Intercontinental community convergence of ecology and morphology in desert lizards

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Evolutionary ecologists have long debated the extent to which communities in similar environments but different geographic regions exhibit convergence. On the one hand, if species' adaptations and community structure are determined by environmental features, convergence would be expected. However, if historical contingencies have long-lasting effects convergence would be unlikely. Most studies to date have emphasized the differences between communities in similar environments and little quantitative evidence for convergence exists. The application of comparative phylogenetic methods to ecological studies provides an opportunity to further investigate hypotheses of convergence. We compared the evolutionary patterns of structural ecology and morphology of 42 species of iguanian lizards from deserts of Australia and North America. Using a comparative approach, we found that evolutionary convergence of ecology and morphology occurs both in overall, community-wide patterns and in terms of pairs of highly similar intercontinental pairs of species. This result indicates that in these desert lizards, deterministic adaptive evolution shapes community patterns and overrides the historical contingencies unique to particular lineages.

Keywords: convergence; evolution; Agamidae; Iguanidae; historical contingency; community ecology

1. INTRODUCTION

The structure of communities that occur in the same environmental conditions is expected to be similar if the environment drives evolution in predictable directions (MacArthur 1972; Orians & Paine 1983). Nonetheless, most investigations that look for community-level convergence—including studies of plants (Latham & Ricklefs 1993), birds (Ricklefs 1987; Wiens 1991), fish (Winemiller & Pianka 1990), snakes (Cadle & Greene 1993) and lizards (Pianka 1986)—find that the differences that characterize communities in different regions out-weigh the similarities. In fact, examples of community convergence seem mostly restricted to island biotas (e.g. Losos *et al.* 1998; Blackledge & Gillespie 2004; Gillespie 2004), whereas for continental communities, lack of convergence seems the norm.

One likely cause for the failure of communities to converge are historical contingencies, defined as an unpredictable sequence of antecedent states (Gould 1989) that affect both lineages and areas. For example, due to the geographic aspects of diversification, evolutionary lineages are not equally represented in all geographic areas. As a result, communities in different areas are likely to contain species representing different lineages. In turn, these lineages have experienced different evolutionary histories and, thus, exhibit different ecologically relevant traits. The result of these two factors is that the structure of communities in different areas—composed as they are of different lineages—often can be quite distinct, even if the environments they occupy are nearly identical (Losos 1994; Vitt & Pianka 2005).

A classic example is Pianka's study of desert lizard communities across three continents (Pianka 1986). The herpetofaunas of North America, Africa and Australia are dominated by different lizards: e.g. the Varanidae—the family of large and often carnivorous monitor lizards—is species-rich in Australia, represented by several species in Africa, and absent in North America. Similarly, the Gekkonidae and Scincidae are diverse in Australia and Africa, but depauperate in North America. Because lizard families tend to be ecologically distinctive (Pianka & Vitt 2003; Vitt *et al.* 2003; Vitt & Pianka 2005), it is thus not surprising that the structure of lizard communities on different continents varies so greatly (for another herpe-tological example see Cadle & Greene 1993).

Such historical contingencies do not preclude community convergence. Even if entire communities fail to converge due to the presence of different evolutionary lineages, one might still hypothesize that convergence would occur among those lineages that are shared across communities. To examine this idea, we need closely related species that have diversified independently in disparate areas. Moreover, these species must comprise an important element of communities in both areas. The iguanian lizard assemblages of Australian and North American deserts provide an ideal comparison for such an approach. The Agamidae and Iguanidae (following the traditional taxonomy; Macey *et al.* 2000), which occur in the Old and New Worlds, respectively, are sister taxa (comprising the Iguania), and species across this group are generally similar in their morphology (robust, powerful limbs) and behavioural ecology (usually territorial, sit-and-wait foragers). In addition, these groups comprise a significant proportion of the lizard fauna on each continent. Both agamids and iguanids constitute

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Table 1. Summary of study species, where they were found, number measured for morphological characters. (WA, Western Australia; NT, Northern Territory; CA, California; AZ, Arizona.)

species	field sites	N	general habit description
Australia			
Caimanops amphiboluroides	WA	2	arboreal
Ctenophorus caudicinctus	NT, WA	32	saxicolous
Ctenophorus clayi	NT, WA	11	ground-dwelling
Ctenophorus cristatus	WA	25	ground-dwelling
Ctenophorus femoralis	WA	6	ground-dwelling
Ctenophorus fordi	WA	21	ground-dwelling
Ctenophorus isolepis	NT, WA	35	ground-dwelling
Ctenophorus nuchalis	NT, WA	69	ground-dwelling, low perches
Ctenophorus pictus	NT	28	ground-dwelling
Ctenophorus reticulatus	WA	18	ground-dwelling
Ctenophorus salinarum	WA	25	ground-dwelling
Ctenophorus scutulatus	WA	25	ground-dwelling
Diporiphora winneckei	NT	24	arboreal
Lophognathus gilberti	NT	27	arboreal
Lophognathus longirostris	NT	33	semi-arboreal
Moloch horridus	NT, WA	7	ground-dwelling
Pogona vitticeps	NT	18	semi-arboreal
Pogona mitchelli	NT	4	semi-arboreal
Pogona minor	WA	8	semi-arboreal
Tympanocryptis centralis	NT	28	ground-dwelling
Tympanocryptis cephalus	WA	6	ground-dwelling
USA			
Callisaurus draconoides	CA, AZ	51	ground-dwelling
Cophosaurus texanus	AZ	15	ground-dwelling
Crotaphytus collaris	AZ	20	saxicolous
Dipsosaurus dorsalis	CA	45	ground-dwelling
Gambelia wislizenii	CA, AZ	56	ground-dwelling
Holbrookia maculata	AZ	20	ground-dwelling
Phrynosoma cornutum	AZ	22	ground-dwelling
Phrynosoma modestum	AZ	15	ground-dwelling
Phrynosoma platyrhinos	CA	45	ground-dwelling
Phrynosoma solare	AZ	4	ground-dwelling
Sauromalus obesus	CA	16	saxicolous
Sceloporus clarkii	AZ	6	semi-arboreal
Sceloporus jarrovii	AZ	20	ground-dwelling, low perches
Sceloporus magister	CA, AZ	43	semi-arboreal
Sceloporus occidentalis	CA, AZ	15	saxicolous
Sceloporus scalaris	AZ	23	ground-dwelling
Sceloporus virgatus	AZ	23	ground-dwelling
Uma scoparia	CA	36	ground-dwelling
Urosaurus graciosus	CA	12	arboreal
Urosaurus ornatus	AZ	22	ground-dwelling, low perches
Uta stansburiana	CA	31	ground-dwelling, low perches

the only sit-and-wait diurnal lizards in the Australian and North American deserts and they are a numerically important component of the lizard fauna in each desert system (Pianka 1986).

We examined whether convergence has occurred in assemblages of iguanian lizards in Australian and North American deserts. We choose to focus on the evolutionary relationship between locomotor morphology and habitat use. The adaptive basis of correlations between morphology and habitat use has been extensively studied in iguanians (e.g. Herrel *et al.* 2002; Glor *et al.* 2003). Furthermore, performance-based studies have demonstrated an evolutionary functional link between these two sets of traits (Garland & Losos 1994). Two lines of evidence would indicate that community convergence in these traits has occurred—evolution of similar ecology/ morphology patterns across taxa and convergence of pairs

of species between communities. Here we develop and apply new statistical comparative tests for each of these patterns of convergence. Using phylogenetic analyses based on mitochondrial DNA sequence data and micro-habitat and morphology data collected over a five year period, we tested the hypothesis of evolutionary convergence in ecological morphology at both the species and community level.

2. MATERIAL AND METHODS
(a) *Study systems and data collection*
We studied 42 iguanian species: 21 species in the family Agamidae in two desert regions in Australia and 21 species of the Iguanidae in two desert regions of southwestern USA (table 1). In North America, the two study sites used were located in the Mojave Desert (California) and the overlap

region between the Sonoran and Chihuahuan Deserts (southern Arizona and New Mexico). The two Australian study sites are in the interior of the continent: Great Victoria Desert (Western Australia) and central Australian deserts (Northern Territory).

In this study, we use the term 'community' in the broad sense to mean the study of all similar species that occur together. Thus, our use of community is equivalent to what some would call an 'assemblage' (Fauth *et al.* 1996). Focusing exclusively on iguanian lizards is appropriate as we know of no skinks, geckos or other lizards on either continent that are morphologically similar to iguanians. In addition, iguanians are the only diurnal, sit-and-wait predators in both regions of our study (Pianka 1986).

Structural microhabitat characteristics and morphology of species were recorded at the four study areas (see table 1 for sample sizes and localities). The data were recorded by driving or walking throughout each field site from approximately 07.00 to 19.00 h, capturing lizards opportunistically. This method ensured coverage of the entire range of structural microhabitats available. Data were only collected on sunny warm days when lizards could be fully active.

We recorded nine morphological measurements, selected to be relevant to locomotion through an animal's structural habitat (Schulte *et al.* 2004): snout–vent length (SVL); tail length (only individuals with intact tails were included in analyses); pelvis width; humerus length (distance from shoulder to apex of elbow); antebrachium length (distance from elbow apex to centre of wrist); forefoot length (distance from centre of wrist to claw tip of longest toe (IV)); femur length (distance from insertion of hind leg at pelvis to apex of knee); crus length (distance from apex of knee to heel); and hind foot length (distance from heel to claw tip of longest toe (IV)).

We also recorded 10 structural characteristics of the microhabitat surrounding each lizard caught or sighted: (i) visual estimate of per cent canopy cover in a $3 \, \text{m}^2$ radius surrounding lizard; (ii) visual estimate of per cent shrub cover in a $3 \, \text{m}^2$ radius surrounding lizard; (iii) visual estimate of per cent ground and grass cover in a $3 \, \text{m}^2$ radius surrounding lizard; (iv) perch height of lizard in cm; (v) distance to the nearest vegetation in cm; (vi) distance to the nearest shelter in cm (e.g. rock, litter, vegetation, litter); (vii) perch diameter in cm; (viii) visual estimate of percentage cover by rocks less than 50 cm in diameter in a $3 \, \text{m}^2$ radius surrounding lizard; (ix) visual estimate of percentage of cover by rocks greater than 50 cm in diameter in a $3 \, \text{m}^2$ radius surrounding lizard; and (x) visual estimate of percentage of cover by gravel in a $3 \, \text{m}^2$ radius surrounding lizard.

(b) *Phylogenetic relationships*
The phylogeny used is based on 1799 aligned positions of the mitochondrial genome from three protein-coding genes (*ND1*, *ND2* and *COI*) and eight intervening tRNA genes (see Macey *et al.* 2000; Melville *et al.* 2001; Schulte *et al.* 2003 for GenBank accession numbers). Sequence for this region of mitochondrial DNA was not available for *Uma scoparia*; instead its sister species *Uma notata* was used (Wilgenbusch & De Queiroz 2000). Likelihood settings from best-fit model GTR+G+I were selected using Model test v. 3.06, with optimal model parameters of: empirical base frequencies (A=0.426; C=0.314; G=0.063; T=0.197); substitution rates (A : C=0.493; A : G=3.809; A : T=0.660; C : G= 0.357; C : T=4.829; G : T=1.000); gamma shape (0.655);

Table 2. Summary of partial Mantel tests describing relationship between ecology and morphology. (*p*-value is based on permutation test of 9999 randomizations; significant *p*-values are indicated in bold.)

	body size included		body size removed	
	Z	p	Z	p
overall significance value	81.15	**0.012**	103.13	**<0.001**
within Australia	9.93	0.227	15.68	**0.026**
within USA	29.82	**0.005**	34.80	**<0.001**
between continents	41.41	**0.016**	52.68	**<0.001**

and proportion of variable sites (0.139). Maximum likelihood trees were estimated using PAUP* beta version 4.0b4a with no assumption of a molecular clock that resulted in a single trees with a likelihood score of $-\ln L = 25625.31$.

(c) *Statistical analyses*
All morphological variables were log transformed prior to analysis. Arcsine square root transformations were conducted on all ecological variables that were percentages. Normality of all variables was ensured prior to analysis. For both the morphological and the habitat use data sets, we carried out principal components analyses (PCA) using the correlation matrix of the species' means. These axes represent statistically independent axes of ecological and morphological variation. All principal component axes were used in the subsequent analyses.

A hypothesis of community-wide convergence predicts that the relationship between morphology and ecology will be similar in independently evolved and assembled communities. We tested for community-level convergence using a modified version of the Mantel test, a permutation-based test used to compare similarity/dissimilarity matrices. In a traditional Mantel test, one would estimate the correlation between the morphological and ecological difference matrices, while controlling for the effect of the phylogenetic matrix. In this traditional context, the Mantel test statistic Z represents the correlation between ecology and morphology combining comparisons of species both within and between continents. However, community convergence only implies a correlation in the between-continent comparisons of morphology and ecology. Thus, to test this hypothesis, we took advantage of the additive nature of the Mantel statistic by partitioning it into between and within-continent correlations, using the following formula:

$$Z_{\text{total}} = Z_{\text{within North America}} + Z_{\text{within Australia}} + Z_{\text{between continents}}.$$

This partitioning is analogous to the partitioning of between- and within-group distances in an analysis of molecular variance (Excoffier *et al.* 1992). Like that test, our hypothesis concerned the between-group (intercontinental) species pairs; thus, we focused on $Z_{\text{between continents}}$. We assessed the significance of this statistic using a permutational significance test. To do this, we carried out 9999 standard Mantel permutations of the entire matrix. We then calculated $Z_{\text{between continents}}$ for each of these permuted matrices to generate a null distribution. This permutation is statistically equivalent to randomly assigning half of the 42 lizard species to each continent; our test is thus related to
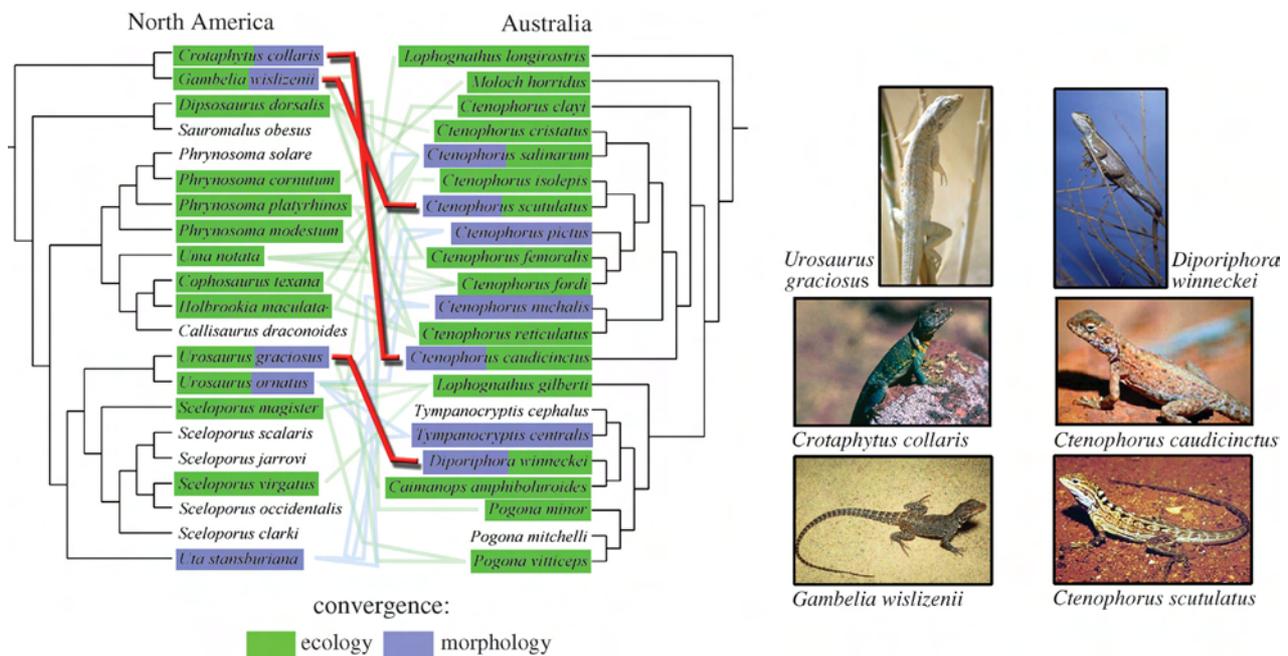
Figure 1. Phylogenetic relationships within iguanian study species using maximum likelihood tree based on 1799 aligned positions of mitochondrial DNA sequence. Species that show significant intercontinental convergence in ecology and/or morphology are highlighted (green and blue, respectively) and lines between species indicate convergent pairs. Three species pairs that are significantly convergent in both ecology and morphology are connected by bold red lines. Images of the three species pairs convergent in both ecology and morphology are shown below the main figure. Images provided by: *Diporiphora winneckei*, Gerald & Buff Corsi, California Academy of Sciences; *Gambelia wislizenii*, John H. Tashjian, California Academy of Sciences; *Ctenophorus scutulatus*, M. Peterson, Western Australia Museum.

the 'pseudocommunity' approach developed by other authors (e.g. Pianka 1986). We compared our actual test statistic to this null distribution to calculate a one-sided p-value, with $p = 1 - ($ rank of actual test-statistic in null distribution$)/($ number of permutations $+ 1)$. A significant between-continent comparison means that, for all cross-continental pairs, species from each continent that are more similar in their ecology also tend to be more similar in their morphology than expected based on the permuted data sets, and thus the ecomorphological structure of the communities is convergent.

To conduct our modified Mantel permutation analysis, we produced three dissimilarity matrices representing the distance between all species pairs in microhabitat use, morphology and phylogenetic relatedness. For the microhabitat and morphological distance matrices, mean factor scores of species from the PCAs of microhabitat and morphological data were used to produce matrices of Euclidean distances between each pair of species in each respective space. A patristic distance matrix was produced from the phylogenetic tree using TREE EDIT V1 (Rambaut & Charleston 2001). A modified Mantel permutation analysis was then carried out using the three data matrices, using the methods described above.

We also identified ecologically and morphologically similar species pairs between continents within a phylogenetic framework. To achieve this, we calculated the Euclidean distance between all pairs of species in the 10-dimensional PCA of morphology or ecology. We then compared these distances to what would be expected under a null model of traits evolving under Brownian motion. To do this, we simulated the data on the phylogeny using this null model, constraining the rate of evolution so that the terminal species (the tips of the phylogeny) had the same variance as the

original data on each PC axis. The distances between all possible pairs of species were calculated and the closest pair of species for each of the 1000 simulations was identified. This provided a null distribution of the smallest morphological or ecological distance expected for a transcontinental species pair. Based on this null distribution, we considered any intercontinental pair of species to be more similar than expected by chance if their degree of similarity fell within the lower 5% tail of the distribution.

We conducted all analyses twice, once with body size (represented by SVL) included and again with body size removed from all variables (ecology and morphology), as the influence of allometry on the convergence of species was uncertain. The effect of SVL was removed from variables by regressing SVL against the variable and using the residuals in further analyses. For the morphological analysis, ln-transformed SVL was regressed against ln-transformed morphological variables of individuals and species means of the residuals were used in the PCA.

3. RESULTS

As predicted by the community convergence hypothesis, Australian and North American desert lizard communities are significantly similar in ecomorphological structure; the similarity in microhabitat occupation of an intercontinental pair of species (i.e. of two species, one from each continent) can be predicted from their morphological similarity, as indicated by a Mantel test controlling for phylogenetic relationships ($Z_{\text{between continents}} = 103.13$, $p < 0.001$). Results from both sets of analyses, with body size either included or removed, were qualitatively equivalent with the same pattern of community convergence (table 2).

Table 3. Summary of intercontinental species pairs, which are significantly similar ecologically and morphologically, within a phylogenetic framework. (The Euclidean distances between all possible pairs of species were calculated and the closest pair of species for each of the 9999 simulations was identified. Probability values were calculated as the number of distances that are smaller than the actual distance, divided by the number of simulations (9999); significant p-values are indicated in bold.)

species pairs		body size included		body size removed	
Australia	USA	Euclidean distance	p	Euclidean distance	p
ecology					
Diporiphora winneckei	*Urosaurus graciosus*	0.61	**<0.001**	0.34	**<0.001**
Ctenophorus caudicinctus	*Crotaphytus collaris*	0.64	**<0.001**	1.12	**0.003**
Ctenophorus salinarum	*Holbrookia maculata*	1.24	**<0.001**	0.85	**<0.001**
Ctenophorus femoralis	*Uma scoparia*	1.41	**<0.001**	0.92	**<0.001**
Ctenophorus fordi	*Uma scoparia*	1.57	**0.001**	1.03	**0.001**
Lophognathus gilberti	*Sceloporus magister*	1.59	**0.001**	1.83	0.134
Ctenophorus salinarum	*Phrynosoma modestum*	1.61	**0.001**	0.85	**<0.001**
Ctenophorus salinarum	*Cophosaurus texanus*	1.61	**0.001**	0.96	**<0.001**
Ctenophorus reticulatus	*Cophosaurus texanus*	1.64	**0.002**	1.03	**0.001**
Ctenophorus scutulatus	*Phrynosoma platyrhinos*	1.77	**0.004**	1.27	**0.006**
Ctenophorus clayi	*Uma scoparia*	1.79	**0.004**	1.18	**0.004**
Ctenophorus reticulatus	*Phrynosoma modestum*	1.81	**0.004**	1.01	**0.001**
Lophognathus longirostris	*Urosaurus ornatus*	1.91	**0.006**	1.20	**0.004**
Ctenophorus pictus	*Uta stansburiana*	1.92	**0.007**	1.63	0.540
Ctenophorus scutulatus	*Dipsosaurus dorsalis*	2.05	**0.011**	1.25	**0.005**
Ctenophorus reticulatus	*Holbrookia maculata*	2.09	**0.012**	1.26	**0.005**
Ctenophorus femoralis	*Phrynosoma platyrhinos*	2.13	**0.015**	1.50	**0.026**
Ctenophorus fordi	*Phrynosoma platyrhinos*	2.14	**0.015**	1.42	**0.016**
Ctenophorus isolepis	*Uma scoparia*	2.14	**0.015**	1.40	**0.015**
Moloch horridus	*Phrynosoma cornutum*	2.19	**0.018**	1.51	**0.027**
Ctenophorus scutulatus	*Gambelia wislizenii*	2.20	**0.019**	1.34	**0.011**
Ctenophorus cristatus	*Dipsosaurus dorsalis*	2.29	**0.027**	1.52	**0.029**
Lophognathus longirostris	*Sceloporus magister*	2.36	**0.035**	1.85	0.137
Ctenophorus cristatus	*Phrynosoma platyrhinos*	2.37	**0.036**	1.62	0.051
Ctenophorus femoralis	*Dipsosaurus dorsalis*	2.41	**0.042**	1.39	**0.014**
Ctenophorus fordi	*Dipsosaurus dorsalis*	2.44	**0.045**	1.36	**0.014**
Caimanops amphiboluroides	*Urosaurus graciosus*	3.90	0.670	0.89	**<0.001**
Pogona vitticeps	*Urosaurus ornatus*	3.36	0.389	1.43	**0.017**
Ctenophorus fordi	*Gambelia wislizenii*	2.88	0.163	1.51	**0.028**
Ctenophorus salinarum	*Dipsosaurus dorsalis*	2.64	0.088	1.55	**0.036**
Ctenophorus femoralis	*Gambelia wislizenii*	2.81	0.137	1.57	**0.041**
Lophognathus gilberti	*Sceloporus virgatus*	2.85	0.155	1.58	**0.041**
Pogona minor	*Dipsosaurus dorsalis*	2.77	0.124	1.58	**0.042**
Lophognathus gilberti	*Urosaurus ornatus*	2.77	0.126	1.60	**0.046**
Ctenophorus reticulatus	*Dipsosaurus dorsalis*	2.86	0.158	1.60	**0.046**
Pogona vitticeps	*Sceloporus magister*	3.28	0.347	1.60	**0.047**
morphology					
Diporiphora winneckei	*Urosaurus graciosus*	0.19	**<0.001**	0.69	**<0.001**
Ctenophorus caudicinctus	*Crotaphytus collaris*	0.35	**<0.001**	0.69	**<0.001**
Ctenophorus pictus	*Uta stansburiana*	0.83	**<0.001**	0.69	**<0.001**
Tympanocryptis centralis	*Uta stansburiana*	1.55	0.125	0.96	**0.015**
Ctenophorus nuchalis	*Urosaurus ornatus*	1.58	0.139	0.98	**0.016**
Tympanocryptis centralis	*Urosaurus ornatus*	1.16	**0.013**	1.07	**0.035**
Ctenophorus salinarum	*Uta stansburiana*	1.29	**0.031**	1.07	**0.036**
Ctenophorus nuchalis	*Uta stansburiana*	1.72	0.239	1.08	**0.039**
Ctenophorus scutulatus	*Gambelia wislizenii*	0.99	**0.003**	1.09	**0.042**
Diporiphora winneckei	*Urosaurus ornatus*	1.29	**0.032**	1.29	0.124
Ctenophorus pictus	*Urosaurus ornatus*	1.32	**0.036**	1.26	0.105

We also investigated whether particular intercontinental species pairs were more convergent in ecology and morphology than would be expected by chance. Using phylogenetic simulations, we demonstrate that nine intercontinental species pairs are more morphologically similar than expected by chance and 32 are more similar in microhabitat occupation than expected by chance; moreover, three species pairs qualified on both counts (figure 1).

When body size was included in the analysis, eight intercontinental species pairs are more morphologically similar than expected by chance and 26 are more similar in microhabitat occupation than expected by chance; the same three species pairs again qualify on both counts (table 3). The three pairs of species that are significantly similar in both ecology and morphology are: *Diporiphora winneckei* and *Urosaurus graciosus* (twig/grass species);

Ctenophorus caudicinctus and *Crotaphytus collaris* (rock-dwelling species); and *Ctenophorus scutulatus* and *Gambelia wislizenii* (open ground-dwelling species).

4. DISCUSSION

Although examples of community convergence have been reported, both in terms of convergence of species' characters and higher-level community attributes (Mooney & Dunn 1970; Mooney 1977; Ben-Moshe et al. 2001), most studies emphasize the dissimilarities among communities that occupy comparable environments on different continents (Pianka 1986; Ricklefs 1987; Winemiller & Pianka 1990; Wiens 1991; Cadle & Greene 1993; Latham & Ricklefs 1993). Such differences, for example, are evident in Pianka's (1986) pioneering studies of desert lizard assemblages and Cadle & Greene's (1993) study of neotropical snake assemblages. In both cases, significant differences were found in community structure between the continents despite broad similarities in available habitats.

Nonetheless, we hypothesized that if closely related species had diversified independently on two continents and that these species were important components of communities on both continents then intercontinental convergence in specific traits might be detected. To test this hypothesis, we examined desert lizard communities, focusing on lizards in the clade Iguania, which includes Agamidae and Iguanidae.

Comparison of iguanian lizards from Australia and North America confirmed this prediction. Using phylogenetic analyses based on mitochondrial DNA sequence data, we found that evolutionary convergence in eco-morphological traits occurs at the species and community level. Two lines of evidence strongly suggest that community convergence has occurred in desert iguanian species—evolution of similar ecology/morphology patterns across taxa and convergent evolution of pairs of species between communities.

Our study examined particular traits (locomotor morphology and habitat use) and found strong evidence of convergence. It is probable that different aspects of an animal's biology are under differing selection forces (Blackledge & Gillespie 2004), providing the opportunity that convergence may not occur in all dimensions of a community. Thus, other niche dimensions, such as diet and thermal biology, would provide an interesting avenue to test the multi-dimensional nature of convergence. Nonetheless, we have demonstrated convergence in two aspects of community evolution, providing strong evidence of the significance of environmental conditions as a driving force in evolution on a continental mainland.

These results relate to the discussion about the relative frequency of convergence among mainland and island communities. Whereas previous non-phylogenetic studies have rarely demonstrated convergence on mainlands, it has been found much more frequently in island communities. Recent phylogenetically based island examples include spiders (Blackledge & Gillespie 2004; Gillespie 2004), lizards (Losos et al. 1998) and cichlid fish (for which East African Rift Lakes are the equivalent of islands—Arnegard et al. 1999). It is possible that differing analytical methods (i.e. phylogenetic versus non-phylogenetic) have influenced these differing results between continental and insular island communities; however, other possible causes need to be considered. In each case of insular convergence, communities on different islands are composed of relatively closely related species. Thus, just as members of the same lineage might converge in communities on different continents, one might also expect convergence among entire island communities when those communities are composed of members of the same lineage. By the same token, one would not expect community convergence when islands are occupied by different lineages and, in fact, such cases are rare.

Nonetheless, one might suggest that an important difference exists between continental lizard assemblages of North America and Australia and members of island communities. The clear distinction is that of divergence time. Most examples of convergent island communities are relatively young (e.g. <5 million years in Hawaiian *Tetragnatha* spiders (Blackledge & Gillespie 2004; Gillespie 2004), perhaps as much as 30–40 million years in Caribbean *Anolis* lizards (Shochat & Dessauer 1981)). By contrast, the iguanian lizards of Australia and North America have been evolving separately for as much as 150 million years (Schulte et al. 2003).

Consequently, even if Australian and North American iguanian lizards are members of the same clade, given the antiquity of their divergence, one might predict that they would have evolved enough differences in their biology and natural history to preclude convergence, for the very same reason that entire continental communities fail to converge. Why the contingencies of history have failed to produce the lineage-specific differences that preclude convergence in Australian agamid lizards and North American iguanids is an interesting question deserving of further study.

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