

## INVITED REVIEW

# Lizards as model organisms for linking phylogeographic and speciation studies

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## Abstract

Lizards have been model organisms for ecological and evolutionary studies from individual to community levels at multiple spatial and temporal scales. Here we highlight lizards as models for phylogeographic studies, review the published population genetics/phylogeography literature to summarize general patterns and trends and describe some studies that have contributed to conceptual advances. Our review includes 426 references and 452 case studies: this literature reflects a general trend of exponential growth associated with the theoretical and empirical expansions of the discipline. We describe recent lizard studies that have contributed to advances in understanding of several aspects of phylogeography, emphasize some linkages between phylogeography and speciation and suggest ways to expand phylogeographic studies to test alternative pattern-based modes of speciation. Allopatric speciation patterns can be tested by phylogeographic approaches if these are designed to discriminate among four alternatives based on the role of selection in driving divergence between populations, including: (i) passive divergence by genetic drift; (ii) adaptive divergence by natural selection (niche conservatism or ecological speciation); and (iii) socially-mediated speciation. Here we propose an expanded approach to compare patterns of variation in phylogeographic data sets that, when coupled with morphological and environmental data, can be used to discriminate among these alternative speciation patterns.

[Correction made after online publication (28/07/2010): (minor deletion in the last line of the abstract)].

*Keywords:* adaptation, divergence, lizards, molecular markers, phylogeography, speciation

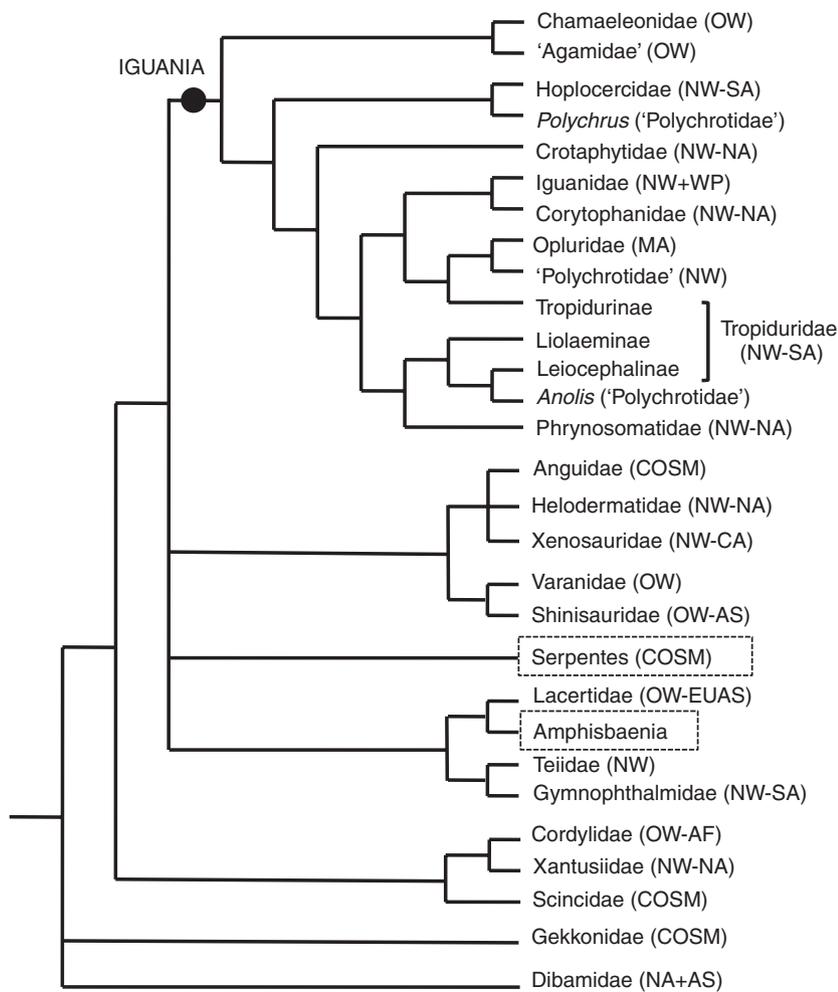
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## Introduction

'Lizards' are a paraphyletic group of non-avian reptiles that, together with the odd 'worm lizards' (Amphisbaenia) and the snakes (Serpentes), comprise the clade Squamata (Lee *et al.* 2004; Pough *et al.* 2004). The well-supported clades Amphisbaenia and Serpentes are unambiguously nested within the Squamata but for simplicity we refer to lizards as all squamates that do not belong to these other clades. This group includes at least 5354 species (The Reptile Database: <http://www.reptile-database.org/> accessed on 15 February 2010) in about 25–26 crown clades usually recognized

as families (Pough *et al.* 2004). Figure 1 depicts a phylogenetic hypothesis from Townsend *et al.* (2004) that summarizes relationships and distributions in these major groups and while this arrangement has been challenged (Lee *et al.* 2004; Vidal & Hedges 2005; Conrad 2008), we present the hypothesis merely to acquaint readers with some aspects of the evolutionary history of the group. Lizards are widely distributed geographically, occupy a wide range of habitats and are characterized by a striking range of morphologies, ecologies and body sizes (Pianka & Vitt 2003; Vitt & Caldwell 2009). As a group, lizards show about 150 independent origins of lateral toe fringes (for sand running; Luke 1986), about 100 independent origins of viviparity (lizards + snakes; Blackburn 2006), multiple transitions to a snakelike body form with limb reduction (Greer 1991;

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**Fig. 1** Schematic phylogeny of squamate reptiles showing relationships of major lizard clades with non-lizard taxa (Amphisbaenia and Serpentes), modified from Townsend *et al.* (2004). The geographic distributions of lizard lineages are identified as follows: NW: New World; NA: North America; SA: South America; CA: Central America; WP: West Pacific; MA: Madagascar; OW: Old World; COSM: Cosmopolitan; AS: Asia; EUAS: Eurasia; AF: Africa. The relationships within the clade Iguania were taken from Schulte *et al.* (2003).

Wiens *et al.* 2006; Brandley *et al.* 2008) and multiple origins of obligate parthenogenesis (Kearney *et al.* 2009).

Numerous symposia (Milstead 1967; Huey *et al.* 1983; Vitt & Pianka 1994; Fox *et al.* 2003; Reilly *et al.* 2007) and texts (Roughgarden 1995; Pianka & Vitt 2003; Losos 2009) have focused on lizards as model organisms, because they share attributes relevant to the study of many biological processes and they are often abundant and easy to manipulate. In this review, we: (i) summarize some important aspects of lizard diversity and evolution; (ii) describe some advantages lizards offer as models for phylogeographic studies; (iii) identify some emerging themes and review available lizard phylogeographic studies to summarize trends and patterns; (iv) describe case studies which have yielded important insights into broader aspects of phylogeography; (v) emphasize some explicit linkages between phylogeography and patterns of speciation and alternative speciation models; and (vi) synthesize the current state of knowledge and suggest ways to capitalize on attributes of lizards to improve resolution of phylogeographic

studies capable of discriminating among alternative speciation patterns. Such questions can be framed in several alternative speciation contexts and we suggest that multi-disciplinary studies can highlight linkages of phylogeographic patterns to divergence processes and integrate some aspects of both phylogeographic and pattern-based speciation studies to allow deeper and more synthetic levels of inquiry.

### Lizards as models for evolutionary studies

Lizards have become model organisms for evolutionary studies due to the accumulated knowledge of long-term demographics, life history strategies and adaptive ecophysiology and ecophysiology, which together provide an ideal framework for phylogeographic and speciation studies. Lizards are easy to find, approach and capture in the field for mark-release-recapture methods. They tolerate experimental manipulation, such as *in vivo* ablation of egg yolk mass (Sinervo & Huey 1990), alteration of body mass (Olsson *et al.* 2009) and removal of energy reserves by caudal autotomy (Naya *et al.* 2007).

Long-term demographic studies of several species (Bull 2000; Sinervo & McAdam 2008; Vercken *et al.* 2008) have provided deep pedigrees leading to novel insights into microevolutionary processes (Sinervo *et al.* 2007, 2008), patterns of heritable variation and covariation (see Pemberton 2008, for general issues) and patterns of natural selection (Sinervo & McAdam 2008). As an example, *Uta stansburiana* has one of the deepest vertebrate pedigrees in existence that covers both sexes; the pedigree for long-term demographic studies at Los Baños, California, currently spans 21 generations and 7464 individuals (1988–2008; 400 years in the human sense of time; Sinervo & McAdam 2008).

Some of the earliest tests of the theory of density-dependent natural selection, based on *r*- vs. *K*-selected life history strategies (MacArthur & Wilson 1967; Pianka 1970), were carried out on lizards (Tinkle *et al.* 1970; Pianka & Parker 1975). Thermal biology and biophysical ecology models in lizards that emerged from early physiological studies (Huey 1982; Tracy 1982; Porter *et al.* 2000) are now being applied to estimate geographic distributions based on thermal requirements and climate (Kearney & Porter 2004, 2009; Buckley 2008; Sinervo *et al.* 2010), whereas comparative ecophysiological methods have been used to explain multi-species distributional patterns (Navas 2002). Lizards have been ideal for investigating the mechanisms and targets of selection based on locomotor performance (Irschick 2000; Van Damme *et al.* 2008), showing that morphological variation is functionally and ecologically relevant because it translates into performance differences (Goodman 2007). These and related population processes have been emphasized in frameworks for studying the biological basis for allopatric speciation (Wiens 2004a) and we return to this point at the end of this review.

### Emerging themes in phylogeographic research

The term 'phylogeography' originally described analyses of gene genealogies within species or among closely-related species in explicit geographic contexts (Avice *et al.* 1987). Hewitt (2001) expanded phylogeography to also include considerations of hybrid zone dynamics and speciation patterns, especially in the context of Quaternary & Holocene histories of regional biotas. Moreover, because the original goal of phylogeography was and still is, to bridge population genetics with phylogenetics, the analysis of genotypic and allele frequency data for phylogeographic inference of very recent events or ongoing processes has been incorporated into a more inclusive discipline (Garrick *et al.* 2010). As recent reviews attest, the field is experiencing rapid growth in many directions (Knowles 2004; Beheregaray 2008; Riddle *et al.* 2008; Avice 2009; Brito & Edwards 2009;

Edwards 2009; Knowles 2009; Nielsen & Beaumont 2009). The availability of nuclear genetic markers, advances in coalescent theory and new GIS tools for generating ecological niche and paleoclimate models, are rapidly increasing the scope of phylogeographic studies (Swenson 2008; Buckley 2009; Hickerson *et al.* 2010; Sinervo *et al.* 2010). For example, some studies incorporate external climatic and geologic data to generate a priori predictions that can then be tested with molecular phylogeographic approaches (e.g. Richards *et al.* 2007; Knowles *et al.* 2007; Knowles & Carstens 2007a; Moriarty-Lemmon *et al.* 2007; Carnaval & Moritz 2008; Werneck *et al.* in review), but statistical methods can also estimate phylogeographic history without a priori hypotheses (Templeton 2004, 2010a,b; Lemmon & Moriarty-Lemmon 2008). The application of multi-locus coalescence methods to link phylogeography to species delimitation issues is growing rapidly (Carstens & Knowles 2007; Liu & Pearl 2007; Brumfield *et al.* 2008; Liu *et al.* 2008; Degnan & Rosenberg 2009; Yang & Rannala 2010), as are multi-species assessments of the role of gene flow vs. natural selection across environmental gradients (Rosenblum 2006), biodiversity patterns and processes in regional landscapes (Leaché *et al.* 2007; Victoriano *et al.* 2008; Carnaval *et al.* 2009; Hurt *et al.* 2009; Moritz *et al.* 2009) and the incorporation of these data into conservation planning (Davis *et al.* 2008). Statistical and computational issues remain challenging (Knowles 2008; Nielsen & Beaumont 2009; Templeton 2009a,b, 2010a,b; Beaumont *et al.* 2010), but phylogeography will continue to expand and incorporate other disciplines (Beheregaray 2008; Avice 2009; Knowles 2009).

### Lizard phylogeography: patterns and trends

Similar to other organisms (Beheregaray 2008), population genetic and phylogeographic studies of lizards have grown rapidly due to the refinement of data collection and analytical techniques, including the use of molecular markers with finer resolving power (Avice 2000; Garrick *et al.* 2010), coupled with increasingly powerful analytical methods (Hickerson *et al.* 2006; Richards *et al.* 2007; Nielsen & Beaumont 2009; Templeton 2009a). Here we review the primary literature published on population genetics and phylogeography of lizards. While phylogeography originally referred to molecular studies linking the geographic distribution and genealogical relationships among intraspecific evolutionary lineages (Avice *et al.* 1987) and population genetics did not incorporate a genealogical component, we review both for two reasons. First, early population genetic studies often established a basis for subsequent phylogeographic studies and second, the biology of population isolation and divergence, which ultimately drives speciation

(Wiens 2004a,b), requires the integration of multiple approaches based on different data sets relevant to different time scales (Hewitt 2001; Templeton 2001; Swenson 2008; Buckley 2009; Garrick *et al.* 2010; Sobel *et al.* 2010). The same is true for the issue of species delimitation, and both tree-based (coalescent) and non-genealogical gene flow methods are relevant to these interrelated issues (Knowles & Carstens 2007b; Petit & Excoffier 2009; Carstens & Dewey in press).

The search for published studies of lizards and the information extracted from these publications to analyse temporal, geographical, taxonomical and methodological trends are described in Appendix S1. We found 426 references representing 452 study cases (some studies included multiple taxa) (Table 1, Appendix S1). Seventeen families and 117 genera were included in these studies, with the European lacertid *Podarcis* being the most commonly studied genus (40 references), followed by the North American phrynosomatid *Sceloporus* (35) and the Caribbean *Anolis* (35) (Appendix S2). The first references appeared in 1980 (population genetic studies), while the first phylogeographic study (*sensu* Avise *et al.* 1987) appeared in 1989 (Sites & Davis 1989). Numbers of papers remained relatively stable with slight increases through 1996 and in 1997 the increase began a trajectory of nearly exponential growth (Fig. 2). These studies have been published in a total of 87 different journals with the most frequent being 'Molecular Ecology' (63), 'Molecular Phylogenetics and Evolution' (56) and 'Evolution' (33).

Most studies were based in North America (24%), followed by Europe, Australia, and Asia (14–18%), the West Indies and Africa (~10% each), then South America with Atlantic and Pacific oceanic islands (3–6%); other regions include less than 1% of the studies (some studies cover more than one region; Appendix S2). Coverage is taxonomically biased; the Lacertidae and Phrynosomatidae (the dominant clades in Europe and North America, respectively) are over-represented relative to their species diversity, while the species-rich clades Scincidae and Gekkonidae are under-represented. At the level of generic diversity, these families plus the Agamidae are well represented, but other families remain poorly studied (e.g. Gymnophthalmidae; Appendix S2). Lizards are better studied in the Southern Hemisphere proportional to their diversity; 33% of all studies were based in Africa, Australia or South America, a much higher proportion relative to their diversity than for other groups of vertebrates (Beheregaray 2008).

Mitochondrial DNA has been the most frequently used (51%) marker, followed by allozymes (25%), mini- and microsatellites (16%), and AFLP/RFLP/RAPD markers (10%), chromosomes (8%) and nuclear

sequences (5%). Allozymes were the earliest used, then mtDNA [restriction sites (1989) and (1993)], microsatellites in 1997 and since 1998 both have been preferred for different temporal scales, with nuclear sequences incorporated since 2004 (Fig. 3). The reconstruction of intraspecific (or congeneric) phylogenies and networks (category E; Table 2) has been the most common method employed (63%), usually together with estimates of differentiation and gene flow (A, B and D; 58%; Appendix S2). Tests of population structure (C) have been common (28%), but new phylogeographic/population genetic methods (F, G and H) are becoming popular (16%), while classification and correlation methods (I and J) have infrequently been applied (16%). From 1999–2009, new methods (Nested Clade Phylogeographic Analysis = NCPA, coalescent, assignment/clustering algorithms; F, G and H, respectively) were applied in ~21% of all studies. Over this same time frame, mtDNA use has remained about the same (53%), while nDNA and microsatellites usage almost doubled (11% and 28%, respectively) and allozymes and RFLP/AFLP/RAPD were rarely used (5% and 2%, respectively). The average sampling design was similar for studies using the newer methods (12.4 individuals per locality, SD = 13.9,  $N = 70$ ) relative to that used across all studies in 1999–2009 (12.7, SD = 36.3,  $N = 329$ ).

### Conceptual contributions to phylogeography from lizards

#### *Ecotones and hybrid zones*

Studies of ecological gradients and parapatric hybrid zones can suggest what evolutionary forces may have contributed to divergence/adaptation to different habitats (Ogden & Thorpe 2002; Rosenblum 2006), while studies of narrow contact zones can reveal patterns such as linkage disequilibrium, heterozygote deficits and coincident clines suggestive of post-zygotic selection against hybrids (Phillips *et al.* 2004). Novel investigations of divergence across ecotones include the Schneider *et al.* (1999) study of the skink *Carlia rubrigularis* in the Australian Wet Tropics. Morphology (body size, limb length and head shape) and life history (age at maturity) in this species shift abruptly across a sharp ecotone between forest types and avian predation (as estimated from beak marks on plasticine models) was one likely driver of this divergence despite gene flow. Rosenblum (2006) studied phenotypic transitions of three lizard species [*Holbrookia maculata*, *Sceloporus undulatus* (Phrynosomatidae) and *Aspidoscelis inornata* (Teiidae)] characterized by 'blanched' colour morphs on the gypsum dunes, wild type morphs on brown soils and intermediate colours in the narrow ecotones [colour

**Table 1** Summary of phylogeographic studies of lizards published by family (Fig. 1) through 31 December 2009. All details for each study are given in Appendix S1. The second column shows the number of genera and species in each family based on the Reptile Database (<http://www.reptile-database.org>). The third column shows the number of genera sampled and the number of studies reviewed in each family. The fourth column is the mean number of localities and the fifth column represents the mean number of individuals sampled per locality (range in parentheses). Geographic region: AS = Asia, AF = Africa, AU = Australia, NA = North America, EU = Europe, SA = South America, WI = West Indies, PI = Pacific Ocean islands, AI = Atlantic Ocean islands, IO = Indic Ocean islands. Genetic marker: MT = mitochondrial DNA, NU = nuclear DNA, AZ = allozymes, MS = microsatellites, AFLP = amplified fragment length polymorphism, RFLP = restriction fragment length polymorphism, RAPD = random amplification of polymorphic DNA, CS = chromosomes. Analytical method: (A) within-population differentiation, (B) between-population differentiation, (C) tests of population structure, (D) gene flow estimates, (E) tree-based methods, (F) nested clade phylogeographic analysis, (G) coalescent-based methods, (H) clustering/assignment/non-coalescent methods, (I) ordination and classification methods, (J) correlation analyses, (K) neutrality and equilibrium tests, (L) mating system/parentage/relatedness, and (M) cline analysis and hybrid indices

Family	Genera/ species	Genera/ studies	Geographic region	Number of localities	Sample size	Genetic marker
Agamidae	55/424	11/24	AS/AF/AU	16.2	11.5 (1–80)	MT/AZ/MS/RAPD/AFLP
Anguidae	12/115	2/3	NA	22.7	1.3 (1–3)	MT
Anniellidae	1/2	1/2	NA	26.5	2.0 (1–6)	MT/NU
Chamaeleonidae	9/183	4/6	AF/EU	32.4	1.5 (1–7)	MT/RAPD
Cordylidae	3/55	2/2	AF	9.0	5.2 (1–10)	MT
Crotaphytidae	2/12	3/7	NA	47.4	9.3 (1–189)	RFLP/AZ/MS/MT
Gekkonidae	10/1283	21/47	AU/EU/AS/PI/ AF/NA/WI/AI	25.9	6.8 (1–87)	MT/AZ/NU/CS/RAPD/RFLP
Gymnophthalmidae	41/221	2/4	SA/WI	11.6	2.9 (1–16)	MT/CS/AZ
Iguanidae	8/39	9/14	PI/NA/CA/WI	17.2	16.3 (1–186)	MS/MT/AZ/RFLP/NU
Lacertidae	32/303	16/122	EU/AF/AS/AI	18.0	16.0 (1–542)	MT/AZ/MS/RAPD/RFLP/NU/CS
Phrynosomatidae	10/136	8/54	NA	24.9	9.5 (1–131)	MT/NU/AZ/CS/RFLP/AFLP/MS
Polychrotidae	9/409	1/35	WI/NA	29.8	12.5 (1–57)	MT/NU/AZ/MS/AFLP
Scincidae	133/1445	29/79	EU/AS/AF/AU/ AI/PI/NA/IO/SA	21.0	16.9 (1–202)	MT/MS/RFLP/NU/AZ/CS
Teiidae	9/127	5/27	SA/WI/NA	11.7	35.9 (1–88)	AZ/MT/RAPD/NU/CS/RFLP/MS
Tropiduridae	11/367	4/20	SA/PI	24.8	10.6 (1–64)	MT/CS/AZ/MS/RFLP
Varanidae	1/69	1/3	AS	10.7	10.7 (6–27)	MS/MT
Xantusiidae	3/30	1/4	NA	66.8	2.2 (1–18)	MT/AZ/NU

Family	A	B	C	D	E	F	G	H	I	J	K	L	M
Agamidae	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	
Anguidae					✓		✓				✓		
Anniellidae			✓		✓								
Chamaeleonidae		✓	✓		✓		✓						
Cordylidae					✓								
Crotaphytidae			✓	✓	✓					✓			
Gekkonidae	✓	✓	✓	✓	✓			✓	✓	✓	✓		✓
Gymnophthalmidae	✓				✓								
Iguanidae	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	
Lacertidae	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	
Phrynosomatidae	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Polychrotidae	✓	✓	✓	✓	✓		✓	✓	✓	✓	✓		✓
Scincidae	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Teiidae	✓	✓	✓	✓	✓	✓	✓	✓	✓		✓	✓	✓
Tropiduridae	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓		
Varanidae	✓	✓	✓	✓	✓	✓	✓				✓		
Xantusiidae	✓				✓	✓			✓		✓		

morphs have a genetic basis (Rosenblum 2005)]. Neutral processes could not explain colour variation but natural selection was sufficiently strong to produce divergent phenotypic responses despite species-specific differ-

ences in population structure, demographic history and ecology (Rosenblum 2006). Rosenblum *et al.* (2010) have now shown that different molecular mechanisms in the same gene have produced these blanched phenotypes.

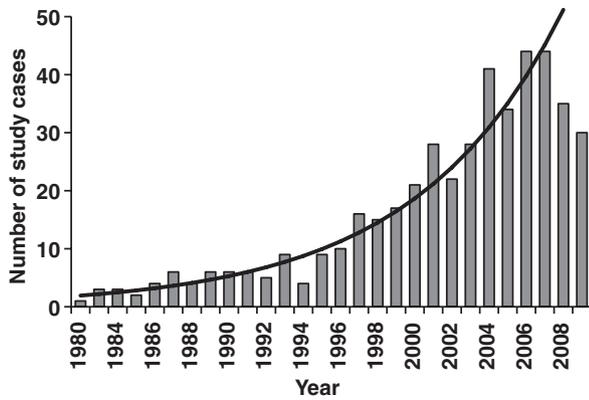


Fig. 2 Annual number of phylogeographic studies published between 1980 and 2009. The curve represents the best-fit exponential function for the period 1980–2008 ( $R^2 = 0.92$ ,  $P < 0.01$ ). Studies from 2009 were not included in the regression analysis because the number of references from last year found in the internet databases is probably an underestimate of the real number of publications.

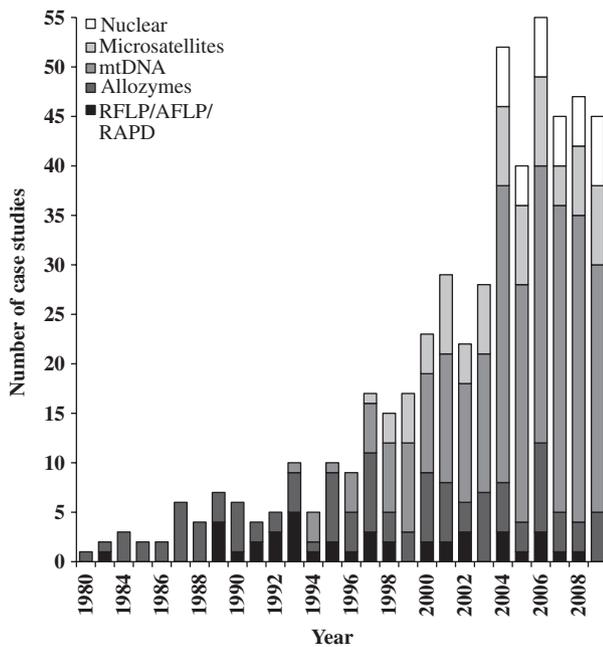


Fig. 3 Annual distribution of study cases between 1980–2009 for four classes of genetic markers, allozymes, RFLP/AFLP/RAPD, mtDNA, nuclear DNA and microsatellites.

In Mexico, two chromosomal races of *Sceloporus grammicus* (Phrynosomatidae) form a hybrid zone in a pine-oak/chaparral ecotone characterized by steep concordant clines in three diagnostic autosomal markers. Sites *et al.* (1995) used tension zone theory (Barton & Hewitt 1985; Barton & Gale 1993) to calculate a cline width (~830 m) and inferred that this zone is likely maintained by both endogenous (genetic) and exoge-

nous (environmental) selection adapting the races to different habitats. Studies of (i) fitness correlates in hybrid/back-cross males heterozygous for different autosomal rearrangements (Reed *et al.* 1995a,b); (ii) female fecundity among parental, F<sub>1</sub> and back-cross genotypes (Reed & Sites 1995); (iii) cyto-nuclear structure (Sites *et al.* 1996); and (iv) modeling of cline shapes for multiple unlinked markers (Marshall & Sites 2001) confirmed earlier findings and provided among the first multi-faceted studies of the dynamics of a vertebrate mosaic hybrid zone. Recent detailed studies of a contact zone between two mtDNA haploclades of *Lacerta schreiberi* in the Iberian Peninsula found a steep cline (Godinho *et al.* 2008) with asymmetric gene flow unrelated to female mating preferences (Stuart-Fox *et al.* 2009a), but consistent with body condition (based on parasite load) or male colour (associated with aggressiveness) (Stuart-Fox *et al.* 2009b).

### Species delimitation

Species delimitation has become inter-connected with phylogeography because (i) phylogeography deals with patterns and processes occurring at the intra/interspecific boundary; and (ii) coalescent methods are relevant to both topics (Knowles & Carstens 2007b; Knowles 2009; O'Meara 2010; Carstens & Dewey 2010). Methods of species delimitation have already been the topic of several recent reviews (Sites & Marshall 2003, 2004; Padial & De la Riva 2006; Wiens 2007) and lizards have served as models for new approaches.

Wiens & Penkrot (2002) described tree-based species delimitation methods using molecular and morphological data, to test species boundaries in the Mexican *Sceloporus jarrovi* complex. Gene trees were constructed and an inference key used to assess species boundaries, which identified a total of five species in this group but only two of these were identical across different data and criteria. This was among the earliest studies to test performance of clearly articulated methods for concordance in the species recovered. Morando *et al.* (2003) sequenced multiple mtDNA regions in the Patagonian *Liolaemus elongatus-kriegi* complex (Tropiduridae) and described an efficient hierarchical sampling design to simultaneously evaluate intra- and interspecific variation in poorly known clades and to identify 'candidate species' for further study. Raxworthy *et al.* (2007) used GIS-based ecological niche modeling (ENM; Phillips *et al.* 2006) to delimit species in two complexes of *Phelsuma* geckos endemic to Madagascar based on niche overlap predictions. The ENM of all named taxa combined was expected to overpredict niche space if the taxa occupied different niches and results revealed that both species complexes included taxa that occupied

**Table 2** Expected patterns of divergence between sister species (or phylogroups) in allopatry, under alternative speciation scenarios

Pattern-based divergence	Non-adaptive (passive) divergence	Adaptive divergence	Phenotypic stasis	Socially-mediated speciation
Morphological variation (size or shape)*	Variance and co-variance of traits within lineages proportional to those between lineages Divergence correlated with neutral molecular variation	Divergence due to adaptation to a novel environment reflected in divergent ecomorphological traits Ecomorphological traits correlated with distinct niche envelopes but not correlated with neutral molecular variation	No divergence due to failure to adapt to novel environment reflected in conserved ecomorphological traits Ecomorphological traits correlated with similar niche envelopes but not correlated with neutral molecular variation	If male based polymorphism, then colour genes will have effect on male size and accentuate sexual dimorphism
Sexual dimorphism <sup>†</sup>	Divergence as above	Divergence in allopatry (or no divergence)	Divergence in allopatry (or no divergence)	Female only morphs—females larger than males; male only morphs, males larger than females
Colour pattern polymorphism <sup>‡</sup>	Divergence as above	Divergence in allopatry (or no divergence)	Divergence in allopatry (or no divergence)	Correlated to shifts in mating strategies (1 → 2 → 3, in phylogenetic sequence) in males OR in females <i>r</i> - vs. <i>K</i> -strategies

\*These are characters thought to be influenced by natural selection favouring adaptation to niche dimensions such as crypsis, microhabitat, thermoregulation or interactions related to competition, predation, or parasitism.

<sup>†</sup>Characters such as colour and/or body size differences usually attributed to the influence of sexual selection or natural selection on female fecundity or male resource defence.

<sup>‡</sup>Characters such as colour polymorphisms segregating within a single breeding group and attributed to frequency-dependent selection on local mating dynamics.

divergent niche space. In some cases morphological data corroborated ENM inferences for species, despite low levels of molecular divergence (0.47% uncorrected mtDNA p-distance).

Marshall *et al.* (2006) compared the performance of several species delimitation methods in the *Sceloporus grammicus* complex by designating four 'hypothesized evolutionary species' (HES) from molecular data and then evaluating the accuracy of five methods in recovering four HES units. No single method strongly delimited all of these, but two showed some support of all four, revealing that co-dominant markers are likely to be successful at delimiting species by any number of methods, given their success in this complex characterized by recent race diversification and multiple hybrid zones.

Leaché *et al.* (2009) integrated mitochondrial and nuclear gene sequences, niche envelopes and morphometric assessments of horn shape, to delimit species in the *Phrynosoma coronatum* complex. The mtDNA gene tree recovered five haploclades distributed linearly from central California south through the Baja Peninsula. The other data sets were largely congruent with each other

and the mtDNA haploclades at the deepest divergence levels, but at recent levels of divergence the other data sets were discordant and nuclear gene flow between these could not be rejected. The authors recognized three species concordant with the deepest mtDNA haploclades, all of which were ecologically and morphologically diagnosable.

#### *Novel single species studies*

GIS-based ENM is now routine in many phylogeographic studies, but biophysical niche modeling methods (Kearney 2006) can decipher functional links between organismal physiology and predictor variables that may limit species distributions (Kearney & Porter 2004, 2009). Strasburg *et al.* (2007) integrated this approach in a phylogeographic reconstruction of Pleistocene range expansions in two parthenogenetic forms of the Australian gecko *Heteronotia binoei*. Both have had relatively recent origins and subsequently expanded at different times; the 3N1 race at ~24 000 years ago and the 3N2 race at ~7000 years (estimates from NCPA and mismatch distribution

analyses). ENM and biophysical modeling (Kearney & Porter 2004) supported these conclusions and showed that the southern range limit of one bisexual race coincides closely with the thermal limit for successful egg development, an inference that could not have been made from correlational modeling alone.

Rosenblum *et al.* (2007) studied colonization histories of *Sceloporus undulatus* (= *S. cowlesi*, in Leaché & Reeder 2002) in novel habitats in the Tularosa Basin of New Mexico. Geologically recent 'islands' of white sand dunes (dated to ~10 000 yr BP) and black rocks (Carrizozo lava flow; ~5000 yr BP) provide independent but analogous experiments in selection. Multiple loci used in an Approximate Bayesian Computation (ABC) framework (Hickerson *et al.* 2006) revealed that: (i) population reductions were associated with initial colonization of both habitats; and (ii) these were more severe during colonization of the black lava habitat. Reductions in inbreeding effective population size ( $N_e$ ) may be more dramatic when colonization is accompanied by a change in selection regime, an idea consistent with a demographic cost of adaptation to novel environments (Haldane 1957; Lande & Shannon 1996).

Gifford & Larson (2008) used multiple loci to infer two fragmentation events concordant with Pliocene and Pleistocene marine transgressions in *Ameiva chrysolema* (Teiidae) on the island of Hispanola. Multi-locus NCPA (Templeton 2010a,b) and Bayesian coalescent analyses recovered signatures of population expansion and asymmetric migration consistent with the relative magnitude and duration of inundations for each region. In the Iberian Peninsula, Godinho *et al.* (2008) described a hybrid zone between two lineages of the lacertid *Lacerta schreiberi*, delineated by a combination of slow- and fast-evolving markers; a sharp transition between mtDNA clades but smooth clines in the nuclear data suggested a chronology of historical events including a late Pliocene fragmentation, recontact during glacial cycles with formation of a hybrid zone and recent population expansions.

#### Novel multi-species studies

McGuire *et al.* (2007) investigated patterns of mtDNA paralogy in 12 species of the family Crotaphytidae (*Crotaphytus* and *Gambelia*) in southwestern North America, coupled with GIS-modeling of current and 'last glacial maximum' (LGM, ~21 000 yr BP) distributions to identify contact areas today or in the recent past. This revealed a unique pattern of mtDNA variation that suggested repeated cycles of introgression of *C. collaris* mtDNA haplotypes into *C. bicinctores*. The authors hypothesized an 'introgression conveyor' model with three phases of unidirectional introgression,

followed by substantial mtDNA divergence between each of the three events.

Dolman & Moritz (2006) estimated isolation and divergence in the Australian skink genus *Carlia*, using three well-defined mtDNA clades representing the sister species *Carlia rubrigularis* and *C. rhomboidalis* to assess interaction between geographic isolation, genetic drift, introgression and divergent selection, on speciation and divergence processes in rainforest faunas (Moritz *et al.* 2000). A coalescent method (IM; Hey & Nielsen 2004) applied to sequence data from seven nuclear genes revealed large  $N_e$  in *C. rhomboidalis*, suggesting that drift did not likely contribute to its divergence from *C. rubrigularis*, while the processes that maintained phenotypic stasis within *C. rubrigularis* and drove divergence between the two species were not clear. Recent studies on co-distributed lizard species in this same region, such as Moussalli *et al.* (2009) evaluation of climatic niche specialization in *Saproscincus* skinks, focused on responses Quaternary cycles of forest contraction/expansion. Current climate preferences of these species extrapolated to past climates were concordant with geographic patterns of mtDNA genetic diversity, suggesting that all have maintained their respective climate preferences at least through the late Pleistocene and that niche conservatism (Wiens & Graham 2005) contributed to genetic diversification within this system.

Victoriano *et al.* (2008) implemented a super-trees approach [Lapointe & Rissler (2005)], to estimate co-divergence in three species of *Liolaemus* (Tropiduridae) with partially overlapping distributions in the Chilean Andes. Concordance of area trees was tested by treating co-occurring taxa as host-parasite associations and congruent patterns were inferred when tests were significant. Environments from three a priori recognized climate zones were quantified by six variables and tested against a null model (no difference) by permutation. Significant spatial co-divergence between *L. tenuis* and *L. pictus* and between *L. tenuis* and *L. lemniscatus* and significant positive correlations between the super-tree distance and the climate matrixes, suggest that, in sympatry, these species have responded in parallel to shared historical events.

Leaché *et al.* (2007) tested for simultaneous divergence across a shared phylogeographic break [the mid-peninsular seaway in 12 species co-distributed along the Baja Peninsula (mtDNA from four lizards, two snakes, and six rodents)]. A hierarchical Approximate Bayesian Computation (hABC) analysis suggested two temporally disjunct divergence events; seven taxon pairs diverged ~2.3–15.3 Ma, while five diverged ~0.6–3.4 Ma. In the Australian Wet Tropics, Moritz *et al.* (2009) included nine lizard species in a comparative phylogeographic analysis of a 'suture zone' [a region

where an assemblage of species establish secondary contact (Remington 1968; Swenson & Howard 2004)] and showed that individual hybrid zones were significantly clustered in a region between two major Quaternary refugia and most of these occurred in areas of low environmental suitability relative to the adjacent refugia. MtDNA sequence divergences varied between sister lineages (2–15%), as did the extent of reproductive isolation [random admixture to speciation by reinforcement (Hoskin *et al.* 2005)]. Moritz *et al.* (2009) suggested that suture zones are better defined by shared expansion times to contact, rather than common divergence times.

### Linking phylogeography to population divergence and speciation

#### *Speciation modes and patterns*

An integrated phylogeographic perspective can provide important insights into three components of speciation research: (i) the geographic context of speciation; (ii) the processes driving divergence; and (iii) the origin of reproductive isolation (Nosil 2008, 2009; Nosil *et al.* 2009; Sobel *et al.* 2010). Speciation patterns have been categorized by geographic modes since the modern synthesis (Mayr 1942); the classical allopatric (Mayr 1963) and more recently peripatric, parapatric and sympatric modes (Coyne & Orr 2004). This classification spans the continuum of geographic modes and clarifies some key questions in speciation research (Butlin *et al.* 2008), but despite theoretical (Gavrilets 2004) and empirical treatments (Coyne & Orr 2004; Futuyma 2005; Price 2008) on the frequency of these modes, the allopatric model remains widely corroborated (Barraclough & Vogler 2000; Coyne & Orr 2004; Phillimore *et al.* 2008; Price 2008).

A classification of speciation modes by evolutionary processes was presented by Losos (2009), and recognized 'adaptive' vs. 'non-adaptive' patterns. In a theoretical context, Gavrilets (2004) has recognized stochastic vs. deterministic factors responsible for the origin of reproductive isolation, which are responsible for 'non-adaptive' and 'adaptive' patterns of speciation. In practice, Futuyma (2005) suggested formulating and testing a null hypothesis of speciation due to stochastic forces, which in the simplest case is the 'passive divergence' or 'drift-only' paradigm, because rejecting this hypothesis is probably easier than demonstrating the action of other evolutionary forces.

Stochastic processes alone are considered unlikely to drive speciation because drift is relatively inefficient in producing reproductive isolation (Sobel *et al.* 2010), but if species are independent evolutionary lineages

(de Queiroz 1998) that can be detected using neutral genetic markers and coalescent-based methods (O'Meara 2010), then a phylogeographic approach can distinguish among some modes of speciation. Simulation studies show that, given enough loci, coalescent methods can delimit species at shallow levels of divergence ( $\sim 0.3 N_e$ ) when they still display considerable incomplete lineage sorting (Knowles & Carstens 2007b); these stochastic forces therefore have a role in generating independent lineages. Gene trees and geographic distributions alone are insufficient to distinguish among geographic modes of origin because assumptions about the distributional ranges of the populations/species may not be met (Losos & Glor 2003). Here we suggest that a phylogeographic focus on population/species divergence in terms of the spatio-temporal isolation of lineages, combined with environmental and phenotypic data, are sufficient to discriminate 'drift only' vs. 'selection-driven' divergence and then among some three classes of the latter. Establishment of a strongly corroborated pattern would then require follow-up studies to explicitly link lineage divergence to the origin of reproductive isolation (Sobel *et al.* 2010; Wiens 2004a,b).

#### *What modes can phylogeographic patterns distinguish?*

Ecologically-based adaptive processes can produce selectively-driven departures from a neutral divergence pattern in two different ways. First, niche conservatism can limit gene flow and therefore promote divergence between allopatric sister lineages by constraining adaptation at the geographic barrier separating them (Wiens 2004a; Kozak & Wiens 2006). Alternatively, adaptation to different ecological niches can also limit gene flow between allopatric or parapatric lineages and lead to 'ecological' speciation when these changes result in reproductive isolation (Rundle & Nosil 2005; Nosil *et al.* 2009; Schluter 2009). The niche conservatism scenario is predicted to produce more similar ENMs between species' ranges relative to the unoccupied region separating them, whereas the adaptive divergence model predicts more different ENMs relative to the barrier region (Hua & Wiens 2010). Although the environmental factors used in ENM can distinguish between divergent ecological niches, it is important to evaluate if these factors have diverged beyond expectations due to geographic distance. In this vein, McCormack *et al.* (2010) developed null expectations for differentiation in ENM to distinguish between adaptive patterns (causing niche divergence or conservatism) and differentiation due to geographic separation only. This approach can be strengthened by quantification of morphological divergence (or absence thereof) in isolated populations, because this information will capture some niche

dimensions not included in climate modeling. For example, if the two lineages have similar ENM, we would expect them to also display similar phenotypes as a result of adaptation to 'identical' ecological niches. Alternatively, if ENM are different, divergent ecological selection is expected to drive some phenotypic divergence between the lineages.

A third alternative is the hypothesis of socially mediated speciation, in which hybrid unfitness is due to alternative local mating systems, rather than divergent ecological forces underlying adaptive traits (Sinervo & Svensson 2002; Hochberg *et al.* 2003). The well-studied 'rock-paper-scissors' (RPS) mating system in the lizard *Uta stansburiana*, in which three male throat colour morphs fluctuate via frequency-dependent selection within local populations, has been suggested as an example of speciation by this mode (Corl *et al.* 2010b; the genetic basis for these phenotypes, details of the model for divergence and possibly reproductive isolation, are described in Appendix S3). Corl *et al.* (2010b) suggested that geographic variation in the RPS polymorphism among *Uta* populations offers the opportunity for speciation when ancestral tri-morphic systems collapse to di- or mono-morphic systems in isolated populations and reproductive isolation then evolves upon secondary contact due to an interaction of natural and sexual selection forces. Loss of one or two male colour morphs in novel environments alters the 3-morph RPS equilibrium and this is followed by 'character release' and rapid phenotypic evolution of the remaining colour morphs in body size, sexual dimorphism and probably other life history traits such as clutch size (Corl *et al.* 2010a). Body size and clutch size are likely not the only traits that have diverged with morph loss, because these morphs also differ in other heritable traits including behaviour, hormone levels, clutch size, egg mass and immunocompetence (see Appendix S3) and strong correlational selection on the colour locus and other trait loci (e.g. multi-trait selection) generates the highest standing levels of linkage disequilibrium observed within a species (Sinervo *et al.* 2006). Divergence in colour traits involved in male signaling and female choice can then promote reproductive isolation through assortative mating by colour (Bleay & Sinervo 2007), multi-trait female preference (Lancaster *et al.* 2009) and/or operation of reinforcement processes on post-zygotic (Dobzhansky-Mueller) differences between populations (see details in Appendix S3). The rapid phenotypic divergence of isolated di- or mono-morphic populations (some recognized as different species or subspecies) suggests that a 'morphic' speciation process has been operating in *Uta stansburiana* (Corl *et al.* 2010b). Because colour polymorphism may be the first step in speciation in this mode (Levene 1953; Maynard-Smith 1966) and

reproductive isolation may arise from social competition rather than ecology *per se* (West-Eberhard 1983, 1986, 2003), we view this as a distinct alternative to the ecological modes described above. Table 2 summarizes patterns of ecological and morphological divergence expected among these speciation modes.

#### *What kinds of data are needed?*

*Geographic sampling.* Dense geographic sampling and geo-referencing of specimens are necessary to document distributions of species accurately (Buckley 2009), which can then be used to address a range of ecological and evolutionary questions (Wiens & Graham 2005; Kozak *et al.* 2008). Ideally, sampling design should be based on a priori knowledge of population structure and life history, guided by the assumptions of the analytical methods to be used and included as another parameter in analyses to evaluate the impact of sampling on the inferences (Buckley 2009). Sampling impact can be minimized by correcting for ascertainment bias due to poor sampling of rare polymorphisms (Rosenblum & Novembre 2007), assessing sampling completeness (Dixon 2006) and evaluating limitations of inferences made from finite samples (Templeton 2009a).

*Genetic data.* While mtDNA will likely remain the preferred phylogeographic 'first pass' marker for lizards, as in most other organisms (Beheregaray 2008; Zink & Barrowclough 2008; Avise 2009; Barrowclough & Zink 2009), the continued development of new markers and analytical methods will expedite the incorporation of multiple loci into phylogeographic studies (Knowles 2009; Nielsen & Beaumont 2009; Templeton 2009a; Hickerson *et al.* 2010). Multiple loci increase the accuracy of estimation of parameters such as population sizes and divergence times (Edwards & Beerli 2000; Felsenstein 2006; Heled & Drummond 2008; Kuhner 2008) and the resolving power of coalescent-based species delimitation methods even at shallow time horizons (Knowles & Carstens 2007b). While the discovery of nuclear markers with sufficient variability for phylogeographic analysis is still challenging, anonymous loci seem to be promising for these purposes and even for phylogenetic inference (Brito & Edwards 2009). Complementary studies of hybrid zones and gene flow will likely rely on microsatellite markers (Petit & Excoffier 2009).

*Morphological data.* Many studies have identified morphological traits relevant to functional performance with fitness consequences, including body size, limb proportions and head size/shape, as these relate to

locomotion, microhabitat use, niche convergence, anti-predator behaviour and social interactions (Harmon *et al.* 2005, 2007, 2008; Losos *et al.* 2006; Calsbeek 2008; Vervust *et al.* 2007; Herrel *et al.* 2008; Losos 2009). Frequency of tail autotomy provides information on predation efficiency/intensity (Medel *et al.* 1988; Cooper *et al.* 2004; Pafilis *et al.* 2009) and/or intrasexual competition (Hofmann & Henle 2006; Corl *et al.* 2010a). Body colour patterns display adaptive variation in association with habitat (Thorpe 2002; Rosenblum 2006; Schneider 2008) and in cases of sexual dimorphism, colour patterns or morphs usually act as signaling traits carrying relevant information for social interactions and mate recognition (Lancaster *et al.* 2009). If sexual dimorphism in colour is relevant, then phenotypes can be scored by eye from photographs (Sinervo *et al.* 2006, 2007) or spectrophotometry if colours are beyond the visible range (e.g. UV; Côte *et al.* 2008; Vercken *et al.* 2008) and some pigmentation patterns can be quantified from museum vouchers (Leaché & Cole 2007), especially melanism (Camargo *et al.* unpub. data).

*Environmental layers/niche modelling.* Climate and topographic data with global coverage at several levels of geographic resolution are available from public databases (i.e. <http://www.worldclim.org>) and vegetation and soil properties can be derived from remote-sensing data (Zimmermann *et al.* 2007). GIS software enables preparation of these environmental layers for subsequent analyses to ensure identical resolution and area coverage and to extract data associated with point localities. These layers represent the input data, together with georeferenced localities from field-collected specimens for estimating ENM under alternative scenarios. While most studies use the maximum entropy approach (Phillips *et al.* 2006; Phillips & Dudík 2008), mechanistic methods are emerging (Kearney & Porter 2009; Monahan 2009) and recent reviews have highlighted the utility of ENM for addressing questions in speciation research (Wiens & Graham 2005; Rissler & Apodaca 2007; Kozak *et al.* 2008).

#### *What kinds of analyses are appropriate?*

*Genetic data.* DNA sequences can be analysed by a number of methods for testing species boundaries, thus delimiting the units to be compared with phenotypic and environmental data. Coalescent-based approaches statistically test the fit of gene genealogies to alternative hypotheses of species boundaries, including likelihood methods that accommodate incomplete lineage sorting (Knowles & Carstens 2007b) and extensions (O'Meara

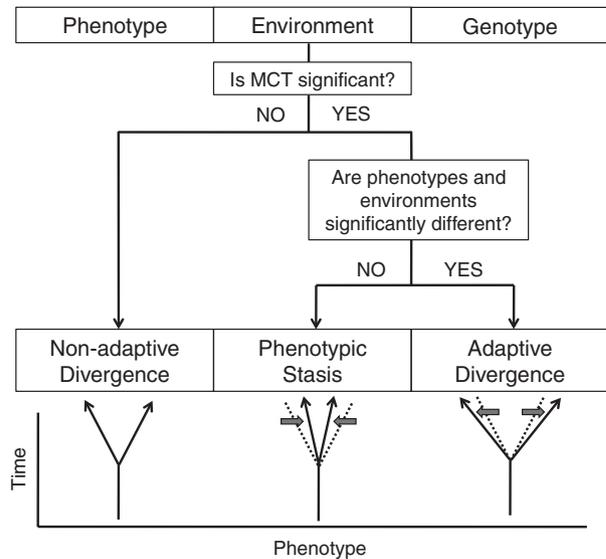
2010) to search simultaneously for both the optimal delimitation of multiple species and the species tree. We anticipate that the current surge of coalescent methods, including likelihood (STEM, Kubatko *et al.* 2009) and Bayesian approaches (BEST, Liu & Pearl 2007; \*BEAST, Heled & Drummond 2010; GLASS, Mossel & Roch 2010), will continue to improve by accommodating other processes (i.e. gene flow) that may occur between recently diverged species. Genetic data can also be used to calculate distance matrices based on pairwise comparisons between population mean values or individual values ( $F_{ST}$  for example).

*Morphological data.* Differentiation based on morphological data can be summarized with the  $P_{ST}$  statistic, a surrogate for the quantitative genetic differentiation ( $Q_{ST}$ ) under some assumptions (Gay *et al.* 2009). Multivariate analyses can be applied to extract a few major axes that account for most of the variation in phenotypic variables (e.g. morphometric or meristic data, co-ordinates from geometric morphometrics, etc.) and multidimensional Euclidean distances between individuals can be obtained from the data space defined by these axes. Obviously neither the environmental nor the morphological data may fully capture some variables linked directly to adaptive change and they may fail to detect adaptive divergence, but a focus on traits for which links between direct fitness and adaptive processes have been documented should minimize this problem. In lizards, differences in body size, shape, colouration or limb and head proportions (Harmon & Gibson 2006; Harmon *et al.* 2007) are most often associated with adaptive responses to shifts in habitat (Losos *et al.* 2000, 2001; Ogden & Thorpe 2002; Kearney & Porter 2004, 2009; Calsbeek & Sinervo 2007; Calsbeek & Smith 2007), climate (Guillette 1993; de Fraitpont *et al.* 1996) or biotic interactions (e.g. competitors, parasites, prey, or predators) (Kearney 2006; Buckley 2008; Stuart-Fox *et al.* 2009b).

*Environmental data.* Ecological niche modeling (ENM) for species can be tested for significant between-species differences with new methods (ENM Tools, Warren *et al.* 2008; McCormack *et al.* in press). Further, environmental data extracted from georeferenced localities can be used to obtain environmental distances between localities based on Euclidean distances derived from multivariate approaches such as principal components analysis. In addition to the usual climatic and topographic layers, remote-sensing data that are strongly associated with habitat differences and have low spatial autocorrelation can increase the resolving power of ENM analyses (see McCormack *et al.* 2010).

*Integrating genetic, phenotypic and environmental data into tests of alternative speciation modes.* Neutral genetic markers can be used to assess the significance of ecological/phenotypic divergence between populations, since they represent the predicted levels of differentiation due to drift only (within populations) or drift and gene flow (between populations; Nosil *et al.* 2008; Gay *et al.* 2009). Phenotypic divergence exceeding or discordant with neutral expectations suggests the influence of selection in driving divergence and if also correlated with environmental divergence, a causal mechanism can be hypothesized for observed patterns. ENM can be used to test for significant niche divergence by accommodating the effect of geographic distance separating species/populations and distinguishing between selection-driven ecological divergence vs. niche differentiation due strictly to geographic separation (McCormack *et al.* 2010). Because tests of niche differentiation may be insufficient to distinguish between adaptive and non-adaptive speciation modes, we suggest that the inclusion of neutral genetic and morphological data provide a more inclusive context for ENM differentiation. We propose that by looking at both (i) the divergence between lineages in each dataset; and (ii) the correlations between these three datasets, we can distinguish among the three alternative speciation patterns addressed above.

The first step consists of obtaining distance matrices for the three genetic, morphological (or other phenotypic) and environmental data sets. As explained above,  $F_{ST}$  distances based on genetic variation and Euclidean distances from multivariate analyses of morphological and environmental data can provide these matrices. The next step uses a partial matrix correspondence (Mantel) test (MCT) to evaluate possible correlations between environmental and phenotypic matrices, while accommodating neutral genetic variation based on the residuals of the pairwise correlations with the genetic distance matrix (Smouse *et al.* 1986; Thorpe *et al.* 1996; Thorpe 2002); this is required in order to hypothesize a potential adaptive phenotypic response to the environmental conditions. A partial MCT is then used to test the null hypothesis that drift alone explains the phenotypic differentiation, by evaluating the correlation between phenotypic and environmental distance matrices, after controlling for the genetic differentiation in neutral markers (Thorpe & Stenson 2003; Rosenblum 2006; Rosenblum *et al.* 2007; Richards & Knowles 2007). There are two alternative outcomes of this test (Fig. 4). If the partial MCT is not significant, we can infer that drift explains the observed phenotypic differentiation between lineages, as expected under non-adaptive divergence. Alternatively, if the partial MCT (between ENM and multivariate summary of morphological data)



**Fig. 4** Diagram of inferential steps for evaluating three common speciation modes. First, a partial matrix correlation test (MCT) between phenotype and environment controlled by genotype (based on neutral markers) is used to test the null expectation: random drift accounts for the observed phenotypic divergence. Absence of significant correlation is consistent with the null model. Significant MCT between-lineage differences in phenotype and environment (based on niche models) support an adaptive divergence scenario and indistinguishable phenotypes and environments are consistent with a niche conservatism/phenotypic stasis model. The bottom panel summarizes patterns of phenotypic divergence under the three speciation modes: (A) non-adaptive divergence of phenotypes in isolated lineages due to random drift; (B) retention of conserved phenotypes more similar to each other than expected due to phenotypic stasis; and (C) phenotypes are more different from each other than expected due to adaptive divergence. Solid lines indicate the realized phenotypic divergence and dotted lines represent the expected pattern due to non-adaptive divergence. Socially-mediated speciation can potentially occur under all three scenarios since sexual selection can produce divergence in phenotypic traits (e.g. colour morphs) linked to mating systems and RPS dynamics (see text).

shows significant differentiation between lineages, we can hypothesize a process of adaptive divergence. Another possible outcome would be significantly conserved niches and morphologies, which would support an hypothesis of niche conservatism and phenotypic stasis (Fig. 4).

Additional evidence of demographic history can reveal important perspectives that might clarify results of the MCT and the evolutionary forces involved in divergence of lineages. For example, support for both an adaptive divergence model in MCT analyses and a model of isolation-with-migration in IM analyses, suggests that selective forces have maintained differentiation in spite of gene flow (Nosil 2008; Hey 2009).

Multi-locus coalescent-based analyses may also detect population bottlenecks, providing evidence for selection associated with adaptive differentiation to the new habitat (Rosenblum *et al.* 2007). Alternatively, phenotypic divergence explained by neutral genetic divergence (non-significant MCT) coupled with a strict isolation model without significant gene flow, is more consistent with non-adaptive divergence. In summary, the interplay of evolutionary forces (drift, gene flow and selection) during population divergence can result in two distinct divergence patterns (adaptive divergence with gene flow or neutral divergence in isolation) that are being currently examined with empirical data (usually in single species pairs; Nosil *et al.* 2008; Nosil 2009; Gay *et al.* 2009).

Under socially-mediated speciation model, divergence leading to possible reproductive isolation can result from a build-up or loss of colour morphs (see Sinervo *et al.* 2008), which Corl *et al.* (2010b) refer to as morphic speciation (a sub-category of SMS, Appendix S3). One-strategy (monomorphic) systems can be invaded and converted to two-strategy systems (dimorphic), which can be invaded by a third to generate a trimorphic RPS dynamic; this system can then collapse back to a two or a one-morph system, and these can be reconstructed in a well-designed phylogeographic study (Fig. 5). Lineage diversification is expected to be non-random under a SMS mode (Corl *et al.* 2010b) and closely related tip lineages should be more dissimilar in social systems, presumably for the same reasons as noted above for ecologically-driven speciation based on divergent selection. If social systems contribute to lineage divergence and the buildup of reproductive isolation, then upon secondary contact they should begin to limit gene flow via pre-reproductive isolating mechanisms or by reinforcement processes if hybrid fitness is reduced by Dobzhansky-Muller incompatibilities (Corl *et al.* 2010b). If morphs evolve in both sexes (or in females only) the expected phylogeographic patterns become more complex and will likely relate to social strategies of density regulation (Sinervo *et al.* 2000, 2007; Corl *et al.* 2010b). Because completion of SMS may require evolution of a reinforcement mechanism (Butlin 1989), it does not fit the strict 'origin of allopatry' research paradigm described by Wiens (2004a). Further, lineage-based phylogeographic predictions derived from this mode of speciation [any number of social forces can drive this system besides morphs *per se* (Hochberg *et al.* 2003; Sinervo & Clobert 2008; Sinervo *et al.* 2008)] are distinctly different from both passive and adaptive divergence expectations (Table 2).

Potential limitations of this approach should be considered to reduce over-confidence in the interpretations. First, the approach represents a minimum test to reject

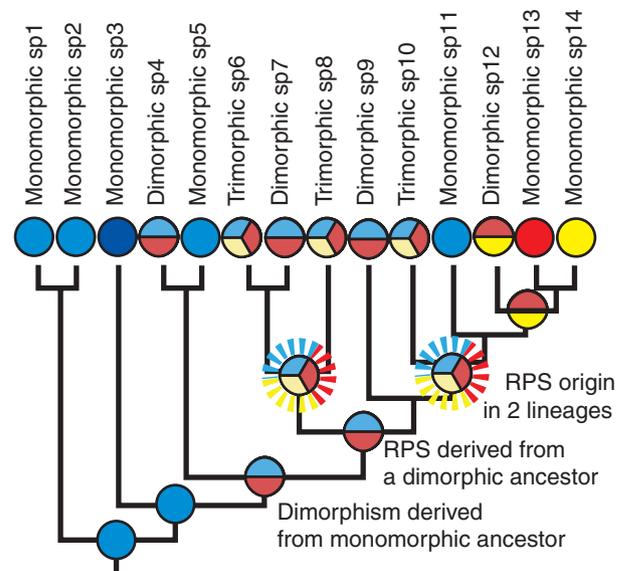


Fig. 5 Hypothetical phylogeny illustrating taxa with the predicted signature of socially mediated speciation based on a RPS set of colour morphs. Monomorphic outgroups suggest a blue ancestral colour/mating system, which was subsequently invaded by orange to create a dimorphic mating system, which is then invaded by yellow to create the full complement of three colours. This RPS mating system can also generate new mono- and dimorphic taxa by subsequent loss of morphs. Notice that the three monomorphic descendants of an RPS ancestor exhibit only one morph, but each descendant species is a different colour. We label terminals as species here for convenience, but these can also be divergent intra-specific clades (Corl *et al.* 2010b).

non-adaptive explanations for observed between-lineage patterns of variation, but alone it does not imply that divergence in phenotypic traits is directly responsible for speciation (if this has indeed occurred) because correlations alone do not link the diverged phenotypes to the origin of reproductive isolation. For example, Rundell & Price (2009) pointed out that ecological and morphological differentiation between species can either occur together with reproductive isolation ('ecological' speciation) or evolve after non-adaptive speciation. In this case, coalescent-based methods can clarify whether divergence occurred in complete isolation (e.g. no gene flow), supporting the hypothesis of 'non-adaptive' speciation (Nosil 2008) even if species show different niches and phenotypes today. Second, there is the possibility that phenotypic similarity between lineages is due to 'counter-gradient selection' in which genetic and environmental factors compensate each other across an ecological gradient, with a net outcome of apparently conserved phenotypes (Conover & Schultz 1995; Conover *et al.* 2009). Third, these correlation tests cannot point unambiguously to a single process underlying observed patterns because different processes can be responsible

for similar patterns (Revell *et al.* 2008). For example, phenotypic divergence following a neutral Brownian-like pattern can be due to either pure genetic drift or randomly fluctuating selection over time (Losos 2008).

Lastly, other kinds of analyses can also be used to evaluate association between genotype and phenotype or ecology; matrix correlation approaches are not the only options. For example, a nested random permutation procedure has been developed to test for 'cohesion' species based on significant associations between genetic lineages (inferred from past fragmentation events in a NCPA) and reproduction-related phenotypic and/or ecological traits (Templeton *et al.* 2000; Templeton 2001).

### Synthesis and future directions

The lizard studies of ecotones and hybrid zones described provide strong evidence for the influence of natural selection in promoting population divergence across narrow environmental gradients with ongoing gene flow, in a variety of taxa and ecological contexts. Rapid ecomorphological divergence documented within some species as a result of adaptive change to different environments (Losos *et al.* 1997, 2006; Rosenblum 2006; Vervust *et al.* 2007; Herrel *et al.* 2008) also suggests that phenotypic divergence can occur quickly given strong selection pressures, even in the presence of gene flow. Future studies of lizard hybrid zones will continue to rely on dense sampling, multiple genetic markers and the use of well-developed cline theory (Sites *et al.* 1995; Phillips *et al.* 2004), but there is room for a greater focus on the role of colour and other cues as these relate to mating preferences and the fitness consequences of mate selection (Stuart-Fox *et al.* 2009b; Corl *et al.* 2010b). Further, quantification of colour traits coupled with an emerging understanding of the genetic basis of colouration (Morrison *et al.* 1995; Sinervo *et al.* 2001, 2006; Rosenblum *et al.* 2004, 2010), will permit advancement of mechanistic hypotheses about the role of colour signals in promoting reproductive isolation under ecological and/or social modes of speciation. Genomics data sets will also expedite searches of 'outlier loci' possibly linked to 'speciation genes' under divergent selection (Hendry 2009; Nosil *et al.* 2009; Schluter 2009).

Lizards have figured prominently in species-delimitation studies, including the development of various approaches, comparisons of performance of different methods and syntheses of multiple data sets. The increasing availability of nuclear markers will enhance coalescent frameworks for estimating species trees and parameters such as ancestral population sizes, divergence times and demographic histories (Butlin *et al.* 2009). We suggest here also a place for non-model

based approaches to the same issue, for example the two-stage hypothesis testing protocol outlined by Templeton (2001). This approach is based on the use of NCPA to: (i) test for presence of separate evolutionary lineages as indicated by an inference for historical fragmentation at some clade level, and upon rejection of the null (panmixia), this is followed by (ii) a test that these separate lineages constitute different cohesion species. This second test evaluates whether these different lineages are genetically exchangeable and/or ecologically interchangeable within themselves, but not across lineage boundaries (Templeton 2001). Comparative evaluations of the performance of model vs. non-model approaches would be instructive in a few well-studied systems and should different approaches prove discordant with respect to species numbers and boundaries, the reasons would likely be apparent and informative about the validity of assumptions made by each approach (Wiens & Penkrot 2002; Marshall *et al.* 2006).

Bioclimatic (ENM) contributions will likely remain important for species delimitation, testing speciation hypotheses (Graham *et al.* 2004), predicting extinctions (Sinervo *et al.* 2010) and generating a priori phylogeographic predictions (Richards *et al.* 2007; Carnaval & Moritz 2008; Werneck *et al.* accepted). Detailed biophysical data will not be available for the majority of species, and while limitations of ENM data as assessments of 'niche' are widely appreciated (omission of soils, vegetation etc.), we suggest that morphological and other kinds of 'niche' data available from museum specimens have yet to be fully explored. For example, morphological and morphometric data can be used to assess features of niche divergence not included in ENM (sexual dimorphism, differences in trophic structure etc.; Fontanella *et al.* in review) and this approach could easily be expanded to assess potential competitors (congeneric species in sympatry or allopatry, for example). Other data available from vouchers include parasites and diets (food items are retained longer in poikilotherms in general; Pianka & Vitt 1994), both of which are likely to be informative about similarities or differences in niches.

The issue of sampling effects on phylogeographic inference has received little attention (but see Maddison & Knowles 2006) and future studies should distinguish among four aspects of sampling: number of individuals, number of loci, sequence length (Brito & Edwards 2009) and the number and distribution of sampling localities relative to the geographical range (Templeton 2009a; Leaché 2009). The relative impact of these different levels of sampling could be assessed by sub-sampling, which will help to incorporate ascertainment bias (Rosenblum & Novembre 2007) and to design better sampling strategies targeted to specific research questions.

Relative to other vertebrate taxa (Beheregaray 2008), fewer comparative studies of co-distributed taxa have been carried out in lizards (<4% of the studies summarized here) and we predict an increase in these kinds of studies, given rapid developments of methods for testing across multiple taxa for spatial and temporal co-divergence (see in examples in Leaché *et al.* 2007; Victoriano *et al.* 2008; Moussalli *et al.* 2009) and other shared historical events (Moritz *et al.* 2009). Well-designed comparative lizard studies are also likely to contribute to biodiversity conservation via continued discovery of cryptic species, identification of regions of high diversity and endemism and regions where evolutionary processes are likely to continue to operate (Davis *et al.* 2008).

We envision future phylogeographic and speciation research based on more explicit integration of multiple kinds of data from several disciplines, especially from earth sciences (Beheregaray 2008) and geography (Kidd & Ritchie 2006) and expanded assessments of phylogeographic patterns based on phenotypic and ecological data. Here we have outlined one correlative approach to compare genetic, morphological and ecological divergence patterns in a framework easily applied to phylogeographic studies and suggest that such data sets are capable of discriminating among alternative speciation patterns.

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A. Camargo is interested in the use of coalescent methods for species delimitation and phylogeography; B. Sinervo is interested in the evolution of social behaviours and social systems and their role in macroevolutionary processes; and J.W. Sites, Jr is interested in phylogeography, speciation patterns and hybrid zone interactions.

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## Supporting Information

Additional supporting information may be found in the online version of this article.

**Appendix S1** List of published studies on lizard phylogeography.

**Appendix S2** Number of published studies across families, general, continents and methods.

**Appendix S3** Details of the socially-mediated model of speciation.

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