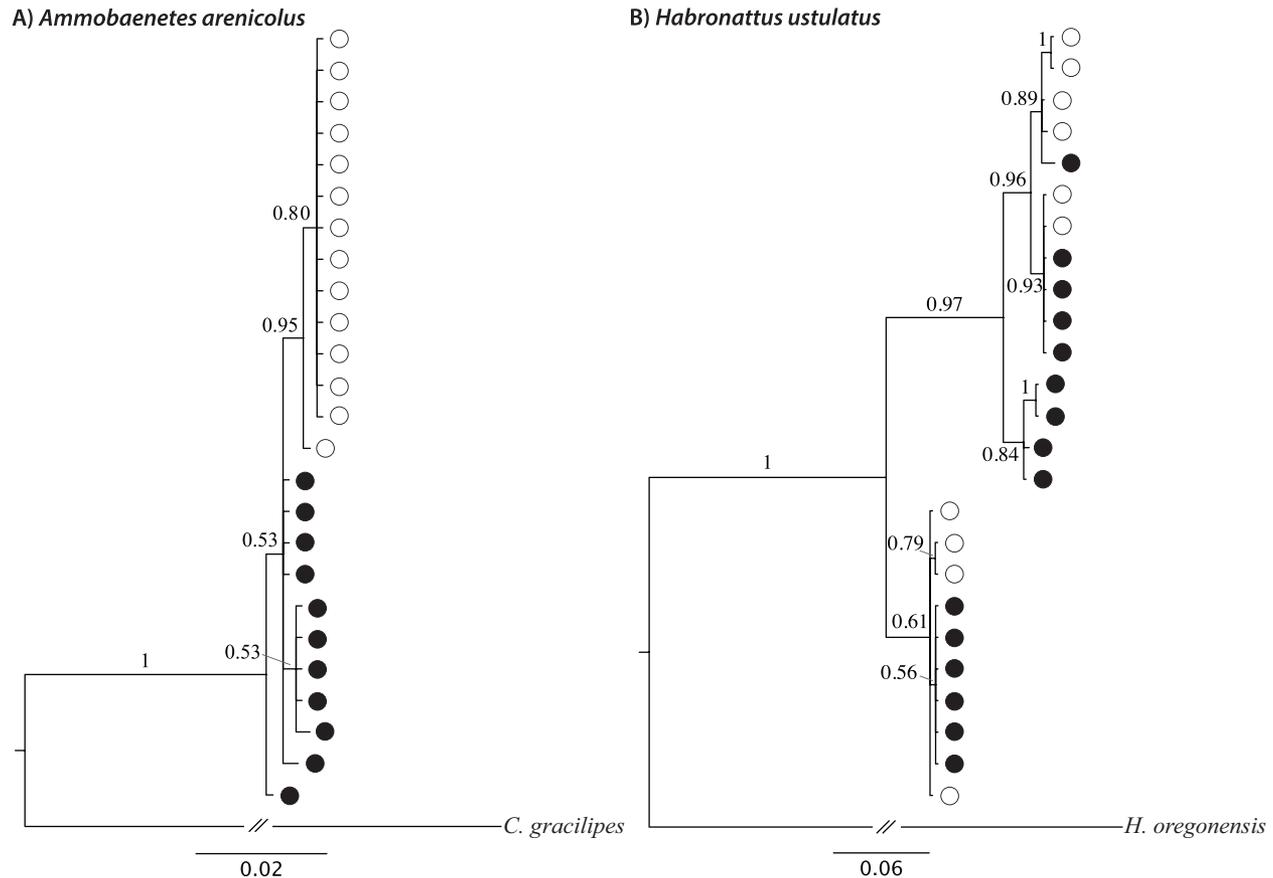
#### *Arthropod Demographic History*

Another possible explanation for differences in phenotypic response across the White Sands ecotone is differences in underlying demography (e.g., population size, colonization history, contemporary patterns of gene flow). Convergence in dorsal coloration is accompanied by conspicuously different demographic histories in *A. arenicolus* and *H. ustulatus*.

The sand-treader cricket *A. arenicolus* exhibits strong population structure, while the jumping spider *H. ustulatus* exhibits little genetic differentiation across the White Sands ecotone. The cricket mitochondrial gene tree shows a well-supported monophyletic White Sands clade (fig. 3), and the



**Figure 2:** Dorsal color variation for *Ammobaeetes arenicolus* (A) and *Habronattus ustulatus* (B): mean dorsal color (and standard error of the mean) for White Sands (open symbols) and dark-soil (closed symbols) samples. Circles, squares, and triangles represent female, male, and substrate samples, respectively. Note that Y-axes differ because color was quantified differently for the two species (see “Color Quantification” in app. A, available online). PC1 = principal component 1.



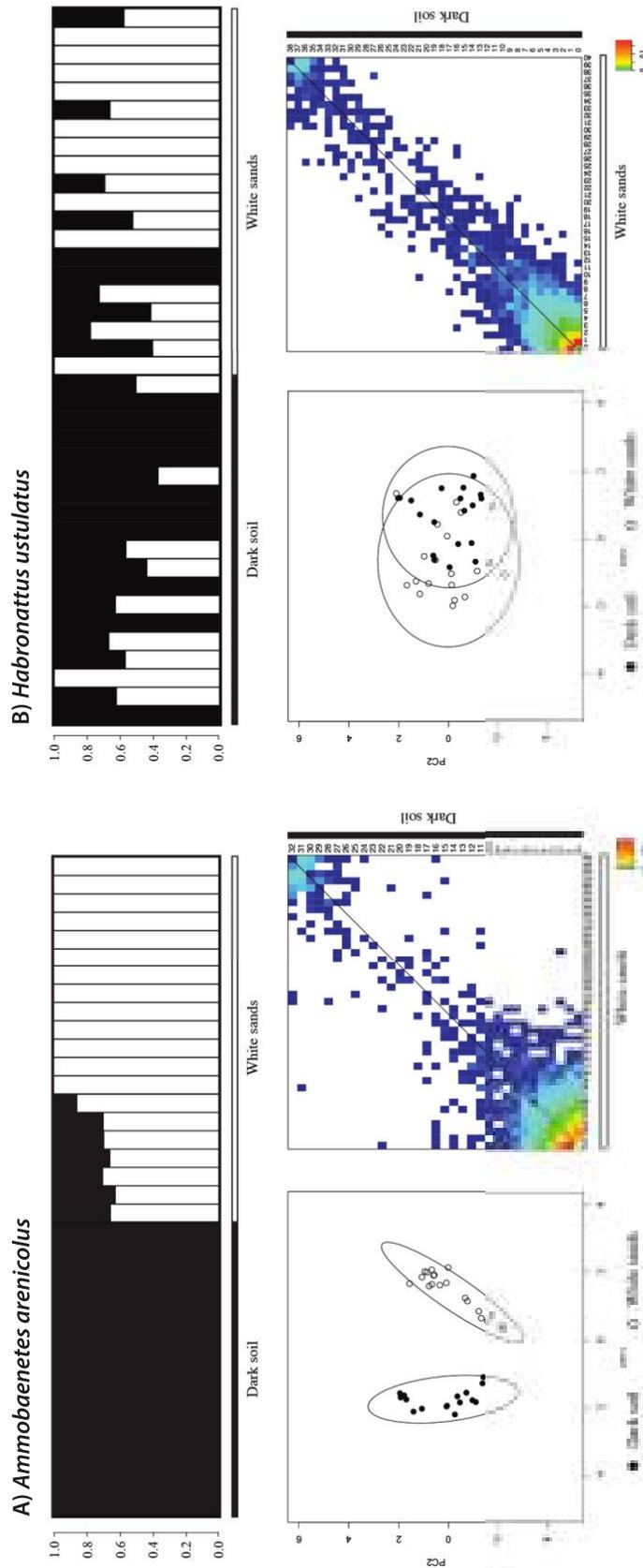
**Figure 3:** Contrasting demographic patterns based on mitochondrial *cytochrome c oxidase subunit I* gene sequences for *Ammobaenetes arenicolus* (A) and *Habronattus ustulatus* (B): Bayesian inference, with numbers at nodes representing posterior probabilities. The branches for the outgroup species are shortened by half, indicated by the “//” symbol. Open and filled symbols represent samples collected in White Sands and dark-soil habitats, respectively.

RADseq data show strong population structure, with White Sands and dark-soil individuals clearly in separate genetic clusters (fig. 4). In contrast, the spider mitochondrial gene tree shows no clear clustering by habitat (fig. 3). Although there is support for multiple clades in the spider tree, these clades contain both White Sands and dark-soil individuals (with no substructure based on dark-soil collecting locality). Consistent with the mitochondrial data, the spider RADseq data show largely overlapping clusters of White Sands and dark-soil individuals, with little structuring of genetic variation by habitat (fig. 4).

Metrics of population differentiation also show strong differences in genetic patterns between the spider and cricket data sets. For the mitochondrial data set,  $F_{ST}$  is more than an order of magnitude higher for the crickets ( $F_{ST} = 0.45$ ) than for the spiders ( $F_{ST} = 0.03$ ; table 1). Moreover, the mitochondrial data suggest dramatically reduced diversity in the White Sands cricket population but not in the spider population. For the crickets, both nucleotide diversity ( $\pi$ )

and Watterson's  $\theta$  are more than an order of magnitude smaller for the White Sands population than for the dark-soil population (table 1), whereas for the spiders,  $\pi$  and  $\theta$  are high and comparable for the White Sands and dark-soil populations (table 1). Mitochondrial nucleotide diversity is more than two orders of magnitude higher in the White Sands spiders than in the White Sands crickets. Mitochondrial and RADseq data give concordant results in the spiders but show slightly different patterns in the crickets. Specifically, for the crickets,  $\pi$  and  $\theta$  are substantially higher and  $F_{ST}$  is substantially lower for the RADseq data set than for the mitochondrial data set, but both data sets indicate much stronger population structure for the crickets than for the spiders.

Our molecular results are consistent with different demographic scenarios in the two focal invertebrate species. For the crickets, our results are consistent with a simple colonization history (likely with a reduced population size), limited ongoing gene flow, and strong genetic divergence



**Figure 4:** Contrasting patterns of population structure based on restriction site-associated DNA sequencing (RADseq) data for *Ammobaenetes arenicolus* (A) and *Habronattus ustulatus* (B). A, For *A. arenicolus*, the population structure plot (top) for  $K = 2$  shows strong population structure. Each individual is represented by a vertical bar and labeled as dark soil (black horizontal bar) or White Sands (white horizontal bar). The genetic principal-component analysis (PCA) plot (bottom left) shows no overlap between dark-soil (filled circles) and White Sands (open circles) individuals. Ellipses represent 95% confidence intervals for the dark-soil and White Sands populations. The joint site frequency spectrum (bottom right) shows only loosely correlated allele frequencies. B, For *H. ustulatus*, the population structure plot (top) shows less structure and more admixture between the two populations for  $K = 2$ . There is substantial overlap between the dark-soil and White Sands individuals in the genetic PCA plot (bottom left), and the joint site frequency spectrum shows strongly correlated allele frequencies (bottom right).

**Table 1:** Estimates of the nucleotide diversity ( $\pi$ ), Watterson's theta ( $\theta$ ), and  $F_{ST}$  for the mitochondrial and nuclear data sets

Data set, measure	<i>Ammobaenetes arenicolus</i>		<i>Habronattus ustulatus</i>	
	Dark soil	White Sands	Dark soil	White Sands
COI:				
$\pi$	.0030	.0002	.0294	.0261
$\theta$	.0048	.0003	.0177	.0154
$F_{ST}$	.4541		.0295	
RAD sites:				
$\pi$	.0213	.0198	.0210	.0220
$\theta$	.0316	.0215	.0336	.0347
$F_{ST}$	.0312		.0140	

Note: COI = cytochrome c oxidase subunit I gene; RAD = restriction site-associated DNA sequencing.

across habitats. For the spiders, our results suggest admixture across the White Sands ecotone, and different scenarios could underlie the lack of population structure, including multiple colonization events, a large recent founding population with substantial genetic variation, and high levels of ongoing gene flow. Our results are consistent with patterns observed in other groups of jumping spiders. Hybridization, introgression, interspecific gene flow, and incomplete lineage sorting are not uncommon in the *Habronattus* clade, and gene trees often fail to resolve geographic or phenotypic groups (e.g., Maddison and McMahon 2000; Masta 2000; Hedin and Lowder 2009). To refine our understanding of the relationship between initial colonization history and ongoing gene flow in these species, we will need more thorough sampling throughout the Tularosa Basin (i.e., within species replication) and more explicit modeling of alternative demographic scenarios.

### Convergence across the Community at White Sands

Cases of convergent evolution have long been used as evidence that species can exhibit similar evolutionary responses when exposed to comparable selection pressures (e.g., Arendt and Reznick 2008; Losos 2011; McGhee 2011; Wake et al. 2011; Conte et al. 2012). However, myriad factors influence whether species will adapt along parallel trajectories. Studying evolutionary outcomes across diverse lineages provides replicated variation in factors that can influence adaptive convergence (e.g., trait heritability, population size, gene flow, behavior). Further, comparisons across species in a single environment (e.g., where colonization time is geologically constrained and abiotic context is shared) can reduce complexity and analytical noise. Thus, we can better understand whether adaptation is constrained in similar ways across diverse species and which key factors modulate evolutionary response.

Our work thus far on White Sands lizards and arthropods shows both shared and unique patterns across species ex-

posed to a common ecotone. While the direction of color evolution is typically convergent in the White Sands fauna, the magnitude of phenotypic change varies across species. Moreover, differences in phenotypic response appear to correlate with variation in underlying demographic patterns. Specifically, species with more genetic differentiation across the White Sands ecotone (e.g., *Holbrookia maculata* and *Ammobaenetes arenicolus*) typically exhibit more phenotypic differentiation. Thus, population demography appears to be an important modulator of phenotypic evolution in this system. Our research also suggests that subtle variation in the dynamics of natural selection and differences in genomic architecture across species can influence patterns of phenotypic convergence.

Moving forward, the White Sands system can be used to address important outstanding questions about the interplay among natural selection, genetic architecture, and population demography. For example, what is the role of phenotypic plasticity in promoting or hindering phenotypic divergence? How do different species experience the same environment? How similar are underlying molecular and functional mechanisms of adaptation in closely versus distantly related species? How do levels of gene flow and strength of selection interact to determine phenotypic outcome? What null expectations are most appropriate to use when studying convergent evolution?

Developing a general understanding of the factors that facilitate and constrain convergent evolution at White Sands will be promoted by studying additional species. Other animal species exhibit blanched forms on the dunes and can be integrated into a broader community-scale study. For example, the moth *Euxoa misturata* and the pocket mouse *Perognathus flavescens* also have blanched forms in the gypsum habitat that contrast with nearby dark forms. In addition to these dramatic examples, White Sands is home to multiple endemic species of Lepidoptera that are pale compared to close relatives (Metzler 2014).

Although White Sands is a relatively depauperate ecosystem, the species that have survived on the dunes typically exhibit thriving populations. For example in the herpetofauna, 28 species of reptiles and amphibians are found in the immediate vicinity (Prival and Goode 2005), but only three of these species are found commonly in the heart of the dunes. These three species exhibit dramatic density compensation, with much higher local population densities at White Sands than in nearby dark-soil environments (Des Roches et al. 2011). Relatively high densities allow for a diversity of research approaches to be applied at White Sands. Integrating natural history studies, manipulative lab and field experiments, detailed phenotypic analysis, genomic sequencing, and demographic modeling across the entire White Sands community will ultimately shed light on the factors governing the probability—and the degree—of convergent evolution in natural systems.

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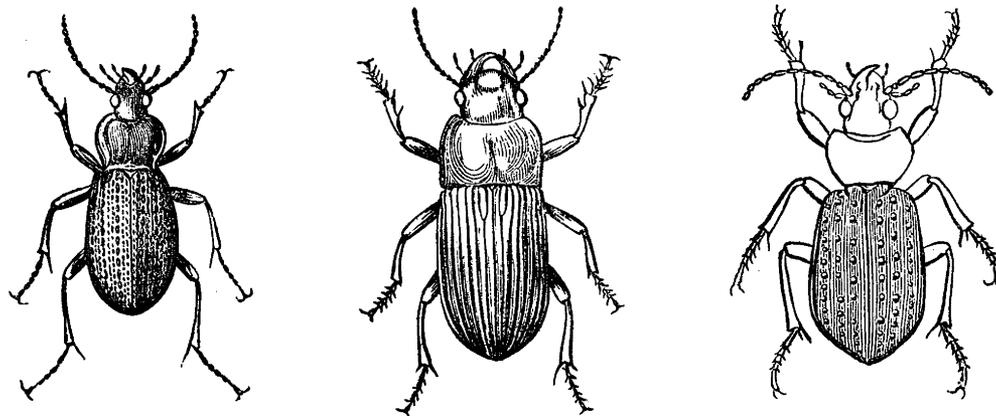
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“The farmer should know his true insect friends as well as his insect foes. We introduce to our readers a large family of ground-beetles (*Carabidæ*, from *Carabus*, the name of the typical genus) which prey on those insects largely injurious to crops.” From “Entomological Calendar” (*The American Naturalist*, 1868, 2:110–111).