

Biome evolution and biogeographical change through time

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Abstract. Keystone plant groups can be used to infer the evolution of biomes and biogeographical change of communities and taxa. In this thesis I investigated whether lineages in Trachycarpeae palms could be used to track different forest types through time and whether change in biome or biogeographic region had an effect on species diversification. These questions were approached using genetic data integrated with fossil record, species distribution, and speciation models. Although the three chapters of my thesis had additional foci outside of the main goal of inferring biogeographic change and diversification through time, they come together to paint a clear picture of how fine-scale and interdisciplinary studies can lead to more robust hypothesis testing and conclusions. I found that outside of tracking tropical forests through time, palms are useful for understanding island biogeography and the formation of other types of biomes.

Keywords. Areaceae, biogeography, macroevolution, phylogeny

Introduction

The inference of biogeography and diversification is an integral window into the past that enables the investigation of how geographic regions, biomes, and communities are assembled through time and how they may evolve in the future. By integrating data, for example from geology, genetics, fossils, species distribution and abundance, and morphology, we can reach a more comprehensive framework for the understanding of biogeographical evolution (Figure 1). The importance of these types of studies reaches beyond basic biodiversity science and the discovery of important evolutionary processes, and underscores cutting edge conservation research (Rolland et al. 2011). Understanding how biodiversity evolved can inform modeling of the past, present and future of that biodiversity and can aid in, for example, the design of protected areas that take into account diverse evolutionary processes (Sarker et al. 2006), or the definition of how climate change may affect the future availability of resources (Piao et al. 2010).

The use of model groups to understand evolutionary patterns is commonplace, particularly in systems like *Drosophila* (*Drosophila* 12 Genomes Consortium 2007) and *Arabidopsis* (Koch and Matschinger 2007), but for evolutionary stud-

ies of biodiversity and biogeography, other model groups have proved equally important. One example lies in leguminous plants, where studies have shown that endemic legume clades track South American seasonally dry tropical forests (SDTF) through time (Pennington et al. 2010, Särkinen et al. 2012). These clades are geologically old and evolutionary distinct, as evidenced by the deep divergences within and amongst species. These studies suggest that SDTFs are ancient biomes that were separated by the rise of the Andes and could be excellent models for understanding vicariance processes if complemented with ancestral area analysis. Another model plant group for understanding biome evolution is the palms (Couvreur and Baker 2013). Because palms are primarily restricted to the tropics and subtropics due to structural constraints, they represent keystone tropical rainforest (TRF) clades. A recent study by Couvreur et al. (2011) inferred that a TRF-like biome was present in Laurasia during the mid-Cretaceous, suggesting that ancient and steady evolutionary processes contribute to the present day species richness in TRFs. One caveat of their analysis is that it was based on a genus-level phylogeny that, even with missing species grafted onto appropriate branches, is not robust to the sampling bias introduced in the diversification

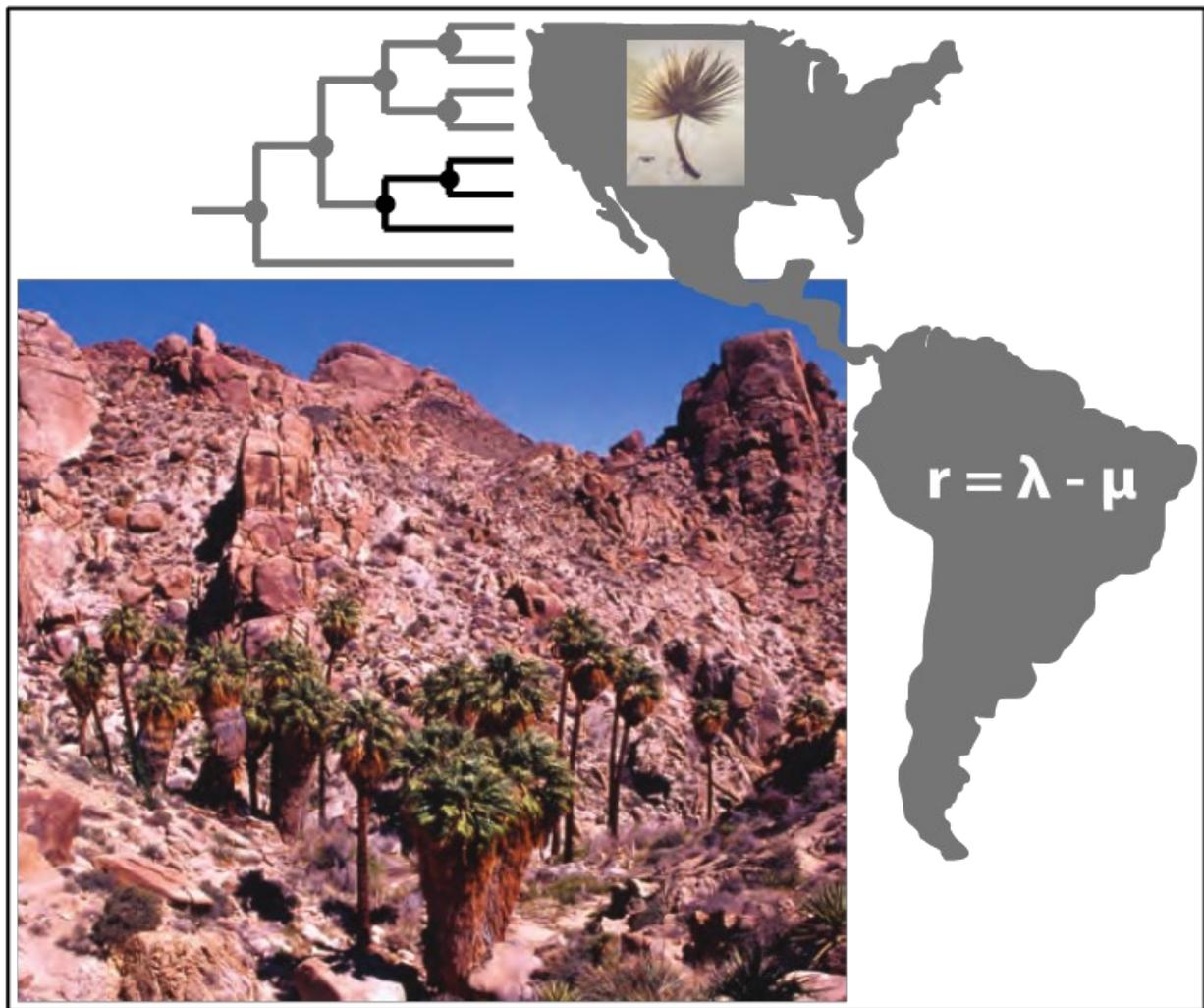


Figure 1. By integrating data—for example from geology, genetics, fossils, species distribution and abundance, and morphology—a more comprehensive framework for the understanding of biogeographical evolution can be reached. For example, to infer the timing and geographic location of desert biomes a time-calibrated molecular phylogeny of endemic desert lineages can be reconstructed and species distributions and diversification rates (r = diversification rate, λ = speciation rate, μ = extinction rate) are optimized on the tree. Taken together, these results can be used to understand the evolutionary processes that contribute to the formation of this biome and its respective biota. Photo by John Dransfield with permission.

models (Cusimano and Renner 2010).

To infer biome evolution and biogeographical change through time, my dissertation focused on Trachycarpeae palms. Trachycarpeae encompasses three insular radiations found in the Hawaiian Islands, the Caribbean, and the area surrounding Wallace's Line. My first goal was to understand the common evolutionary processes that contributed to the repeated diversification on islands in the tribe (Bacon et al. 2012a). Focusing on the Hawaiian radiation, species delimitation methods were compared to not only robustly infer species diversity and biogeography, but also to under-

stand plant evolutionary processes, such as incomplete lineage sorting and hybridization (Bacon et al. 2012b). Lastly, to understand the relative importance of taxonomic identity and biogeographic area in shaping the patterns of diversification and forming the bimodal biogeographical pattern observed in palm lineages in the Southeast Asian region, the tempo and mode of species diversification were inferred for a clade distributed across Wallace's Line (Bacon et al. 2013a). What sets this dissertation apart from previous studies is the fine scale view of biogeographical processes that was achieved by incorporating dif-

ferent types of data—phylogeny, fossil, species distributions, population genetics—and mathematical models, which were analyzed in a complementary fashion (divergence times, biogeography, diversification) to examine biome evolution and biogeographical patterns.

Methods

To understand evolutionary processes of biome evolution based on DNA sequence data, we used a fossil calibrated molecular phylogeny. The most cited method for estimating divergence times is conducted in a Bayesian framework (BEAST; Drummond et al. 2006), which is desirable considering that uncertainty in topology and calibration points can be explicitly incorporated. For Trachycarpeae, a review of the fossil palm record revealed three macrofossils that were well dated and sufficiently known to confidently place constraints on nodes leading to certain taxa (Bacon et al. 2012a). Calibrations were set at nodes using a lognormal distribution with the mean age of the fossil used as the offset value of the lognormal curve and the standard deviation encompassing the variation in age of the fossil strata (Ho 2007). A Yule tree prior was used, which assumes a constant lineage birth rate for each branch in the tree, and is the most suitable for species-level phylogenies (Heled and Drummond 2012). After five independent iterations of 50 million MCMC chains, results were compared, combined, and examined for convergence.

With a calibrated phylogeny, the temporal information of clades can be used to infer the origin and biogeographical evolution across the tree. New methods in biogeographical analysis have been advancing the field at a rapid rate. For example, the DEC likelihood model (Ree and Smith 2008) is a powerful method of hypothesis testing where the dated phylogeny can be split up into time slices, which can in turn be constrained to limit dispersal between regions that are thought to lack connectivity in particular geological times. Bayesian statistics are also implemented in reconstructing biogeographical change through time (Yu et al. 2010). User-defined biogeographical areas are optimized on a fossil calibrated topology (or

set of topologies) to infer ancestral areas in time across the phylogeny and with these results, biogeographic events such as dispersal, vicariance, cladogenesis, and local extinction are inferred. In the dissertation study, both RASP (Yu et al. 2010) and DEC were implemented to infer the geographic change in ancestral distribution areas through time in Trachycarpeae lineages.

A fundamental question in evolution involves the factors that influence speciation and extinction. For example, has the evolution of a particular trait or the dispersal into a biogeographic region increased speciation rates? The estimation of diversification rate has improved in recent years and many advances towards understanding the interplay between speciation and extinction have been made (Alfaro et al. 2009, Stadler 2011). In Trachycarpeae lineages distributed across Wallace's Line, I compared the likelihoods of various models of diversification to determine whether constraints associated with either taxonomic identity, biogeographic area, or both have contributed to shape the patterns of diversification observed in the clade of Southeast Asian palms.

Results

Examining the three datasets in this dissertation allowed for the inference of tempo and mode of diversification in Trachycarpeae palms. Higher-level relationships and the inference of their ancestral areas show dispersal and vicariance events across the tree corresponding to geological processes such as tectonic plate movement and the emergence of land bridges. The number of dispersal events inferred for the island lineages was particularly high and primarily occurred in the Miocene (Bacon et al. 2012a). Results from species delimitation showed that long-distance dispersal and rapid island radiation were fundamental in the biogeography of species and corresponded to the geological age of each of the island groups (Bacon et al. 2012b). We detected significant diversification rate shifts in the lineages that crossed Wallace's line, which we interpreted as a function of the evolution new morphological traits within new biogeographical areas (Bacon et al.

2013a). Furthermore, lineages that crossed Wallace's Line migrated in geological time corresponding to the reduction of the oceanic seaway between islands, facilitating dispersal. These results taken together suggest that biogeographic regions and biomes can be tracked through time through the study of Trachycarpeae palms.

Discussion

Results stemming from my dissertation research suggest that beyond TRF evolution, palms can be used to track biomes more generally. We showed that open-forest, savanna endemic palm lineages evolved in North America in open, tropical grasslands, and dispersed through the Isthmus of Panama region, into savannas in northern South America (Bacon et al. 2013b). If a phylogenetic niche conservatism hypothesis is assumed, the dispersal of dry-adapted palms that are resistant to intermittent flooding may indicate the presence of savanna-type ecosystems during the early formation of the isthmus region. This result is important because the implications of the timing of biotic dispersal can illuminate the debate about the geological formation of the isthmus (Stone 2013). In conjunction with other analyses such as hindcasting (Wake et al. 2009 and references therein) and climatology, the analyses used in my dissertation can help scientists infer paleoenvironments with greater precision.

Advancements in the estimation of coalescent species trees will be essential to using phylogenies for inference of biogeographical change through time as they improve topologies and the inference of species relationships (Yang and Rannala 2010) by accounting for incomplete lineage sorting (Heled and Drummond 2010) and hybridization (Kubatko et al. 2009). Furthermore, future work in the area of biome evolution and biogeography should focus on complementing phylogenetics with emerging biogeographical (Goldberg et al. 2011) and macroevolutionary analyses to allow for reciprocal illumination amongst analyses. For example, ecological niche modeling can help researchers forecast how climate change and degradation of habitats will affect the biogeography and diversification of species and clades. Furthermore,

studying macroevolutionary patterns such as trait-based diversification (Fitzjohn 2012) or phylogenetic community structure (Webb et al. 2002) can illuminate essential processes involved in morphological change and community assembly, which in turn need to be protected from anthropological disturbance.

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