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An adult male *Leiocephalus personatus* from near Juanillo, La Altagracia Province. This wide-ranging species reaches the westernmost extent of its range along the southern coast in association with a sharp ecotone near Baní.

Ecotones and Hybrid Zones: Implications for Conservation Illustrated by Ground-dwelling Lizards from Hispaniola

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Hybrid zones have been of great interest to evolutionary biologists for quite some time. However, only in the last few decades have they received much attention. This change follows a paradigm shift from viewing hybrid zones as rare occurrences in the general distribution of "pure" forms to their potential importance as regulators and creators of biodiversity (Harrison 1993). The resultant research effort has created a realization that the analysis of hybrid zones can provide information with far-reaching implications for speciation, adaptation, and even conservation (Arnold 1997, Harrison 1993). With this in mind, the following article discusses hybrid zones in the context of their consequences for speciation and conservation, focusing on an area identified as a zone of secondary contact between two lineages of the lizard *Ameiva chrysolaema* in the Dominican Republic.

Hybrid zones can be defined as regions (either narrow or broad) of genetic or anatomical changes that separate otherwise continuous and homogeneous "taxa." "Taxa" is placed in quotes here to represent not only recognized species but also divergent

Ameiva chrysolaema from 5 km west of Duvergé, Independencia Province. Two distinct lineages of this species meet at the ecotone near Baní.

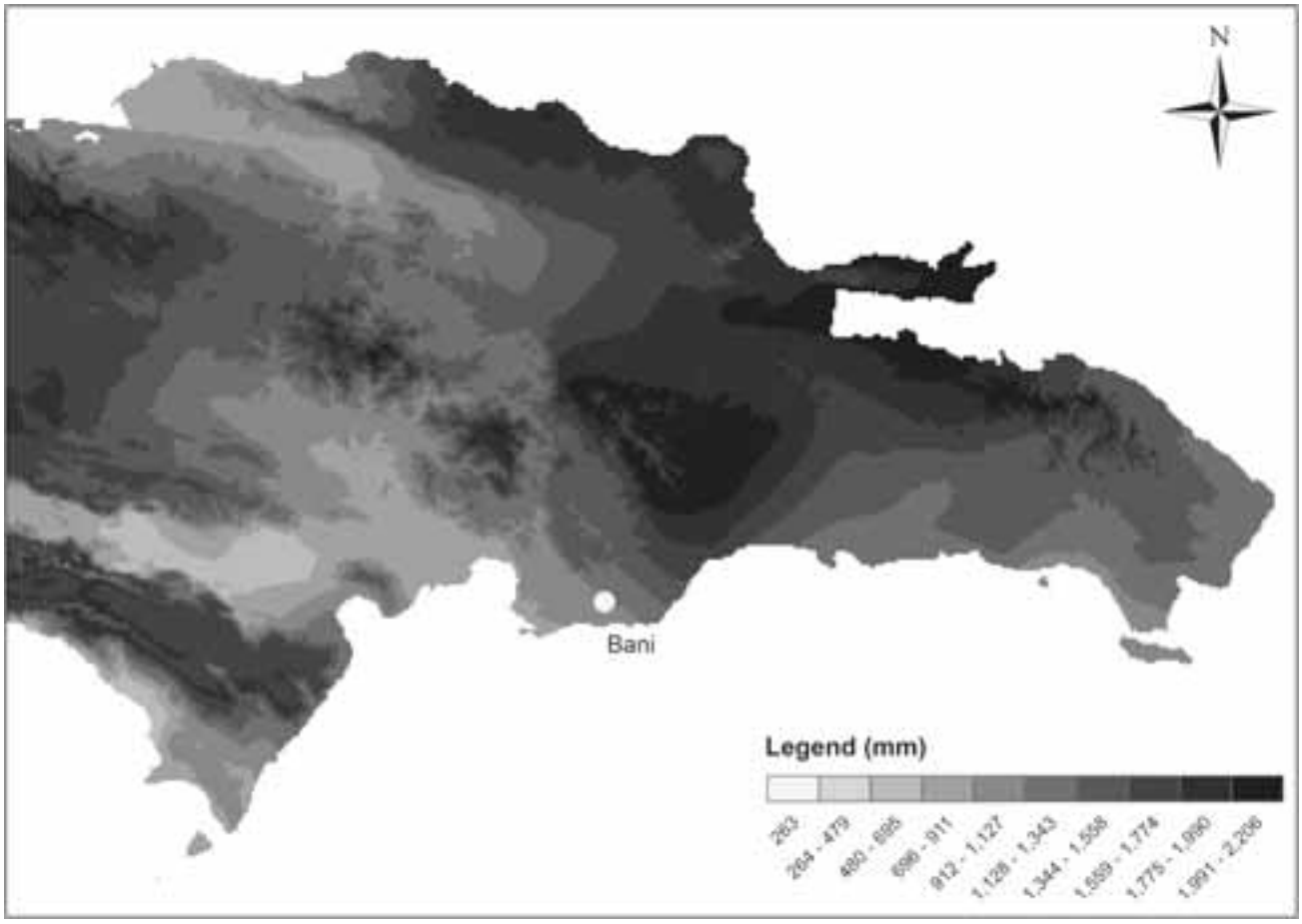
lineages that may or may not be formally recognized. The advent of new methodologies and availability of increasingly detailed genetic data has revealed that previously unknown lineages are common and characterize most widely distributed groups of organisms. Areas of contact between lineages many times result in interbreeding among members of these lineages. Such zones provide unique opportunities to study the process of speciation and adaptation. Combined analyses of different types of characters (genetic and anatomical) provide information on the processes that maintain hybrid zones or contribute to their collapse (Barton and Hewitt 1985). Hybrid zones can form in areas of continuous habitat or at habitat transitions (i.e., ecotones). The hybrid zone discussed herein is associated with a prominent ecotone in the south-central Dominican Republic near the city of Baní.

The island of Hispaniola has had a dynamic geological history highlighted by periodic inundation of the Cul de Sac-Neiba Valley in the central portion of the island. These inundations separated Hispaniola into two paleoislands at various times during the Miocene to Pleistocene epochs (~15–1 million years ago [mya]; Mann et al. 1999, McLaughlin et al. 1991, Taylor et al. 1985). After recession of seawater, habitable land likely became emergent during the late Pleistocene and Holocene. Genetic data suggest that these seawater inundations fragmented populations of *Ameiva chrysolaema*, forming eastern and western lineages along the southern coast of the island (Gifford et al. 2004). This study also identified a restricted area (in the vicinity of Baní) where these two lineages have come into secondary contact.

The diverse topography of the island contributes to a vast array of environmental conditions and creates near Baní a sharp environmental shift from relatively moist conditions in the east to extremely dry conditions in the west. Character shifts in *A. chrysolaema* associated with this ecotone include body size (SVL), dorsal scale size, and both nuclear and mitochondrial genetic characters (unpubl. data). In the following section, I consider what these character shifts imply about the nature of the hybrid zone and discuss the implications of these shifts for speciation, adaptation, and conservation in the group. Please note that this discussion is based on preliminary data and is used only to illustrate a thesis. Additional data collected during future field seasons will be necessary to further characterize this hybrid zone and test the hypotheses discussed here.

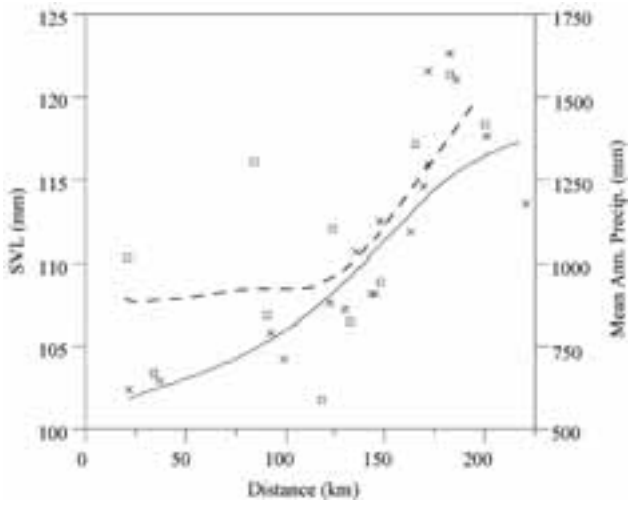
Patterns of character variation across the zone

Mitochondrial genetic characters show a sharp change in frequency from those characterizing the western lineage being found in essentially all individuals in those populations west of the ecotone, to being absent from populations on the east side of the ecotone. However, two populations within the ecotone contain characters of both lineages (Gifford et al. 2004). Preliminary data from studies of nuclear genetic material show a similar pattern, but the area over which the change occurs



Map of mean annual precipitation (mm) for the Dominican Republic. The ecotone discussed in the text refers to the area in the vicinity of Baní.

appears to be wider. Anatomical characters also seem to exhibit comparable relationships across the contact zone. In the case of body size, populations in dry habitats to the west tend to contain smaller individuals than populations in the moister eastern environments. This is illustrated clearly by a positive correlation between precipitation and SVL across the contact zone.



Morphological (dashed line) and environmental (solid line) clines for populations of *Ameiva chrysolaema* sampled across the ecotone. Boxes represent mean SVL (mm) for each sampled population along the transect. Crosses represent mean annual precipitation (mm) for each sampling point along the transect. The x-axis represents distance (in km) from an arbitrary locality on the western side of the ecotone.

Implications of contact zones for speciation and adaptation

The coincidence of contact zones (i.e., the occurrence of zones corresponding to several characters in similar geographic locales) and the concordance of changes (i.e., similar rates of change over the contact zones for different characters) have been used as evidence that natural selection can maintain a hybrid zone (Endler 1977, Barton and Hewitt 1985). However, two types of selection could be responsible and are indistinguishable from one another. Selection may work against individual hybrids, which would suffer a decrease in fitness relative to "pure" forms. Alternately, selection may favor local adaptation to different selective pressures on either side of the zone. One may be able to distinguish between these types of selection by using additional data. For example, the first hypothesis may be supported if populations in the hybrid zone are found in a population density trough (i.e., have decreased population densities), which is a testable prediction. That hypothesis would be further strengthened if reciprocal transplant experiments indicated a decreased fitness of hybrids in all transplanted habitats. Although testing these predictions takes considerable time and effort, the important point here is that natural selection is important in structuring the hybrid zone.

Variation among transition zones for anatomical characters could arise in several ways. Some characters may be under selection while others are effectively neutral. That could lead to transition zones for neutral characters governed most strongly by totally random factors (as opposed to selection). Variation among transition zones for genetic characters might be gener-

Leiocephalus semilineatus from 5 km west of Duvergé, Independencia Province. This very drought-tolerant species is largely confined to the very dry Cul de Sac-Neiba Valley and reaches the easternmost extent of its range at the ecotone near Baní.

ated by the different properties of mitochondrial versus nuclear genes. The latter generally evolve more rapidly, so differences might be coupled with the age of the hybrid zone. If genetic variation is minimal and anatomical variation pronounced, natural selection on anatomical features may be very strong. Different patterns may suggest that the lineages are diverging while others might indicate that they are merging in a fashion that could result eventually in a single genetic lineage.

Implications of hybrid zone studies for conservation

At first glance, the presence of a hybrid zone may cause problems for conservationists. These problems likely stem from the lack of consensus about the appropriate methods by which we should identify species. By viewing speciation as an extended process and species as elements of populations-level lineages (*sensu* de Queiroz 1998), some of these problems may be

Leiocephalus schreibersii from 5 km west of Duvergé, Independencia Province. This species is largely associated with very dry habitats; like *L. semilineatus*, it reaches the easternmost extent of its range at the ecotone near Baní.

Leiocephalus lunatus from Catuano, Isla Saona, La Altagracia Province, Dominican Republic. Although this individual is not from the main island of Hispaniola, the species is fairly uniform in pattern across its range. This species has a largely coastal distribution that reaches its westernmost extent at the ecotone near Baní.

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Ameiva lineolata from Isla Catalina, La Romana Province. Although most populations of this drought-tolerant species are found in the very dry Cul de Sac-Neiba Valley west of the ecotone near Baní, some apparently relict isolates are found far to the east.

addressed more effectively. The goal of conservation is to preserve biodiversity. Biodiversity can be defined as the natural diversity of independently evolving lineages (as opposed to formally recognized species or even higher taxa; see, for example, Powell 2004 and references therein). Consequently, we must understand the evolutionary consequences of lineage contact and the processes acting to either maintain lineage differences or facilitate lineage merger. Ecotonal contact zones mark the confluence of different environmental conditions that may also represent the limits of other species adapted to the alternative environments. As such, these ecotones represent areas of high faunal turnover and, hence, high diversity. By conserving these areas, we may preserve the selective pressures (environmental heterogeneity) that have shaped the current distribution of taxa and the processes that maintain and structure biodiversity. Other ground-dwelling lizards whose distributional limits are located at this particular ecotone include *Leiocephalus semilineatus*, *L. schreibersii*, and *Ameiva lineolata* on the dry western side and *L. personatus* and *L. lunatus* on the moister eastern side.

Literature Cited

Arnold, M.L. 1997. *Natural Hybridization and Evolution.* Oxford University Press, New York.

Barton, N.H. and G.M. Hewitt. 1985. Analysis of hybrid zones. *Annual Review of Ecology and Systematics* 16:113–148.

de Queiroz, K. 1998. The general lineage concept of species, species criteria, and the process of speciation: A conceptual unification and terminological recommendations, pp. 57–75. In: D.J. Howard and S.H. Berlocher (eds.), *Endless Forms: Species and Speciation.* Oxford University Press, New York.

Endler, J.A. 1977. *Geographic Variation, Speciation, and Clines.* Princeton University Press, Princeton, NJ.

Gifford, M.E., R. Powell, A. Larson, and R.L. Gutberlet, Jr. 2004. Population structure and history of a phenotypically variable teiid lizard (*Ameiva chrysolaema*) from Hispaniola: The influence of a geologically complex island. *Molecular Phylogenetics and Evolution* 32:735–748.

Harrison, R.G. 1993. Hybrids and hybrid zones: Historical perspectives, pp. 3–12. In: R.G. Harrison (ed.), *Hybrid Zones and the Evolutionary Process.* Oxford University Press, New York.

Mann, P., P.P. McLaughlin, W.A. van den Bold, S.R. Lawrence, and M.E. Lamar. 1999. Tectonic and eustatic controls on Neogene evaporitic deposition in the Enriquillo basin, Dominican Republic, pp. 287 – 341. In: P. Mann and K.J. Hsü (eds.), *Sedimentary Basins of the World: Caribbean Basins.* Elsevier, Amsterdam, The Netherlands.

McLaughlin, P.P., W.A. van den Bold, and P. Mann. 1991. Geology of the Azua and Enriquillo basins, Dominican Republic; 1, Neogene lithofacies, biostratigraphy, biofacies, and paleogeography, pp. 337–366. In: P. Mann, G. Draper, and J.F. Lewis (eds.), *Geologic and Tectonic Development of the North America-Caribbean Plate Boundary in Hispaniola.* Geological Society of America Special Papers, vol. 262.

Powell, R. 2004. Species and subspecies: What do they mean and why should we care? *Iguana* 11:108–113.

Taylor, F.W., P. Mann, S. Valastro, Jr., and K. Burke. 1985. Stratigraphy and radiocarbon chronology of a subaerially exposed Holocene coral reef, Dominican Republic. *Journal of Geology* 93:311–332.