

## INVITED PAPER

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

# American amphitropical disjuncts: Perspectives from vascular plant analyses and prospects for future research<sup>1</sup>

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**PREMISE OF THE STUDY:** Historical patterns and processes of plants with an American amphitropical disjunct (AAD) distribution have long interested botanists and biogeographers. Here we update examples of AAD vascular plants, their biogeographic history, and aspects of their biology elucidated by recent studies to make inferences about common patterns of AAD plants and formulate future research questions.

**METHODS:** All known examples of AAD vascular plants were tabulated, along with data on plant duration and habit, chromosome number, dispersal direction, and divergence time. The data were then compared with regard to taxonomic categories, AAD bioregions, and character evolution.

**KEY RESULTS:** We clarify the definition of amphitropical and summarize features of AAD plants. We identify 237 AAD plant divergence events. Timing of these events generally corresponds with taxonomic category. Plant duration and habit are associated with AAD bioregions. Increases in chromosome number mostly occurred in members of the recipient area. The AAD plants of bipolar or temperate bioregions entirely or largely dispersed from North to South America, whereas almost half of desert plants dispersed from South to North America.

**CONCLUSIONS:** Tabulating AAD plants by taxonomic group and bioregion yields insight into character evolution and processes of divergence. Phylogenetic studies provide information on the timing and direction of dispersal. However, more research on AAD plants is needed to draw inferences regarding general patterns and processes, especially those at the clade level. Our AAD Working Group website provides current information on AAD vascular plants to aid workers doing research in this field.

**KEY WORDS** Biogeography; biogeographic patterns; disjunction; long-distance dispersal; divergence; North America; polyploidy; South America

Plants with a native (i.e., naturally occurring or nonanthropogenic) American amphitropical disjunct (AAD) distribution, occurring on both sides of, but not within, the American tropics, have long been recognized as a repeating biogeographic pattern found in a number of plant groups (Gray and Hooker, 1880; Bray, 1898, 1900; Raven, 1963; Cruden, 1966; Thorne, 1972; Carlquist, 1983; Wen and Ickert-Bond, 2009). The mechanisms giving rise to AAD

distributions, the geological timing of AAD dispersal events, and the evolution of plant features associated with AAD taxa have long fascinated botanists, biogeographers, and ecologists.

Here we review and summarize some features of AAD vascular plants with suggestions for future research on this topic and provide an up-to-date compendium of examples. Insightful research, including molecular phylogenetic analyses, have enabled us to tabulate more precise data about relationships of AAD plants, possible mechanisms giving rise to their disjunct distributions, number and timing of evolutionary divergences, and attributes of plant duration, substrate preference, reproductive biology, propagule morphology, changes in chromosome number, genetic divergence, speciation rate, and direction of dispersal. These data may ultimately allow us to elucidate common patterns of AAD events, in concert with the geologic and climatic history of the Americas.

Although bryophytes and lichens make up a large percentage of AAD organisms (Du Rietz, 1940), including approximately 66 species of mosses, 24 species of liverworts, and 160 species of

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lichens (Lewis et al., 2014a), we only consider vascular plants in this study. See the articles by Lewis et al. (2017) and Garrido-Benavent and Pérez-Ortega (2017) in this issue for updated studies on bryophytes and lichens, respectively.

## MATERIALS AND METHODS

We used Raven (1963) as a starting point, updating nomenclature and checking the listed species of vascular plants for those with a native AAD distribution in North America (NA) and South America (SA). We then added examples from more recent literature references, including those of phylogenetic studies of AAD vascular plants. We checked nomenclature using The Plant List (<http://www.theplantlist.org>), International Plant Names Index (<http://www.ipni.org>), Catálogo de las Plantas Vasculares del Cono Sur (Zuloaga et al., 2008), and the companion and continually updated website Flora del Cono Sur (2017; <http://www.darwin.edu.ar/Proyectos/FloraArgentina/Familias.asp>), Flora of North America (Flora of North America Editorial Committee, 1993+; <http://floranorthamerica.org>), or recent taxonomic studies. We noted synonymy where new taxonomic concepts have been accepted in the above references. We also checked the native vs. introduced status of a taxon with various sources, particularly the USDA-NRCS (2017) database for NA north of Mexico (<http://plants.usda.gov>), Rebman et al. (2016) and Villaseñor (2016) for Mexico, Zuloaga et al. (2008) and Flora del Cono Sur (2017) for the “Southern Cone” of SA, and regional floras including the Bolivia Catalogue (Jørgensen et al., 2014; <http://www.tropicos.org/Project/BC>). We checked distributions using the Global Biodiversity Information Facility (GBIF, 2017; <http://www.gbif.org>) or the Encyclopedia of Life (2017; <http://www.eol.org>). We listed each example as having a typical AAD distribution or deviating as “trans-AADs” or “eastern-AADs” (see *Definition of amphitropical* section, below). In some cases where taxonomy was complicated, we assessed distributions from original records. We then compiled each AAD example by general plant group, family, genus, and species/infraspecies and by type of taxonomic category (see *AAD taxonomic categories* section), both for NA and SA. We also listed, where available, chromosome numbers of NA and SA samples (*not* those from other regions), using cited references from the Index to Plant Chromosome Numbers (Goldblatt and Johnson, 1979–present), or other sources. We tabulated plant duration and plant habit from the literature, verified using the USDA-NRCS (2017) database for NA plants north of Mexico and Zuloaga et al. (2008) or Flora del Cono Sur (2017) for SA plants of the “Southern Cone” region. We recorded dispersal direction where known from phylogenetic or rigorous taxonomic studies, either NA to SA, SA to NA, or equivocal; in some cases, dispersal direction was inferred by us, if not explicitly stated in a research study. Where data were available, we listed the time of evolutionary divergence (mean and range, if available) in millions of years ago (Ma) for the most recent common ancestor of NA and SA lineages. If there was conflict in data, e.g., between plastome markers and ITS, we averaged the two means and listed the extreme ranges. For nine molecular phylogenetic studies in which divergence dates were not listed, we calculated them from the data presented (these indicated with an asterisk in the Time of Divergence–Div. Ma–column of Appendices 1–3; see below). For ITS data, we used median values from Kay et al. (2006) (calculated by us from their data) of  $3.72 \times 10^{-9}$  substitutions/site/

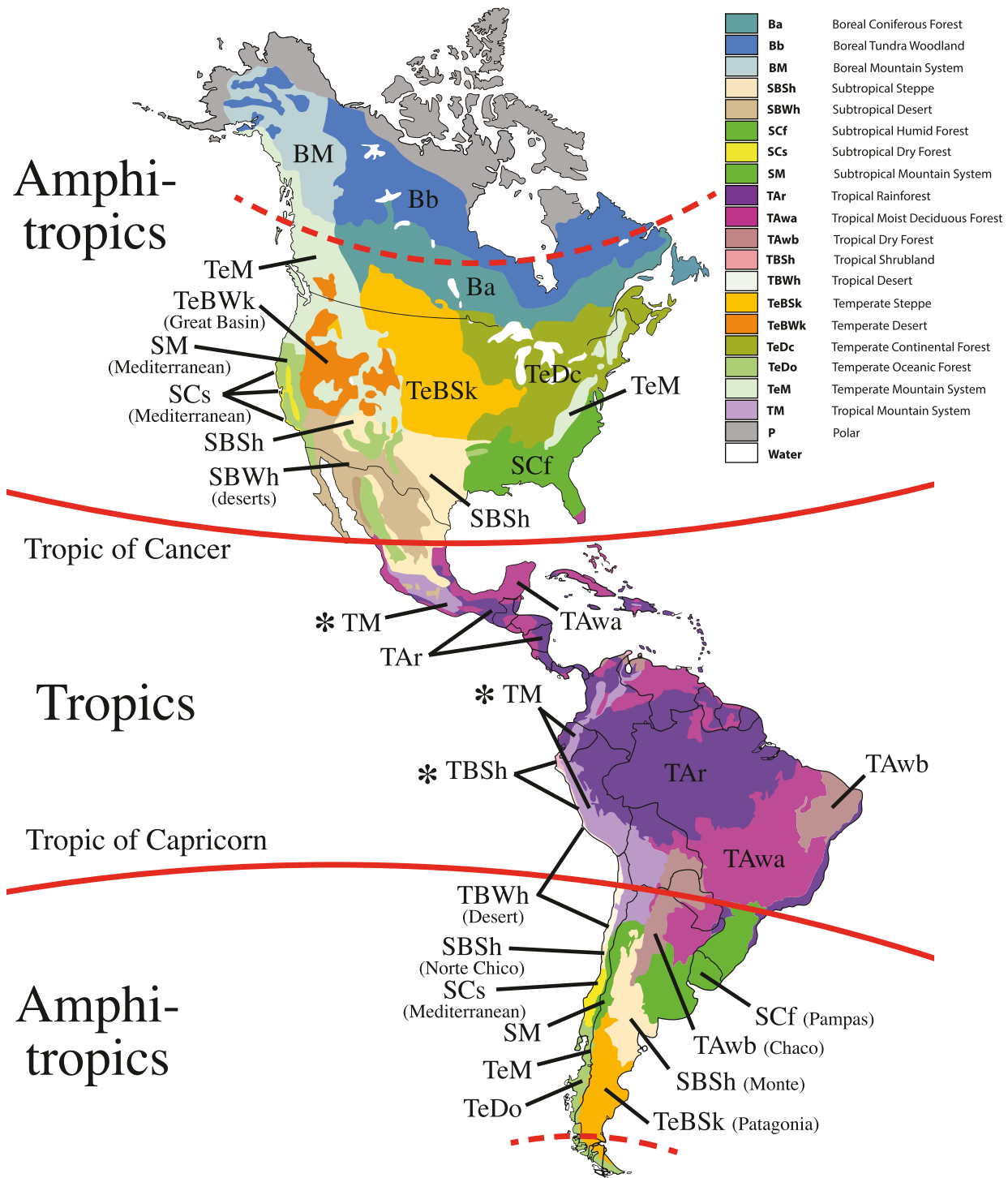
year for annual or perennial herbs and  $1.86 \times 10^{-9}$  substitutions/site/year for woody perennials. These are slightly different from the mean values of  $4.13 \times 10^{-9}$  and  $2.5 \times 10^{-9}$  substitutions/site/year, respectively, listed by these authors, but should provide better estimates by removing the potential effect of outliers in this small data set. We note, however, that Kay et al. (2006) listed ranges of  $1.72 \times 10^{-9}$  to  $8.34 \times 10^{-9}$  substitutions/site/year for herbaceous annuals/perennials and  $0.38 \times 10^{-9}$  to  $7.83 \times 10^{-9}$  for woody perennials, spanning 5-fold and 20-fold differences in magnitude, respectively. For single-copy intergenic chloroplast markers, we used the average value of  $2.1 \times 10^{-9}$  substitutions/site/year (Gaut, 1998; Muse, 2000; synonymous and nonsynonymous substitutions averaged). When the phylogenetic trees in a given study were not ultrametric, the branch lengths along sister lineages were averaged, with ranges in the appendices listing minimum and maximum values of ITS and chloroplast markers together. If no detectable variation in sequences was reported, we assigned a value of zero. We realize these calculations are approximations only and await refinement in future, more precisely calibrated molecular studies. (See *Future directions* section.)

We compiled all of these data, organized by general AAD *bioregions* (Appendices 1–3; see below), and designating those AAD plants that additionally occur on other continents. We also created a listing of rejected AAD taxa (Appendix 4). We used these data to summarize various features of AAD plants (see Tables). Finally, we have established an American Amphitropical Disjunction Working Group website (see *Future directions* section), where we present a compendium of this information, such that known AAD examples and their supporting data may be continually checked and revised, as a resource to those doing research on this topic.

## RESULTS AND DISCUSSION

**Definition of amphitropical**—The term “amphitropical” refers to either side of the tropics, in this case within the western hemisphere. The tropical zone is technically the geographic region between the Tropic of Cancer and the Tropic of Capricorn (approximately  $23^{\circ}26'N$  and  $S$ ; Fig. 1), where the sun is directly overhead at the time of the summer solstice of the two hemispheres. Strictly speaking, an amphitropically distributed taxon occurs on both sides of this tropical zone *but not within it*. A plant species with a typical AAD distribution is exemplified by *Amsinckia tessellata* A.Gray (Fig. 2A), with NA and SA populations well on either side of the tropical zone. However, here we are defining “amphitropical” to also include disjuncts with populations in the amphitropical zone but that may also have additional occurrences within the strict tropical zone (examples in Fig. 2B–D). We recognize the problem in distinguishing such AAD examples from those that have a continuous distribution in the western hemisphere, and we attempt to clarify this distinction by categorizing these encroachments of some AAD plants into the tropics (see below).

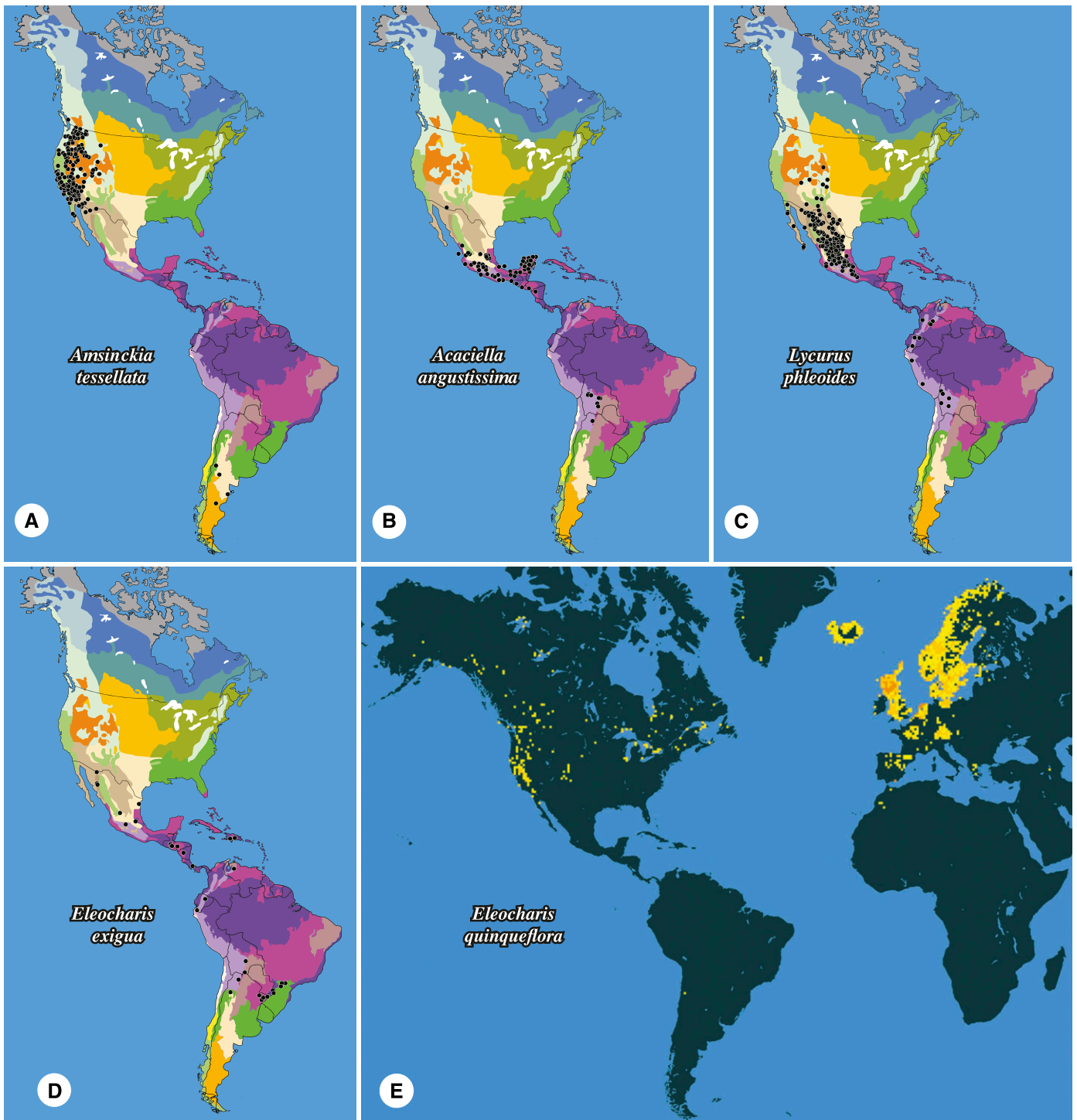
Vegetation regions, which are a function largely of climate, topography, geology, and biotic interactions, are likely even more important in understanding AAD distributions than simply considering northern and southern sides of the tropics. By this reasoning, the “amphitropical” zone would not be limited by the strict boundaries of the tropics and could be justifiably expanded to include vegetative regions that extend from amphitropical regions into strict tropical ones (Fig. 1). There are innumerable vegetation/



**FIGURE 1** Map of North and South America showing boundaries of strict tropical and amphitropical regions and Global Ecological Zones, redrawn from Davis and Holmgren (2001) with abbreviations after this system. Zone labels with an asterisk (\*) are those within the tropical zone but included for (trans) AAD plants. Dotted lines indicate approximate boundaries of bipolar plants using the criteria of Moore and Chater (1971).

plant community systems (see, e.g., Josse et al., 2003 for Latin America) that may serve as a basis for defining the amphitropical vs. tropical regions. Here, we cite the Global Ecological Zoning for the Global Forest Resources conducted by the United Nations Food and Agriculture Organization (Davis and Holmgren, 2001; reproduced

in Fig. 1). By this system (with their abbreviations), the tropics would be inclusive of tropical rain forest (TAr), tropical moist deciduous forest (TAwa), tropical dry forest (TAWb), tropical shrubland (TBSh), tropical desert (TBWh), and tropical mountain systems (TM) of NA and SA. The amphitropical region would include, for



**FIGURE 2** Examples of American amphitropical disjunct (AAD) vascular plant distributions. (A) *Amsinckia tessellata* (Boraginaceae), showing a typical AAD distribution in central western North and southern South America. (B) *Acaciella angustissima* (Fabaceae), showing a “trans-NA” AAD distribution into Central America. (C) *Lycurus phleoides* (Poaceae), showing a “trans-SA” AAD distribution into northwestern South America. (D) *Eleocharis exigua* (Cyperaceae), showing a “trans-NASA” AAD distribution. (E) *Eleocharis quinqueflora*, having a typical AAD distribution but with populations also occurring in Asia, Europe, and possibly Africa and Australia. (A–D), Distribution map data from GBIF (2017), superposed on Global Ecological Zones map, redrawn from Davis and Holmgren (2001).

SA, the subtropical steppe (SBS<sub>h</sub>), subtropical dry forest (SC<sub>f</sub>), subtropical humid forest (SC<sub>f</sub>), subtropical mountain systems (SM), temperate steppe (TeBS<sub>k</sub>), temperate oceanic forest (TeDo),

and temperate mountain systems (TeM); for NA, amphitropical includes these same ecological zones plus the boreal mountain systems (BM), boreal tundra woodland (Bb), boreal coniferous forest



(Ba), subtropical desert (SBWh), temperate desert (TeBwk), and temperate continental forest (TeDc) (see Fig. 1 and AAD *bioregions* section, below). We realize that these vegetation zones are only a rough estimate of plant habitats, as microecological conditions are also important in the establishment, survivorship, and spread of plants.

Some of the ecological zones outlined above extend continuously from an amphitropical region to a tropical one. Thus, another option for relaxing a strict latitudinal requirement for designating an amphitropical distribution is to encompass all ecological zones exclusive of the wet tropical rain forest and tropical moist deciduous forest. We elected to do this, including the tropical shrubland (TBSH) and tropical mountain systems (TM) as AAD distributions. In NA, this expansion would extend the amphitropical zone into southern Mexico and the cordillera of Central America. In SA, this would extend the amphitropical zone into the Andean cordillera of Peru, Ecuador, Colombia, and even Venezuela. Though this might seem excessive, doing so would permit the recognition of so-called stepwise (stepping-stone) patterns (see below) for amphitropical plants that might otherwise not be classified as AADs. Scientists investigating AAD plants would have to evaluate whether a plant exhibiting such a pattern should even be considered having an AAD distribution (vs. one that is continuous), as these more extensive distributions, though interesting, might be the result of different general processes. Here, we designate such examples as “trans-AADs”, either as “trans-NA”, those with a distribution significantly entering the tropical region of NA [e.g., *Acaciella angustissima* (Mill.) Britton & Rose, Fig. 2B]; “trans-SA”, those with a distribution significantly entering the tropical region of SA (e.g., *Lycurus phleoides* Kunth, Fig. 2C); or “trans-NASA”, those with a distribution significantly entering the tropical regions of both NA and SA [e.g., *Eleocharis exigua* (Kunth) Roem. & Schult., Fig. 2D]. Given that most AAD examples occur in western NA and SA, we also tabulate “eastern-AADs”, those that occur in eastern NA or eastern SA. (See Appendices 1–3.)

Some plants normally identified as having an AAD distribution are also found on other continents [e.g., *Eleocharis quinqueflora* (Hartmann) O.Schwarz, which also occurs in Europe, Asia, and northern Africa; Fig. 2E]; these are designated in Appendices 1–3. This distribution pattern is true of most bipolar AAD plants (see below). It is important to consider in these cases whether the NA and SA populations are each other’s closest relative. If so, then the AAD distribution still can be explained as a unique “AAD event”. If either North or South American populations are shown to be more closely related to those of other continents, they should be excluded as AAD examples. Their attributes may not correlate with those potentially associated with true AAD distributions, adding noise to efforts to discover such character associations, if not known. Of course, these “false” AAD plants might be shown to have interesting attributes of their own.

In conclusion, the definition of the term amphitropical may vary with different authors and with different systems of ecological or vegetation zones. When there is doubt, it is best to explicitly state the distributions involved and the definition of amphitropical used. Allowing significant deviation from the classic amphitropical definition may introduce different parameters as to biogeographic history as well as obfuscate patterns in morphology or evolution that are otherwise common using a stricter definition.

**Anthropogenic AAD plants**—A distinction must be made between a “natural” AAD distribution and one due to human activity. In our

comparisons, we are only considering AAD events that are not of anthropogenic origin. However, native vs. adventive distributions are not always easy to discern, and mistakes have been made in the past. For example, the sea fig, *Carpobrotus chilensis* (Molina) N.E.Br. (Aizoaceae), was not long ago considered to have a naturally occurring AAD distribution, but evidence points to its introduction by humans in both North and South America (Bicknell and Mackey, 1998; Vivrette, 2003). *Nuttallanthus texanus* (Scheele) D.A.Suttonis (Plantaginaceae) is considered native to NA (Preston and Wetherwax, 2012; USDA-NRCS, 2017) but is now thought introduced to SA (Zuloaga et al., 2008).

A human introduction from one region to the other would likely be characterized by extreme similarity between members of the two intercontinental populations. Detailed molecular phylogenetic techniques (e.g., along the lines of Valliant et al., 2007) might be capable of discerning whether a long-distance dispersal event occurred in historical times and might be human mediated. One might also expect that with anthropogenic dispersals, considerably less morphological or genetic variation would be present in the recipient (“sink”) region than in the source region because of a genetic bottleneck associated with the introduction. However, this prediction would also be expected in a recent natural AAD event, but to less of an extreme. As an example of the latter, Peterson and Ortíz-Díaz (1998), using enzyme electrophoresis, determined that in the conspecific AAD *Muhlenbergia torreyi* (Kunth) Hitchc. ex Bush (thought to be native to both continents), populations in SA are less variable, implying that dispersal likely occurred from NA to SA.

Several AAD plants are known from historical records to have been dispersed anthropogenically between the two western hemisphere continents. For example, the California poppy, *Eschscholzia californica* Cham., was dispersed by humans from the mediterranean climatic region of the California Floristic Province of NA (Howell, 1957) and is now naturalized in similar climatic regions of Chile and other South American countries, where it may be locally common. In addition, it may be difficult to detect past introductions by indigenous peoples during pre-European times with certainty. A study of known anthropogenic AAD events is a separate topic, but might yield insight into the AAD phenomenon, particularly with regard to morphological and reproductive features, mechanisms of establishment, and potential subsequent evolutionary or ecological change of these taxa.

#### **AAD taxonomic categories and evolutionary divergence time—**

Along with consideration of what constitutes an amphitropical distribution is the question of which taxonomic categories might be useful in making comparisons and inferences about AAD plants. Early AAD research, such as that of Raven (1963), was based on the identification of mostly minimum-ranked taxa (species or infraspecies), using traditional comparative morphology and sometimes cytogenetics. However, more recent phylogenetic studies have resulted in many transfers in rank and position of historically named taxa and new insights into the groups of comparison from the northern and southern hemispheres. These phylogenetic studies have also led in some cases to the recognition of clades as the product of an AAD event.

There are a number of examples of AAD plants in which taxonomic concepts have varied, resulting in rampant synonymy. Continuing taxonomic research is critical to clarifying species and infraspecies concepts of past classifications. For example, the

species *Chenopodium philippianum* Aellen [*C. carnosulum* Moq. var. *patagonicum* (Phil.) Wahl], native to south-central Chile and Argentina, was long considered present also in coastal California and perhaps Mexico, an example of an AAD plant species. However, Benet-Pierce and Simpson (2010) concluded from morphological studies that these were different taxa, naming the California populations a new species. (Note, however, that future phylogenetic studies could demonstrate these now separate taxa are in fact AAD species pairs.) In another example, the study of *Collomia* and *Navarretia* (Polemoniaceae) by Johnson et al. (2012) and Johnson and Porter (2017, in this issue) exemplify the need to address a complicated taxonomy with careful study of morphology from herbarium specimens.

We currently tabulate a total of 237 examples of AAD vascular plant events; see below. Of this total, the families with the most AAD representatives are the Poaceae with 51 examples, Boraginaceae (after Chacón et al., 2016, excluding Ehretiaceae and Hydrophyllaceae) with 19 examples, Asteraceae with 16 examples, Fabaceae with 16 examples, Cyperaceae with 15 examples, and Polemoniaceae with 11 examples (Appendices 1–3).

We use the following taxonomic categories for classifying AAD events. We realize that these categories are not strictly comparable as evolutionary units, yet feel they are useful in comparing the temporal history of AAD events. For this purpose, we are relaxing the term “taxonomic category” to include not just named taxa at different ranks but also clades, which may or may not be formally named. (Ideally, all named taxa would correspond to clades, but we use the latter for a monophyletic group of two or more named species.) As summarized by Wen and Ickert-Bond (2009), the date of divergence of AAD plants varies significantly depending on the specific group. Here we tabulate the known divergence times of AAD vascular plants relative to their taxonomic category, yielding some insight as to their degree of divergence. We note that only 72 of the 237 (about 30%) recognized vascular plant AAD examples have divergence dates, including the nine calculated by us from published data.

**Conspecific AADs**—A starting point for AAD plants are those classified as the same species occurring in both North and South America, termed here conspecific AADs. Conspecific AADs are the most common category, with a total of 135 examples or 57% of all AADs (Table 1). If infraspecific examples (below) are excluded, there are 118 examples of conspecifics (almost 50% of the total). Three examples of conspecific distributions (not involving infraspecies; see below) are illustrated in Fig. 2A–E and 3A–C.

The relatively few studies that have dated the divergence times of North and South American conspecifics indicate a relatively recent age: a mean of about 0.63 Ma if intraspecific AADs (below) are included or 0.62 Ma if infraspecifics are excluded (Table 1). Examples include two species of *Sanicula* (Apiaceae), *S. crassicaulis* Poepp. ex DC. and *S. graveolens* DC., both conspecific AADs, with divergence times of ca. 1 Ma and 2 Ma, respectively (Vargas et al., 1998; Fig. 3A–C). Conspecifics are generally thought to have arisen by unidirectional dispersal in relatively recent times. The recency of dispersal may be the primary explanation for the observed lack of morphological differences, with less time available for evolutionary changes between the isolated intercontinental populations.

**Intraspecific AADs**—Some conspecific AADs contain infraspecies (i.e., varieties or subspecies; Table 1). These may be the same

infraspecies on both continents, termed here “conintraspecific” AADs, or the intercontinental infraspecies can be different, unique to one or both of the two continents. Additional infraspecies of that species, other than those representing AADs, could also occur on either or both of the continents. We currently tabulate a total of 17 infraspecific AAD examples, representing 7.2% of the total (Table 1), separated into eight conintraspecific examples and nine examples of different infraspecies.

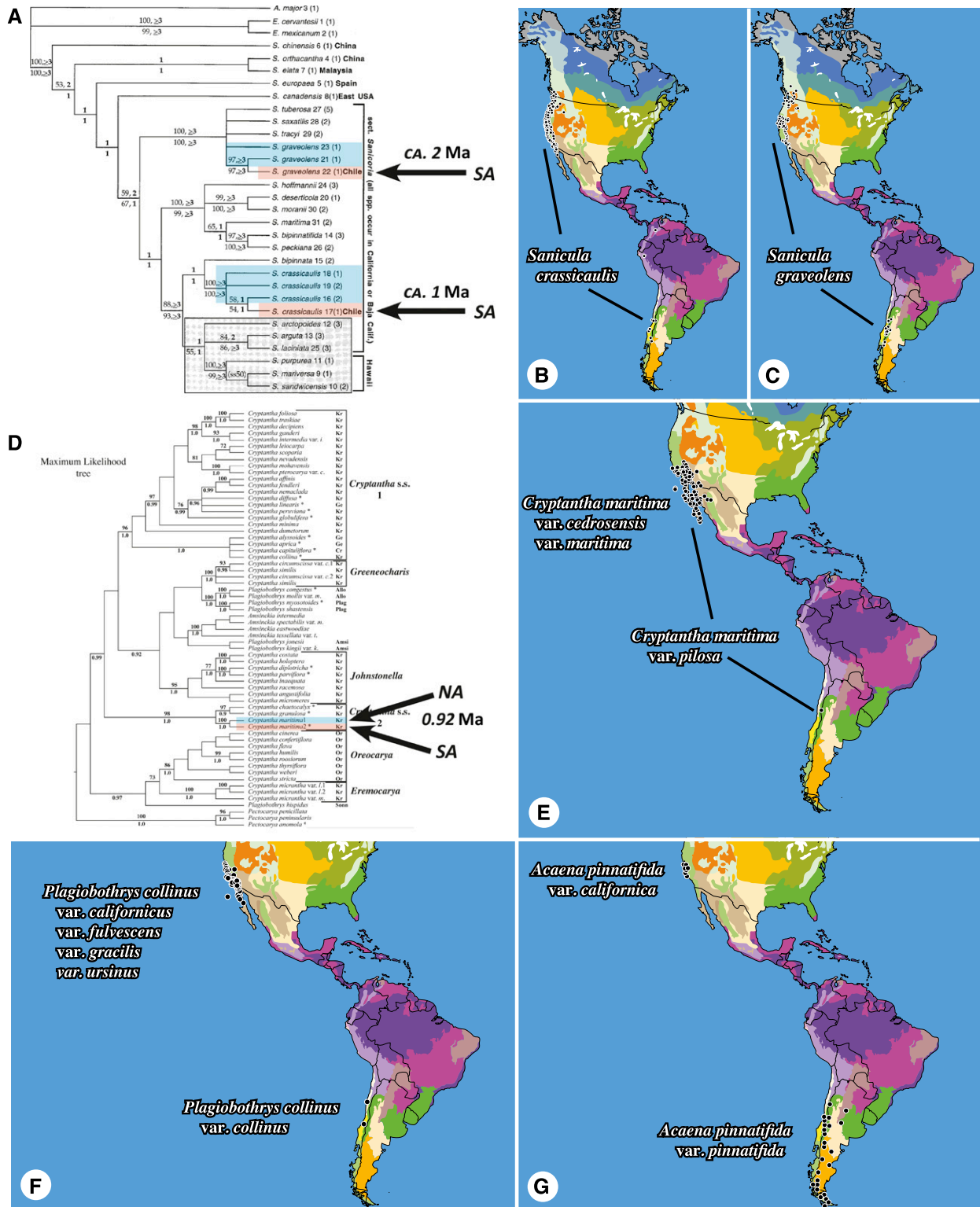
An example of a conintraspecific AAD is *Cryptantha maritima* (Greene) Greene var. *pilosa* I.M. Johnst., Boraginaceae (Fig. 3D, E). This variety occurs in both North and South America, but the other two recognized varieties [*C. maritima* var. *maritima* and *C. maritima* var. *cedrosensis* (Greene) I.M. Johnst.] are found only in NA. In this case, there is good evidence that the amphitropically distributed variety dispersed unidirectionally from North to South America (Hasenstab-Lehman and Simpson, 2012; Williams et al., 2017, in this issue), with an estimated time of divergence from molecular data of about 0.92 Ma (K.E. Hasenstab-Lehman, Santa Barbara Botanic Garden, personal communication). One could speculate that the species occurred in NA for some time before dispersal into SA, allowing time for its divergence into three varieties in NA, only one of which subsequently dispersed to SA; however, the details of this complex have yet to be worked out.

In another example in the Boraginaceae, *Plagiobothrys collinus* (Phil.) I.M. Johnst., as presently treated, contains five varieties. *Plagiobothrys collinus* var. *collinus* is restricted to SA, and the other four varieties are found only in NA (Fig. 3F). Again, the evidence points to a single, unidirectional dispersal from North to South America of a *Plagiobothrys collinus* propagule, with an estimated divergence time of 1.48 Ma (Williams et al., 2017). In this particular example, the evidence shows that the North American populations diverged into the four recognized varieties (as well as one taxon at the species level that is phylogenetically nested in *P. collinus*) after this dispersal event, given that *P. collinus* var. *collinus* is sister to the four North American varieties (Williams, 2015). This pattern might imply that relative evolutionary stasis occurred in the SA population following the AAD dispersal event.

Finally, *Acaena pinnatifida* Ruiz & Pav. (Rosaceae) is often recognized to have two varieties, with *Acaena pinnatifida* var. *californica* (Bitter) Jeps. restricted to NA (Macmillan and Ertter, 2017) and *Acaena pinnatifida* var. *pinnatifida* restricted to Chile and Argentina (Fig. 3G). Although no divergence time estimates are known, this AAD event would be predicted to have occurred relatively recently, but generally slightly older than conspecific AADs not having infraspecies.

It is expected that the average divergence time for infraspecific taxa would be similar to that of conspecific taxa, given that both represent morphologically indistinguishable populations in the two continents. We found infraspecific examples (mean of 0.65 Ma) to be very slightly older than conspecific examples (mean of 0.62 Ma, not including infraspecifics); see Table 1. An older divergence time for different infraspecifics than for conintraspecifics might be expected, given that generally more time would be needed for evolutionary divergence into what are classified as different taxa. Among infraspecific examples, the two examples of conintraspecific taxa had a mean divergence time of 0.63 Ma, and that of different infraspecies is only slightly older, at 0.66 Ma (Table 1).

**Species pairs**—A pair of species, each considered the closest relative of the other, are the second most common taxonomic category of



**FIGURE 3** (A) Phylogenetic tree of the genus *Sanicula* (Apiaceae), with arrows highlighting two conspecific AADs, average divergence times indicated. From Vargas et al. (1998, p. 239), with permission; copyright 1998 National Academy of Sciences, USA. (B) Distribution map of *Sanicula crassicaulis*. (C) Distribution map of *Sanicula graveolens*. (D) Phylogenetic tree of the genus *Cryptantha* (Boraginaceae), with arrows highlighting two infraspecific AADs of *C. maritima*, average divergence time indicated. From Hasenstab and Simpson (2012, p. 743), with permission. (E) Distribution map of *C. maritima* infraspecies, three in North America, one (*var. pilosa*) in both North and South America. (F) Distribution map of infraspecies of *Plagiobothrys collinus* (Boraginaceae), four in North America and a fifth solely in South America. (G) Distribution map of two AAD infraspecies of *Acaena pinnatifida* (Rosaceae). NA = North America; SA = South America. Distribution map data from GBIF (2017), superposed on Global Ecological Zones map, redrawn from Davis and Holmgren (2001).



**TABLE 1.** Taxonomic categories of the 237 American amphitropical disjunct vascular plants, showing the total number, percentage of the total, and mean time of evolutionary divergence (including range of individual means) based on phylogenetic studies. [M] = number of studies from which mean divergence time was calculated. See Appendices for sources of data.

Taxonomic category	Total number	Percent of total	Mean divergence time (Range), Ma [M]
Conspecific (including infraspecies)	135	57.0	<b>0.63</b> (0–2.45) [27]
Conspecific (excluding infraspecies)	118	49.8	<b>0.62</b> (0–2.45) [22]
Infraspecific	17	7.2	<b>0.65</b> (0.20–2.46) [5]
Conintraspecific	8	3.4	<b>0.63</b> (0.33–0.92) [2]
Different infraspecies	9	3.8	<b>0.66</b> (0.20–1.48) [3]
Species-species pairs	54	22.8	<b>3.14</b> (0–14.9) [21]
Species-clade, clade-species, & clade-clade	48	20.3	<b>6.29</b> (0.61–24.78) [24]
Species-clade & clade-species	21	8.9	<b>4.51</b> (0.61–14.50) [13]
Species-clade	11	4.6	<b>4.81</b> (0.61–14.50) [8]
Clade-species	10	4.2	<b>4.40</b> (1.37–5.53) [4]
Clade-clade	27	11.4	<b>8.40</b> (0.98–24.78) [11]

AAD plants. We cite a total of 54 AAD species pairs, about 23% of the total (Table 1). An example is seen in the North American *Lilaeopsis occidentalis* J.M.Coult. & Rose and the South American *L. macloviana* (Gand.) A.W.Hill (Apiaceae; Spalik et al., 2010) (Fig. 4A; Appendix 3). Some of these AAD species pairs have been shown to be sister species from phylogenetic analyses; others are presumed to be from comparative studies, but lacked phylogenetic evidence at the time. As an example of the latter, *Lasthenia glaberrima* DC. of NA (Asteraceae) and *L. kunthii* (Less.) Hook. & Arn. of Chile and were considered close relatives based on morphology and taxonomy, being the only species of section *Lasthenia* (Ornduff, 1963). Only relatively recently did a phylogenetic study (Emery et al., 2012) confirm that they are indeed sister species.

Species pairs indicate enough change in one or both lineages following an AAD event (see below) that the two products of the divergence are classified as separate. Biosystematic studies (e.g., Moore and Raven, 1970) have shown that the great majority of artificial crosses between intercontinental AAD species pairs result in sterile hybrids, with observed chromosome structural changes in some cases. Thus, in most cases examined, reproductive isolation has occurred between the products of an AAD species pair.

The average divergence time of species pairs would be expected to be older than that of conspecific or infraspecific examples. This prediction is supported by our data in that the average mean divergence time for species pairs by our summary is 3.14 Ma, 5× that of conspecific AADs, including infraspecific AADs or not (Table 1).

**Clades**—In addition to AADs that are conspecific or species pairs, phylogenetic studies provide examples of clades that represent species diversification of one or both lineages following an AAD event. This diversification could result in a clade that is sister to a single species or sister to another clade. Note that we distinguish between a “species-clade”, in which diversification into a clade occurred in the recipient region, and a “clade-species”, in which clade diversification occurred in the source region. An example of the former is seen in the study by Moore et al. (2006), in which the North American species *Tiquilia paronychioides* (Phil.) A.Richardson of the source region is sister to the recipient South American “*Tiquilia plicata*” clade (Appendix 2). An example of the latter is seen in *Lycium* (Levin et al., 2007), in which a clade of two source South American *Lycium* species is sister to the North American *L. californicum* Nutt. ex A.Gray (Appendix 2). Finally, an example of sister clades is exemplified by the genus *Cryptantha* (Boraginaceae), in which

two large South American clades (termed the “*Cryptantha/Geocarya*” and “*Globulifera*” clades; Fig. 4B) are each sister to other clades, with each clade representing species diversification following a unique AAD event (Mabry, 2015; Mabry and Simpson, in press; Guilliams et al., 2017; Simpson et al., 2017; Appendix 3). AAD events involving clades (species-clade, clade-species, or clade-clade events combined) are less commonly known than conspecific or species pairs, with 48 examples, or about 20% of the total (Table 1).

One would expect divergence times involving clades to be the oldest of the categories we have outlined, given that more time would be required for diversification of a

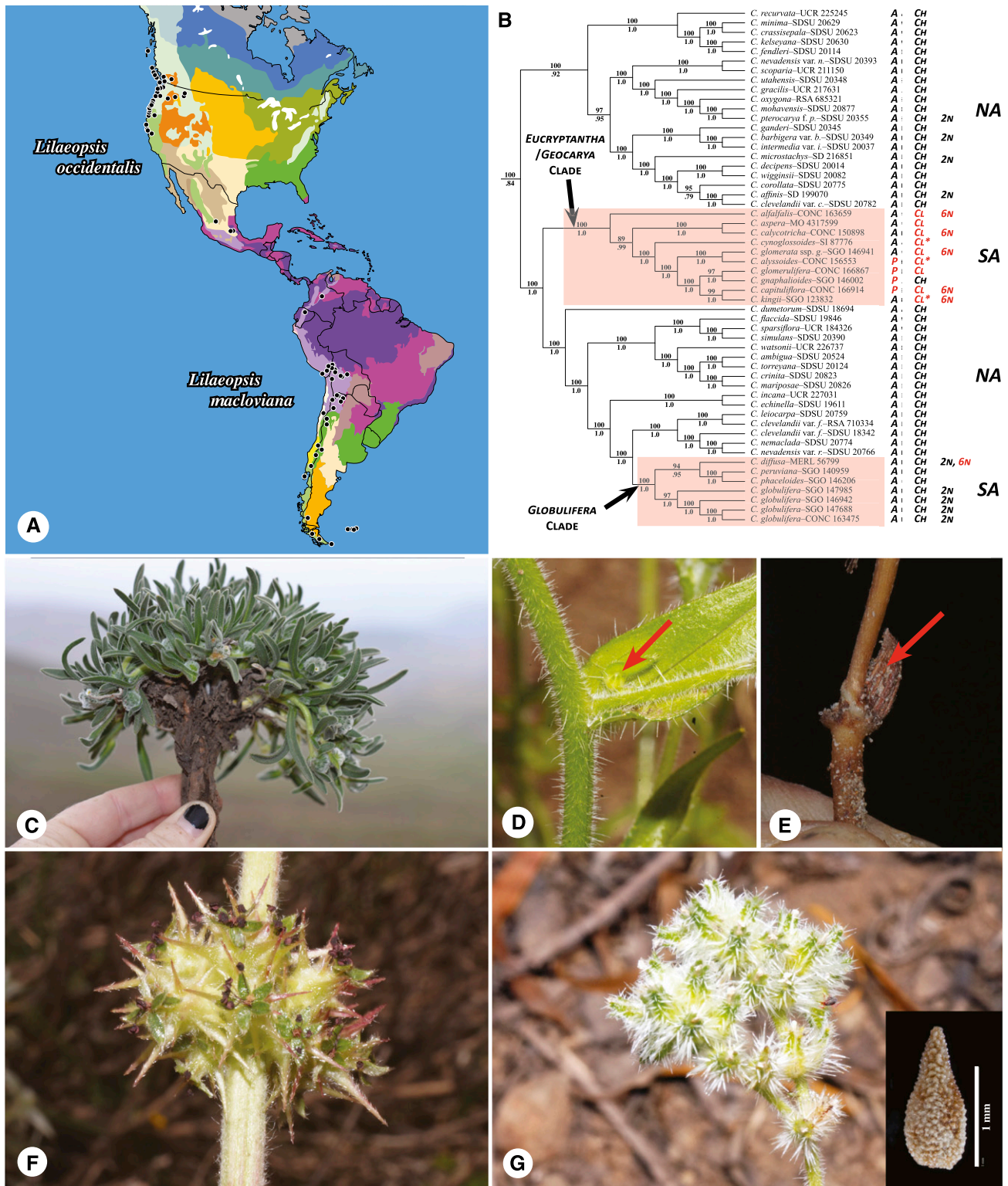
single taxon into multiple lineages/species within a clade. This is what the data show, with a pooled mean divergence time of 6.29 Ma, 10× the average of conspecifics (Table 1). Also, as might be expected, species-clades and clade-species examples together have a more recent average divergence time of about 4.51 Ma, with clade-clade examples having the oldest average divergence time, about 8.40 Ma, the latter over 13× that of conspecifics (Table 1).

**AAD events**—An important insight from evaluating AAD taxonomic categories is the consideration of the divergence of North and South American plant taxa to be the product of a unique “AAD event”. The changes that occur in the two lineages following that event will be influenced by a number of factors, but the amount of elapsed time following the event is a predictor of the AAD taxonomic category, which is itself a proxy for the degree of diversification. As discussed above, if the event occurred in the distant past, enough diversification could occur to form one or more clades from one or both of the AAD descendant lineages. If it occurred in the recent past, there would be little genetic and morphological change in the AAD descendants, which would be classified as the same species or perhaps infraspecies. A plot of divergence times for each of the taxonomic categories shows the general trend of mean divergence time becoming progressively more recent in time, from clade-clades to species-clades or clade-species to species pairs to infraspecies to conspecifics alone (Fig. 5A); however, the differences among the last two categories are minor.

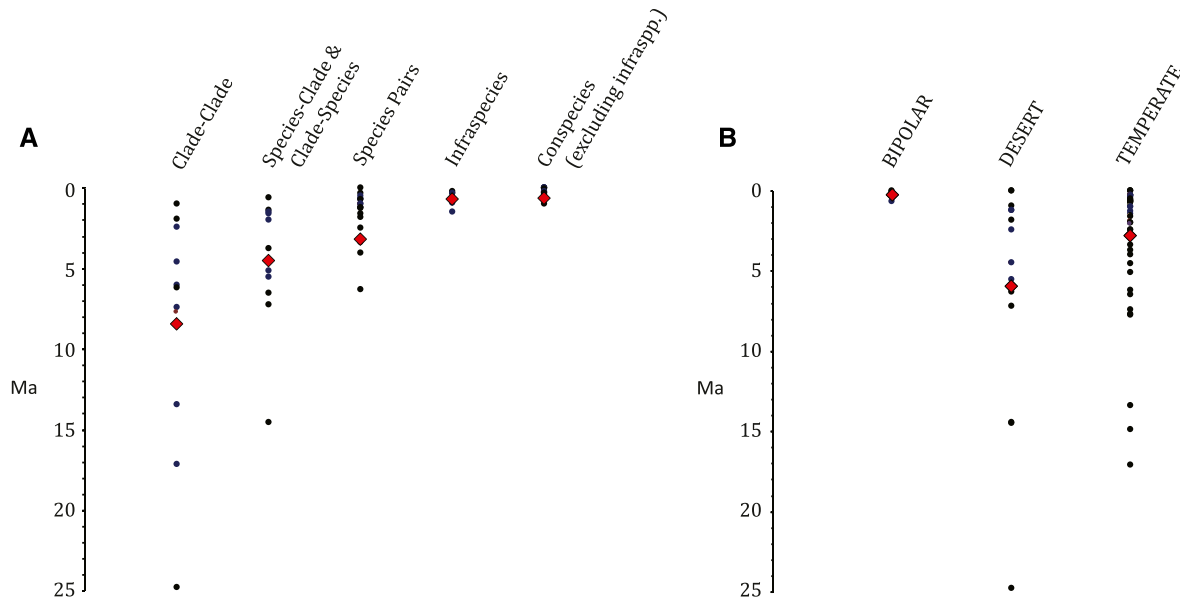
**AAD bioregions**—A convenient and logical way to partition AAD bioregions is into bipolar regions, temperate regions, and desert regions, as done by Raven (1963). Although this is not always a clear-cut division, it yields insight into different patterns and evolutionary mechanisms that vary among these regions without excessively fragmenting the landscape as would, for example, using the ecological zones mapped in Fig. 1.

**Bipolar AAD plants**—Vascular plants with a bipolar AAD distribution have been defined in two general ways. Raven (1963) simply defined bipolar AAD plants as those that “occur at high latitudes”, whereas Moore and Chater (1971) quantified this definition by considering taxa with a bipolar distribution as those whose populations reached >55°N and >52°S (dashed lines of Fig. 1). One thing to consider is whether bipolar AAD plants must *only* occur at these higher latitudes or if only some populations must occur in these





**FIGURE 4** (A) Distribution map of two sister AAD species, *Lilaeopsis occidentalis* and *L. macloviana* (Apiaceae). (B) Phylogenetic tree of the genus *Cryptantha* (Boraginaceae), showing two major South American (SA) clades nested within all North American taxa. Within the *Eucryptantha/Geocarya* clade, note the evolution of a perennial plant duration (P) from the ancestral annual plant duration (A, the latter found in all other *Cryptantha* species), the evolution of cleistogamy (CL) from the ancestral chasamogamy (CH, the latter found in all other *Cryptantha* species), the evolution of specialized cleistogenes (CL\*) among some of the cleistogamous members, and the evolution of hexaploids (6n) from the ancestral diploid (2n), the latter found in all other *Cryptantha*, except one member of the *Globuliferae* clade, which has both diploid and hexaploid counts. Modified from Mabry (2015), with permission. (C) *Cryptantha capituliflora*, with a perennial rootstock. (D) *Cryptantha glomerata*, with cauline cleistogamous flowers (arrow). (E) *Cryptantha*



**FIGURE 5** (A) Plot of mean divergence time (Ma = millions of years before present) for all known examples relative to taxonomic category: clade-clade, species-clade & clade-species, species pairs, intraspecies (conintraspecies and different intraspecies pooled), and conspecific (these excluding intraspecies values). Mean for each category indicated by red diamond symbol. Note general trend toward more recent divergence times. (B) Plot of mean divergence time for each of the three AAD bioregions. Symbols as in "A".

regions with other populations located closer to the equator. Alternatively, one might consider AAD plants to be bipolar if only one of the North American or South American populations meet these distributional criteria, but not both. We have elected to require that, to be designated bipolar, both NA and SA taxa must have populations occurring at high latitude but not exclusively, allowing for some distributions into more temperate zones. Using the ecological zone classification of Davis and Holmgren (2001), bipolar AAD plants may occur in the boreal mountain system (BM), most of the boreal tundra woodland (Bb), and the northern parts of the boreal coniferous forest (Ba) and temperate mountain system (TeM) of NA. South American bipolar plants are less easily delimited by vegetation regions and are generally found in the extreme southern parts of the temperate oceanic forest (TeDo) and the temperate steppe (TeBSk: extreme southern Patagonia) (Fig. 1).

Our tabulation of bipolar AAD plants includes 27 examples, making up about 11% of the total (Appendix 1; Table 2), including two ferns, 15 monocots, and 10 eudicots (Appendix 1). Three species or species pairs that were not considered to be bipolar AAD plants by Moore and Chater (1971) are included by us (Appendix 1), as they occur in both bipolar regions of NA (>55°N) and SA (>52°S), but also get well into temperate regions. With regard to plant families, Cyperaceae and Poaceae have the greatest number of bipolar AADs with seven examples each. The genus *Carex* has the greatest number of bipolar AADs of any genus, with six examples. In our listing (Appendix 1), we clarify the taxonomy of species of *Carex* from recent studies (Murray, 2002; Wheeler and Guaglianone, 2003; Escudero et al., 2010; Villaverde et al., 2015a, b, 2017a

[this issue]). One of two AAD examples of *Botrychium* (Ophioglossaceae) cited by Raven (1963) is rejected (Appendix 4) because of changes in taxonomic concepts (Farrar and Stensvold, 2017, in this issue; Meza-Torres et al., 2017). We also reject as bipolar AAD plants the species *Honckenya peploides* (L.) Ehrh (Caryophyllaceae), *Lathyrus japonicus* Willd. (Fabaceae), and *Poa glauca* Vahl. (Poaceae) (Appendix 4), all cited by Raven (1963). The first is no longer considered to occur in SA (Chile) (Wagner, 2005), and the last two are now thought to be nonnative in SA (Zuloaga et al., 2008).

The mean divergence time of bipolar AAD events was calculated as 0.25 (range of means 0–0.69) Ma, considerably more recent in time than temperate or desert examples (Table 2). The only bipolar AAD shrub, *Empetrum* spp., had a significantly older mean divergence time of 0.69 Ma, the oldest of this bioregion. The generally late dispersal times of bipolar AADs agrees with Raven's (1963) postulation that these plants attained their current distribution relatively recently, primarily because their high latitude habitats formed late in geologic time. (See also Donoghue, 2011.) This recency of divergence of bipolar AADs is supported by the fact that the great majority (21 examples, 77.8% of the total) are single species, with the rest (6 examples, 22.2% of the total) being species-species pairs; there are no bipolar clade examples (Appendix 1). Bipolar AAD plants are almost entirely (about 96%) perennial, and all but one (*Empetrum* spp.) of these are or include perennial herbs (Table 2; see *Character evolution* section, below). The available phylogenetic studies indicate that all bipolar AAD events had a NA to SA dispersal direction, with one being equivocal (Table 2; see *Dispersal direction* section, below).

← *aprica*, showing a ground-level to subterranean cleistogeme (arrow). (F, G) Examples of epizoochoric propagules. (F) *Acaena pinnatifida* var. *pinnatifida* (Rosaceae), in which a hardened, glochidiate hypanthium surrounding the seeds acts as an effective dispersal mechanism. (G) *Cryptantha globulifera*, in which the bristly calyx enclosing the fruits (nutlets, see inset) may function in animal attachment and subsequent dispersal. (C–G) Photographs by Michael G. Simpson. Distribution map data from GBIF (2017), superposed on Global Ecological Zones map, redrawn from Davis and Holmgren (2001).

**TABLE 2.** American amphitropical disjunct vascular plants, organized by general bioregions, listing total number of plant taxa, percentage of the total, mean divergence time (including range of individual means), percentage of perennials and annuals, and percentage of taxa inferred to have had a dispersal or migration from North American (NA) to South America (SA). [N] = number of studies from which mean divergence time or direction is calculated. See Appendices for source of data.

Bioregion	Total (%)	Mean (Range) divergence time, Ma [N]	% Annuals	% Perennials	% NA→SA [N]
Bipolar	27 (11.4)	<b>0.25</b> (0–0.69) [6]	4.0	96.0	100 (1 equivocal) [7]
Desert	52 (21.9)	<b>5.96</b> (0–41.5) [16]	18.2	81.8	53.8 (2 equivocal) [26]
Temperate	158 (66.7)	<b>2.79</b> (0–17.11) [49]	54.5	45.5	90.5 (7 equivocal) [63]

*Desert AAD plants*—Desert AAD plants include those that occur in the subtropical desert (SBWh), subtropical steppe (SBSH), tropical desert (TBWh), and temperate desert (TeBWk), using the ecological zone classification of Davis and Holmgren (2001). These ecoregions are inclusive of the Great Basin and the Chihuahuan, Mohave, and Sonoran deserts of NA and the Atacama and Monte deserts of SA (Fig. 1). Desert AADs are sometimes difficult to differentiate from those of temperate regions because of intergradation of these bioregions, especially in SA. For example, the subtropical steppe Norte Chico of Chile is an interface region between the dry Atacama Desert (part of the tropical desert) and the mediterranean subtropical dry forest (Davis and Holmgren, 2001), whereas this region is considered part of mediterranean Chile in other classifications (e.g., Josse et al., 2003). In addition, plants of some desert regions actually occupy more mesic conditions. For example, within the Atacama Desert, coastal areas up to several hundred meters in elevation receive minimal annual precipitation levels measured in millimeters, yet plants can thrive because of drip precipitation from the “camanchaca”, or coastal fog (Johnston, 1929; see Zuloaga et al., 2008). In general, we considered the subtropical and temperate steppes (Patagonian and Monte deserts) and perhaps part of the tropical dry forest (chaco) of Argentina to house desert plants, although a variety of habitats of varying moisture regimes occur in these regions. In addition, clades of species may have a mixture of AAD bioregions, e.g., the genus *Verbena* (Verbenaceae).

Despite these issues, we currently estimate a total of 52 desert AAD plants, making up almost 22% of the total (Table 2). These include no ferns, one Gnetales (*Ephedra*), 18 monocots, and 33 eudicots. With regard to plant families, Poaceae have the greatest number of desert AADs with 18 examples (all of the monocots), followed by Fabaceae with seven examples (Appendix 2). The mean divergence time of desert AAD events was calculated at 5.96 (range of means 0–41.5) Ma, considerably older than bipolar examples and somewhat older than temperate ones (Table 2; see below). The great majority (about 82%) of desert AADs are perennials, with about 61% of these herbs and 39% shrubs, subshrubs, or trees. From available phylogenetic data, slightly over half (about 53.8%) of the desert AAD plants dispersed from North to South America, a trend that contrasts with the other two bioregions. (See *Dispersal direction* section, below.)

*Temperate AAD plants*—Temperate plants comprise the largest group of AAD plants, with 158 examples, making up about 67% of the total (Table 2). For our purposes, temperate plants occupy the vegetation zones other than those of the bipolar and desert regions (although intergradation with the latter can occur) and other than the tropical rainforest (TA<sub>r</sub>), tropical moist deciduous forest (TA<sub>wa</sub>), tropical dry forest (TA<sub>wb</sub>), and tropical shrubland (TB<sub>sh</sub>) (Davis and Holmgren, 2001; Fig. 1). Temperate regions include the subtropical dry forests (SCs) and subtropical mountain systems

(SM) of NA and SA, which encompass the regions of Mediterranean-type climates of the two continents (Fig. 1; see Dallman, 1998; Moreira-Muñoz, 2011). Temperate plants also include the subtropical humid forest (SC<sub>f</sub>: southeastern coniferous forest of the NA, pampas of SA), temperate continental forest (TeDc: eastern deciduous forest of NA), temperate mountain system (TeM: Appalachian cordillera of NA, southern Andes of SA), part of the subtropical steppe (SBSH: Norte Chico of SA), and temperate steppe (TeBSk: Great Plains of NA). We note that some of the plants we classified as temperate may also occur in bipolar regions of either NA or SA (but not both) and recall that many plants classified as bipolar also occur in more temperate regions.

Temperate AAD plants include two ferns, 37 monocots, and 119 eudicots. With regard to plant families, Poaceae have the greatest number of temperate AADs with 26 examples, followed by Boraginaceae with 15 examples, Asteraceae with 14 examples, and Apiaceae, Fabaceae, and Polemoniaceae each with 9 examples (Appendix 3). Among the AAD temperate plants, a number are found in both western NA and western SA, but there are some that range into eastern NA and/or, perhaps more commonly, into eastern SA. The mean divergence time of temperate AAD events was calculated at 2.79 (range of means 0–17.11) Ma, a little less than half that of desert examples and over 11× of bipolar regions (Table 2). The majority (almost 55%) of temperate AADs are annuals, in contrast to those of bipolar and desert regions. From available phylogenetic studies, almost 91% of temperate AADs dispersed from North to South America. (Table 2; see *Dispersal direction* section, below.)

*Divergence times vs. AAD bioregion*—A plot of divergence times for each of the AAD bioregions shows the general trend of very recent divergence times in bipolar regions (mean = 0.25 Ma, with little variance), which, as discussed, is reflective of the recent establishment of those habitats. Mean divergence times of desert and temperate regions are earlier, 5.96 vs. 2.79 Ma, respectively, both with considerably more variance (Fig. 5B). Why desert plants have a generally older divergence time is unclear, but possibly related to plant duration or dispersal mechanism (see below).

*Extra-western hemisphere AADs*—A total of 38 AAD examples have native distributions also occurring beyond the western hemisphere (Appendices 1–3). Most of these (22, about 58%) are bipolar plants, only one (about 3%) is a desert plant, and the remainder (15, about 39%) are temperate plants. Their preponderance in bipolar plants, and to a degree in temperate plants, may be indicative about a more probable long-distance dispersal mechanism in these two bioregions (below).

*Rejected AAD examples*—We list a total of 22 taxa that had been considered examples of AAD plants in the past but that are rejected



based on our analyses. All of these are no longer believed to be native to either NA or SA (Appendix 4).

**Dispersal direction**—Evolutionary divergence occurs when a common ancestor gives rise to two, independent lineages. An AAD distribution pattern arises when the products of one lineage end up in amphitropical NA and those of the other in amphitropical SA. What we are terming dispersal direction is the direction of geographic change of the spatially altered lineage relative to the common ancestor, following this divergence event. Although dispersal is not the only explanation for current AAD distributions, we elect to use this term given it is by far the most probable explanation (see *Mechanisms of AAD distribution* section, below).

Taxonomic studies have traditionally been used to assess the direction of intercontinental dispersal. However, dispersal direction is most rigorously inferred from phylogenetic studies, the primary source of our comparative data (Appendices 1–3). As reviewed under *AAD bioregions*, a NA to SA direction of dispersal is the most common of all AAD patterns, occurring in about 81% of all AAD plants for which this is known. All bipolar AAD plants have the NA to SA pattern, with one case possibly equivocal (Table 2). Among temperate AADs, the great majority, over 90%, are NA to SA (Table 2). Both of these patterns have generally been explained by long-distance dispersal by migratory birds, some of which can fly long distances, e.g., along the Pacific Flyway (see below). However, as also concluded by Wen and Ickert-Bond (2009), desert AAD plants show a different pattern; about 46% by our calculations having a SA to NA direction of dispersal/migration (Table 2), exemplified by *Hoffmannseggia* (Simpson et al., 2005; Fig. 6A) and *Larrea* (Lia et al., 2001; Fig. 6B, C). Different mechanisms of propagule movement are likely involved for these desert plants (see Park, 2016; Schenk and Saunders, 2017, in this issue). Dispersal vectors likely show common patterns with regard to the AAD bioregion and timing of divergence.

**Character evolution**—Phenotypic and genotypic features in AAD plants are of great interest. We can first consider features possessed by AAD plants that may have facilitated their transportation, survival, and reproduction in the novel habitat of another continent. These features may be termed pre-AAD adaptations. We can also assess changes that occurred after transport to the new continent, so-called post-AAD adaptations. The following are some of the more recognizable features of AAD plants that appear important as pre- or post-AAD adaptations.

**Plant duration**—The duration of AAD plants is generally correlated with their AAD bioregion. As previously discussed, in bipolar AAD plants, about 96% are perennials, all but one of these perennial herbs. This predominant plant duration may be a function of their habitat, as most plants that live in extreme altitudes are perennials, and most of these are herbs. This agrees with the general recognition of a predominance of perennial plants in high latitude and high altitude conditions (Bliss, 1971). In contrast, about 55% of temperate AAD plants are annuals and 45% perennials (Table 2). Of the temperate perennial plants, almost all are perennial herbs, with about 3% of the perennials being shrubs. Finally, the great majority, about 82%, of desert AAD plants are perennials, with about 40% of these being woody trees or shrubs and the remainder being perennial herbs. These differences in desert AADs may be indicative of a different mechanism of dispersal, timing of dispersal

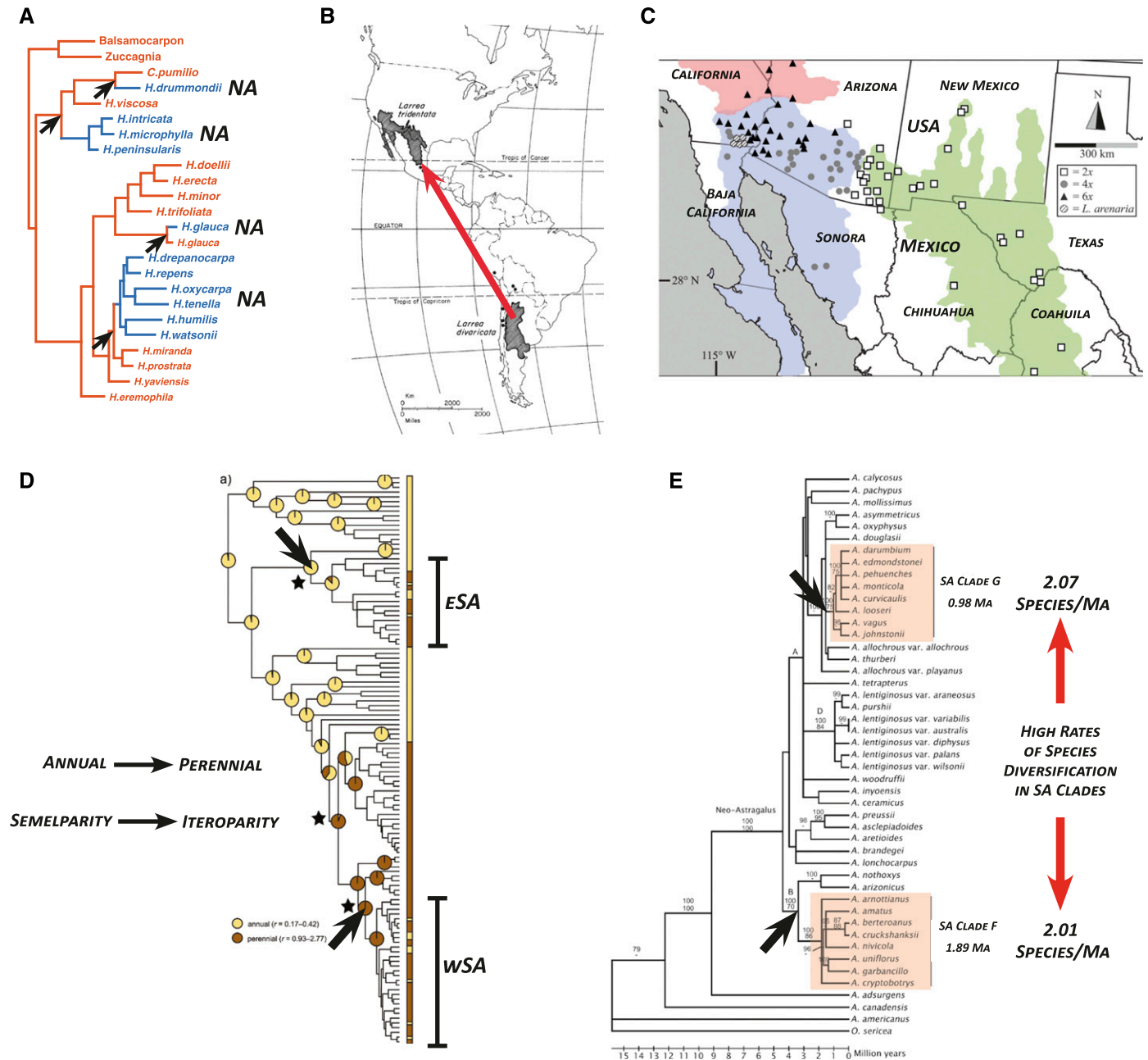
opportunity vs. propagule availability in annuals vs. perennials, or differences in the ability to establish populations postdispersal in an environment where conditions likely fluctuate with greater amplitude year to year compared to bipolar and temperate regions.

In the great majority (about 92%) of AAD examples, plant duration of the source vs. recipient taxa undergo no change following dispersal. However, a shift in plant duration is seen following a few AAD events. In several cases, the shift occurs from annual to perennial duration. For example, in *Cryptantha* (Boraginaceae), many members of a relatively large SA clade (termed the *Eucryptantha/Geocarya* clade, after Mabry, 2015; Mabry and Simpson, in press), which is the product of a single dispersal from North to South America, evolved a perennial duration (Fig. 4B, C). All other members of *Cryptantha* on both continents are annuals, the ancestral condition for the genus, as currently defined. We can only speculate as to the possible adaptive significance of this shift in plant duration. It may be related to the (at least initial) dearth of pollinators and selection for iteroparity, permitting multiple sexual reproductive events over a lifetime. However, some of these South American *Cryptantha* species occur at high altitude in the Andes Mountains, where the selective pressure for a perennial plant duration may have helped to survive the cold, alpine conditions (Bliss, 1971). A similar shift from annual to perennial plant duration is exemplified in other AAD examples. In the genus *Plagiobothrys* (Boraginaceae), most (seven of nine) of the perennial species occur only in SA (Johnston, 1927, 1932); thus, a perennial duration is thought to be derived, verified in part by Guillems (2015). In the genus *Chorizanthe* (Polygonaceae), all of the SA species are perennial; although we lack precise phylogenetic data, the perennial duration is presumed to have been derived on that continent from an ancestral annual one. Finally, Drummond et al. (2012) showed a shift from annual to perennial plant duration in clades of *Lupinus* (Fabaceae), one of these before and the other after two independent dispersals from North to South America (Fig. 6D). This change in plant duration corresponds with a shift from semelparity to iteroparity. Perennial plant duration is often cited as being the ancestral feature (Johnston, 1927; Raven, 1963), but in many AAD cases, it is clearly derived, apparently in the majority of cases after long-distance transport from North to South America.

A contrasting shift from a perennial plant duration in the common ancestor of the source region to annual in the recipient region is seen in other AAD events. For example, the desert grass genus *Munroa*, there is a shift from perennial (characteristic of the North American *M. pulchella* (Kunth) Amarilla and all outgroups studied) to annual (characteristic of all five species of a clade sister to *M. pulchella*) following presumed long-distance dispersal to SA (Amarilla et al., 2015; Appendix 2). Interestingly, no change in plant duration occurred following a later back dispersal from South to North America in this five species clade.

A comparison of plant duration and evolutionary divergence time shows some differences with respect to AAD bioregions. When all bioregions are pooled, there is little difference in mean divergence times between annuals (2.31 Ma) and perennials (2.77 Ma; Table 3). As already discussed, AAD plants of bipolar regions are predominantly perennial (about 96%), with a very recent mean divergence time (0.25 Ma), no data being available for the single annual species (Table 3). Among desert AAD plants, perennials have a somewhat older mean divergence time (6.07 Ma) than that of annuals (4.27 Ma; Table 3). Among temperate plants, the divergence times between annuals and perennials are more similar, 1.81





**FIGURE 6** (A) Cladogram of *Hoffmannseggia* (Fabaceae), showing four dispersal events (arrows), all from South America (lineages/taxa in orange) to North America (NA; lineages/taxa in blue). Modified from Simpson et al. (2005, p. 21), with permission. (B) Distribution map of *Larrea* (Zygophyllaceae), showing hypothesized dispersal from South to North America. Modified from Hunter et al. (2001, p. 525), with permission. (C) Distribution map of *Larrea* spp., showing North American 2n, 4n, and 6n chromosome races. From Laport et al. (2012, p. 155), with permission. (D) Cladogram of *Lupinus* (Fabaceae), showing evolutionary shift from annual (light yellow) to perennial (dark brown) habit, associated with a similar shift from semelparity to iteroparity, and two independent dispersals from North to South America (arrows). Stars indicate increases in species diversification rates. Modified from Drummond et al. (2012, p. 452), with permission. (E) Cladogram of *Astragalus* (Fabaceae), showing shift of species diversification rate correlated with two independent dispersals from North to South America (arrows). Modified from Scherson et al. (2008, p. 1034), with permission.

vs. 2.31 Ma, respectively (Table 3). However, we note that this includes only examples for which plant duration is unambiguous.

In general, differences in divergence time between annuals and perennials between AAD bioregions seems significant, but within an AAD bioregion appears to be small. Further studies may provide more insight into the evolution of plant duration in AAD

plants, e.g., with respect to both bioregion and source and sink habitats.

*Substrate preference*—Virtually nothing is known about shifts in substrate preference in AAD plants. In a single known example, Simpson et al. (2005) mention that the source South American

**TABLE 3.** American amphitropical vascular disjunct plants, comparison of number, percentage, and mean divergence time (with range of individual means) of annual vs. perennial plants for all regions, biopolar plants only, desert plants only, and temperate plants only. Only nonequivocal data listed. Those taxa listed in the literature ambiguously as either annual or perennial (or a combination with biennial) were omitted. [N] = number of examples from which mean divergence time is calculated. — = no available data. See Appendices for source of data.

Plant duration	Total number	Percent of total	Mean divergence time, Ma (Range) [N]
<b>All regions</b>			
Annuals	82	40.6	<b>2.31</b> (0–14.9) [29]
Perennials	120	59.4	<b>2.77</b> (0–24.78) [26]
<b>Bipolar only</b>			
Annuals	1	4.0	—
Perennials	24	96.0	<b>0.25</b> (0–0.69) [7]
<b>Desert only</b>			
Annuals	8	18.2	<b>4.27</b> (0.03–14.42) [6]
Perennials	36	81.8	<b>6.07</b> (0–24.78) [7]
<b>Temperate only</b>			
Annuals	73	54.9	<b>1.81</b> (0.26–14.90) [23]
Perennials	60	45.1	<b>2.31</b> (0–7.69) [12]

species of *Hoffmannseggia* are limited to sandy or rocky soils, but the recipient North American species can occupy these plus clay or calcareous soils. The implication in this observation was that a shift in diversification of substrate tolerance occurred following dispersal.

**Reproductive biology**—The great majority of AAD plants are reported to be self-compatible (Chambers, 1963; Constance, 1963; Heckard, 1963; Ornduff, 1963; Raven, 1963; Moore and Raven, 1970; not tabulated in our study). Self-compatibility and bisexuality (e.g., either a hermaphroditic or monoecious plant sex) are likely necessary conditions for survival after long-distance transport, given that this transport might involve a single propagule with an unlikely chance of cross-pollination (i.e., Baker's Rule; Baker, 1955; see Carlquist, 1966 for an alternative viewpoint). However, long-term vegetative propagation (not investigated here) could also allow persistence of a propagule in the recipient region following dispersal.

A specialized type of self-compatibility is cleistogamy, in which the corolla remains closed as the stamens and pistils mature. Thus, cleistogamous flowers are self-compatible and self-pollinating within a single flower, ensuring propagule production in the total absence of pollinators. The ability to produce cleistogamous flowers might be under selective pressure following dispersal to a novel environment, and some of the AAD plants are known to have cleistogamous flowers. Among AAD plants, cleistogamy is reported in *Cryptantha* spp., sections *Cryptantha* and *Geocarya* (Boraginaceae); *Dichondra* (Convolvulaceae); *Epilobium campestre* (Jeps.) Hoch & W.L. Wagner (Onagraceae); *Nuttallanthus texanus* (Plantaginaceae); *Bromus berteroi* Colla, *Deschampsia danthonioides* (Trin.) Benth., *D. monandra* Parodi, *Festuca octoflora* Walt., *Phalaris angusta* Nees ex Trin., and possibly *Phalaris lemmonii* Vasey and *P. platensis* Henrard ex Heukels (Poaceae); *Collomia grandiflora* Douglas ex Lindl., *C. soehrensii* Phil., *Leptosiphon pusillus* (Benth.) J.M. Porter & L.A. Johnson, and *Polemonium micranthum* Benth. (Polemoniaceae; Johnston, 1927; Raven, 1963; Johnson and Porter, 2017, this issue), and *Acaena pinnatifida* Ruiz

& Pav. (Rosaceae; Marticorena, A. 2006). Cleistogamy in *Collomia* and *Polemonium* can be considered a pre-AAD adaptation that may have facilitated establishment in South American, while cleistogamy in the SA *Leptosiphon pusillus* is not known among its North American sister species and appears to be a post-AAD adaptation following dispersal (Johnson et al., 2012; Johnson and Porter, 2017, this issue). One notable example of cleistogamy among AAD plants are certain South American species of *Cryptantha* (Boraginaceae; Fig. 4D). Cleistogamy, like a perennial plant habit, is predominant among members of the aforementioned *Eucryptantha/Geocarya* clade (Mabry and Simpson, in press; Fig. 4B). An interesting avenue of research will be investigation into a possible interaction between cleistogamy and a perennial duration in these taxa. Interestingly, among members of this clade are species (of section *Geocarya*; Johnston, 1927) that have evolved a specialized type of cleistogamous flower, one that originates at ground level and can, in fact, be pulled underground during development. These geocarpic fruits, termed “cleistogenes”, are enlarged and morphologically different from the apical fruits that are the produce of chasmogamous flowers (Grau, 1983; Fig. 4E), an intriguing example of a potential post-AAD adaptation.

**Propagule morphology and physiology**—If long-distance dispersal is invoked as a mechanism of intercontinental movement, then the propagules (diaspores) would need to be adapted for such transport, with specializations either for water (oceanic hydrochory, also termed nautochory), wind (anemochory or chamaechory, the “tumbleweed” mechanism), or animal (zoochory) dispersal. The propagule units of angiosperms are generally seeds or fruits/fruit parts, though rarely whole plants or plant parts, as in the tumbleweeds. If animal transport is invoked as a mechanism for dispersal, which many authors think most probable, the transport was likely by either endozoochory or epizoochory (see *Mechanisms of AAD distribution* section, below). Endozoochory involves passing through an animal's gut unharmed, whereby fruits or seeds would require a thick, resistant outer covering (pericarp and/or seed coat) to survive. Epizoochory (also termed ectozoochory) requires attachment to the fur, feathers, or appendages of an animal. Fruits or seeds that are relatively small, mucilaginous, or have hairs, viscid glands, barbs, or processes would have a higher probability of remaining attached during long-distance transport (Carlquist, 1981). Because some migratory birds can travel great distances in a single flight, bird migration has been invoked as the most probable mechanism of long-distance dispersal (see Lewis et al., 2014a for evidence of bird epizoochory). Size and sculpturing of seeds or fruits may also correlate with their ability to be transported by epizoochory.

A good example of epizoochory is seen in *Acaena pinnatifida*, in which the glochidiate processes of the fruit very effectively attach to the fur or features of a passing animal (Fig. 4F). Similarly, the bristly calyces enclosing the nutlets of several members of the subtribe Amsinckinae (Boraginaceae, after Chacón et al., 2016) may provide an effective animal transport mechanism (Fig. 4G; see Guillems et al., 2017). *Phacelia* (Hydrophyllaceae) shows variation in propagule morphology, with most South American members having relatively nonadherent seeds released from the capsule at maturity. However, in some members of the *P. magellanica* complex, presumed to have been dispersed from North to South America by long-distance dispersal, the seeds are retained within the capsule and surrounded by a bristly calyx, making attachment to an

animal more probable (Heckard, 1963). Temperate Polemoniaceae have small seeds that either remain unchanged when wetted or that produce mucilage/spiracles from the seed coat when wetted; yet, all AAD exemplars in this family involve species with mucilaginous seeds, likely more easily dispersed via epizoochory (Johnson and Porter, 2017, this issue). Williams (2015), in a comparative phylogenetic study of the fruits (nutlets) of members of the subtribe Amsinckiinae (Boraginaceae), showed a positive correlation with regard to a rough sculpturing and a negative correlation with respect to size in members of the subtribe occurring in SA. Here, all South American taxa or clades were inferred to be the product of NA to SA dispersal events. In this case, taxa possessing propagules with putative adaptations for long-distance transport by birds seem more likely to be present in South America.

Schenk and Saunders (2017, this issue) tabulate propagule morphology of AAD plants and evaluate the mechanisms of possible propagule dispersal.

**Chromosome number and polyploidy**—Few trends in chromosome number changes can be recognized in AAD plants because of the paucity of chromosome counts, especially of South American taxa or populations. In our tabulation, where counts are available, not ambiguous (e.g., without multiple, overlapping numbers reported), and show changes in number associated with an AAD event, most examples point to polyploidy evolving in the recipient (sink) populations. It is not always clear, however, whether the chromosomal shift occurred prior to or after dispersal.

Among bipolar AAD plants, shifts in chromosome number include the source North American *Botrychium spathulatum* ( $2n = 90, 2x$ ) vs. the recipient South American *Botrychium dusenii* (reported as  $4x$ ; Appendix 1). In addition, the conspecific *Anemone multifida* Poir. (Ranunculaceae) is thought to be of hybrid origin, the possible parents all from NA. This species is polyploid ( $4x$ ) in NA, but recipient populations in SA show more variation, being  $2x$ ,  $4x$ , or  $6x$  (Appendix 1). Its hybrid nature is hypothesized to be correlated with its variability and the diversity of habitats occupied in NA and SA (Meyer et al., 2010; Hoot et al., 2012). (See Appendix 1.)

Among desert AAD plants, Yuan and Olmstead (2008) showed a shift from diploidy to polyploidy in the recipient North American members of *Glandularia* (Verbenaceae) relative to the source members in SA. All members of the recipient South American clade (“Blue-flowered group”) of *Tiquilia* spp. (Ehretiaceae), derived via a NA to SA long distance dispersal, are tetraploid, whereas their sister species, the North American source species *T. palmeri* (A.Gray) A.T.Richardson, is diploid (Moore et al., 2006; see also Soltis et al., 2014). The genus *Larrea* (Zygophyllaceae) is thought to have been dispersed from SA to NA (Lia et al., 2001; Fig. 6B), with the subsequent postdispersal evolution of polyploidy (tetraploidy and hexaploidy) only in some North American populations (Laport et al., 2012; Fig. 6C). (See Appendix 2.)

Among temperate AAD plants a shift occurred relative to the source North American *Primula alcalina* Cholewa & Dougllass M.Hend. + *P. specuicola* Rydb. clade ( $2n = 18, 2x$ ) vs. the recipient South American *P. magellanica* Lehm. ( $2n = 72, 8x$ ). Ornduff (1963) speculated that the Chilean *Blennosperma chilense* Less. ( $2n = 32$ ) arose following an allopolyploidy event within a North American *Blennosperma* species complex ( $2n = 14, 18$ ). In a more detailed study, Johnson et al. (2012) hypothesized that the South American (Patagonian) tetraploid *Collomia biflora* (Ruiz & Pav.) Brand (Polemoniaceae) originated via an allopolyploid event

following hybridization between two South American species, after long-distance transport to SA. The recipient South American *Gilia crassifolia* Benth. has both tetraploid and octoploid populations ( $2n = 36, 72$ ), while its most likely source North American relatives, either *G. salticola* Eastw. or *G. clokeyi* H.Mason are diploid ( $2n = 18$ ; Morrell et al., 2000; Johnson and Porter, 2017, this issue). Several members of the recipient South American *Eucryptantha/Geocarya* clade of the genus *Cryptantha* are hexaploid (Fig. 4B), whereas all others in the genus are diploid, except for one sample of a single member of the South American *Globuliferae* clade, other members of which are diploid (Fig. 4B; see Appendix 3).

Adaptive features of polyploids, especially allopolyploids, include amelioration of inbreeding depression, increased ecological tolerance, and increased chance of genetic novelties (Mummenhoff and Franzke, 2007). All of these may have enhanced the survival and reproduction of AAD plants dispersed to a new continent. The possibility that the derivation of polyploidy in recipient AAD taxa may be somehow correlated with or causative of other morphological and reproductive features, such as the perennial plant duration and cleistogamy in certain *Cryptantha* (above), will be interesting to investigate.

**Genetic divergence**—The study of genetic divergence following the establishment of a taxon in a new region might give insight as to the genetic mechanisms following introduction of a single propagule to a new environment. For example, van Houten et al. (1994) examined the genotypic variation in coastal vs. inland populations of the Chilean annual *Microseris pygmaea*, which was presumed to have become established in SA following long-distance dispersal from NA (see Lohwasser et al., 2004). By studying molecular markers in the F2 population resulting from crosses of two individuals of the most ecologically diverse populations, the authors identified significant genetic variation between the two populations (including the identification of 18 quantitative trait loci), which they surmised may represent radiation of an AAD plants following a presumed single colonization.

**Species diversification rate**—A few phylogenetic studies have demonstrated an increase in species diversification rate following an AAD event. Hughes and Eastwood (2006) demonstrated a high species diversification rate in an AAD recipient clade of Andean *Lupinus* (81 spp.) of 2.49–3.72 species per million years, with the diversification rate increase occurring after the uplift of the northern Andes. They hypothesized the formation of diverse island-like montane habitats following the Andean uplift as the driving factor for this high species diversification rate. Scherson et al. (2008) inferred two separate AAD clades of South American *Astragalus* species (Fig. 6E), each with high rates of species diversification (2.01 and 2.07 species/million years). Both of these studies demonstrate a probable adaptive radiation event following the introduction of a propagule into a novel habitat, potentially driven by new niche availability, reduced competition, and/or reduced predation.

**Phylogeography**—Although there are very few published examples, phylogeographic methods (e.g., Matzke, 2013) are now available to infer the source and sink areas of an AAD event in terms of present day ecoregions. For example, assignment of current biogeographic regions to taxa in an phylogeographic analysis of the



genus *Cryptantha* (Mabry, 2015; Mabry and Simpson, in press) indicates that the common ancestors of each of the two major South American clades were the products of single long-distance dispersals, from a Mediterranean-type climate region of NA to a Mediterranean-type climate region of Chile in SA, with later dispersals to the subtropical mountain system of the Andes or subtropical steppe or desert (Fig. 7). Of course, these phylogeographic studies trace the history of plant lineages in terms of the current ecoregions occupied. Knowledge of the past climate, geology, and vegetation of source and sink regions of AAD plants are needed to fully understand the history of an AAD event, as current ecoregions may be different from those present at the time of the dispersal or migration.

*Mechanisms of AAD distribution*—Different mechanisms have been proposed to explain the distribution of AAD plants. One early hypothesis is that a given AAD plant distribution arose by vicariance, via the splitting of an ancestrally continuous range, such as by the formation of the wet tropical region. It is also possible that a common ancestor restricted in distribution to a currently intermediate region (e.g., ancestrally within what is now the neotropics) could have given rise to lineages to the north and to the south, with these intermediate populations going extinct. Both of these hypotheses could be tested with study of intermediate populations. However, given that, by definition, AAD plants lack such tropical intermediates, no fossil evidence of geographic intermediates has been described, and events that may have led to vicariance are generally not correlated with AAD divergence time estimates, these hypotheses are not widely accepted.

A general assumption in evaluating AAD distributions is that the products of the spatially disjunct lineage (relative to the common ancestor) were transferred to a region different from the common ancestor by a dispersal event. The most accepted hypothesis is that the great majority of AAD taxa acquired their current ranges via long-distance dispersal. Direct dispersal, in a single, relatively rapid event, is generally accepted as the primary means of long-distance dispersal between the continents. Birds are considered the most likely vector of this direct dispersal. (See Schenk and Saunders, 2017, this issue.) A number of migratory bird species, with combined annual numbers likely in the millions, fly between western NA and Chile/Argentina (Collins, 1974; Carlquist, 1983) along the well-known Pacific Flyway. As mentioned earlier, propagule dissemination by birds may have occurred by endozoochory or epizoochory. There are empirical studies demonstrating the occurrence of seeds in the gut contents of migratory birds, some of these retained there for many days (see Carlquist, 1983 and references therein). And, as previously alluded to, Lewis et al. (2014a) demonstrated the presence of plant fragments on the outer bodies of migratory birds, indicating the possibility of epizoochory for long-distance dispersal. The distribution of AAD plants well within the amphitropical zone, e.g., in western NA and western or southern SA (as in Fig. 2A), is thought to support the long-distance dispersal hypothesis, likely by migratory birds given the great distance between intercontinental populations.

Another hypothesis of long-distance dispersal is that at least some AAD plants attained their current distribution by a slower, more gradual stepwise or stepping-stone dispersal process across Central America and the northern Andes of SA. In addition to birds, other animals, including mammals, could be the vector of transport in this scenario, e.g., perhaps associated with the Great

American Biotic Interchange (e.g., Woodburne, 2010). A stepwise distribution pattern, showing “trans” populations along the cordillera of Central America or northern SA (e.g., as seen in Fig. 2B–D) might be indicative of this type of movement. One could argue that most AAD plants must have been dispersed long distance because they cannot survive or persist in the wet tropics, although it is certainly possible that they did survive in tropical regions for a time, in a stepwise migration, but later went extinct there, making this hypothesis virtually untestable. Fine-scale molecular studies may be capable of differentiating between a long-distance vs. stepwise dispersal hypotheses. For example, Lewis et al. (2014b) determined from phylogenetic studies that the moss *Tetraplodon* attained its current AAD distribution by direct long-distance dispersal from NA to SA, probably in a single flight by a migratory bird. In this case, putative stepwise populations were refuted as the mechanism of AAD distribution, because the spatially intermediate neotropical populations of this taxon were found to be more distantly related to the sister amphitropical populations of North and South America.

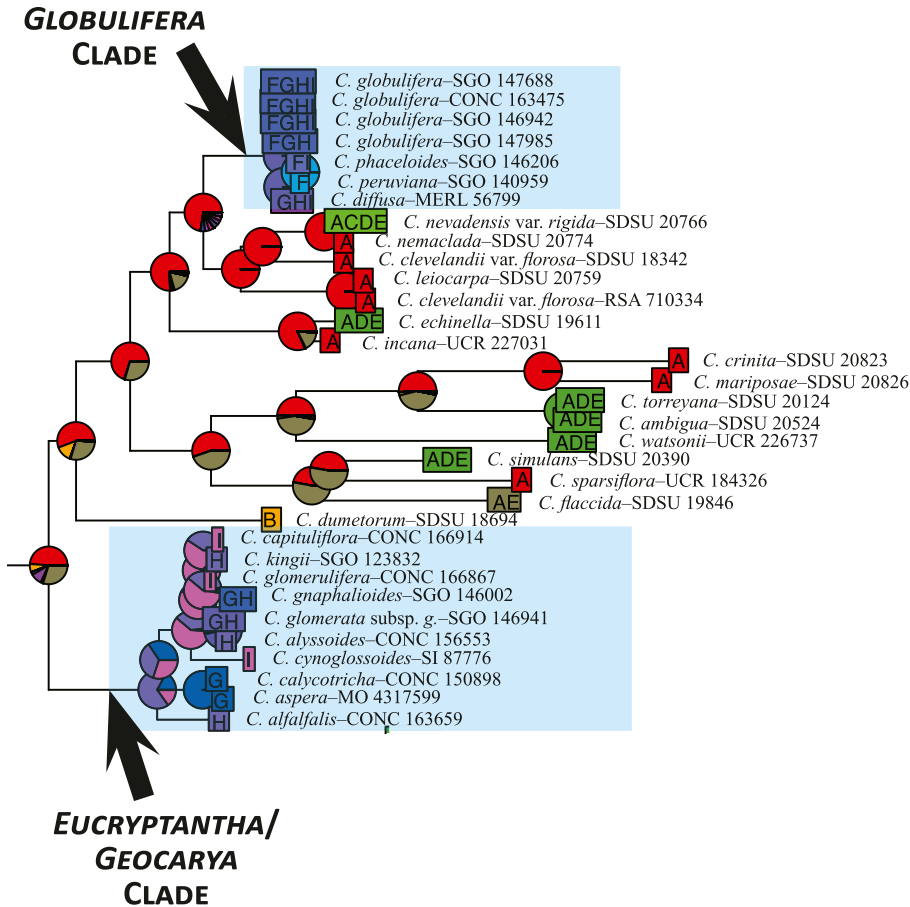
Our tabulations of deviations from a typical AAD distribution yielded the following summaries. A total of 38 AAD examples have distributions also outside the western hemisphere. Most of these (22) are in bipolar regions, one is a desert plant, and 15 are in temperate regions. All but three of these otherwise have a typical AAD distribution occurring in western NA or western to southern SA. A total of 20 AAD examples deviate significantly in east–west range from a typical AAD distribution, these fairly evenly split between desert and temperate plants. Six AAD examples have representatives occurring in eastern NA (one desert, five temperate), six in both eastern and western NA (all temperate), two in eastern SA (one desert, one temperate), and six in both eastern NA and SA (three desert, three temperate) (Appendices 2, 3). Finally, a total of 38 examples of the general desert and temperate bioregions have distributions that we deemed to encroach well beyond the amphitropical zone, into Central America and northern SA. Four of these occur in what we termed “trans-NA” (three desert, one temperate), 15 occur in “trans-SA” (seven desert, eight temperate), and 19 occur in “trans NA-SA” (four desert, 15 temperate).

Aside from the fact that most bipolar AADs are also found outside of NA and SA, no clear trends or correlations were noted in these distribution deviations. However, these examples might be scrutinized for mechanisms of dispersal in attaining their current distribution, including possible stepwise long-distance dispersal.

## CONCLUSIONS

Evaluating what constitutes an amphitropical distribution is important in discriminating among different types of biogeographic patterns, with potentially different mechanisms at play by which current distributions became established. Consideration of anthropogenic AAD introductions is critical, and study of known examples of human introductions may give insight into the mechanisms, patterns, and levels of variation of naturally distributed AADs. Continuing taxonomic research is critical to verifying specific AAD plant distribution hypotheses. Consideration of taxonomic category—conspecific, infraspecific, species pairs, and clade relationships—is valuable in giving insight into the amount of evolutionary divergence that has taken place in different groups. It is





**FIGURE 7** Phylogeographic graphical output using BioGeoBEARS (Matzke, 2013), showing the most likely ancestral range for *Cryptantha*, highlighting the two major South American groups: the *Globulifera* clade and the *Eucryptantha/Geocarya* clade. From Mabry (2015), with permission. Legend for ecological zones (modified from Davis and Holmgren, 2001): red = North America subtropical dry forest and mountain system; green = North America temperate desert; blue = South America tropical desert; purple = South America subtropical steppe and dry forest.

best to view the split between NA and SA plant lineages as a unique AAD event, which in some cases is followed by at least one lineage resulting in diversification into a clade of species. Classifying AAD plants by bioregion—bipolar, desert, and temperate—is useful, as these comparisons may point out different dispersal mechanisms and different processes of evolutionary divergence.

Evaluating character evolution with respect to plant duration, substrate preference, aspects of reproductive biology, propagule features, chromosome number changes, and genetic divergence helps to understand AAD adaptations, both before (pre-AAD) and after (post-AAD) dispersal. Additional studies detailing other features, such as the molecular evolutionary changes causative for shifts in such features as a perennial duration, polyploidy, or cleistogamy, will constitute intriguing, new avenues of research.

Phylogenetic studies can more clearly establish the timing and direction of dispersal in an AAD event, especially if associated with bioregion or plant characteristics. These phylogenetic methods can also provide precise information on species diversification rate, this sometimes increasing following an AAD event, signaling a rapid radiation. Detailed phylogeographic studies, combined with knowledge of climatic and geologic changes in source and sink regions,

can yield insight into mechanisms of AAD events, elucidating the range and habitats of common ancestors and their descendants. However, phylogenetic and phylogeographic studies of AAD plants are still few in number. More are needed to more fully evaluate potentially common patterns of divergence resulting in an AAD distribution in concert with knowledge of climatic and geologic history of AAD regions.

Though long-distance dispersal is thought to be a rare, chance event, occurring at various times during biogeographic history, the great majority of AAD plants likely attained their current distributions by relatively rapid, direct long-distance dispersal, most likely by migratory birds. However, stepwise long-distance dispersal hypotheses may be viable alternatives in some cases, especially those with “trans” incursions into the tropical zone.

**Future directions**—Continued research on AAD plants is needed to accumulate sufficient data to evaluate whether the events that have led to current patterns of distribution show common patterns and to elucidate correlations between these patterns and past geological or climatic events that shaped the survival and evolution of plants in novel habitats. Future directions will include refining our current tabulation of AAD plants to stimulate needed research. Continued phylogenetic studies will give us additional and more precise estimates of divergence times (e.g., with fossil calibration) and species diversification rates, both still grossly undocumented. These studies are likely to provide even more examples of clade-level AADs, which are likely underreported by us, having been difficult to demonstrate with the earlier focus on minimum-ranked taxa.

To facilitate continued research in this field, we have established an American Amphotropical Disjunction Working Group ([https://figshare.com/projects/American\\_Amphotropical\\_Disjunctions\\_AAD\\_Working\\_Group/25510](https://figshare.com/projects/American_Amphotropical_Disjunctions_AAD_Working_Group/25510)), for which our objective is to continuously update both the list of AADs (<http://dx.doi.org/10.6084/m9.figshare.5479822>) and the data associated with them, including the features listed in Appendices 1–3 here and additional features, such as propagule morphology and other documented features of reproductive biology. Critical to this listing is a clarification of the taxonomy of each AAD example and its precise distribution based on data from georeferenced herbarium specimens. The value of herbaria as repositories of the taxa of study, and the importance of specimen annotations by experts cannot be overstated. Our most ambitious plan is to link each AAD example with one or more distribution maps, ideally with layers of vegetation regions, topography, climate data, and even soils. Our desire is to stimulate and encourage ongoing discussion among the members of the scientific community to facilitate updates, keep these lists current, and provide a resource to the botanical community at large.

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**APPENDIX 1**

List of vascular plants with a native, bipolar American amphitropical disjunct (AAD) distribution. **Tax.** = taxonomic unit of comparison; **Sp** = single species (conspecifics) occurring in both North America (NA) and South America (SA); **Sp-Ind** = two different infraspecies (varieties or subspecies) occurring in both NA and SA; **Sp-Sp** = two different species, either sister or closely related, occurring in NA and SA. Taxa names in square brackets [ ] = synonym(s). (**Dist.**) = distribution: **AAD** = American amphitropical disjunct distribution generally well outside of tropical regions; \* = native distribution also occurring outside the western hemisphere. **C#-NA** = chromosome number of North American taxon; **C#-SA** = chromosome number of South American taxon, number in curly brackets { } = source for chromosome counts (key at bottom of table). **Dur.-Hab.** = plant duration, **A** = annual, **B** = biennial, **P** = perennial, or a combination; plant habit, **H** = herb, **S** = shrub, or a combination, with differences between NA and SA indicated by "/". **Disp. dir.** = direction of dispersal from source area to recipient area as determined from phylogenetic studies, either **N→S** (NA to SA), **S→N** (SA to NA), or **Equiv** = equivocal. **Div. Ma** = mean time of divergence (mean ranges in parentheses) of NA and SA taxa/clades. **Lit. source** = Source of phylogenetic or pertinent taxonomic studies, including those citing direction or time of divergence. "—" = missing information. \*\* = not considered bipolar by Moore and Chater (1971).

GROUP / Family/ Genus	Tax./(Dist.)	AAD Taxon/Clade-NA	C#-NA	AAD Taxon/Clade-SA	C#-SA	Dur.-Hab.	Disp. dir.	Div. Ma (Mean range)	Lit. source
<b>FERNS</b>									
<b>Ophioglossaceae</b>									
<b>Botrychium</b>	<b>Sp-Sp (AAD)</b>	<i>Botrychium spathulatum</i> W.H.Wagner [ <i>Botrychium lunaria</i> (L.) Sw. x <i>Botrychium campestre</i> W.H.Wagner & Farrar]	B. l.: 2n = 90 [2x] {2}	<i>Botrychium dusenii</i> (Christ) Alston [ <i>Botrychium lunaria</i> (L.) Sw. var. <i>dusenii</i> Christ]	[4x] {10}	<b>P-H</b>			Farrar and Stensvold, 2017; Meza-Torres et al., 2017
<b>Pteridaceae</b>	<b>Sp-Sp (AAD)</b>	<i>Cryptogramma acrostichoides</i> R.Br. [ <i>Cryptogramma crista</i> (L.) R.Br. ex Hook. var. <i>acrostichoides</i> (R.Br.) C.B.Clarke]	—	<i>Cryptogramma fumariifolia</i> Christ [ <i>Cryptogramma crista</i> var. <i>chilensis</i> (Christ) Loosel]	—	<b>P-H</b>			
<b>MONOCOTS</b>									
<b>Cyperaceae</b>									
<b>Carex</b>	<b>Sp (AAD*)</b>	<i>Carex arctogena</i> L.	—	"	—	<b>P-H</b>	<b>N→S</b>	<b>0</b>	Villaverde et al., 2015a
	<b>Sp (AAD*)</b>	<i>Carex canescens</i> L. s.l.	2n = 54, 56 {9}	"	—	<b>P-H</b>	<b>N→S</b>	<b>0.05</b> (0–0.17)	Villaverde et al., 2017b
	<b>Sp (AAD)</b>	<i>Carex macloviana</i> D'Urv.	2n = 86 {9}	"	—	<b>P-H</b>	<b>Equiv</b>	<b>0.27</b> (0.09–0.48)	Escudero et al., 2010; Márquez-Corro et al., 2017
	<b>Sp-Ind (AAD)</b>	<i>Carex magellanica</i> Lam. subsp. <i>irrigua</i> (Wahlenb.) Hitonen	2n = ca. 60 {9}	<i>Carex magellanica</i> Lam. subsp. <i>magellanica</i>	—	<b>P-H</b>	<b>N→S</b>	<b>0.2</b> (0–0.39)	Escudero et al., 2010
	<b>Sp (AAD*)</b>	<i>Carex maritima</i> Gunnerus, s.l. [ <i>Carex incurva</i> Lightf.]	2n = 60 {9}	"	—	<b>P-H</b>	<b>N→S</b>	<b>0.23</b> (0.03–0.51)	Villaverde et al., 2017b
	<b>Sp (AAD*)</b>	<i>Carex microglochyn</i> Wahlenb.	—	"	—	<b>P-H</b>			Escudero et al., 2010
<b>Eleocharis</b>	<b>Sp (AAD*)</b>	<i>Eleocharis quinqueflora</i> (Hartmann) O.Schwarz s.l.** [ <i>Eleocharis pauciflora</i> (Lightf.) Link, <i>Eleocharis atacomensis</i> Phil.]	2n = ca. 136 {8}	"	—	<b>P-H</b>			
<b>Juncaginaceae</b>	<b>Sp (AAD*)</b>	<i>Triglochin palustris</i> L.	2n = 24 {8}	"	—	<b>P-H</b>			
<b>Poaceae</b>	<b>Sp (AAD*)</b>	<i>Alopecurus magellanicus</i> Lam. [ <i>Alopecurus alpinus</i> J.E.Sm., <i>Alopecurus antarcticus</i> Vahl]	—	"	—	<b>P-H</b>			

continued

## APPENDIX 1, Continued

GROUP / Family/ Genus	Tax./ (Dist.)	AA/Taxon/Clade-NA	C#-NA	AA/Taxon/Clade-SA	C#-SA	Dur.-Hab.	Disp. dir.	Div. Ma (Mean range)	Lit. source
<i>Avenella</i>	Sp (AAD*)	<i>Avenella flexuosa</i> (L.) Drejer [ <i>Deschampsia flexuosa</i> (L.) Trin.]	—	"	—	P-H			
<i>Calamagrostis</i>	Sp (AAD*)	<i>Calamagrostis stricta</i> (Timm) Koel. [ <i>Calamagrostis neglecta</i> (Ehrh.) P.Gaertn., B.Mey. & Schreb.]	—	"	—	P-H			
<i>Catabrosa</i>	Sp (AAD*)	<i>Catabrosa aquatica</i> (L.) Beauv.	2n = 20 {8}	"	—	P-H			
<i>Deschampsia</i>	Sp (AAD*)	<i>Deschampsia caespitosa</i> (L.) P.Beauv.	2n = 26, 28 {8}	"	—	P-H			
<i>Phleum</i>	Sp (AAD*)	<i>Phleum alpinum</i> L.	2n = 28 {1}	"	2n = 28 {7}	P-H			
<i>Vahlodea</i>	Sp (AAD*)	<i>Vahlodea atropurpurea</i> (Wahlenb.) Fr. [ <i>Deschampsia atropurpurea</i> (Wahlenb.) Scheele]	2n = 14 {13}	"	—	P-H			
<b>EUDICOTS</b>									
<b>Brassicaceae</b>									
<i>Cardamine</i>	Sp-Sp (AAD*)	<i>Cardamine pratensis</i> L.	—	<i>Cardamine glacialis</i> (G.Forst.) DC.	—	P-H			
<i>Draba</i>	Sp-Sp (AAD*)	<i>Draba incana</i> L.	—	<i>Draba magellanica</i> Lam.	—	BP-H			
<b>Ericaceae</b>									
<i>Empetrum</i>	Sp-Sp (AAD*)	<i>Empetrum nigrum</i> L.	—	<i>Empetrum rubrum</i> Vahl ex Willd.	—	P-S	N→S	0.81 (0.45–1.35)	Popp et al., 2011
<b>Gentianeaceae</b>									
<i>Gentiana</i>	Sp (AAD*)	<i>Gentiana prostrata</i> Haenke	—	"	—	ABP-H			
<b>Plantaginaceae</b>									
<i>Hippuris</i>	Sp (AAD*)	<i>Hippuris vulgaris</i> L.	—	"	—	P-H			
<i>Plantago</i>	Sp (AAD*)	<i>Plantago maritima</i> L. [ <i>Plantago maritima</i> L. subsp. <i>juncoides</i> (Lam.) Hulten]	—	"	—	P-H			
<b>Plumbaginaceae</b>									
<i>Armeria</i>	Sp (AAD*)	<i>Armeria maritima</i> (Mill.) Willd. [ <i>Armeria maritima</i> (Mill.) Willd. subsp. <i>californica</i> (Boiss.) A.E.Porsild]	2n = 18 {8}	"	—	P-H			
<b>Polygonaceae</b>									
<i>Koenigia</i>	Sp (AAD*)	<i>Koenigia islandica</i> L.	2n = 28 {8}	"	—	A-H			
<b>Ranunculaceae</b>									
<i>Anemone</i>	Sp (AAD)	<i>Anemone multifida</i> Poir.**	2n = 32 [4x] {5}	"	2n = 16, 32 [4x], 64 [6x] {7,13}	P-H	N→S		Meyer et al., 2010; Hoot et al., 2012
<i>Ranunculus</i>	Sp-Sp (AAD*)	<i>Ranunculus hyperboreus</i> Rottb.**	2n = 32 {5,3,6, 11,12}	<i>Ranunculus fuegianus</i> Speg.**	2n = 48 {7}	P-H	N→S?		Paun et al., 2005

Key to literature citations of chromosome numbers: {1} = Dalgaard, 1988; {2} = Dauphin, et al., 2016; {3} = Engelskjøn, 1979; {4} = Krogulevich, 1976; {5} = Löve, 1982a; {6} = Malakha, 1990; {7} = Moore, 1981; {8} = Raven, 1963; {9} = Roalson, 2008; {10} = Stensvold and Farrar, 2017; {11} = Zhukova, 1980; {12} = Zhukova, 1982; {13} = Ziman et al., 2006.

**APPENDIX 2**

List of vascular plants with a native, desert, American amphitropical disjunct (AAD) distribution. **Tax.** = taxonomic unit of comparison: **Sp** = single species (conspicuous) occurring in both North America (NA) and South America (SA); **Sp-InC** = two infraspecies (coninfraspecifics) occurring in both NA and SA; **Sp-IND** = two different infraspecies (varieties or subspecies) occurring in both NA and SA; **Sp-Sp** = two different species, either sister or closely related, occurring in NA and SA; **Sp-Cl** = a single species in the source region sister to a clade (of two or more species) in the recipient region; **Cl-Cl** = a clade sister to another clade. Taxa names in square brackets [] = synonym(s). (**Dist.**) = distribution: **AAD** = American amphitropical disjunct distribution generally well outside of tropical regions; **eN** = AAD distribution in eastern North America; **eS** = AAD distribution in eastern South America; **eNS** = AAD distribution in eastern North America and eastern South America; **tN** = trans-North America, distribution significantly entering North American tropical zone; **tS** = trans-South America, distribution significantly entering South American tropical zone; **tNS** = trans-North and South America, distribution significantly entering North American and South American tropical zones; \* = native distribution also occurring outside the western hemisphere. **C#-NA** = chromosome number of North American taxon; **C#-SA** = chromosome number of South American taxon, number in curly brackets {} = source for chromosome counts (key at bottom of table). **Dur.-Hab.** = plant duration, **A** = annual, **B** = biennial, **P** = perennial, or a combination; plant habit, **H** = herb, **S** = shrub, **T** = tree, or a combination, with differences between NA and SA indicated by "/". **Disp. dir.** = direction of dispersal from source area to recipient area as determined from phylogenetic studies; either **N→S** (NA to SA), **S→N** (SA to NA), or **Equiv** = equivocal. **Div. Ma** = mean time of divergence (mean ranges in parentheses) of NA and SA taxa/clades, either stated in or calculated from (\*) literature sources. **Phyl./Tax. Lit. Source** = source of phylogenetic or pertinent taxonomic studies, including those citing direction or time of divergence. "—" = missing information.

GROUP / Family/Genus	Tax./(Dist.)	AAD Taxon/Clade-NA	C#-NA	AAD Taxon/Clade-SA	C#-SA	Dur.-Hab.	Disp. dir.	Div. Ma (mean range)	Phyl./Tax. Lit. source
<b>GNETALES</b>									
<b>Ephedraceae</b>									
<b>Ephedra</b>									
	<b>Cl-Cl (tS)</b>	Two NA CLADES: <i>Ephedra nevadensis</i> S.Watson, <i>Ephedra pedunculata</i> Engelm. ex S.Watson, <i>Ephedra torreyana</i> S.Watson, <i>Ephedra trifurca</i> Torr. ex S.Watson, <i>Ephedra viridis</i> Coville + <i>Ephedra antisiphilitica</i> Berland. ex C.A.Mey., <i>Ephedra aspera</i> Engelm. ex S.Watson, <i>Ephedra californica</i> S.Watson, <i>Ephedra compacta</i> Rose, <i>Ephedra coryi</i> E.L.Reed, <i>Ephedra cutleri</i> Peebles, <i>Ephedra fasciculata</i> A.Nelson, <i>Ephedra funerea</i> Coville & C.V.Morton	2n = 28 <b>{7}</b>	Two SA CLADES: <i>Ephedra multiflora</i> Phil. ex Stapf, <i>Ephedra ochreate</i> Miers, <i>Ephedra rupestris</i> Benth., <i>Ephedra triandra</i> Tul., <i>Ephedra tweediana</i> C.A.Mey. + <i>Ephedra americana</i> Humb. & Bonpl. ex Willd., <i>Ephedra andina</i> Poepp. ex C.A.Mey. [ <i>Ephedra chilensis</i> C.Presl], <i>Ephedra boelckei</i> F.A.Roig, <i>Ephedra breana</i> Phil., <i>Ephedra chilensis</i> C.Presl, <i>Ephedra frustillata</i> Miers, <i>Ephedra gracilis</i> Phil.	—	<b>P-S</b>	<b>Equiv</b>	<b>24.78</b> (8.84–41.53)	Ickert-Bond et al., 2009
<b>MONOCOTS</b>									
<b>Poaceae</b>									
<b>Blepharidachne</b>									
	<b>Sp-Sp (AAD)</b>	<i>Blepharidachne kingii</i> (S.Watson) Hack.	2n = 14 <b>{27}</b>	<i>Blepharidachne benthamiana</i> Hitchc.	2n = 14 <b>{27}</b>	<b>P-H</b>	<b>N→S</b>	<b>1.2</b>	Amarilla et al., 2015
<b>Bothriochloa</b>									
	<b>Sp (eNS)</b>	<i>Bothriochloa exaristata</i> (Nash) Henrard [ <i>Andropogon exaristatus</i> (Nash) Hitchc.]	2n = 60 <b>{1}</b>	"	—	<b>P-H</b>			Allred and Gould, 1983
	<b>Sp-InC (eNS/tN)</b>	<i>Bothriochloa laguroides</i> (DC.) Herter subsp. <i>laguroides</i>	2n = 60 <b>{1}</b>	"	—	<b>P-H</b>			Allred and Gould, 1983

continued



## APPENDIX 2, Continued

GROUP / Family/Genus	Tax. (Dist.)	AAD Taxon/Clade-NA	C#-NA	AAD Taxon/Clade-SA	C#-SA	Dur.-Hab.	Disp. dir.	Div. Ma (mean range)	Phyl./Tax. Lit. source
	<b>Sp-InC (eNS)</b>	<i>Bothriochloa lagurooides</i> (DC.) Herter subsp. <i>torreyana</i> (Steud.) Allred & Gould	2n = 60 {1}	"	—	<b>P-H</b>			Allred and Gould, 1983
<b>Bouteloua</b>	<b>Sp (tS)</b>	<i>Bouteloua simplex</i> Lag. [ <i>Chondrosium simplex</i> (Lag.) Kunth]	—	"	—	<b>A-H</b>			
<b>Cottea</b>	<b>Sp (tS)</b>	<i>Cottea pappophoroides</i> Kunth	—	"	—	<b>AP-H</b>			
<b>Disakisperma</b>	<b>Sp (AAD)</b>	<i>Disakisperma dubium</i> (Kunth) P.M. Peterson & N. Snow [Leptochloa <i>dubia</i> (Kunth) Nees]	—	"	—	<b>P-H</b>			
<b>Dissanthelium</b>	<b>Sp (AAD)</b>	<i>Dissanthelium calycinum</i> (J.Presl) Hitchc. [ <i>Poa</i> <i>calycina</i> (J.Presl) Kunth]	—	"	—	<b>?</b>			
<b>Enneapogon</b>	<b>Sp (AAD*)</b>	<i>Enneapogon desvauxii</i> P.Beauv.	—	"	—	<b>P-H</b>			
<b>Erioneuron</b>	<b>Sp (AAD)</b>	<i>Erioneuron avenaceum</i> (Kunth) Tateoka [ <i>Erioneuron avenaceum</i> var. <i>kurtzianum</i> (Parodi) Anton, <i>Erioneuron</i> <i>avenaceum</i> var. <i>longiflume</i> (Parodi) Anton, <i>Erioneuron</i> <i>avenaceum</i> var. <i>pygmaeum</i> (Hack.) Anton]	—	"	—	<b>P-H</b>			
<b>Lycurus</b>	<b>Sp (tS)</b>	<i>Lycurus phleoides</i> Kunth [ <i>Muhlenbergia</i> <i>phleoides</i> (Kunth) J.T.Columbus]	—	"	—	<b>P-H</b>			
<b>Muhlenbergia</b>	<b>Sp (AAD)</b>	<i>Muhlenbergia</i> <i>alopeurooides</i> (Griseb.) P.M. Peterson & Columbus [ <i>Lycurus</i> <i>alopeurooides</i> Griseb., <i>L. serosus</i> (Nutt.) C. Reeder]	—	"	—	<b>P-H</b>			
<b>Munroa</b>	<b>Sp-CI (AAD)</b>	<i>Munroa pulchella</i> (Kunth) Amarilla [ <i>Dasychloa p.</i> (Kunth) Willd. ex Rydb.]	2n = 16 {2}	CLADE of <i>Munroa</i> <i>andina</i> Phil.,	2n = 16 {2}	<b>P-H/A-H</b>	<b>N→S</b>	<b>7.2</b> (6.5–8.2)	Amarilla et al., 2015
		<i>Munroa argentina</i> Griseb., <i>Munroa decumbens</i> Phil., <i>Munroa mendocina</i> Phil.,	2n = 16 {2} 2n = 16 {2} 2n = 16 {2}						

continued

APPENDIX 2, Continued

GROUP / Family/Genus	Tax./Dist.)	AAD Taxon/Clade-NA	C#-NA	AAD Taxon/Clade-SA	C#-SA	Dur.-Hab.	Disp. dir.	Div. Ma (mean range)	Phyl./Tax. Lit. source
<b>Pappophorum</b>	<b>Sp-Sp (AAD)</b>	<i>Munroa squarrosa</i> (Nutt.) Torr.	2n = 16 {2}	+ <i>Munroa squarrosa</i> (Nutt.) Torr.	2n = 16 {2}				
	<b>Sp (eS/tNS)</b>	<i>Pappophorum vaginatum</i> Buckley [Pappophorum mucronulatum Nees]	—	"	—	<b>P-H</b>	<b>S→N</b>	<b>1.8</b> (0.8–2)	Amarilla et al., 2015
	<b>Sp (AAD)</b>	<i>Scleropogon brevifolius</i> Phil.	—	"	—	<b>P-H</b>			
	<b>Sp (tNS)</b>	<i>Trichloris pluriflora</i> E.Fourn.	—	"	—	<b>P-H</b>			
	<b>Sp-InD (AAD)</b>	<i>Willkommia texana</i> Hitchc. var. <i>texana</i>	—	<i>Willkommia texana</i> var. <i>stolonifera</i> Parodi [ <i>Wilblebia stolonifera</i> (Parodi) Herter]	—	<b>P-H</b>			
<b>EUDICOTS</b>									
<b>Asteraceae</b>									
<b>Grindelia</b>	<b>Cl-CI (AAD)</b>	CLADE of at least 31 species of NA <i>Grindelia</i>	2n = 12, 24 [2x, 4x] {21}	CLADE of at least 17 SA <i>Grindelia</i> species	2n = 12, 24, 36 [2x, 4x, 6x] {21}		<b>N→S?</b>		Moore et al., 2012
	<b>Sp (AAD)</b>	<i>Picradeniopsis multiflora</i> (Hook. & Arn.) B.G.Baldwin [ <i>Schuhria multiflora</i> Hook. & Arn.]	—	"	2n = 22, 24 {34; 29}	<b>A-H</b>			
<b>Boraginaceae</b>	<b>Cryptantha</b>	<b>Sp (AAD)</b>	—	"	—	<b>A-H</b>	<b>N→S</b>	<b>2.45</b>	Guilliams et al., 2017
		<b>Cl-CI (AAD)</b>	CLADE of <i>Cryptantha albidia</i> (Kunth) I.M.Johnst. + <i>C. mexicana</i> I.M.Johnst.	—	CLADE of <i>Cryptantha albidia</i> (Kunth) I.M.Johnst. + <i>C. mexicana</i> I.M.Johnst.	<b>A-H</b>	<b>N→S</b>	<b>6.01</b>	Guilliams et al., 2017
		<b>Sp-InC (AAD)</b>	<i>Cryptantha maritima</i> (Greene) Greene var. <i>pilosa</i> I.M.Johnst. + <i>Johnstonella diplotricha</i> (Phil.) Reiche	—	+ <i>Johnstonella diplotricha</i> (Phil.) Hasenstab & M.G.Simpson [ <i>Cryptantha diplotricha</i> (Phil.) Reiche]	2n = 36 {15}	<b>A-H</b>	<b>N→S</b>	<b>0.92</b>
<b>Cl-Sp (AAD)</b>	CLADE of <i>Cryptantha maritima</i> (Greene) Greene + <i>Johnstonella echinosepala</i> (J.F.Macbride) Hasenstab & M.G.Simpson	—	<i>Cryptantha subamplexicaulis</i> (Phil.) Reiche	—	<b>A-H/P-H</b>	<b>N→S</b>	<b>5.53</b>	Guilliams et al., 2017	

continued

## APPENDIX 2, Continued

GROUP / Family/Genus	Tax. (Dist.)	AAD Taxon/Clade-NA	C#-NA	AAD Taxon/Clade-SA	C#-SA	Dur.-Hab.	Disp. dir.	Div. Ma (mean range)	Phyl./Tax. Lit. source
<b>Capparaceae</b> <i>Atamisquea</i>	<b>Sp</b> <b>(AAD)</b>	<i>Atamisquea emarginata</i> Miers ex Hook. & Am. [ <i>Capparis</i> <i>atamisquea</i> Kuntze]	2n = 16 {24}	"	2n = 16 {8}	<b>P-S</b>			
<b>Convolvulaceae</b> <i>Cressa</i>	<b>Sp</b> <b>(AAD)</b>	<i>Cressa nudicaulis</i> Griseb.	—	"	2n = 28 {4}	<b>P-H</b>			
<b>Evolvulus</b> <i>Evolvulus</i>	<b>Sp</b> <b>(AAD)</b>	<i>Evolvulus arizonicus</i> A.Gray	—	"	—	<b>P-H</b>			
<b>Ehretiaceae</b> <i>Tiquilia</i>	<b>Sp</b> <b>(AAD)</b>	<i>Tiquilia nuttallii</i> (Benth. ex Hook.) A.T.Richardson [ <i>Coldenia nuttallii</i> Benth. ex Hook.]	—	"	—	<b>A-H</b>	<b>N→S</b> <b>0.003</b>	Moore et al., 2006	
	<b>Sp-CI</b> <b>(ts)</b>	<i>Tiquilia cuspidata</i> (L.M.Johnst.) A.T.Richardson	—	CLADE of <i>Tiquilia darwinii</i> (Hook.f.) A.T.Richardson, <i>Tiquilia fusca</i> (Hook.f.) A.T.Richardson, <i>Tiquilia galapagoa</i> (J.T.Howell) A.T.Richardson, <i>Tiquilia nesiotica</i> (J.T.Howell) A.T.Richardson, + <i>Tiquilia paronychioides</i> (Phil.) A.T.Richardson	—	<b>P-H</b>	<b>N→S</b> <b>4.5</b> (3–6)	Moore et al., 2006	
	<b>Sp-CI</b> <b>(AAD)</b>	<i>Tiquilia palmeri</i> (A.Gray) A.T.Richardson	[2x] {20}	CLADE ("Blue-flowered group") of <i>Tiquilia</i> <i>atacamensis</i> (Phil.) A.T.Richardson, <i>Tiquilia conspicua</i> (L.M.Johnst.) A.T.Richardson, <i>Tiquilia dichotoma</i> (Ruiz & Pav.) Pers., <i>Tiquilia elongata</i> (Rusby) A.T.Richardson, <i>Tiquilia ferreyrae</i> (L.M.Johnst.) A.T.Richardson, <i>Tiquilia grandiflora</i> (Phil.) A.T.Richardson, <i>Tiquilia litoralis</i> (Phil.) A.T.Richardson, + <i>Tiquilia tacnensis</i> A.T.Richardson	[4x] {20; 30}	<b>P-H</b>	<b>N→S</b> <b>4.5</b> (3–6)	Moore et al., 2006	

continued



APPENDIX 2, Continued

GROUP / Family/Genus	Tax./Dist.)	AAD Taxon/Clade-NA	C#-NA	AAD Taxon/Clade-SA	C#-SA	Dur.-Hab.	Disp. dir.	Div. Ma (mean range)	Phyl./Tax. Lit. source
<b>Fabaceae</b>									
<b>Acaciella</b>	<b>Sp (tN)</b>	<i>Acaciella angustissima</i> (Mill.) Britton & Rose var. <i>angustissima</i> [ <i>Acacia angustissima</i> (Mill.) Kuntze var. <i>angustissima</i> ]	—	"	—	<b>P-H</b>			
<b>Errazurizia</b>	<b>Cl-Sp (AAD)</b>	CLADE of <i>Errazurizia benthamii</i> (Brandegee) I.M.Johnst. + <i>Errazurizia megacarpa</i> (S.Watson) I.M.Johnst. <i>Hoffmannseggia glauca</i> (Ortega) Eifert <i>Hoffmannseggia drummondii</i> Torr. & A.Gray [ <i>Caesalpinia drummondii</i> (Torr. & A.Gray) Fisher]	2n = 28 {28}	<i>Errazurizia multifoliolata</i> (Clos) I.M.Johnst.	—	<b>P-S</b>		McMahon, 2005	
<b>Hoffmannseggia</b>	<b>Sp (AAD)</b>	<i>Hoffmannseggia intricata</i> Brandegee, <i>Hoffmannseggia microphylla</i> Torr., + <i>Hoffmannseggia peninsularis</i> (Britton & Rose) Wiggins	—	"	2n = 24 {40}	<b>P-HSu</b>	<b>S→N</b>		Simpson et al., 2005
	<b>Sp-Sp (AAD)</b>	<i>Hoffmannseggia drummondii</i> Torr. & A.Gray [ <i>Caesalpinia drummondii</i> (Torr. & A.Gray) Fisher]	—	<i>Hoffmannseggia pumilio</i> (Griseb.) B.B.Simpson [ <i>Caesalpinia pumilio</i> Griseb.]	—	<b>P-SSu</b>	<b>S→N</b>		Simpson et al., 2005
	<b>Cl-CI (tS)</b>	CLADE of <i>Hoffmannseggia intricata</i> Brandegee, <i>Hoffmannseggia microphylla</i> Torr., + <i>Hoffmannseggia peninsularis</i> (Britton & Rose) Wiggins	—	CLADE of: <i>Hoffmannseggia pumilio</i> (Griseb.) B.B.Simpson, <i>Hoffmannseggia viscosa</i> Hook. & Arn., + <i>Hoffmannseggia drummondii</i> Torr. & A.Gray (NA)	—	<b>P-S</b>	<b>S→N</b>		Simpson et al., 2005
	<b>Cl-CI (AAD)</b>	CLADE of <i>Hoffmannseggia drepanocarpa</i> A.Gray, <i>Hoffmannseggia humilis</i> (M.Martens & Galeotti) Hemsl., <i>Hoffmannseggia oxycarpa</i> A.Gray, <i>Hoffmannseggia repens</i> (Eastw.) Cockerell, <i>Hoffmannseggia tenella</i> Tharp & L.O.Williams, + <i>Hoffmannseggia watsonii</i> (Fisher) Rose	—	CLADE of <i>Hoffmannseggia miranda</i> Sandwith, + <i>Hoffmannseggia prostrata</i> DC.	—	<b>P-H</b>	<b>S→N</b>		Simpson et al., 2005
<b>Prosopidastrum</b>	<b>Sp-Sp (AAD)</b>	<i>Prosopidastrum mexicanum</i> (Dressler) Burkart [ <i>Prosopis globosa</i> Gillies ex Hook. & Arn. var. <i>mexicana</i> Dressler]	—	<i>Prosopidastrum globosum</i> (Hook. & Arn.) Burkart [ <i>Prosopis globosa</i> Gillies ex Hook. & Arn.]	—	<b>P-T</b>			

continued

## APPENDIX 2, Continued

GROUP / Family/Genus	Tax. (Dist.)	AAD Taxon/Clade-NA	C#-NA	AAD Taxon/Clade-SA	C#-SA	Dur.-Hab.	Disp. dir.	Div. Ma (mean range)	Phyl./Tax. Lit. source
<b>Koerberliniaceae</b>									
<b>Koerberlinia</b>									
<b>Sp-Sp (AAD)</b>		<i>Koerberlinia spinosa</i> Zucc.	2n = 44, ca.88 {10}	<i>Koerberlinia holacantha</i> W.C.Holmes, K.L.Yip & A.E.Rushing	—	<b>P-ST</b>			
<b>Loasaceae</b>									
<b>Mentzelia</b>									
<b>Sp (AAD)</b>		<i>Mentzelia albescens</i> (Gillies ex Arn.) Griseb.	—	"	—	<b>P-H</b>	<b>N→S 0</b>		Schenk and Hufford, 2011
<b>Martyniaceae</b>									
<b>Proboscidea</b>									
<b>Sp (AAD)</b>		<i>Proboscidea althaeifolia</i> (Benth.) Decne.	—	"	—	<b>P-H</b>			
<b>Polemoniaceae</b>									
<b>Dayia</b>									
<b>Sp-Sp (AAD)</b>		<i>Dayia scabra</i> (Brandege) J.M.Porter [ <i>Gilia scabra</i> Brandege]	2n = 18 {25}	<i>Dayia glutinosa</i> (Phil.) J.M.Porter [ <i>Gilia glutinosa</i> Phil., <i>Bryantiella glutinosa</i> (Phil.) J.M.Porter; <i>Bryantiella glutinosa</i> (Phil.) J.M.Porter]	—	<b>A-H</b>	<b>N→S</b>	14.42 (12.84–16.41)	Porter and Cuéller, cited in Johnson and Porter, 2017
<b>Giliastrum</b>									
<b>Sp-CI (AAD)</b>		<i>Giliastrum incisum</i> (Benth.) J.M.Porter [ <i>Gilia incisum</i> Benth.]	2n = 18 {35}	CLADE of <i>Giliastrum castellanosii</i> J.M.Porter [ <i>Gilia castellanosii</i> (J.M.Porter) V.E.Grant] + <i>Giliastrum foetidum</i> (Gillies) 2n = 18 {12} ex Benth. J.M.Porter [ <i>Gilia foetida</i> Gillies ex Benth.]	—	<b>P-H</b>	<b>N→S</b>	14.5 (4.8–19.4)	Johnson and Porter, 2017
<b>Solanaceae</b>									
<b>Lycium</b>									
<b>CI-Sp (tNS)</b>		<i>Lycium californicum</i> Nutt. ex A.Gray	2n = 24, 36, 48 {6}	CLADE of <i>Lycium nodosum</i> Miers + <i>Lycium vimineum</i> Miers	2n = 24 {3; 32}	<b>P-S</b>	<b>S→N</b>		Levin et al., 2007
<b>CI-CI (tS)</b>		CLADE of <i>Lycium berlandieri</i> Dun. + <i>Lycium exsertum</i> A.Gray + <i>Lycium fremontii</i> A.Gray, 120 {6}	2n = 24 {6}	CLADE of <i>Lycium americanum</i> Jacq. + <i>Lycium infaustum</i> Miers	2n = 24 {3}	<b>P-S</b>	<b>S→N</b>		Levin et al., 2007
<b>CI-CI (eN)</b>		<i>Lycium parishii</i> A.Gray, <i>Lycium texanum</i> Correll, + <i>Lycium torreyi</i> A.Gray	2n = 24 {6}	CLADE of <i>Lycium brevipes</i> Benth. + <i>Lycium carolinianum</i> Walter	2n = 24 {6}	<b>P-S</b>	<b>Equiv</b>		Levin et al., 2007
<b>Verbenaceae</b>									
<b>Aloysia</b>									
<b>CI-CI (AAD?)</b>		CLADE of <i>Aloysia macrostachya</i> (Torr.) Moldenke + <i>A. wrightii</i> A.Heller	—	CLADE of 19 spp. of <i>Aloysia</i> , common ancestor SA	—	<b>P-S</b>	<b>S→N</b>		Lu-Irving et al., 2014; Frost et al., 2017, this issue

continued

APPENDIX 2, Continued

GROUP / Family/Genus	Tax./Dist.)	Sp-InC (AAD)	AA Taxon/Clade-NA	C#-NA	AA Taxon/Clade-SA	C#-SA	Dur.-Hab.	Disp.dir.	Div. Ma (mean range)	Phyl./Tax. Lit. source
							P-S	S→N		
<b>Glandularia</b>	<i>Aloysia gratisissima</i> (Gillies & Hook. ex Hook.) Tronc. var. <i>g.</i> [Aloysia lycioides Cham.]									
	CLADE of <i>Glandularia</i> <i>bipinnatifida</i> (Schauer) Nutt., <i>Glandularia chiricahensis</i> Umber [Glandularia <i>bipinnatifida</i> var. <i>latilobata</i> (L.M.Perry) B.L.Turner], <i>Glandularia gooddingii</i> (Briq.) Solbrig var. <i>gooddingii</i> , <i>Glandularia verecunda</i> Umber, + <i>Glandularia wrightii</i> (A.Gray) Umber [ <i>Glandularia</i> <i>bipinnatifida</i> (Nutt.) Nutt. var. <i>ciliata</i> (Benth.) B.L.Turner]	2n = 30 {33}	CLADE of <i>Glandularia</i> <i>aurantiaca</i> (Speg.) Botta,	[2x] {39}		AP-H	S→N		Frost et al., 2017, this issue	
		2n = 20 [4x]	<i>Glandularia araucana</i> (Phil.) Botta,	[2x] {39}						
		2n = 20 [4x]	<i>Glandularia flava</i> (Gillies & Hook.) Schnack & Covas, <i>Glandularia microphylla</i> (Kunth) Cabrera, <i>Glandularia parodi</i> Covas & Schnack,	[2x] {39}						
		2n = 20 [4x]		[2x] {39}						
		2n = 20 [4x]		[2x] {39}						
		2n = 20 [4x]		[2x] {39}						
		2n = 20 [4x]		[2x] {39}						
		2n = 20 [4x]		[2x] {39}						
		2n = 20 [4x]		[2x] {39}						
<b>Verbena</b>	CLADE of 15 NA species: <i>Verbena bracteata</i> Cav. ex Lag. & Rodr., <i>Verbena californica</i> Moldenke, <i>Verbena canescens</i> Kunth, <i>Verbena carnea</i> Medik., [ <i>Stylodon carneus</i> (Medik.) Moldenke] <i>Verbena halei</i> Small, <i>Verbena hastata</i> L.,	2n = 14 {18}; 38		<i>Glandularia sulphurea</i> (DDon) Schnack & Covas, <i>Glandularia tenera</i> (Spreng.) Cabrera, + <i>Glandularia venturii</i> (Moldenke) Botta CLADE of 11 <i>Verbena</i> species: <i>Verbena alata</i> Otto ex Sweet or <i>V. alata</i> Cham., <i>Verbena bonariensis</i> L., [ <i>Juniella tridactylites</i> (Lag.) Moldenke] <i>Verbena demissa</i> Moldenke, <i>Verbena glabrata</i> Kunth, <i>Verbena hispida</i> Ruiz & Pav., <i>Verbena intermedia</i> Gillies & Hook. ex Hook.,			ABP-H	S→N		Frost et al., 2017, this issue

continued



## APPENDIX 2,

Continued

GROUP / Family/Genus	Tax. (Dist.)	AAD Taxon/Clade-NA	C#-NA	AAD Taxon/Clade-SA	C#-SA	Dur.-Hab.	Disp. dir.	Div. Ma (mean range)	Phyl./Tax. Lit. source
	<i>Verbena hirtella</i> (L.M.Perry) G.L.Nesom, [ <i>V. neomexicana</i> (A.Gray) Briq. var. <i>hirtella</i> L.M.Perry]		—	<i>Verbena litoralis</i> Kunth,	—				
	<i>Verbena lasiostachys</i> Link,		—	<i>Verbena montevidensis</i> Spreng.,	—				
	<i>Verbena macdougalii</i> A.Heller,		2n = 14 {37}	<i>Verbena rigida</i> Spreng.,	2n = 42 {11}				
	<i>Verbena mentifolia</i> Benth.,		—	<i>Verbena scabra</i> Vahl, [ <i>V. rigida</i> Spreng.]	—				
	<i>Verbena officinalis</i> L.,		2n = 14, 28 {19}	+ <i>Verbena sedula</i> Moldenke [ <i>Verbena litoralis</i> Kunth]	—				
	<i>Verbena orcuttiana</i> L.M.Perry [V. <i>simplex</i> Lehm. var. <i>orcuttiana</i> (L.M.Perry) N.O'Leary]		—						
	<i>Verbena perennis</i> Wootton,		2n = 14 {38}						
	<i>Verbena urticifolia</i> L., + <i>Verbena</i> <i>valerianoides</i> Kunth		2n = 14, 16 {9}						
<b>Zygophyllaceae</b>									
<b>Fagonia</b>									
<b>Sp-Sp (AAD)</b>	<i>Fagonia villosa</i> D.M.Porter		—	<i>Fagonia chilensis</i> Hook. & Arn.	—		<b>P-S</b>	<b>N→S</b>	1.22*
<b>Sp-Sp (AAD)</b>	<i>Larrea tridentata</i> (DC.) Coville		2n = 26, 52, 78 [2x, 4x, 6x] {14}	<i>Larrea divaricata</i> Cav.	2n = 26 [2x] {14}		<b>P-S</b>	<b>S→N</b>	6.3 (4.2–8.4)
									Beier et al., 2004 Lia et al., 2001

Key to citations of chromosome numbers: {1} = Allred and Gould, 1983; {2} = Amarilla et al., 2015; {3} = Bernardello, 1982; {4} = Bernardello, et al., 1990; {5} = Chaw et al., 1986; {6} = Chiang, 1982; {7} = Choudhry, 1984; {8} = Covas and Schnack, 1946; {9} = Gervais et al., 1997; {10} = Goldblatt, 1977; {11} = Hanson et al., 2005; {12} = Johnson and Porter, 2017; {13} = Kumar and Dutt, 1989; {14} = Laport et al., 2012; {15} = Las Peñas, 2003; {16} = Las Peñas, 2005; {17} = Leitch et al., 2001; {18} = Löve, 1982b; {19} = Löve, 1982c; {20} = Moore et al., 2006; {21} = Moore et al., 2012; {22} = Nakata and Oginuma, 1989; {23} = Ohri and Khoshoo, 1986; {24} = Pinkava et al., 1992; {25} = Porter, 1996; {26} = Rattenbury, 1959; {27} = Reeder and Reeder, 1973; {28} = Reveal and Moran, 1977; {29} = Robinson et al., 1981; {30} = Soltis et al., 2014; {31} = Stiefkens and Bernardello, 2000; {32} = Stiefkens and Bernardello, 2002; {33} = Turner and Powell, 2005; {34} = Turner et al., 1979; {35} = Turner, 1994; {36} = Umber, 1979; {37} = Ward and Spellenberg, 1988; {38} = Ward, 1984; {39} = Yuan and Olmstead, 2008; {40} = Zanin and Cangiano, 2001.

**APPENDIX 3**

Vascular plants with a native, temperate American amphitropical disjunct (AAD) distribution. **Tax.** = taxonomic unit of comparison: **Sp** = single species (conspecifics) occurring in both North America (NA) and South America (SA); **Sp-InC** = the same two infraspecies (coninfraspecifics) occurring in both NA and SA; **Sp-IND** = two different infraspecies (varieties or subspecies) occurring in both NA and SA; **Sp-Sp** = two different species, either sister- or closely related, occurring in NA and SA; **Sp-Cl** = a single species in the source region sister to a clade (of two or more species) in the recipient region; **Cl-Sp** = a clade (of two or more species) in the source region sister to a single species in the recipient region; **Cl-Cl** = a clade sister to another clade. Taxa in square brackets [] = synonym(s). **(Dist.)** = distribution: **AAD** = American amphitropical disjunct distribution generally well outside of tropical regions; **eN** = AAD distribution in eastern North America; **eS** = AAD distribution in eastern South America; **eNS** = AAD distribution in eastern North America and eastern South America; **ewN** = AAD distribution in eastern and western North America; **tN** = trans-North America, distribution significantly entering North American tropical zone; **tS** = trans-South America, distribution significantly entering South American tropical zone; **tNS** = trans-North and South America, distribution significantly entering North American and South American tropical zones; \* = native distribution also occurring outside the western hemisphere. **C#-NA** = chromosome number of North American taxon; **C#-SA** = chromosome number of South American taxon. {} = literature citation for chromosome counts (key at bottom of table). **Dur.-Hab.** = plant duration. **A** = annual, **B** = biennial, **P** = perennial, or a combination; plant habit, **H** = herb, **S** = shrub, **T** = tree, **V** = vine, or a combination, with differences between NA and SA indicated by "/". **Disp. dir.** = direction of dispersal from source area to recipient area as determined from phylogenetic studies, either **N→S** (NA to SA), **S→N** (SA to NA), or **Equiv** = equivocal. **Div. Ma** = mean time of divergence (mean ranges in parentheses) of NA and SA taxa/clades, either stated in or calculated from (\*) literature sources. **Phyl./Tax. Lit. source** = Literature source of phylogenetic or pertinent taxonomic studies, including those citing direction or time of divergence. "—" = missing information.

GROUP / Family / Genus	Tax. / (Dist.)	AAD taxon / Clade-NA	C#-NA	AAD taxon / Clade-SA	C#-SA	Dur.-Hab.	Disp. dir.	Div. Ma	Phyl./Tax. Lit. source
<b>FERNS</b>									
<b>Pteridaceae</b>									
<i>Pellaea</i>	<b>Sp-Sp (AAD)</b>	<i>Pellaea andromedifolia</i> (Kaulf.) Fée	2n = 58 {110}	<i>Pellaea myrtilifolia</i> Mett. ex Kuhn	—	P-H			
<i>Polystichum</i>	<b>Sp-Sp (AAD)</b>	<i>Polystichum lemmonii</i> Underw.	2n = 82 {97}	<i>Polystichum mohrioides</i> (Bory) Presl	—	P-H			
<b>MONOCOTS</b>									
<b>Cyperaceae</b>									
<b>Amphiscirpus</b>									
<i>Amphiscirpus</i>	<b>Sp (AAD)</b>	<i>Amphiscirpus nevadensis</i> (S.Watson) Oteng-Yeb. [ <i>Scirpus nevadensis</i> S.Watson]	—	"	—	P-H			
<i>Bolboschoenus</i>	<b>Sp-IND (tNS*)</b>	<i>Bolboschoenus maritimus</i> (L.) Palla [ <i>Scirpus maritimus</i> L.]	2n = 104 {56}	<i>Bolboschoenus maritimus</i> (L.) Palla subsp. <i>paludosus</i> (A.Nelson) T.Koyama	—	P-H			
<i>Carex</i>	<b>Sp (tS)</b>	<i>Carex praegracilis</i> W.Boott	2n = 60 {56}	"	—	P-H			
<i>Cyperus</i>	<b>Sp (AAD*)</b>	<i>Cyperus pseudocyperus</i> L.	2n = 66 {56}	"	—	P-H			
<i>Eleocharis</i>	<b>Sp (eN)</b>	<i>Cyperus cephalanthus</i> Torr. & Hook.	—	"	—	P-H			
<i>Eleocharis</i>	<b>Sp (AAD*)</b>	<i>Eleocharis pachycarpa</i> E.Desv.	—	"	—	P-H			
<i>Eleocharis</i>	<b>Sp (tNS)</b>	<i>Eleocharis exigua</i> (Kunth) Roem. & Schult. [ <i>Eleocharis radicans</i> (A.Dietr.) Kunth]	—	"	—	P-H			
<i>Schoenoplectus</i>	<b>Sp (tNS*)</b>	<i>Schoenoplectus tabernaemontani</i> (C.C.Gmel) Palla [ <i>Scirpus validus</i> Vahl]	2n = 42 {101}	"	—	P-H			
<i>Juncaceae</i>	<b>Sp (AAD*)</b>	<i>Juncus acutus</i> L.	2n = 48 {96}	"	—	P-H			
<i>Juncus</i>	<b>Sp (AAD)</b>	<i>Juncus lesueurii</i> Bol. [ <i>Juncus lescurii</i> Bol., orth. var.]	—	"	—	P-H			

continued

## APPENDIX 3, Continued

GROUP / Family / Genus	Tax./ (Dist.)	AAID taxon/Clade-NA	C#-NA	AAID taxon/Clade-SA	C#-SA	Dur.-Hab.	Disp. dir.	Div. Ma	Phyl./Tax. Lit. source
<b>Juncaginaceae</b>									
<b>Triglochin</b>									
	Sp (AAD*)	<i>Triglochin maritima</i> L. [ <i>Triglochin concinna</i> Burt. Davy var. <i>concinna</i> , <i>Triglochin concinna</i> var. <i>debilis</i> (M.E.Jones) J.T.Howell]	2n = 48 {58}	" [ <i>Triglochin concinna</i> var. <i>deserticola</i> (Phil.) J.T.Howell]	—	P-H			
<b>Poaceae</b>									
	Sp (AAD)	<i>Agrostis idahoensis</i> Nash.	—	"	—	P-H			
	Sp (AAD)	<i>Bromus berteroi</i> Colla [ <i>Bromus tirii</i> E.Desv. var. t.]	2n = 41 {87}	"	2n = 42 {87}	A-H			
	Sp (AAD)	<i>Danthonia californica</i> Bol. [ <i>Danthonia californica</i> Boland. var. <i>americana</i> (Scribn.) Hitchc; <i>Danthonia grandiflora</i> Phil., nom. illeg.]	2n = 36 [6x] {87}	"	—	P-H			
	Sp-Sp (AAD)	<i>Deschampsia danthonioides</i> (Trin.) Benth.	—	<i>Deschampsia monandra</i> Parodi [ <i>D. glauca</i> (E.Desv.) Parodi, hom. illeg.]	—	A-H/P-H			
	Sp AAD	<i>Deschampsia elongata</i> (Hook.) Munro ex Benth.	2n = 26 [4x] {87}	"	—	P-H			
	Sp (ewN)	<i>Festuca octoflora</i> Walter [ <i>Vulpia octoflora</i> (Walter) Rydb.]	2n = 14 {87}	"	2n = 14 {87}	A-H			
	Sp-CI (AAD)	<i>Hordeum brachyantherum</i> Nevski	2n = 28 {7; 76}	CLADE of <i>Hordeum chilense</i> Roem. & Schult., <i>Hordeum comosum</i> J.Presl, <i>Hordeum cordobense</i> Bothmer, <i>Hordeum erectifolium</i> Bothmer, <i>Hordeum euclaston</i> Steud., <i>Hordeum flexuosum</i> Steud., <i>Hordeum muticum</i> J.Presl, <i>Hordeum patagonicum</i> (Hauman) Covas, <i>Hordeum pubiflorum</i> Hook.f., <i>Hordeum intercedens</i> Nevski (NA), + <i>Hordeum pusillum</i> Nutt. (NA)	2n = 14 {9} 2n = 14 {55} 2n = 14 {55} 2n = 14 {9; 55} 2n = 14 {69} 2n = 14 {55} 2n = 14 {69} 2n = 14 {90}	P-H	N→S	3.73 (2.53–5.25)	Blattner, 2006
	Sp-Sp (AAD)	<i>Hordeum intercedens</i> Nevski	2n = 14 {76; 90}	<i>Hordeum euclaston</i> Steud.	2n = 14 {55; 69}	A-H	S→N	1.00 (0.42–1.60)	Blattner, 2006
	Sp-Sp (ewN)	<i>Hordeum pusillum</i> Nutt.	2n = 14 {76; 90}	<i>Hordeum erectifolium</i> Bothmer, N.Jacobsen & R.B.Jørg.	2n = 14 {10; 55}	A-H	S→N	1.27 (0.40–3.07)	Blattner, 2006

continued

APPENDIX 3, Continued

GROUP / Family / Genus	Tax. / (Dist.)	AAD taxon/Clade-NA	C#-NA	AAD taxon/Clade-SA	C#-SA	Dur.-Hab.	Disp. dir.	Div. Ma	Phyl./Tax. Lit. source
<b>Muhlenbergia</b>									
Sp (AAD)		<i>Muhlenbergia asperifolia</i> (Nees & Mey.) Parodi	2n = 20 {57}	"	—	P-H	N→S		Peterson and Ortiz-Diaz, 1998
Cl-Sp (tNS)		CLADE of <i>Muhlenbergia filiformis</i> (Thurb.) Rydb. + <i>Muhlenbergia vaginata</i> Swallen	2n = 18 {79; 81}	<i>Muhlenbergia caxamarcensis</i> Laegaard & Sánchez Vega	—	AP-H	N→S		Peterson and Ortiz-Diaz, 1998; Peterson et al., 2010
Sp-Sp (AAD)		<i>Muhlenbergia ligulata</i> (E.Fourn.) Scribn. & Merr. [ <i>Chaboissaea ligulata</i> E.Fourn.]	—	<i>Muhlenbergia atacamensis</i> Parodi [ <i>Chaboissaea atacamensis</i> (Parodi) P.M.Peterson & Annable]	—	P-H / A-H	N→S		Peterson and Ortiz-Diaz, 1998; Peterson et al., 2010
Cl-Sp (tNS)		CLADE of <i>Muhlenbergia dubia</i> E.Fourn., + <i>M. macroura</i> (Kunth) Hitchc. <i>Muhlenbergia paniculata</i> (Nutt.) Columbus [ <i>Schedonnardus paniculatus</i> (Nutt.) Trel.; <i>Muhlenbergia paniculata</i> (Nutt.) P.M.Peterson]	—	<i>Muhlenbergia angustata</i> (J.Presl) Kunth	—	P-H	N→S		Peterson and Ortiz-Diaz, 1998; Peterson et al., 2010
Sp (AAD)		<i>Muhlenbergia paniculata</i> (Nutt.) Columbus [ <i>Schedonnardus paniculatus</i> (Nutt.) Trel.; <i>Muhlenbergia paniculata</i> (Nutt.) P.M.Peterson]	2n = 30 {87}	"	—	P-H			Peterson and Ortiz-Diaz, 1998; Peterson et al., 2010
Sp-Sp (ewN/tS)		<i>Muhlenbergia richardsonis</i> (Trin.) Rydb.	2n = 40 {57}	<i>Muhlenbergia fastigiata</i> (J.Presl) Henrad	—	P-H	N→S		Peterson and Ortiz-Diaz, 1998; Peterson et al., 2010
Sp (ewN)		<i>Muhlenbergia schreberi</i> J.F.Gmel.	—	"	—	P-H	N→S		Peterson and Ortiz-Diaz, 1998; Peterson et al., 2010
Sp (AAD)		<i>Muhlenbergia torreyi</i> (Kunth) Hitchc. ex Bush	2n = 20, 21 {80}	"	—	P-H	N→S		Peterson and Ortiz-Diaz, 1998; Peterson et al., 2010
Sp-Sp (tNS)		<i>Muhlenbergia versicolor</i> Swallen	—	[ <i>Muhlenbergia gracillima</i> Torr.] <i>Muhlenbergia maxima</i> Laegaard & Sánchez Vega	—	P-H	N→S		Peterson and Ortiz-Diaz, 1998; Peterson et al., 2010
Sp-Sp (tS)		<i>Muhlenbergia viliflora</i> Hitchc. [ <i>Muhlenbergia viliflora</i> Hitchc. var. <i>villosa</i> (Swallen) Morden]	—	<i>Muhlenbergia</i> <i>palmirensis</i> Grignon & Laegaard	—	P-H	N→S		Peterson and Ortiz-Diaz, 1998; Peterson et al., 2010
Sp (AAD*)		<i>Phalaris angusta</i> Nees ex Trin.	2n = 14 {87}	"	2n = 14 {87}	A-H	Equiv 0.3* (0.27–0.33)		Voshell et al., 2011
Sp-Sp (eS)		<i>Phalaris lemmonii</i> Vasey	2n = 14 {87}	<i>Phalaris platensis</i> Henrad ex Heukels	2n = 14, 56 {87}	A-H	Equiv		Voshell et al., 2011
Sp-Sp (AAD*)		<i>Phippsia aligida</i> (Sol.) R.Br.	2n = 28 {87}	<i>Phippsia wilczekii</i> Hack.	—	P-H			
Sp-Sp (AAD)		<i>Poa douglasii</i> Nees	—	<i>Poa cumingii</i> Trin.	—	P-H			
Sp (AAD*)		<i>Poa secunda</i> J.Presl	2n = 42 {98}	"	—	P-H			
Sp (AAD)		<i>Poa stanantha</i> Trin.	—	"	—	P-H			

continued



## APPENDIX 3, Continued

GROUP / Family / Genus	Tax./ (Dist.)	AAID taxon/Clade-NA	C#-NA	AAID taxon/Clade-SA	C#-SA	Dur.-Hab.	Disp. dir.	Div. Ma	Phyl./Tax. Lit. source
<i>Stipa</i>	Sp (AAD)	<i>Stipa speciosa</i> Trin. & Rupr. [ <i>Achnatherum speciosum</i> (Trin. & Rupr.) Barkworth; <i>Jarava speciosa</i> (Trin. & Rupr.) Peñailillo; <i>Pappostipa speciosa</i> (Trin. & Rupr.) Romaschenko]	2n = 60, 62, 68 [6x] {87}	"	2n = 66 {87}	P-H			
<b>EUDICOTS</b>									
<b>Apiaceae</b>									
<i>Bowlesia</i>	Sp (AAD)	<i>Bowlesia incana</i> Ruiz & Pav.	—	[ <i>Bowlesia septentrionalis</i> J.M.Coult. & Rose]	2n = 32 [4x] {87}	A-H	S→N		Constance, 1963
<i>Daucus</i>	Sp (AAD)	<i>Daucus pusillus</i> Michx.	2n = 22 {5; 23}	"	2n = 22 {23}	A-H	1.5		Spalik et al., 2010
<i>Lilaeopsis</i>	Sp eN	<i>Lilaeopsis carolinensis</i> J.M.Coult. & Rose [ <i>Lilaeopsis attenuata</i> (Hook. & Arn.) Fernald]	—	"	2n = 22 {26}	P-H	0.4		Spalik et al., 2010
<i>Osmorhiza</i>	Sp-Sp (tS)	<i>Lilaeopsis occidentalis</i> J.M.Coult. & Rose	2n = 44 {23}	<i>Lilaeopsis macloviana</i> (Gand) A.W.Hill	—	P-H	0.65		Spalik et al., 2010
	Cl-Sp (AAD?)	Two polytomous CLADES of mostly NA <i>Osmorhiza</i> species	—	<i>Osmorhiza glabrata</i> Phil.	—	P-H	N→S	1.59*	Wen et al., 2002
	Sp (AAD)	<i>Osmorhiza berteroi</i> DC.	—	"	2n = 22 {23}	P-H	N→S	0	Constance, 1963; Wen et al., 2002
	Sp (AAD)	[ <i>O. chilensis</i> Hook. & Arn.]	2n = 44 {60}	"	2n = 22 {23; 71}	P-H	N→S	0	Constance, 1963; Wen et al., 2002
	Sp (AAD)	<i>Osmorhiza depauperata</i> Phil.	—	[ <i>Osmorhiza obtusa</i> (J.M.Coult. & Rose) Fernald]	—	P-H	N→S	1	Vargas et al., 1998
<i>Sanicula</i>	Sp (AAD)	<i>Sanicula crassicaulis</i> Poepp. ex DC.	2n = 32 [2x], 48 [4x], 64 [6x] {6}	"	—	PB-H	N→S	2	Vargas et al., 1998
	Sp (AAD)	<i>Sanicula graveolens</i> DC.	2n = 16 {87}	"	—	PB-H	N→S	2	Vargas et al., 1998
<b>Asteraceae</b>									
<i>Agoseris</i>	Sp-Sp (AAD)	<i>Agoseris heterophylla</i> (Nutt.) Greene	2n = 18 [2x], 2n = 36 [4x] {18}	<i>Agoseris coronopifolia</i> (d'Urv.) K.L.Chambers	2n = 18 [2x] {18}	A-H			
<i>Amblyopappus</i>	Sp (AAD)	<i>Amblyopappus pusillus</i> Hook. & Arn.	2n = 16 {87}	"	—	A-H			
<i>Ambrosia</i>	Sp (AAD)	<i>Ambrosia chamissonis</i> (Less.) Greene [ <i>Franseria bipinnatifida</i> (Less.) Nutt.]	2n = 36 {87}	"	2n = 36 {87}	P-H			
<i>Antennaria</i>	Cl-Sp (AAD)	CLADE of <i>Antennaria rosea</i> (D.C.Eaton) Greene subsp. <i>pulvinata</i> (Greene) R.J.Bayer [ <i>Antennaria straminea</i> Fern.] + <i>Antennaria umbrinella</i> Rydb.	2n = 28, 56 (Au.) {20}	<i>Antennaria chilensis</i> Remy [ <i>Antennaria magellanica</i> Sch.-Bip.]	2n = 56 [4x] {87}	P-H			
<i>Blennosperma</i>	Cl-Sp (AAD)	CLADE or possible hybrid parents of <i>Blennosperma bakeri</i> Heiser + <i>B. nanum</i> (Hook.) S.F.Blake	2n = 18 {77}	<i>Blennosperma chilense</i> Less.	2n = 32 {77}	A-H			Omduff, 1963

continued

APPENDIX 3, Continued

GROUP / Family / Genus	Tax. / (Dist.)	AAID taxon/Clade-NA	C#-NA	AAID taxon/Clade-SA	C#-SA	Dur.-Hab.	Disp. dir.	Div. Ma	Phyl./Tax. Lit. source
<b>Gamochoaeta</b>	<b>Sp (ewN*)</b>	<i>Gamochoaeta stagnalis</i> (LMJohnst.) Anderb. [ <i>Gamochoaeta falcata</i> (Lam.) Cabrera, <i>Gnaphalium calviceps</i> Fernald, <i>Gnaphalium stagnalis</i> (LMJohnst.) Anderb.]	—	—	—	A-H	—	—	—
<b>Lasthenia</b>	<b>Sp-Sp (AAD)</b>	<i>Lasthenia glaberrima</i> DC.	2n = 10 {87}	<i>Lasthenia kunthii</i> (Less.) Hook. & Arn.	2n = 10 {77}	A-H	—	—	Emery et al., 2012
<b>Madia</b>	<b>Sp (AAD*)</b>	<i>Madia sativa</i> Mol.	2n = 32 {87}	—	2n = 32 {48}	A-H	—	—	—
<b>Malacothrix</b>	<b>Sp (AAD)</b>	<i>Malacothrix clevelandii</i> A. Gray	2n = 14 {87}	—	—	A-H	—	—	—
<b>Microseris</b>	<b>Sp-Sp (AAD)</b>	<i>Microseris bigelovii</i> (A. Gray) Sch. Bip.	2n = 18 {2; 78}	<i>Microseris pygmaea</i> D. Don [ <i>Microseris brevipes</i> Phil.]	2n = 18 {78}	A-H / AP-H	N → S	1.00*	Lohwasser et al., 2004
<b>Perityle</b>	<b>Sp AAD</b>	<i>Perityle emoryi</i> Torr.	2n = 108 (102–112) {85; 102}	—	—	A-H	—	—	—
<b>Psilocarphus</b>	<b>Sp (AAD)</b>	<i>Psilocarphus brevissimus</i> Nutt.	—	—	—	A-H	—	—	—
<b>Sp-IND (AAD)</b>		<i>Psilocarphus tenellus</i> Nutt. var. <i>tenellus</i> [ <i>Psilocarphus tenellus</i> Nutt.]	—	<i>Psilocarphus tenellus</i> Nutt. var. <i>globiferus</i> (Bertero ex DC.) Morefeld [ <i>Psilocarphus berterii</i> LMJohnst.]	—	A-H	—	—	—
<b>Thelesperma</b>	<b>Sp (AAD)</b>	<i>Thelesperma megapotamicum</i> (Spreng.) Kuntze	2n = 22, 44 {51; 102; 109}	—	2n = 22 {87; 105}	P-H	—	—	—
<b>Boraginaceae</b>									
<b>Amsinckia</b>	<b>Sp (AAD)</b>	<i>Amsinckia tessellata</i> A. Gray	2n = 24 {88}	—	—	A-H	N → S	0.31	Guilliams, 2015
<b>Cryptantha</b>	<b>Sp-Sp (AAD)</b>	<i>Cryptantha minima</i> Ryd.	—	<i>Cryptantha mendocina</i> LMJohnst.	—	A-H	N → S	2.45	Guilliams et al., 2017
<b>CI-CI (AAD)</b>		CLADE of <i>Cryptantha</i> sec. <i>Krynitzkia</i> , at least 16 NA spp. plus at least 4 SA spp. (the <i>Globulifera</i> CLADE)	2n = 14, 20, 24, 56 {40; 54}	CLADE of at least 10 spp. of <i>Cryptantha</i> sec. <i>Geocarya</i> : <i>Cryptantha alfaifalis</i> (Phil.) LMJohnst., <i>Cryptantha alyssoides</i> (DC.) Reiche, <i>Cryptantha aspera</i> (Phil.) Grau,	2n = ca. 120 {40}	A-H / P-H	N → S	17.11	Guilliams et al., 2017
				<i>Cryptantha calycotricha</i> LMJohnst.,	2n = 64 {40}				

continued

## APPENDIX 3, Continued

GROUP / Family / Genus	Tax./ (Dist.)	AAID taxon/Clade-NA	C#-NA	AAID taxon/Clade-SA	C#-SA	Dur.-Hab.	Disp. dir.	Div. Ma	Phyl./Tax. Lit. source
				<i>Cryptantha capituliflora</i> (Clos) Reiche,	2n = 64 {53}				
				<i>Cryptantha cynoglossoides</i> (Phil.) IMJohnst.,	—				
				<i>Cryptantha glomerata</i> Lehmann ex G.Don subsp. <i>glomerata</i> ,	2n = 64, 120 {40}				
				<i>Cryptantha glomerulifera</i> (Phil.) IMJohnst.,	—				
				<i>Cryptantha gnaphalioides</i> (A.DC.) Reiche,	—				
				+ <i>Cryptantha kingii</i> (Phil.) Reiche	2n = 62 {40}				
				Globulifera CLADE of at least 4 spp. of SA <i>Cryptantha</i> sec. <i>Krynitzkia</i> : <i>Cryptantha</i> <i>diffusa</i> (Phil.) IMJohnst.,	2n = 14 {40}; 2n = 56 {54}	A-H	N→S	7.39	Guilliams et al., 2017
				<i>Cryptantha globulifera</i> (Clos) Reiche,	2n = 14 {40}				
				<i>Cryptantha peruviana</i> IMJohnst.,	—				
				<i>Cryptantha phaeceoides</i> (Clos) Reiche	—				
				"	2n = 24 [4x] {87}	A-H	N→S	0.33	Guilliams et al., 2017
<b>Greeneocharis</b>	<b>Sp-InC</b> <b>(AAD)</b>	<i>Greeneocharis circumscissa</i> (Hook. & Arn.) Rydberg var. <i>circumscissa</i>	2n = 24, 36 [4x, 6x] {66; 87}						
<b>Johnstonella</b>	<b>Sp-Sp</b> <b>(AAD)</b>	<i>Johnstonella angelica</i> (IMJohnst.) Hasenstab & M.G.Simpson	2n = 18 {95}	<i>Johnstonella parviflora</i> (Phil.) Hasenstab & M.G.Simpson	2n = 20 {40}	P-H/ A-H	N→S	3.38	Guilliams et al., 2017
<b>Lappula</b>	<b>Sp</b> <b>(AAD)</b>	<i>Lappula redowskii</i> (Hornem.) Greene	2n = 48 {61}	"	—	A-H	N→S		
<b>Pectocarya</b>	<b>Sp</b> <b>(AAD)</b>	<i>Pectocarya linearis</i> (Ruiz & Pav.) DC. subsp. <i>ferocula</i> (IMJohnst.) Thorne [ <i>Pectocarya ferocula</i> (IMJohnst.) Veno, ined.] <i>Pectocarya pusilla</i> (A. DC.) A.Gray	2n = 48 {106}	[ <i>Lappula patagonica</i> (Speg.) MacGloskie]	2n = 72 [6x] {41; 47; 106}	A-H	N→S	0.59	Guilliams et al., 2017
	<b>Sp</b> <b>(AAD)</b>		2n = 24 {106}	"	—	A-H	N→S	0.72	Guilliams, 2015

continued

APPENDIX 3, Continued

GROUP / Family / Genus	Tax. / (Dist.)	AAID taxon/Clade-NA	C#-NA	AAID taxon/Clade-SA	C#-SA	Dur.-Hab.	Disp. dir.	Div. Ma	Phyl./Tax. Lit. source
<b>Plagiobothrys</b>	<b>Sp-IND (AAD)</b>	<i>Plagiobothrys collinus</i> (Phil.) I.M.Johnst. var. <i>californicus</i> (A.Gray) Higgins, <i>Plagiobothrys collinus</i> var. <i>fulvescens</i> (I.M.Johnst.) Higgins, <i>Plagiobothrys collinus</i> var. <i>gracilis</i> (I.M.Johnst.) Higgins, <i>Plagiobothrys collinus</i> var. <i>ursinus</i> (A.Gray) Higgins + possibly nested with <i>Plagiobothrys pringlei</i> Greene	—	<i>Plagiobothrys collinus</i> (Phil.) I.M.Johnst. var. <i>collinus</i>	2n = 24 {41; 47}	A-H	N→S	1.48	Guilliams et al., 2017
	<b>Sp-IND (AAD)</b>	<i>Plagiobothrys fulvus</i> (Hook. & Arn.) I.M.Johnst. var. <i>campestris</i> (Greene) I.M.Johnst.	—	<i>Plagiobothrys fulvus</i> (Hook. and Arn.) I.M.Johnst. var. <i>fulvus</i>	2n = 24 {41; 47}	A-H	N→S	0.3 (0.038–0.66)	Guilliams, 2015, 2017
	<b>Sp-Sp (AAD)</b>	<i>Plagiobothrys greenei</i> (A.Gray) I.M.Johnst.	—	<i>Plagiobothrys gracilis</i> (Ruiz & Pav.) I.M.Johnst.	2n = 36 [3x] {47}	A-H	N→S	0.97	Guilliams et al., 2017
	<b>Cl-Sp (AAD)</b>	CLADE of <i>Plagiobothrys greenei</i> (A.Gray) I.M.Johnst. + <i>Plagiobothrys gracilis</i> (Ruiz & Pav.) I.M.Johnst.	—	<i>Plagiobothrys polycaulis</i> (Phil.) I.M.Johnst.	2n = 24 {41; 47}	A-H	Equip	1.37	Guilliams et al., 2017
	<b>Sp-CI (t57)</b>	<i>Plagiobothrys mollis</i> (A.Gray) I.M.Johnst.	—	CLADE of <i>Plagiobothrys congestus</i> (Wedd.) I.M.Johnst. + <i>Plagiobothrys limifolius</i> (Lehm.) I.M.Johnst.	2n = 24 {47}	A-H	N→S	1.45	Guilliams et al., 2017
	<b>Sp (AAD)</b>	<i>Plagiobothrys myosotoides</i> (Lehm.) Brand [ <i>Plagiobothrys verrucosus</i> (Phil.) I.M.Johnst.]	—	"	2n = 24 {41; 47}	A-H	N→S	0.72	Guilliams, 2015
	<b>Sp (AAD)</b>	<i>Lepidium nitidum</i> Nutt.	—	"	—	A-H			
	<b>Sp-Sp (AAD)</b>	MEMBER of complex of <i>Noccaea fendleri</i> (A.Gray) Holub (& subsp.), <i>Noccaea arctica</i> (A.E.Porsild) Holub, and <i>Noccaea mexicana</i> (Standl.) Holub [ <i>Thlaspi montanum</i> L.; <i>Noccaea montana</i> (L.) F.K.Mey., in part]	2n = 14 [2x] {24; 46}	"	2n = 14 [2x] {24; 46}	BP-H		0*	Koch and Al-Shehbaz, 2004
	<b>Sp-Sp (AAD)</b>	<i>Rorippa curvisiliqua</i> (Hook.) Bessey ex Britton	—	"	2n = 44 {11}	A-H	Equip	0.5*	Bleeker et al., 2002
	<b>Sp (AAD)</b>	<i>Downingia pusilla</i> (G.Don ex A.D.C.) Torr. [ <i>Downingia humilis</i> (Greene) Rattan]	2n = 22 {87}	"	—	A-H			
<b>Sp-Sp (AAD)</b>	<i>Legenere limosa</i> (Greene) McVaugh [ <i>Howellia limosa</i> Greene]	—	"	—	A-H				

continued



## APPENDIX 3, Continued

GROUP / Family / Genus	Tax. / (Dist.)	AAID taxon/Clade-NA	C#-NA	AAID taxon/Clade-SA	C#-SA	Dur.-Hab.	Disp. dir.	Div. Ma	Phyl./Tax. Lit. source
<b>Caryophyllaceae</b>									
<b>Cardionema</b>	<b>Sp (tS)</b>	<i>Cardionema ramosissima</i> (Weinm.) A.Nels. & J.F.Macbr.	—	"	—	<b>P-H</b>			
<b>Mononeuria</b>	<b>Sp (eN)</b>	<i>Mononeuria groenlandica</i> (Retz.) Dillenb. & Kadereit [ <i>Avenaria groenlandica</i> (Retz.) Spreng, <i>Minuartia groenlandica</i> (Retz.) Ostenf., <i>Stellaria groenlandica</i> Retz.]	—	"	—	<b>P-H</b>			
<b>Celastraceae</b>									
<b>Lepuropetalon</b>	<b>Sp (eN)</b>	<i>Lepuropetalon spathulatum</i> (Muhl.) Ell.	2n = 46 { <b>36</b> }	"	—	<b>AP-H</b>			
<b>Chenopodiaceae</b>									
<b>Atriplex</b>	<b>Cl-CI (AAD?)</b>	CLADE of <i>Atriplex acanthocarpa</i> (Torr.) S.Watson, <i>Atriplex canescens</i> (Pursh) Nutt., <i>Atriplex gardneri</i> Aiton, <i>Atriplex leucophylla</i> (Moq.) D.Dietr., <i>Atriplex obovata</i> Moq., <i>Atriplex parishii</i> S.Watson, <i>Atriplex phyllostegia</i> (Torr.) ex S.Watson) S.Watson, <i>Atriplex polycarpa</i> (Torr.) S.Watson, <i>Atriplex powellii</i> S.Watson, <i>Atriplex serenana</i> A.Nelson ex Abrams <i>Chenopodium berlandieri</i> Moq.	2n = 18 { <b>89</b> } 2n = 18, 36, 54 { <b>29</b> } — 2n = 36 { <b>32; 75</b> } 2n = 18 { <b>89</b> }	CLADE of <i>Atriplex cordobensis</i> Gand. & Stuck., <i>Atriplex deserticola</i> Phil., <i>Atriplex imbricata</i> (Moq.) D.Dietr., <i>Atriplex lampa</i> (Moq.) ex Small [A. <i>lampa</i> (Moq.) D.Dietr.] <i>Atriplex patagonica</i> (Moq.) D.Dietr., <i>Atriplex parvifolia</i> Kunth, [Atriplex <i>muricata</i> Humb. & Bonpl. ex Willd.] <i>Atriplex rusbyi</i> Britton, + <i>Atriplex undulata</i> (Moq.) D.Dietr.	2n = 36 { <b>25</b> } — — 2n = 18 { <b>25</b> } — —		<b>N→S</b>	7.72 (4.52–11.08)	Kadereit et al., 2010
<b>Chenopodium</b>	<b>Sp-Sp (tN)</b>	<i>Chenopodium berlandieri</i> Moq.	2n = 36 [4x] { <b>65; 108</b> }	<i>Chenopodium hircinum</i> Schrad.	[4x] { <b>108</b> }	<b>A-H</b>			Walsh et al., 2015
<b>Cistaceae</b>									
<b>Crocanthemum</b>	<b>Sp-Sp (AAD)</b>	<i>Crocanthemum scoparium</i> (Nutt.) Millsp. [ <i>Helianthemum scoparium</i> Nutt.]	—	<i>Crocanthemum brasiliense</i> (Lam.) Spach [ <i>Crocanthemum spartioides</i> (C.Presl) Janch.; <i>Helianthemum spartioides</i> C.Presl]	—	<b>P-H</b>			
<b>Convolvulaceae</b>									
<b>Calystegia</b>	<b>Sp (AAD*)</b>	<i>Calystegia soldanella</i> (L.) R.Br. [ <i>Convolvulus soldanella</i> L.]	—	"	—	<b>P-H</b>			

continued

## APPENDIX 3, Continued

GROUP / Family / Genus	Tax. / (Dist.)	AAID taxon / Clade-NA	C#-NA	AAID taxon / Clade-SA	C#-SA	Dur.-Hab.	Disp. dir.	Div. Ma	Phyl./Tax. Lit. source
<b>Dichondra</b>									
	Sp (AAD)	<i>Dichondra argentea</i> Humb. & Bonpl. ex Willd.	—	"	—	P-H			
	Sp (tNS)	<i>Dichondra sericea</i> Sw.	—	"	—	P-H			
<b>Crassulaceae</b>									
<b>Crassula</b>	Sp (tS)	<i>Crassula connata</i> (Ruiz & Pav.) A. Berger [ <i>Crassula erecta</i> (Hook & Arn.) Berger]	2n = ca. 40–50 {87}	"	—	A-H			
<b>Elatinaceae</b>									
<b>Elatine</b>	Sp (AAD)	<i>Elatine chilensis</i> Gay [ <i>Elatine gracilis</i> H. Mason]	—	"	—	A-H			
				[ <i>Elatine triandra</i> Schkuhr var. <i>triandra</i> ]					
<b>Ericaceae</b>									
<b>Gaultheria</b>	Sp-CI (tS)	<i>Gaultheria shallon</i> Pursh	2n = 44, ca. 88 {19; 67}	CLADE of <i>Gaultheria acuminata</i> Cham. & Schlecht, <i>Gaultheria amoena</i> A.C.Sm., <i>Gaultheria bracteata</i> (Cavanilles) G. Don, <i>Gaultheria domingensis</i> Urb., <i>Gaultheria erecta</i> Vent., <i>Gaultheria eriophylla</i> (Pers.) Mart. ex Sleumer, <i>Gaultheria glomerata</i> (Cav.) Sleumer, <i>Gaultheria gracilis</i> Small, <i>Gaultheria lanigera</i> Hook., <i>Gaultheria reticulata</i> Kunth, <i>Gaultheria schultesii</i> Camp, <i>Gaultheria tomentosa</i> Kunth, + <i>Gaultheria vaccinoides</i> Griseb. ex Wedd.	—	P-S	N→S*	Fritsch et al., 2011	
<b>Fabaceae</b>									
<b>Acmispon</b>	Sp (AAD)	<i>Acmispon wrangelianus</i> (Fisch. & C.A. Mey.) D.D. Sokoloff [ <i>Lotus wrangelianus</i> Fisch. & C.A. Mey., <i>Lotus subpinnatus</i> Lag., misappl.]	2n = 14 {38}	"	—	A-H			
		CLADE of <i>Astragalus allochrous</i> A. Gray var. <i>allochrous</i> , <i>Astragalus thurberi</i> A. Gray,	2n = 22 {99}		—	AP-H	N→S	0.98	Scherson et al., 2008

continued

## APPENDIX 3, Continued

GROUP / Family / Genus	Tax./(Dist.)	AAID taxon/Clade-NA	C#-NA	AAID taxon/Clade-SA	C#-SA	Dur.-Hab.	Disp.dir.	Div. Ma	Phyl./Tax. Lit. source
		+ CLADE of <i>Astragalus asymmetricus</i> E.Sheld., <i>Astragalus oxyphysus</i> A.Gray	2n = 22 {99}	<i>Astragalus edmondstonei</i> (Hook.f.) Robinson, <i>Astragalus johnstonii</i> Gomez-Sosa, <i>Astragalus looseri</i> IMJohnst., <i>Astragalus monticola</i> Phil., <i>Astragalus pehuenches</i> Niederl., + <i>Astragalus vagus</i> Reiche	—				
		+ <i>Astragalus douglasii</i> (Torr. & A.Gray) A.Gray	2n = 22 {99}	2n = 22 {28}	—				
		CLADE of <i>Astragalus arizonicus</i> A.Gray + <i>Astragalus nothoxys</i> A.Gray	2n = 16, 24 {62; 99}	CLADE of <i>Astragalus amatus</i> Clos, <i>Astragalus arnotianus</i> (Gillies) Reiche, <i>Astragalus bertereanus</i> (Moris) Reiche, <i>Astragalus crucksankii</i> (Hook. & Arn.) Griseb., <i>Astragalus cryptobotrys</i> IMJohnst., <i>Astragalus garbancillo</i> Cav., <i>Astragalus nivicola</i> Gomez-Sosa, + <i>Astragalus uniflorus</i> DC.	—	P-H	N→S	1.89	Scherison et al., 2008
<b>Lupinus</b>	<b>Sp (AAD)</b>	<i>Lupinus microcarpus</i> Sims [ <i>Lupinus densiflorus</i> Benth., <i>Lupinus horizontalis</i> A.Heller]	—	"	—	A-H	N→S		
	<b>Cl-CI (?)</b>	CLADE of <i>Lupinus texensis</i> Hook.	2n = 36 {104}	CLADE of <i>Lupinus</i> eastern (1 western) South America group (19 spp.)	—	A-H/P-H	N→S	6.2* (2.5–9.2)	Drummond et al., 2012
	<b>Cl-CI (?)</b>	+ <i>Lupinus havardii</i> S.Watson CLADE of "Lupinus Mexican" group (4–6 spp.)	2n = 36 {104}	CLADE of "Lupinus Andean" group (81 spp.)	—	A-H/P-H	N→S	2.42*	Drummond et al., 2012; Hughes and Eastwood, 2006
<b>Trifolium</b>	<b>Sp (AAD)</b>	<i>Trifolium depauperatum</i> Desv.	—	"	—	A-H			
	<b>Sp (AAD)</b>	<i>Trifolium macraei</i> Hook. & Arn.	—	"	—	A-H			
	<b>Sp (AAD)</b>	<i>Trifolium microdon</i> Hook. & Arn.	—	"	—	A-H			
<b>Gentianaceae</b>	<b>Sp (AAD)</b>	<i>Cicendia quadrangularis</i> (Lam.) Griseb. [ <i>Microcala quadrangularis</i> (Lam.) Griseb.]	—	"	—	A-H			

continued

APPENDIX 3, Continued

GROUP / Family / Genus	Tax./ (Dist.)	AAID taxon/Clade-NA	C#-NA	AAID taxon/Clade-SA	C#-SA	Dur.-Hab.	Disp. dir.	Div. Ma	Phyl./Tax. Lit. source
<b>Haloragaceae</b>									
<i>Proserpinaca</i>		<i>Proserpinaca palustris</i> L.	—	"	—	P-H			
<b>Hydrophyllaceae</b>									
<i>Phacelia</i>									
<b>Sp-Sp (AAD)</b>		<i>Phacelia affinis</i> A.Gray	2n = 22, 24 {15; 17}	<i>Phacelia cumingii</i> (Benth.) A.Gray	2n = 24 {15; 17}	A-H			Heckard, 1963; Hansen et al., 2009; Walden et al., 2014
<b>Cl-CI (?)</b>		CLADE of <i>Phacelia</i> section <i>Glandulosae</i> , incl. <i>Phacelia vossii</i> Atwood	2n = 22 {13; 14; 15; 16; 17}	CLADE of <i>Phacelia</i> section <i>Glandulosae</i> , incl. <i>Phacelia artemisioides</i> Griseb.	2n = 22 {17}	A-H?			Walden et al., 2014
<b>Sp-CI (AAD)</b>		<i>Phacelia heterophylla</i> Pursh	2n = 22 [P, h, subsp. <i>virgata</i> (Greene) Heckard] {94}	CLADE of 4 species, incl. <i>Phacelia brachyantha</i> Benth. [ <i>Phacelia simplicifolia</i> Colla]	2n = 22 {17; 27; 44}	PB-H			
<b>Sp (eNS)</b>		<i>Hypericum gentianoides</i> (L.) Britton, E.E.Sterns & Poggenb.	—	"	—	A-H			
<b>Lamiaceae</b>									
<i>Blephilia-Monarda-Pycnanthemum</i> CLADE									
<b>Cl-CI (eNS)</b>		CLADE of <i>Blephilia hirsuta</i> (Pursh) Benth., <i>Monarda citriodora</i> Cerv. ex Lag., + <i>Pycnanthemum virginianum</i> (L.) T.Durand & B.D.Jacks. ex B.L.Rob. & Fernald	2n = 80 {37}	CLADE of <i>Cunila incana</i> Benth., <i>Cunila microcephala</i> Benth., <i>Cunila spicata</i> Benth., <i>Glechon discolor</i> Epling, <i>Glechon marifolia</i> Benth., <i>Glechon thymoides</i> Spreng., <i>Hedeoma multiflora</i> Benth., <i>Hesperozygis nitida</i> (Benth.) Epling, <i>Hesperozygis rhododon</i> Epling, <i>Hoehnea epilobiodes</i> (Epling) Epling, <i>Rhabdocalon erythrostachys</i> Epling, <i>Rhabdocalon gracilis</i> (Benth.) Epling, <i>Rhabdocalon stenodontum</i> (Briaq) Epling, + <i>Rhabdocalon strictus</i> (Benth.) Epling	2n = 72 {47b}	P-H or ABP-H/ P-H or P-S			Drew et al., 2017

continued



## APPENDIX 3, Continued

GROUP / Family / Genus	Tax./ (Dist.)	AAID taxon/Clade-NA	C#-NA	AAID taxon/Clade-SA	C#-SA	Dur.-Hab.	Disp. dir.	Div. Ma	Phyl./Tax. Lit. source
<b>Clinopodium- Cuminia</b>	<b>Sp-Sp (AAD)</b>	<i>Clinopodium selerianum</i> (Loes.) Govaerts [ <i>Satureja seleriana</i> Loes.]	—	<i>Cuminia fernandezia</i> Colla [ <i>Cuminia eriantha</i> (Benth.) Benth. var. <i>fernandezia</i> (Colla) Harley]	2n = 44 {52; 91}	P-S	4	(1.9–5.1)	Drew et al., 2017
<b>Clinopodium- Kurzamra</b>	<b>Cl-Sp</b>	CLADE of <i>Clinopodium micromerioides</i> (Hemsl.) Govaerts, + <i>Clinopodium hintoniolum</i> (B.L.Turner) Govaerts	—	<i>Kurzamra puichella</i> (Clos) Kuntze	—	P-H	5.1	(2.5–6.9)	Drew et al., 2017
<b>Malvaceae Cressa</b>	<b>Sp (tNS)</b>	<i>Cressa truxillensis</i> Kunth	—	"	—	P-H			
<b>Montiaceae Calandrinia</b>	<b>Sp (AAD)</b>	<i>Calandrinia menziesii</i> (Hook.) Torr. & A.Gray [ <i>Calandrinia ciliata</i> (R. & P.) DC. var. <i>menziesii</i> (Hook.) Macbr.]	—	<i>Calandrinia ciliata</i> (Ruiz & Pavon) DC.	—	A-H			
<b>Nameaceae Nama</b>	<b>Sp-InC (tNS) Sp (AAD)</b>	<i>Nama dichotomum</i> (Ruiz & Pav.) Choisy var. <i>dichotoma</i> <i>Nama undulatum</i> Kunth	2n = 28 {3}	"	2n = 22 {27}	A-H			
<b>Onagraceae Camissonia</b>	<b>Sp-Sp (AAD)</b>	<i>Camissonia strigulosa</i> (Fisch. & C.A.Mey.) P.H.Raven	2n = 28 {70}	<i>Camissonia dentata</i> (Cav.) Reiche [ <i>Oenothera dentata</i> Cav.]	2n = 26, 28 {70}	A-H	N→S		
<b>Clarkia</b>	<b>Sp-Sp (AAD)</b>	<i>Clarkia davyi</i> (Jepps.) H.F.Lewis & M.R.Lewis	2n = 34 {87}	<i>Clarkia tenella</i> (Cav.) H.F.Lewis & M.R.Lewis	2n = 32, 34 {87}	A-H			
<b>Epilobium</b>	<b>Sp (AAD)</b>	<i>Epilobium campestre</i> (Jepps.) Hoch & W.L.Wagner	2n = 30 {87}	"	—	A-H	N→S		
<b>Gayophytum</b>	<b>Sp-Sp (AAD) Sp (AAD)</b>	<i>Gayophytum diffusum</i> Torrey & A.Gray <i>Gayophytum humile</i> Juss.	2n = 28 {87}	<i>Gayophytum micranthum</i> (Presl) Hook. & Arn. "	2n = 28 [4x] {87}	A-H	N→S		
<b>Ludwigia</b>	<b>Sp-InC (tNS)</b>	<i>Ludwigia peploides</i> (Kunth) P.H.Raven subsp. <i>peploides</i>	2n = 16 {86; 87}	" [ <i>Jussiaea repens</i> L. var. <i>montevideensis</i> (Spreng.) Munz]	—	P-H	S→N		
<b>Orobanchaceae Castilleja</b>	<b>Cl-CI (tNS)</b>	CLADE of <i>Castilleja arvensis</i> Cham. & Schltdl., <i>Castilleja auriculata</i> Eastwood var. <i>a.</i> , + <i>Castilleja tenuiflora</i> Benth. var. <i>tenuiflora</i> <i>Castilleja attenuata</i> (A.Gray) T.I.Chuang & Heckard	2n = 24 {22}	CLADE of <i>Castilleja rubigena</i> Kunth, <i>Castilleja purmila</i> (Benth.) Weddell, + <i>Castilleja virgata</i> (Wedd.) Edwin	2n = 24 {22}	A-H	N→S		Tank and Olmstead, 2009
	<b>Sp (AAD)</b>	"	2n = 24 {21}	" [ <i>Orthocarpus attenuatus</i> A.Gray]	2n = 24 {21}	A-H	N→S	0.26*	Tank and Olmstead, 2009

continued

APPENDIX 3, Continued

GROUP / Family / Genus	Tax. / (Dist.)	AAID taxon / Clade-NA	C#-NA	AAID taxon / Clade-SA	C#-SA	Dur.-Hab.	Disp. dir.	Div. Ma	Phyl./Tax. Lit. source
	<b>Cl-CI</b>					<b>P-H</b>	<b>N→S</b>		
		CLADE of <i>Castilleja attenuata</i> (A.Gray) T.I.Chuang & Heckard, <i>Castilleja densiflora</i> (Benth.) T.I.Chuang & Heckard subsp. <i>densiflora</i> , <i>Castilleja lineariloba</i> (Benth.) T.I.Chuang & Heckard, <i>Castilleja nana</i> Eastw., [Castilleja <i>ambigua</i> M.E.Jones subsp. <i>ambigua</i> + <i>Castilleja rubicundula</i> (Jepson) T.I.Chuang & Heckard subsp. <i>rubicundula</i>	— 2n = 24 {21} 2n = 24 {21} 2n = 20 {21}	CLADE of <i>Castilleja alpicola</i> T.I.Chuang & Heckard, <i>Castilleja cerroana</i> Edwin, <i>Castilleja laciniata</i> Hook. & Arn., <i>Castilleja peruviana</i> T.I.Chuang & Heckard, + <i>Castilleja vadosa</i> T.I.Chuang & Heckard	— — 2n = 96 {21}	<b>A-H</b> <b>A-H</b> <b>A-H</b> <b>A-H</b> <b>A-H</b>	<b>N→S</b>		Tank and Olmstead, 2009
<b>Plantaginaceae</b>						<b>A-H</b>			
<b>Plantago</b>		<i>Plantago heterophylla</i> Nutt.	2n = 22 {87}	"	—	<b>A-H</b>			
	<b>Sp (AAD)</b>					<b>A-H</b>			
	<b>Sp (AAD)</b>	<i>Plantago patagonica</i> Jacq.	2n = 20 {60; 87; 92; 93}	[ <i>Plantago purshii</i> Roem. & Schult.]	2n = 20 {87}	<b>A-H</b>			
<b>Plumbaginaceae</b>						<b>P-H</b>			
<b>Limonium</b>		<i>Limonium californicum</i> (Boiss.) Heller	2n = 18 {87}	<i>Limonium guaicuru</i> (Molina) Kuntze	—	<b>P-H</b>			
<b>Polemoniaceae</b>						<b>A-H</b>			
<b>Collomia</b>		<i>Collomia linearis</i> Nutt.	2n = 16 {33; 82; 103}	<i>Collomia biflora</i> (Ruiz & Pav.) Brand (allopolyploid, perhaps with ancestral SA <i>Collomia linearis</i> [ <i>Collomia cavanillesii</i> Hook. & Arn.]	2n = 32 [4x] {64}	<b>A-H</b>	<b>N→S</b>	<b>0.68</b> (0.23–1.13)	Johnson et al., 2012
	<b>Sp-CI (AAD)</b>	<i>Collomia grandiflora</i> Douglas ex Lindl.	2n = 16 [2n = 32 for 4x cell] {33; 82}	CLADE of <i>Collomia grandiflora</i> Douglas ex Lindl., <i>Collomia soehrensii</i> Phil., + allopolyploid <i>Collomia biflora</i> (Ruiz & Pav.) Brand	— 2n = 32 [4x] {64}	<b>A-H</b>	<b>N→S</b>	<b>0.61</b> (0.09–1.13)	Johnson et al., 2012
<b>Gilia</b>		<i>Gilia salicicola</i> Eastw.	2n = 18 {83}	<i>Gilia crassifolia</i> Benth.	2n = 36, 72 [4x·8x] {82}	<b>A-H</b>	<b>N→S</b>		Johnson and Porter, 2017
	<b>Sp-Sp (AAD)</b>	<i>Gilia tricolor</i> Benth. subsp. <i>tricolor</i>	2n = 18 {82}	CLADE of <i>Gilia laciniata</i> Ruiz & Pav. + <i>Gilia valdiviensis</i> Griseb.	2n = 18 {72}	<b>A-H</b>	<b>N→S</b>	<b>2</b> (1–3)	Morrell et al., 2000
	<b>Sp-Sp (AAD)</b>	<i>Ipomopsis pumila</i> (Nutt.) Grant	2n = 14 {87}	<i>Ipomopsis gossypifera</i> (Gill.) Grant	2n = 18 (inferred) {49} 2n = 14 {87}	<b>A-H</b>	<b>N→S</b>	<b>14.9</b>	Porter et al., 2010

continued

GROUP / Family / Genus	Tax. / (Dist.)	AAID taxon / Clade - NA	C# - NA	AAID taxon / Clade - SA	C# - SA	Dur. - Hab.	Disp. dir.	Div. Ma	Phyl. / Tax. Lit. source
<b>Leptosiphon</b>	<b>Sp-Sp (AAD)</b>	<i>Leptosiphon filipes</i> (Benth.) J.M.Porter & L.A.Johnson [ <i>Gilia filipes</i> Benth.]	2n = 18 {87}	<i>Leptosiphon pusillus</i> (Benth.) J.M.Porter & L.A.Johnson [ <i>Gilia pusilla</i> Benth.]	—	A-H	N→S	1.6 (1.2–2)	Bell and Patterson, 2000
<b>Microsteris</b>	<b>Sp (AAD)</b>	<i>Microsteris gracilis</i> (Hook.) Greene	2n = 14 {87}	"	2n = 14 {71; 87}	A-H	N→S	0.27 (0.06–0.64)	Johnson and Porter, 2017
<b>Navarretia</b>	<b>Sp-Sp (AAD)</b>	<i>Navarretia prostrata</i> (A.Gray) Greene (or its ancestor)	2n = 18 {87}	<i>Navarretia involuocrata</i> Ruiz & Pav. (allopolyploid of cf. <i>Navarretia prostrata</i> × <i>Navarretia</i> indet.)	[4x] {49; 50}	A-H	N→S		Johnson et al., 2012
<b>Polemonium</b>	<b>Sp (AAD)</b>	<i>Polemonium micranthum</i> Benth.	2n = 18 {87}	"	2n = 18 {71; 87}	A-H	N→S		
<b>Polygonaceae</b>									
<b>Chorizanthe</b>	<b>Sp-Sp (AAD)</b>	<i>Chorizanthe brevicornu</i> Torr.	2n = 38–42, 46 {43}	<i>Chorizanthe commisuralis</i> J.Rémy	—	A-H			
	<b>Cl-CI (AAD)</b>	CLADE of <i>Chorizanthe angustifolia</i> Nutt., <i>Chorizanthe biloba</i> Goodman var. <i>biloba</i> , <i>Chorizanthe diffusa</i> Benth., <i>Chorizanthe inequalis</i> Stokes, <i>Chorizanthe obovata</i> Goodman,	2n = 38, 40, 42 {43}	CLADE of <i>Chorizanthe dasyantha</i> Phil. + <i>Chorizanthe frankenioides</i> J.Rémy	—	A-H/P-H (C.f.)	N→S		Kempton, 2012
		<i>Chorizanthe palmeri</i> S.Watson, <i>Chorizanthe parryi</i> S.Watson var. <i>fermandina</i> (S.Watson) Jeps., <i>Chorizanthe uniaristata</i> Torr. & A.Gray, + <i>Chorizanthe brevicornu</i> Torr. var. <i>brevicornu</i> , <i>Lastarriaea coriacea</i> (Goodman) Hoover [ <i>Chorizanthe coriacea</i> Goodman]	2n = 38, 40, 42, 44 {43}		—				
<b>Lastarriaea</b>	<b>Sp-Sp (AAD)</b>	<i>Lastarriaea coriacea</i> (Goodman) Hoover [ <i>Chorizanthe coriacea</i> Goodman]	2n = 42, 56–60 {43}	<i>Lastarriaea chilensis</i> J.Rémy	—	A-H	N→S		Kempton, 2012
<b>Oxytheca</b>	<b>Sp-InD (AAD)</b>	<i>Oxytheca dendroidea</i> Nutt. subsp. <i>dendroidea</i> [ <i>Eriogonum dendroideum</i> (Nutt.) S.Stokes]	2n = 40 {31}	<i>Oxytheca dendroidea</i> Nutt. subsp. <i>chilensis</i> (J.Rémy) Ertter	—	A-H			
<b>Rumex</b>	<b>Sp (ewN)</b>	<i>Rumex fueginus</i> Phil. [ <i>Rumex maritimus</i> L., misappl.; <i>Rumex persicarioides</i> L. var. <i>fueginus</i> (Phil.) A.Haines]	—	"	—	AB-H			
<b>Primulaceae</b>									
<b>Androsace</b>	<b>Sp-Sp (AAD)</b>	<i>Androsace occidentalis</i> Pursh	2n = 20 {34; 60}	<i>Androsace salasilii</i> Kurtz	—	A-H			

APPENDIX 3, Continued

GROUP / Family / Genus	Tax. / (Dist.)	AAID taxon/Clade-NA	C#-NA	AAID taxon/Clade-SA	C#-SA	Dur.-Hab.	Disp. dir.	Div. Ma	Phyl./Tax. Lit. source
<b>Primulaceae</b> <i>Primula</i>									
	<b>Cl-Sp (AAD)</b>	CLADE of <i>Primula alcalina</i> Cholewa & Douglass M.Hend. + <i>Primula specuicola</i> Rydb.	2n = 18 [2x] {42}	<i>Primula magellanica</i> Lehm.	2n = 72 [8x] {42}	P-H	N→S		Guggisberg et al., 2009
<b>Ranunculaceae</b> <i>Myosurus</i>									
	<b>Sp-InD (AAD)</b>	<i>Myosurus apetalus</i> Gay var. <i>borealis</i> Whittm., var. <i>montanus</i> (G.R.Campb.) Whittm. [ <i>Myosurus apetalus</i> Gay]	2n = 16 {87}	<i>Myosurus apetalus</i> Gay var. <i>apetalus</i> [ <i>Myosurus apetalus</i> Gay; <i>Myosurus aristatus</i> Benth. ex Hook., illegit.]	—	A-H			
	<b>Sp-Sp (AAD*)</b>	<i>Myosurus minimus</i> L.	—	<i>Myosurus patagonicus</i> Speg [ <i>Myosurus apetalus</i> var. <i>lepturus</i> A.Gray]	—	A-H			
<b>Ranunculus</b>									
	<b>Sp-InC (AAD)</b>	<i>Ranunculus bonariensis</i> Poir. var. <i>triseptalus</i> (Gillies ex Hook. & Arn.) Lourteig	—	"	—	A-H			
	<b>Sp (tNS)</b>	<i>Ranunculus flagelliformis</i> Sm.	—	"	2n = 48 {12}	P-H			Paun et al., 2005
<b>Rosaceae</b> <i>Acaena</i>									
	<b>Sp-InD (AAD)</b>	<i>Acaena pinnatifida</i> Ruiz & Pav. var. <i>californica</i> (Bitter) Jeps. [ <i>Acaena californica</i> Bitter]	—	<i>Acaena pinnatifida</i> Ruiz & Pav. var. <i>pinnatifida</i>	2n = 42 [6x] {68; 71}	P-H			
<b>Fragaria</b>									
	<b>Sp (AAD*)</b>	<i>Fragaria chiloensis</i> (L.) Mill.	2n = 56 [8x] {87; 100}	[ <i>Fragaria chiloensis</i> subsp. <i>lucida</i> (E.Vilm. ex J.Gay) Staudt; <i>Fragaria chiloensis</i> subsp. <i>pacifica</i> Staudt; <i>Potentilla chiloensis</i> (L.) Mabb.]	2n = 56 [8x] {87; 100}	P-H		0.53 (0.19–0.86)	Njuguna et al., 2013
<b>Solanaceae</b> <i>Solanum</i>									
	<b>Cl-CI (eNews)</b>	CLADE of <i>Solanum carolinense</i> L., <i>Solanum dimidiatum</i> Raf., <i>Solanum perplexum</i> Small [S. <i>dimidiatum</i> Raf.], + <i>Solanum pumilum</i> Dunal	2n = 24 {107}	CLADE of <i>Solanum aridum</i> Morong, <i>Solanum comptum</i> C.V.Morton, <i>Solanum juvenale</i> Thell., <i>Solanum moxosense</i> M.Nee, <i>Solanum reineckii</i> Briq., + possibly <i>Solanum hieronymi</i> Kuntze	2n = 24 {107}	P-H	Equip		Wahlert et al., 2015
	<b>Sp (AAD*)</b>	<i>Solanum elaeagnifolium</i> Cav.	2n = 24 {84}	"	2n = 24, 48, 72 {1; 73}	P-H	Equip		Wahlert et al., 2015
	<b>Cl-CI (AAD)</b>	CLADE of <i>Solanum hinsianum</i> Benth.	—	CLADE of <i>Solanum elaeagnifolium</i> Cav. (NA + SA),	2n = 24 (NA); 2n = 24, 48, 72 (SA) {1; 73; 84}	P-H	Equip		Wahlert et al., 2015

continued



## APPENDIX 3, Continued

GROUP / Family / Genus	Tax. / (Dist.)	AAID taxon / Clade-NA	C#-NA	AAID taxon / Clade-SA	C#-SA	Dur.-Hab.	Disp. dir.	Div. Ma	Phyl./Tax. Lit. source
<b>Valerianaceae</b> <b>Plectritis</b>		+ <i>Solanum houstonii</i> Martyn [ <i>Solanum tridynamum</i> Dunal]	2n = 24 {59}	<i>Solanum</i> <i>homalospermum</i> Chiarini, <i>Solanum mortonii</i> Hunz., + possibly <i>Solanum</i> <i>evacanthum</i> Phil.	—	—	—	—	—
	<b>Sp-CI</b> <b>(AAD)</b>	CLADE of <i>Plectritis congesta</i> (Lindl.) DC. subsp. <i>brachystemon</i> (Fisch. & C.A.Mey.) Morey [ <i>Plectritis</i> <i>brachystemon</i> Fisch. & C.A.Mey.], <i>Plectritis congesta</i> (Lindl.) DC., + <i>Plectritis macrocera</i> Torr. & A. Gray	—	<i>Plectritis samolifolia</i> (DC.) Höck [ <i>Valeriana</i> <i>samolifolia</i> (DC.) Höck]	—	<b>A-H</b>	<b>S→N</b>	—	Bell and Donoghue, 2005
	<b>Sp-Sp</b> <b>(tNS)</b>	<i>Valeriana candolleana</i> Gardner [ <i>Valeriana</i> <i>scandens</i> Loefl. ex L. var. <i>candolleana</i> (Gardner) C.A. Muell.]	2n = 32 {30}	<i>Valeriana scandens</i> Loefl. ex L.	2n = 28 {30}	<b>P-HV</b>	<b>N→S</b>	7.69 (4.74– 10.73)	Bell et al., 2012
	<b>Sp</b> <b>(tNS)</b>	<i>Valeriana urticifolia</i> Kunth [ <i>Valeriana tafiensis</i> Borsini]	2n = 64? {30}	"	2n = 64? {30}	<b>P-H</b>	<b>N→S</b>	2.1 (0.67– 5.02)	Bell et al., 2012
<b>CI-CI</b> <b>(AAD)</b>	CLADE of ca. 18 NA <i>Valeriana</i> spp. and 2 SA <i>Valeriana</i> spp., the Central American clade of Bell et al., 2012	—	CLADE of ca. 55 SA <i>Valeriana</i> spp., including suffrutescent vine, Peruvian, Columbian, southern Andean, and Paramo and Peruvian clades of Bell et al., 2012	—	<b>?</b>	<b>N→S</b>	13.4 (10.3– 17.3)	Bell et al., 2012	
<b>CI-Sp</b> <b>(ts)</b>	CLADE of NA <i>Valeriana</i> <i>naiidae</i> Barrie + <i>Valeriana subincisa</i> Benth.	—	<i>Valeriana laurifolia</i> Kunth [ <i>Valeriana</i> <i>clematitis</i> Kunth]	2n = 64 {111}	<b>?/P-V</b>	<b>S→N</b>	6.49 (4.07– 9.33)	Bell et al., 2012	
						<b>?</b>			Bell et al., 2012

Key to literature citations of chromosome numbers: {1} = Acosta et al., 2005; {2} = Bachmann and Price, 1977; {3} = Bacon, 1984; {4} = Baden and Bothmer, 1994; {5} = Bell and Constance, 1957; {6} = Bell, 1954; {7} = Bothmer and Jacobsen, 1989; {8} = Bothmer and Subrahmanyam, 1988; {9} = Bothmer et al., 1980; {10} = Bothmer et al., 1985; {11} = Carrique and Martínez, 1984; {12} = Casas, 1981; {13} = Cave and Constance, 1942; {14} = Cave and Constance, 1944; {15} = Cave and Constance, 1947; {16} = Cave and Constance, 1950; {17} = Cave and Constance, 1959; {18} = Chambers, 1963; {19} = Chinnappa and Chmielewski, 1987; {20} = Chmielewski and Chinnappa, 1988; {21} = Chuang and Heckard, 1982; {22} = Chuang and Heckard, 1993; {23} = Constance et al., 1976; {24} = Dawe and Murray, 1981; {25} = Del Pero Martínez, 1988; {26} = Di Fuluio, 1976; {27} = Diers, 1961; {28} = Dopchiz et al., 1995; {29} = Dunford, 1985; {30} = Engel, 1976; {31} = Erter, 1980; {32} = Flores-Olvera and Mercado-Ruaro, 1997; {33} = Flory, 1937; {34} = Freeman and Brooks, 1988; {35} = Friend, 1982; {36} = Gastony and Soltis, 1977; {37} = Gill, 1981; {38} = Grant, 1997; {39} = Grau, 1971; {40} = Grau, 1983; {41} = Grau, 1988; {42} = Guggisberg et al., 2009; {43} = Hardham, 1989; {44} = Heckard, 1963; {45} = Hersey and Kloet, 1976; {46} = Holmgren, 1971; {47} = Horn, 2000; {47b} = Irving, 1980; {48} = Jansen and Stuessy, 1980; {49} = Johnson and Porter, 2017; {50} = Johnson et al., 2012; {51} = Keil et al., 1988; {52} = Kiehn et al., 2005; {53} = Las Penas, 2005; {55} = Linde-Laursen et al., 1989; {56} = Löve, 1981c; {57} = Löve, 1981a; {58} = Löve, 1981b; {59} = Löve, 1981c; {60} = Löve, 1982b; {61} = Löve, 1985; {62} = Löve, 1986a; {64} = Löve, 1986a; {65} = Marhold, 2006; {66} = Mathew and Raven, 1962; {67} = Middleton and Wilcock, 1990; {68} = Mishima et al., 2002; {69} = Molnar and Fedak, 1989; {70} = Moore and Raven, 1970; {71} = Moore, 1981; {72} = Morrill et al., 2000; {73} = Moscine, 1992; {74} = Nobs, 1978; {75} = Nobs, 1978; {76} = Ørregaard, 1994; {77} = Ornduff, 1963; {78} = Oud et al., 1988; {79} = Peterson and Ortiz-Diaz, 1998; {81} = Peterson, 1988; {82} = Porter, 1996; {83} = Porter, 2012; {84} = Powell and Weedlin, 2005; {85} = Powell, 1968; {86} = Raven and Tai, 1979; {87} = Raven, 1963; {88} = Ray and Chisaki, 1957; {89} = Ruas et al., 2001; {90} = Salomon and Bothmer, 1998; {91} = Sanders et al., 1990; {93} = Sharma et al., 1992; {94} = Shelly, 1989; {95} = Sivinski, 1993; {96} = Snogerup, 1993; {97} = Soltis et al., 1989; {98} = Soereng, 1991; {99} = Spellenberg, 1976; {100} = Staudt, 1962; {101} = Stoeva, 1987; {102} = Strother, 1976; {103} = Sugjura, 1936; {104} = Turner and Powell, 2001; {105} = Turner et al., 1979; {106} = Veno, 1979; {107} = Wählert et al., 2014; {108} = Walsh et al., 2015; {109} = Ward, 1983; {110} = Windham and Yatskevych, 2003; {111} = Xena de Emecht, 1993.

**APPENDIX 4** List of vascular plants considered in some sources to have an American amphitropical disjunct (AAD) distribution, but rejected here. Taxa in square brackets [ ] = synonym(s). Tax. = taxonomic unit of comparison: Sp = single species (conspecifics) occurring in both North America (NA) and South America (SA); Sp-Sp = two different species, either sister or closely related, occurring in NA and SA.

GROUP / Family/Genus	Bioregion	Tax.	Taxon-NA	Taxon-SA	Comments
<b>FERNS</b>					
<b>Ophioglossaceae</b>					
<i>Botrychium</i>	<b>Bipolar</b>	<b>Sp-Sp?</b>	<i>Botrychium hesperium</i> (Maxon & R.T.Clausen) W.H.Wagner & Lellingner [ <i>Botrychium matricarifolium</i> subsp. <i>hesperium</i> Maxon & R.T.Clausen]	<i>Botrychium ramosum</i> A.Gray var. <i>patagonicum</i> Christ [ <i>Botrychium matricarifolium</i> (Döll) A.Braun ex W.D.J.Koch subsp. <i>patagonicum</i> (Christ) R.T.Clausen]	Listed by Raven (1963), but only <i>Botrychium dusenii</i> (Christ) Alston now considered native to SA (Farrar and Stensvold, 2017, this issue)
<b>MONOCOTS</b>					
<b>Poaceae</b>					
<i>Agrostis</i>	<b>Temperate</b>	<b>Sp</b>	<i>Agrostis tandilensis</i> (Kuntze) Parodi [ <i>Bromidium tandilense</i> (Kuntze) Rùgolo]	"	Listed by Raven (1963), but reported non-native in USA (Jepson Flora Project, 2017; USDA-NCRS, 2017) and in Mexico (Rebman et al., 2016, although no voucher reported; not listed by Villaseñor, 2016)
<i>Festuca</i>	<b>Temperate</b>	<b>Sp</b>	<i>Festuca myuros</i> L. [ <i>Festuca megalura</i> Nutt., <i>Vulpia myuros</i> (L.) C.C.Gmel. var. <i>hirsuta</i> Hack., <i>Vulpia myuros</i> f. <i>myuros</i> , <i>Vulpia myuros</i> var. <i>myuros</i> ]	"	Listed by Raven (1963), as <i>Festuca megalura</i> Nutt., but not native to USA (Jepson Flora Project, 2017; USDA-NCRS, 2017) or Mexico (Rebman et al., 2016); <i>Vulpia myuros</i> (L.) C.C.Gmel. var. <i>hirsuta</i> Hack. is considered native to the Southern Cone region of SA (Zuloaga et al., 2008)
<i>Hordeum</i>	<b>Temperate</b>	<b>Sp</b>	<i>Hordeum jubatum</i> L.	"	Listed by Raven (1963); native to NA, but introduced in SA (Baden and Bothmer, 1994; Zuloaga et al., 2008)
<i>Poa</i>	<b>Bipolar</b>	<b>Sp</b>	<i>Poa glauca</i> Vahl.	"	Listed by Raven (1963), but introduced into at least the Southern Cone region of SA (Zuloaga et al., 2008)
	<b>Temperate</b>	<b>Sp</b>	<i>Poa pratensis</i> L. s.s.	"	Listed by Raven (1963, p. 171) as "The circumboreal <i>P. pratensis</i> L. sens. lat. likewise probably occurs as a native in s. SA, but the picture is confused by the cultivation and common introduction of this important pasture grass"; but considered introduced into at least the Southern Cone region of SA (Zuloaga et al., 2008)
<b>EUDICOTS</b>					
<b>Aizoaceae</b>					
<i>Carpobrotus</i>	<b>Temperate</b>	<b>Sp</b>	<i>Carpobrotus chilensis</i> (Mol.) N.E.Br.	"	Listed by Raven (1963), but thought to be introduced by humans from South Africa to Chile, then to North America (Bicknell and Mackey, 1998; Vivrette, 2003)
<b>Asteraceae</b>					
<i>Madia</i>	<b>Temperate</b>	<b>Sp</b>	<i>Madia gracilis</i> (Sm.) Keck	"	Listed by Raven (1963), but apparently does not occur in SA (Zuloaga, et al., 2008)
<i>Malacothrix</i>	<b>Temperate</b>	<b>Sp</b>	<i>Malacothrix coulteri</i> Harv. & A.Gray	"	Listed by Raven (1963); introduced at least into Argentina and Chile, according to Zuloaga et al., 2008
<i>Soliva</i>	<b>Temperate</b>	<b>Sp</b>	<i>Soliva sessilis</i> Ruiz & Pav. [ <i>Soliva daucifolia</i> Nutt.; <i>Soliva pterosperma</i> (Juss.) Less.]	"	Listed by Raven (1963). Native to SA (Zuloaga et al., 2008), but naturalized in Canada and USA (Jepson Flora Project, 2017; USDA-NCRS, 2017)
<b>Boraginaceae</b>					
<i>Myosotis</i>	<b>Temperate</b>	<b>Sp</b>	<i>Myosotis verna</i> Nutt.	"	Listed by Raven (1963). Native to Canada and USA (USDA-NCRS, 2017) but listed as non-native to the Southern Cone region of SA (Zuloaga et al., 2008)

continued

APPENDIX 4, *Continued*

GROUP / Family/Genus	Bioregion	Tax.	Taxon-NA	Taxon-SA	Comments
<b>Caryophyllaceae</b> <i>Honckenya</i>	<b>Bipolar</b>	<b>Sp</b>	<i>Honckenya peploides</i> (L.) Ehrh.	"	Listed by Raven (1963) but no longer considered to occur in Chile (Wagner, 2005). Possibly of anthropochorus origin (Sánchez-Vilas, 2007). See: <a href="http://www.efloras.org/florataxon.aspx?flora_id=1&amp;taxon_id=220006496">http://www.efloras.org/florataxon.aspx?flora_id=1&amp;taxon_id=220006496</a>
<i>Paronychia</i>	<b>Temperate</b>	<b>Sp</b>	<i>Paronychia franciscana</i> Eastw	"	Listed by Raven (1963). Not native to NA (Jepson Flora Project, 2017; USDA-NCRS, 2017); native to SA-CHL (Zuloaga et al., 2008)
<i>Silene</i>	<b>Temperate</b>	<b>Sp</b>	<i>Silene antirrhina</i> L.	"	Native to NA (Jepson Flora Project, 2017; USDA-NCRS, 2017); not native to SA (Zuloaga et al., 2008)
<i>Spergularia</i>	<b>Temperate</b>	<b>Sp</b>	<i>Spergularia platensis</i> (Cambess.) Fenzl var. <i>platensis</i> [ <i>Spergula platensis</i> (Cambess.) Shimmers]	"	Not native to NA (Jepson Flora Project, 2017; USDA-NCRS, 2017); native to SA (Zuloaga et al., 2008); another variety native to SA-ARG, introduced in CHL (Jepson Flora Project, 2017)
<b>Chenopodiaceae</b> <i>Chenopodium</i>	<b>Temperate</b>	<b>Sp</b>	<i>Chenopodium carnosulum</i> Moq.	"	Cited by Raven (1963), but <i>Chenopodium carnosulum</i> is apparently not native to SA (Zuloaga et al., 2008). The species was cited for coastal southern California but is now identified as the native <i>Chenopodium littoreum</i> Benet-Pierce & M.G.Simpson (Benet-Pierce and Simpson, 2010)
<i>Oxybasis</i>	<b>Temperate</b>	<b>Sp</b>	<i>Oxybasis macrosperma</i> (Hook.f.) S.Fuentes, Uotila & Boish [ <i>Chenopodium macrosperma</i> Hook.f.]	"	Cited by Raven (1963, as <i>Chenopodium macrosperma</i> ). Not native to NA (Rebman et al., 2016; Jepson Flora Project, 2017; USDA-NCRS, 2017); two subspp. native to SA-ARG, CHL, PRY (Zuloaga et al., 2008)
<b>Euphorbiaceae</b> <i>Euphorbia</i>	<b>Temperate</b>	<b>Sp</b>	<i>Euphorbia spathulata</i> Lam.	"	Listed by Raven (1963). Native to NA (Jepson Flora Project, 2017). Introduced in ARG, BRA (Zuloaga et al., 2008)
<b>Fabaceae</b> <i>Lathyrus</i>	<b>Bipolar</b>	<b>Sp</b>	<i>Lathyrus japonicus</i> Willd.	"	Listed by Raven (1963), but now considered non-native in the Southern Cone region of SA (Zuloaga et al., 2008)
<b>Onagraceae</b> <i>Oenothera</i>	<b>Temperate</b>	<b>Sp</b>	<i>Oenothera curtiflora</i> W.L.Wagner & Hoch [ <i>Gaura parviflora</i> Douglas ex Lehm.; <i>Gaura parviflora</i> var. <i>lachnocarpa</i> Weath.; <i>Gaura mollis</i> James, nom. rej.]	" [ <i>Gaura parviflora</i> Dougl. ex Hook. var. <i>lachnocarpa</i> ]	Introduced to California, USA (Jepson Flora Project, 2017) and to Baja California, Mexico (Rebman et al., 2016), but native to other parts of USA and Mexico (Villaseñor, 2016; USDA-NCRS, 2017). Introduced to Southern Cone (Zuloaga et al., 2008)
<b>Plantaginaceae</b> <i>Nuttallanthus</i>	<b>Temperate</b>	<b>Sp</b>	<i>Nuttallanthus texanus</i> (Scheele) D.A.Sutton [ <i>Linaria canadensis</i> (L.) Dum.Cours. var. <i>texana</i> (Scheele) Pennell; <i>Linaria canadensis</i> (L.) Chaz., in part, misappl.]	"	Listed by Raven (1963). Native to NA (USDA-NCRS, 2017), but non-native to SA (Zuloaga et al., 2008)
<i>Plantago</i>	<b>Temperate</b>	<b>Sp</b>	<i>Plantago firma</i> Kunze ex Walp. [ <i>Plantago truncata</i> Cham. & Schldl. subsp. <i>firma</i> (Kunze ex Walp.) Pilg.]	"	Listed by Raven (1963) as <i>Plantago truncata</i> . Native to SA (Zuloaga et al., 2008). Introduced in USA (Jepson Flora Project, 2017; USDA-NCRS, 2017)