

Ecological and phylogenetic factors affecting genetic divergence and community structure in Cuban Anolis lizards

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論文内容の要旨

Summary

Understanding the factors that contribute to population genetic divergence and species richness at different geographic levels are long-standing goals in ecology and evolution. In this Thesis, we search for patterns and causal explanations for *Anolis* lizards biodiversity within Cuba. Independent intra-island differentiation on the Greater Antillean islands has produced sets of *Anolis* species that differ morphologically and behaviorally. They are termed “ecomorphs” and are named for the microhabitat they usually occupy (grass-bush, trunk-ground, trunk-crown, crown-giant, and twig). Each of these ecomorphs has evolved independently at least three times in different Caribbean islands. Thus, very similar structured communities (i.e. with the same set of ecomorphs) can be found on those islands.

Two levels of analysis have been considered in this Thesis. First, in Chapter 2 we focus on a particular group of *Anolis* distinguishable by its high diversity in Cuba and the fact that although they are members of the same ecomorph, some species coexist sympatrically at several sites (Collette 1961, Ruibal 1961, Rodríguez-Schettino 1999, Rodríguez-Schettino et al. 2010). Species with different ecomorphs can easily be predicted to sympatrically coexist, but only a limited number of studies have considered the historical and evolutionary processes underlying within-ecomorph species richness on both the regional and local scales (Glor et al. 2003, Glor et al. 2004). In Chapter 2 we assess the relative importance of sympatric coexistence, the number of speciation events, and range expansion for species richness in local assemblages of trunk-ground anole lizards in Cuba. We examined the species richness and thermal microhabitat partitioning (considered to be a measure of ecological interaction) of 12 trunk-ground anole species in 11 local assemblages. We classified species as sympatric when they occurred in the same vegetation type or when they were found in different but contiguous vegetation types. Species were considered allopatric when they were found in different vegetation types without contact points and also when species inhabiting the same vegetation type were not sympatric (i.e., in different locations). Within assemblages, thermal microhabitat type was classified in three categories: open, shade and intermediate. We defined six regions in the Cuban territory based on their high and low land area attributions in the late Pliocene to latest Pleistocene (Iturralde-Vinent 2006): western, western island, central, east-central, west-eastern, and eastern. We inferred the phylogenetic relationships among 247 individuals using mitochondrial DNA (mtDNA) and nuclear genes to estimate the ancestral geographic regions where species originated and the number of speciation events in each region. We tested for nonrandom patterns in the community assemblies using randomly generated null communities of trunk-ground anoles. A phylogenetic distance matrix was constructed by measuring the pairwise phylogenetic distances (i.e. branch lengths in the phylogenetic tree) among all pair of species within the same assemblage. The thermal microhabitat types of

each species (i.e., shade habitat = 1, ecotone habitat = 0.5, open habitat = 0) were used to construct a functional distance matrix to visualize the thermal preference similarity. Phylogenetic and functional dispersion values were calculated using the mean pairwise phylogenetic distances (MPD) (Webb 2000) and mean pairwise functional distances (MFD), which were calculated for all pairwise combinations of species that occurred together at each site. These metrics were subsequently compared with their corresponding null distributions to test whether local assemblages were phylogenetically and functionally clustered or overdispersed.

The results in Chapter 2 indicated that the phylogenetic structure of trunk-ground anole lizard assemblages was random. However, there was an overdispersion of preferences for thermal microhabitat use, which indicates that differences in microhabitat use are likely to occur within assemblages. We suggest that the number of speciation events within regions and the number of sympatrically coexisting species increases species richness at the local level. Migration appeared to be limited, leading to the range expansion of only three species with different thermal requirements. The thermal niches of species were conserved within *Anolis allogus* clade, whereas species within the *Anolis homolechis* and *Anolis sagrei* clades tended to change their thermal niches. Thus, our results suggest that the species composition and richness in local assemblages could be explained by evolutionary history (the number of speciation events and limits to range expansion) and ecological processes (habitat partitioning). Of the ecological factors, the number of thermal (microhabitat use) and structural niches (e.g. vegetation) could limit the potential number of coexisting species within a local assemblage.

After studying the patterns of local species richness within one ecomorph class, we then raise the level of analysis and target all the anole radiation within Cuba. In Chapter 3 we focused on the patterns of genetic divergence in several Cuban *Anolis* species, and the factors affecting it. Patterns of genetic variation often reflect spatial variation in gene flow, which is a direct consequence of a successful dispersion to a new location. Thus, any factor affecting dispersion abilities will influence gen flow, which in turn affect the genetic divergence among populations. How successfully one species disperse is a result of ecological, morphological and geographical factors. Spatially separated populations may experience isolation-by-distance (Wright 1943), in which landscape barriers and geographical distances cause restricted gene flow. In addition, different morphologies are expressed as differences in dispersal abilities (Brown and Maurer 1989; Greenwood 1980). Both phylogenetic history (Abellán and Ribera 2011) and species age (Krug et al. 2008) could also explain historical patterns of dispersion responsible for the current geographic ranges of species. In addition, gen flow can be influenced by isolation-by-environment (Wang and Summers 2010), in which gene flow among populations inhabiting different ecological environments is limited either by selection against dispersers moving between them or by individual preference to remain in a particular environment due to local adaptation. Because genetic divergence can be affected by several factors, it is important to assess which of them are relevant to explain the observed spatial patterns of genetic divergence.

Previous studies indicated a deep interpopulational genetic divergence in several Greater Antillean anoles (Jackman et al. 2002; Glor et al. 2003; Kolbe et al. 2004; Knouft et al. 2006; Rodríguez-Robles et al. 2007; Kolbe et al. 2007, Glor et al., 2004, 2005). These results are unexpected because most of these species have continuous distributions, so impediments to gene flow would not seem to exist, and because no striking geographic variation in morphology has been noted in some of these wide spread species (Losos 2010). Recently, Wang et al. (2013) quantified the relative strengths of ecology (measured as local environmental data) and geography (measured as distance between localities) in spatial genetic divergence in a selection of anoles species from four Greater Antillean island: Cuba (four species), Hispaniola (5 species), Jamaica (three species) and Puerto Rico (5 species). The results showed that geographical isolation explained substantially more genetic divergence than ecological isolation, suggesting that despite the proposed ubiquity of ecological divergence, non-ecological factors play the dominant role in the evolution of spatial genetic divergence.

In Chapter 3, we explore the relative importance of male body size, thermal microhabitat, ecomorph, geographic range, geographic distances, and species age to explain the genetic divergence in 22 Cuban anoles species. We reconstructed a phylogeny for 22 Cuban species (287 samples) to estimate pairwise genetic distances (used as a measure of genetic divergence) among localities, using two nuclear and one mitochondrial gen. A second data set was comprised by 105 species, and it was made using three groups of samples. First, all Cuban *Anolis* species collected by us (56 species, 268 samples) selecting only one sample per locality. Second, a selection of 42 *Anolis* species from all Caribbean Islands (Jamaica, Hispaniola, Puerto Rico, Bahamas, Caymans, and Lesser Antilles) as well as a selection of species from the continent (Central and South America) was included. Third, we added to this phylogeny three additional Cuban species downloaded from the Gen Bank, since these are species we could not collect. Using GLM we tested which of these factors explain the observed genetic divergence among species. GLM analyses were done according to different geographic ranges. One of the GLM included only those localities closer that 200 km (pairwise geographic distance <200km), and the other GLM included only localities located at distances larger than 200 km from each other (pairwise geographic distance >200km). The average genetic distance and geographic distance for each species were used for GLM analysis. Because the sampled localities are usually not the same for all species, geographic distances are also different for each species. Because of this dissimilarity, we expected that geographic distance would affect part of the variation observed in the genetic divergence. By including geographic distance in our GLM analysis, we are removing its effects and we can then analyze which other factors are affecting the intraspecific genetic divergence.

The phylogeny presented in Chapter 3 is the most comprehensive for Cuban anoles. It shows a more parsimonious evolution of anoles ecomorphs within Cuban island, recovering twig anoles as a monophyletic group, which is in disagreement with previous studies. At both geographic scales (geographic distances lower

than 200 km and higher than 200 km) our results showed that geographic distances, ecomorph, and male body size explained the observed variation in the genetic divergence (although the variable “ecomorph” was not included in GLM for geographic distances >200 km). Thus, our results suggest that microhabitat type, range size, and species age are not important for explaining the genetic variation between species. Body size was negatively associated with genetic divergence. Thus, it is a very important factor affecting genetic divergence within the Cuban anole radiation. Previous studies (Losos 1990a, 1990b; Calsbeek and Smith 2007; Calsbeek et al. 2007) suggest that *Anolis* lizards in the Greater Antilles have diversified through natural selection on body size and shape, presumably due to interspecific competition and variation in locomotor performance. Thus, in addition to the well-known effect of body size to explain the variation in locomotor performance, our results showed that variations in body size also accounted for the intraspecific genetic divergence in anole species. Larger animals might exhibit better dispersion abilities. Four trunk-ground anole species accounted for the highest values of genetic divergence among all species: *Anolis allogus*, *A. jubar*, *A. quadriocelifer*, and *A. rubribarbus*, which have highly divergent populations. Two of these species (*A. allogus* and *A. rubribarbus*) inhabit exclusively well-preserved forest, and are restricted to the shaded places within those forests. This habitat specialization might be limiting its dispersal abilities and the gen flow among relatively close populations. Nevertheless, both *A. quadriocelifer* and *A. jubar* do not are restricted to shaded places. Instead, they are found in open and intermediate thermal microhabitat. Thus, this ecological trait (thermal preference) seems not to be the reason for limited dispersion and high levels of genetic divergence. In disagreement to previous findings (Wang et al. 2013), we suggest that isolation-by-distances is not the most important factor affecting genetic divergence in Cuban *Anolis*.

In this Thesis we addressed several questions regarding why are there more species in some regions than others, how do species interact with others within local assemblages and what is the effect of that interaction, and what drives genetic diversification. As was expected, there is no a single factor than can be invoke to explain the current biodiversity anoles in different regions. It is the interplay of both ecological and biogeographical factors that determine the observed patterns. By bringing both community ecology and evolutionary history into a single approach, we gain new insights into questions typically asked by ecologists and evolutionary biologists.

論文審査結果の要旨

アノールトガゲは、カリブ海の島で、異なるニッチに適応放散しており、適応放散、収斂進化のモデル生物として知られている。キューバは、カリブ海の島々の中で最も多様性の高い 64 種が生息している。アノールトガゲにおいて、異なるエコモルフ（形態や行動により分類）を持つ種は、樹冠、幹、枝先、幹-地上(Trunk-Ground)、草地などに生息場所を違えて共存している。しかし、同じエコモルフをもつ種でも数種が共存することが知られている。Antonio Cadiz 氏は、キューバに生息する Trunk-Ground 型の 12 種の局地的な種多様性がどのような要因によって決まっているかを調べた。キューバの 11 の局地群集から 274 個体のサンプルを収集し、系統樹を作成した。また、各局地群集で、同所的に共存している種数を調べた。その結果以下のことが明らかになった。(1)各局地群集に生息する種は系統的にランダムである、(2)オープンな環境、林内の環境、林縁の環境に生息する種は、有意に共存する傾向にある、(3)オープンな環境、林内の環境、林縁の環境に生息するかという生息地利用形質は、系統の中で変化しづらい形質である、(4)局地群集での種数は、そこに何種類まで同所的に共存できるかと、その地域でどれだけ種が生じたかによって決まっている。これらの結果は、種数におよぼす生態学的な要因と歴史的な要因の相対的な重要性を明らかにした重要な成果となった。また、キューバに生息する 22 種、278 個体のサンプルを使って、種内の遺伝的分化におよぼす影響について調べた。その結果、棲息場所や種の生じた時間などについては関係がみられなかったが、体の大きい種ほど、種内の遺伝的分化が低い傾向があきらかになった。これまで、遺伝的分化の程度は、地理的な距離が重要であるという研究はあったが、体のサイズが影響していることを示した最初の研究であり、非常に重要な結果となった。よって、Antonio Cadiz 氏提出の論文は、博士（生命科学）の博士論文として合格と認める。