

INTRODUCTION

For the Special Issue: Patterns and Processes of American Amphitropical Plant Disjunctions: New Insights

Patterns and processes of American amphitropical disjunctions: New insights¹

Michael G. Simpson², C. Matt Guiliams³, and Leigh A. Johnson⁴

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For over a hundred years, botanists and biogeographers have noticed an interesting pattern: the occurrence of the same plant species or very close relatives on either side of the tropics in North America (NA) and South America (SA) (Gray and Hooker, 1880; Bray, 1898, 1900; Johnston, 1940; Constance, 1963; Raven, 1963; Cruden, 1966; Solbrig, 1972; Thorne, 1972; Carlquist, 1983; Wen and Ickert-Bond, 2009). This biogeographic pattern, known as American amphitropical disjunction or AAD (to be distinguished from a European–African amphitropical disjunction), represents the repeated formation of North America–South America sister lineages through dispersal and subsequent diversification on separate continents. General features of this disjunction have been examined by Raven (1963) and Wen and Ickert-Bond (2009), who tabulated examples and described overall trends with respect to the natural history of those taxa exhibiting the American amphitropical disjunction. This disjunction is also a feature emphasized in taxonomic or phylogenetic research on specific plant groups.

Compared to the number of known AAD events, comparatively few studies have investigated this pattern, and even fewer have looked closely at character evolution and processes involved in diversification post dispersal. The time is ripe for a collection of studies focusing on groups that show an AAD distribution pattern and for eventual synthesis of the patterns and processes exhibited. The field of systematics now has the phylogenetic, biogeographic, and

dating tools to assess the evolutionary and biogeographic history of AAD organisms and to begin relating these with common mechanisms of dispersal, climatic shifts, and geologic events. We are pleased to introduce this special issue of the *American Journal of Botany* with 12 contributions pertaining to AAD patterns and processes. We hope that these articles will act as a catalyst to accelerate research in this topic, serving to interface the fields of evolution and biogeography.

A compendium of AAD vascular plants—This issue begins with a new compilation of all instances of vascular plants that exhibit an AAD distribution (Simpson et al., 2017, this issue). As a preamble, the definition of amphitropical is discussed, as is the recognition that some current AAD distributions have been human-mediated. To date, 237 vascular plant examples of AAD have been tabulated from the literature. The bioregions (bipolar, desert, or temperate) of the lineages resulting from these events are also listed. New phylogenetic studies now allow us to add to the growing list of clades that are the result of diversification following the AAD divergence event. Dating the time of the divergence and inferring the direction of biogeographic change (whether NA to SA or SA to NA) have allowed us to trace biogeographic history with a greater precision than available in the past. Here, we use this updated information to evaluate several aspects of character evolution.

Mosses and lichens—The numerous examples of American amphitropical disjuncts that are not vascular plants often go unrecognized or unappreciated in the botanical community. Two articles in this special issue give up-to-date information on mosses (Lewis et al., 2017, this issue) and lichens (Garrido-Benavent and Pérez-Ortega, 2017, this issue). Lewis et al. use extensive molecular data to address the biogeographic history of members of a previously identified AAD lineage within the moss genus *Tetraplodon*. The authors infer a specific North American population that is most closely related to the disjunct South American populations. Garrido-Benavent

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² Department of Biology, San Diego State University, San Diego, California 92128 USA;

³ Department of Conservation and Research, Santa Barbara Botanic Garden, Santa Barbara, California 93105 USA;

⁴ Department of Biology & S.L. Welsh Herbarium, 4102 LSB, Brigham Young University, Provo, Utah 84602 USA; and

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E-mails for correspondence (msimpson@mail.sdsu.edu, mguilliams@sbbg.org, leigh_johnson@byu.edu)

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and Pérez-Ortega summarize the literature for bipolar lichen-forming fungi and their photobionts and provide a checklist of bipolar species shared between regions of high latitudes on both hemispheres. These authors consider the unique biology of lichens and recent molecular studies to discuss the mode, timing, and genetic signatures of dispersal events, as well as prospects for future research.

Vascular plants—The great bulk of American amphitropical disjunction research involves vascular plants. Several articles in this issue span a diverse array of vascular plant groups having this pattern, focusing on interesting biological phenomena associated with their history.

Ferns—Few lineages of ferns exhibit an AAD pattern. Farrar and Stensvold (2017, this issue) concentrate on members of the fern genus *Botrychium* (Ophioglossaceae), providing evidence for only a single AAD dispersal from NA to SA and updating our understanding of the taxonomy of this group based on morphological, genetic, and reproductive data. These authors also enumerate all other examples of fern AADs and review the special features of spore-bearing ferns with respect to long-distance transport and establishment in a novel environment.

Bipolar AAD vascular plants—One article focuses on bipolar AAD taxa, found in high-latitude regions of the two continents. Villaverde et al. (2017a, this issue) review bipolar AAD vascular plants generally. The authors discuss the definition of bipolarity in this context and provide an updated list of bipolar AAD vascular plants, including some outside the Americas. Evidence for the mechanism of the amphitropical distribution pattern is evaluated, as are intrinsic and extrinsic factors involved in the colonization of new areas. Finally, the authors discuss dispersal directions and divergence times of bipolar AAD taxa, considering the impact of past climatic and geological events.

Desert and temperate AAD vascular plants—Other articles in this issue concentrate on AAD examples of desert and temperate regions in various vascular plant families. Drew et al. (2017, this issue) present recent molecular analyses of the subtribe Menthinae of the Lamiaceae. The authors identify three examples of AADs in the group, each diversifying into multispecies clades. They present evidence for the timing, directionality, and possible mechanism for attaining an AAD distribution in these clades.

Frost et al. (2017, this issue) present molecular phylogenetic analyses of the family Verbenaceae, citing examples of desert disjuncts having an AAD pattern. Based on ancestral area reconstructions, the authors infer that North American arid-zone Verbenaceae are derived from South and Central American ancestors via long-distance dispersal, Andean migration corridors, and in situ evolution of desert-adapted species.

Guilliams et al. (2017, this issue) present phylogeographic analyses of the subtribe Amsinckinae of the Boraginaceae, reporting 18 examples of AAD within this group, nearly all with North America to South America directionality. Due to the relatively large number of AAD events in the study group, they are able to evaluate temporal patterns. They interpret a finding of strong asynchrony in the timing of inferred AAD events as supporting a continuous, low-probability phenomenon such as long-distance dispersal by birds as the most likely mechanism for AAD in this group.

Johnson and Porter (2017, this issue) review cases of AAD in the Polemoniaceae combined with new analyses in select groups to illustrate the possible fates of species postdispersal. Their analyses include examples of postdispersal relative stasis, divergence/speciation, hybridization, allopolyploidization, and extirpation. The evolution of cleistogamy, self-incompatibility, and the annual habit may also have occurred following dispersal in some lineages. Species from nine genera of the family have independently dispersed, yet cladogenesis following dispersal has been relatively rare.

Schneider and Moore (2017, this issue) present evidence for the parallel development of an AAD biogeographic pattern in a holoparasitic genus (*Aphyllon*, Orobanchaceae) and one of its hosts (*Grindelia*, Asteraceae). Using DNA sequence data, the authors infer separate time-calibrated phylogenies of the holoparasite and host plants. In the case of *Aphyllon*, which lacks available fossils for primary calibration, the authors implement a novel secondary calibration scheme using a dated horizontal gene transfer event. Biogeographic analysis reveals that *Grindelia* colonized South America from North America in a single dispersal event and then diversified extensively. *Aphyllon* colonized South America from North America in two dispersal events, with the dispersal of the *Aphyllon* lineage that parasitizes *Grindelia* occurring after establishment of its host genus.

Mechanisms of AAD dispersal and adaptation—Finally, two papers in this issue focus on dispersal mechanisms and habitat adaptations of AAD plants, respectively. Schenk and Saunders (2017, this issue) present accumulated data on dispersal modes of over a hundred AAD vascular plants, using analyses of diaspore (propagule) size and structure, habit, habitat, distribution, and dispersal units. They discuss the type of dispersing diaspore and the probable mode of dispersal of these AAD plants. Villaverde et al. (2017b, this issue) present an ecological niche shift analysis of five species of *Carex* that have a bipolar AAD distribution. Using herbarium records and 19 bioclimatic variables, they assess both climatic niche differences and potential distributions and distribution changes with predicted future climate change.

Future directions—Additional studies on American amphitropical disjuncts will further improve our understanding of the AAD biogeographic pattern and the mechanisms by which this pattern has arisen. Basic taxonomic research, especially detailed nomenclatural review and revision, is needed for a number of plant groups to resolve ambiguities, especially with respect to the application of names. Many AAD examples lack molecular phylogenetic analyses, and others that have been analyzed require a greater sampling of populations from one or both continents. Relatively few phylogenetic studies have included divergence time estimation to evaluate the timing of AAD events—only 72 of the 237 (30%) of recognized vascular plant AAD examples (Simpson et al., 2017, including nine calculated by these authors from published data). Dating of AAD divergence events should ideally be based on fossil calibration, but very few published studies include such information. Acquisition of additional chromosome counts, especially of South American taxa, will increase our understanding of shifts in ploidy level in AAD descendants. Additional research on reproductive biology, such as self-compatibility, will permit a better understanding of the role of these features in facilitating long-distance dispersal and establishment, as well as their evolutionary fate following establishment in a novel setting. Studies on AADs showing changes in net

diversification rates in source and recipient regions are very few in number. And only one study that we are aware of has compared substrate preference changes between NA and SA populations. (See Simpson et al., 2017, in this issue for examples and references.)

Research avenues for the future include detailed phylogeographic studies, investigating the correspondence of ecoregions and even microhabitats of source and sink AAD taxa. Additional niche modeling studies may yield a better understanding of the ecological shifts that can occur following dispersal. Evolutionary developmental studies and phylogenomics may illuminate the molecular mechanisms underlying the establishment of organisms to novel conditions of a new continent that are generalizable to other amphitropical disjunctions as well.

We hope that the articles of this issue will pique the interest of many others in studying patterns and processes of the American amphitropical disjunction. To facilitate continued research in AADs, we have established an American Amphitropical Disjunction Working Group and website (https://figshare.com/projects/American_Amphitropical_Disjunctions_AAD_Working_Group/25510) to foster collaboration in the field and allow the continuous updating of a list of AAD examples (e.g., vascular plants at <http://dx.doi.org/10.6084/m9.figshare.5479822>) and the associated data.

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