

The South American Biogeographic Transition Zone: An analysis from Asteraceae

Estrella Urtubey,¹ Tod F. Stuessy,² Karin Tremetsberger³ & Juan J. Morrone⁴

¹ Instituto de Botánica Darwinion, Labardén 200 y E. del Campo, C.C. 22, B1642HYD San Isidro, Buenos Aires, Argentina

² Department of Systematic and Evolutionary Botany, Faculty Center Biodiversity, University of Vienna, Rennweg 14, 1030 Vienna, Austria

³ Departamento de Biología Vegetal y Ecología, Universidad de Sevilla, Apdo. 1095, 41080 Sevilla, Spain

⁴ Museo de Zoología “Alfonso L. Herrera”, Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México (UNAM), Apdo. postal 70-399, 04510 Mexico, D.F., Mexico.

Author for correspondence: Juan J. Morrone, juanmorrone2001@yahoo.com.mx

Abstract In order to elucidate the biotic diversification of Asteraceae inhabiting the South American Transition Zone, we undertook a panbiogeographic analysis (based on a parsimony analysis of endemism) and a cladistic biogeographic analysis. The study units were the six biogeographic provinces of this zone plus the seven subregions of the Neotropical and Andean regions, considered as “outgroups”. Species analyzed belonged to the genera *Arnaldoa*, *Barnadesia*, *Belloa*, *Berroa*, *Chevreulia*, *Chuquiraga*, *Cuatrecasiella*, *Dasyphyllum*, *Doniophyton*, *Dusenilla*, *Facellis*, *Fulcaldea*, *Gamochoetopsis*, *Huarpea*, *Hypochaeris*, *Jalcophila*, *Lucilia*, *Luciliocline*, and *Schlechtendalia*. A parsimony analysis of endemism, based on presence/absence data of the 66 individual tracks ranged on two or more areas, allowed to identify four generalized tracks: (1) Coastal Peruvian Desert and Puna provinces; (2) Central Chilean, Patagonian, and Subantarctic subregions; (3) Amazonian, Chacoan, and Parana subregions; and (4) Puna province and Parana and Chacoan subregions. The Puna and Parana provinces, connected with two different generalized tracks each, constitute nodes. A cladistic biogeographic analysis, based on the paralogy-free subtrees extracted from the taxonomic area cladograms of *Barnadesia*, *Chuquiraga*, *Dasyphyllum*, *Hypochaeris*, and the *Lucilia* group, allowed obtaining a general area cladogram, which indicates a basic separation between the Atacama, Monte, and Prepuna provinces closely related to the Andean region, and the North Andean Paramo, Coastal Peruvian Desert, and Puna provinces closely related to the Neotropical region. Our results corroborate once again the transitional character of the provinces assigned to the South American Transition Zone, and allow speculating on their close affinities with the Andean and Neotropical regions.

Keywords cladistic biogeography; evolutionary biogeography; general area cladogram; generalized tracks; parsimony analysis of endemism; panbiogeography; South America

■ INTRODUCTION

South America is roughly divided into the Neotropical and Andean regions, and the South American Transition Zone (Morrone, 2006). The South American Transition Zone, formerly treated as the Paramo-Punan subregion of the Andean region (Morrone, 2001a,b), extends along the highlands of the Andes from western Venezuela to northern Chile, and central western Argentina (Ruggiero & Ezcurra, 2003; Morrone, 2004a, 2006). The evolution of the biota inhabiting the South American Transition Zone has been greatly influenced by intense vicariance events, associated with the geological history of the Andes, which induced important climatic changes (Stuessy & al., 1996), outlined basically during their final and major uplift toward the end of the Pliocene (Berry, 1982; Taylor, 1991, 1995; Gregory-Wodzicki, 2000). As occurs with other transition zones, the South American Transition Zone possesses a diverse biota (Katinas & al., 1999; Morrone, 2004a,b).

Asteraceae are the largest family of flowering plants, with ca. 23,000 species scattered over the world (Jeffrey, 2007). In South America, they are widely distributed along the Andes, both in the Andean region and the South American Transition

Zone, in different habits from the sea level and reaching 5000 m. Several genera of Andean Asteraceae have been revised in the last years (Anderberg & Freire, 1991; Stuessy & al., 1996, 2009; Urtubey, 1999; Urtubey & Stuessy, 2001; Ezcurra, 2002; Tremetsberger & al., 2006) and phylogenetic hypotheses are available for them. These genera may be used to undertake an evolutionary biogeographic analysis (Morrone, 2008) of the South American Transition Zone.

Our aim is to contribute to the study of the biotic evolution of the South American Transition Zone, identifying generalized tracks and obtaining a general area cladogram based on the phylogenetic evidence available from several genera of Asteraceae. These generalized tracks and the general area cladogram may give us clues to help understand the biotic evolution of this interesting area.

■ MATERIALS AND METHODS

Areas. — The units of the analysis were the six biogeographic provinces of the South American Transition Zone (Fig. 1), which have been identified by analyzing distributional

patterns of several plant and animal taxa (Morrone, 2001a,b, 2006):

- North Andean Paramo province (A): High cordilleras of Venezuela, Colombia, Ecuador, and Peru, above 3000 m altitude.
- Coastal Peruvian Desert province (B): Narrow strip along the Pacific Ocean coast, from northern Peru to northern Chile.
- Puna province (C): Bolivia, northern Argentina and Chile, and southern Peru.
- Atacama province (D): Northern Chile, between 18° and 28° south latitude.
- Prepuna province (E): Central and northwestern Argentina, from Jujuy to northern Mendoza.
- Monte province (F): Central Argentina, between 24° and 43° south latitude, from Salta to northeastern Chubut.

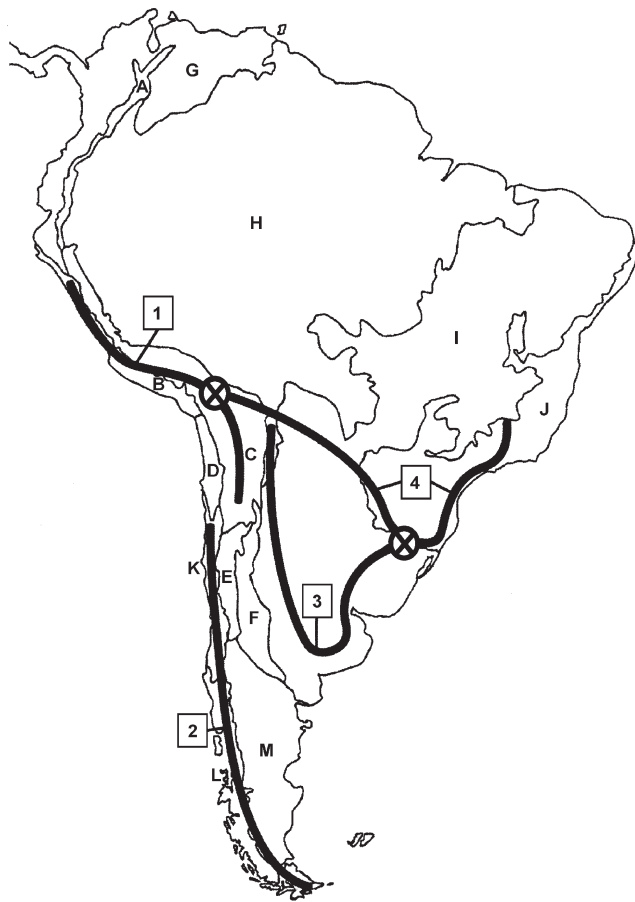


Fig. 1. Areas analyzed, with the generalized tracks and nodes obtained in the track analysis. South American Transition Zone: A, North Andean Paramo province; B, Coastal Peruvian Desert province; C, Puna province; D, Atacama province; E, Prepuna province; F, Monte province. Neotropical region: G, Caribbean subregion; H, Amazonian subregion; I, Chacoan subregion; J, Parana subregion. Andean region: K, Central Chilean subregion; L, Subantarctic subregion; M, Patagonian subregion. Generalized tracks: 1, Coastal Peruvian Desert and Puna provinces; 2, Central Chilean, Patagonian, and Subantarctic subregions; 3, Amazonian, Chacoan, and Parana subregions; 4, Puna province, and Parana and Chacoan subregions.

The seven subregions of the Neotropical region (Caribbean [G], Amazonian [H], Chacoan [I], and Parana [J] subregions) and the Andean region (Central Chilean [K], Patagonian [M], and Subantarctic [L] subregions) (Fig. 1) were also analyzed as “outgroups”, to help test the monophyly of the South American Transition Zone as a whole.

Taxa. — We analyzed 131 species of Asteraceae belonging to the genera *Arnaldoa* (2 species), *Barnadesia* (1), *Chuquiraga* (23), *Dasyphyllum* (29), *Doniophyton* (1), *Dusenilla* (1), *Fulcaldea* (1), *Huarpea* (1), and *Schlechtendalia* (1) of the South American subfamily Barnadesioideae. From the tribe Cichorieae, we analyzed *Hypochaeris* (31 species) and from the tribe Gnaphalieae, the *Lucilia* group, which includes nine genera and 40 species, *Belloa* (9), *Berroa* (1), *Chevreulia* (5), *Cuatrecasiella* (2), *Facellis* (3), *Gamochaetopsis* (1), *Jalco-phila* (3), *Lucilia* (8), and *Luciliocline* (8). The geographical distribution of each species was based on the information contained in revisionary studies and floras (Cabrera, 1963, 1971, 1974, 1978; Anderberg & Freire, 1991; Urtubey, 1999; Urtubey & Stuessy, 2001; Ezcurra, 2002; Tremetsberger & al., 2006), and from material obtained on loan from the following herbaria: BM, CONC, K, LP, LPB, MO, NY, SGO, SI, US and WU.

Track analysis. — A panbiogeographic approach (Craw & al., 1999; Morrone, 2004b, 2009) to identify generalized tracks was applied as a first step of the analysis. Individual tracks are the primary spatial coordinates of species or supra-specific taxa. Operationally, they are line graphs drawn on a map that connects the different localities or distributional areas of a taxon according to their geographic proximity. Generalized tracks result from the significant superposition of different individual tracks, and indicate the preexistence of ancestral biotic components, that became fragmented by geologic or tectonic events. In the areas where two or more generalized tracks superimpose, nodes are recognized. They are complex areas, usually interpreted as tectonic and biotic convergence zones.

Parsimony analysis of endemism or PAE (Rosen, 1988; Morrone, 1994, 2004b) is a quantitative implementation of panbiogeography, which classifies areas that share at least two individual tracks, in order to elucidate possible biotic relationships. An individual track was drawn by hand for each of the species analyzed and a presence/absence data matrix (Table S1 in the Electronic Supplement to this article) was constructed for the 66 individual tracks ranged on two or more areas. The PAE was carried out with programs Winclada v.0.9.99 (Nixon, 1999) and NONA v.2.0 (Goloboff, 1993), rooting the cladograms with a hypothetical area coded with zeros. We applied PAE-PCE or PAE with Progressive Character Elimination (Luna-Vega & al., 2000; García-Barros & al., 2002; García-Barros, 2003), which consists in applying successive parsimony analyses, eliminating in each run the synapomorphic individual tracks that define the area clades, to find alternative groups of areas to the most parsimonious arrangement. From the consensus cladograms obtained in each run, area clades supported by at least two individual tracks were mapped as generalized tracks. Nodes indicating

composite areas were identified where different generalized tracks overlapped.

Cladistic biogeography. — The cladistic biogeographic approach assumes a correspondence between taxonomic relationships and area relationships, and is based on an analogy between biogeography and systematics, using taxa as characters (Morrone & Carpenter, 1994; Humphries & Parenti, 1999; Morrone, 2009). A cladistic biogeographic analysis comprises three basic steps: (1) construction of taxon-area cladograms from taxon cladograms, by replacing the terminal taxa by the area(s) inhabited by them; (2) conversion of taxon-area cladograms into resolved area cladograms, by resolving problems due to widespread taxa, redundant distributions, and missing areas; and (3) derivation of general area cladogram(s), that represent(s) the most logical solution for all the taxa analyzed (Morrone & Carpenter, 1994). General area cladograms represent hypotheses on the biogeographic history of the taxa analyzed and the areas where they are distributed (Morrone, 2009).

In order to obtain the general area cladogram(s), we undertook a parsimony analysis of paralogy-free subtrees (Contreras-Medina & al., 2007) using TASS (Nelson & Ladiges, 1995) to obtain the paralogy-free subtrees from the taxon-area cladograms. Paralogy-free subtrees are derived from the taxon-area cladograms, where geographic data are associated only with informative nodes and areas duplicated or redundant in the descendants of each node are eliminated (Morrone, 2009). Based on the 53 components from the paralogy-free subtrees, a data matrix was constructed (Table S2 in the Electronic Supplement) and analyzed with Winclada v.0.9.99 (Nixon, 1999) and NONA v.2.0 (Goloboff, 1993) to obtain a general area cladogram.

RESULTS

Track analysis. — The PAE of the 66 individual tracks (Table S1 in the Electronic Supplement) produced ten most parsimonious cladograms, with 114 steps, consistency index of 0.57, and retention index of 0.55. Based on the strict consensus cladogram (Fig. 2a), three generalized tracks were identified: (1) Coastal Peruvian Desert and Puna provinces; (2) Central Chilean, Patagonian, and Subantarctic subregions; and (3) Amazonian, Chacoan, and Parana subregions (Fig. 1). The first generalized track, joining the Coastal Peruvian Desert and Puna provinces, is supported by *Barnadesia dombeyana*, *Belloa pickeringii*, *B. piptolepis*, *B. plicatifolia*, *Cuatrecasiella argentina*, *Hypochaeris elata*, *H. sessiliflora*, *Facelis plumosa*, *F. lasiocarpa*, *Luciliocline burkartii*, and *L. lopezmirandae*. The second generalized track, equivalent to Patagonia or the Andean region (sensu Morrone, 2004b, 2006), is supported by ten individual tracks, *Belloa chilensis*, *Chevreulia diemii*, *C. pusilla*, *C. sarmentosa*, *Dasyphyllum diacanthoides*, *Gamochoetopsis alpina*, *Hypochaeris acaulis*, *H. apargioides*, *H. gayana*, and *H. tenuifolia*. The third generalized track joins the Amazonian, Chacoan, and Parana subregions of the Neotropical region, and is supported by 15 species: *Berroa gnaphalioides*, *Dasyphyllum brasiliense*, *D. tomentosum*, *D. synacanthum*, *Lucilia lineariifolia*, *L. lycopodioides*, *Facelis retusa*, *Hypochaeris albiflora*, *H. chillensis*, *H. lutea*, *H. megapotamica*, *H. microcephala*, *H. variegata*, *Lucilia acutifolia*, and *L. nitens*.

A second run, after the synapomorphies defining the previously found clades were deactivated, produced eleven cladograms, with 80 steps, consistency index of 0.51, and retention index of 0.46. Based on the strict consensus cladogram (Fig. 2b), a fourth generalized track was identified, joining

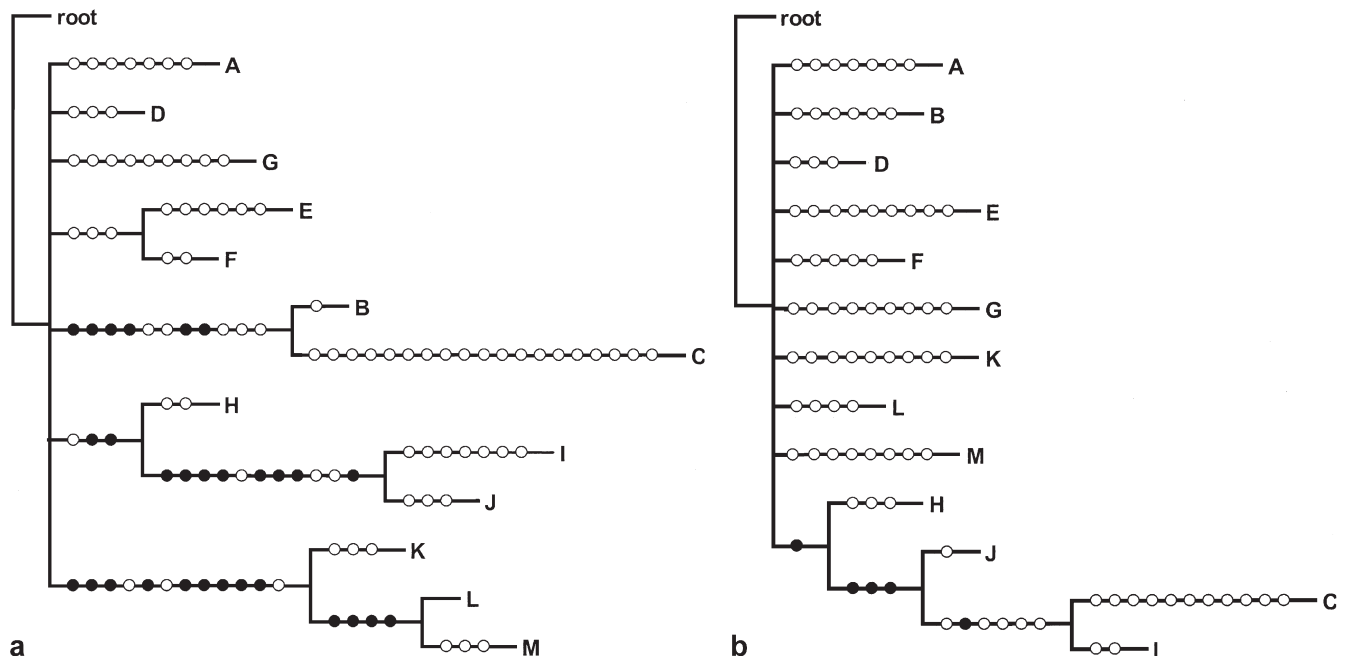


Fig. 2. Strict consensus cladograms resulting from the PAE. **a**, first run; **b**, second run. Areas A–M as in Fig. 1.

the Puna province with the Parana and Chacoan subregions (Fig. 1), supported by *Hypochaeris chillensis*, *H. albiflora* and *Lucilia acutifolia*. A third run did not allow identifying further generalized tracks.

The Puna and Parana provinces are connected with two different generalized tracks each, thus constituting nodes (Fig. 1). This allows speculating on the complex or “hybrid” nature of their biota.

Cladistic biogeography. — The analysis of the taxonomic area cladograms of *Barnadesia*, *Chuquiraga*, *Dasyphyllum*, *Hypochaeris*, and the *Lucilia* group with TASS produced 23 paralogy-free subtrees (Figs. S1–S5 in the Electronic Supplement). Based on the 53 components extracted from them, a data matrix (Table S2 in the Electronic Supplement) was constructed. The parsimony analysis gave five general area cladograms, with 112 steps, a consistency index of 0.46, and a retention index of 0.60. The strict consensus cladogram (Fig. 3) indicates a basic separation between the Atacama, Monte, and Prepuna provinces of the South American Transition Zone closely related to the Andean region, and the North Andean Paramo, Coastal Peruvian Desert and Puna provinces of the South American Transition Zone closely related to the Neotropical region.

DISCUSSION

Two of the generalized tracks obtained corroborate the notion that the Andean and Neotropical regions do constitute natural areas. On the other hand, the provinces of the South American Transition Zone are not joined by any generalized track, which is coherent with its transitional character. Two generalized tracks, however, join the Puna province with the Neotropical and Andean regions, which allows identifying them as nodes, as previously suggested (Katinas & al., 1999; Abrahamovich & al., 2004).

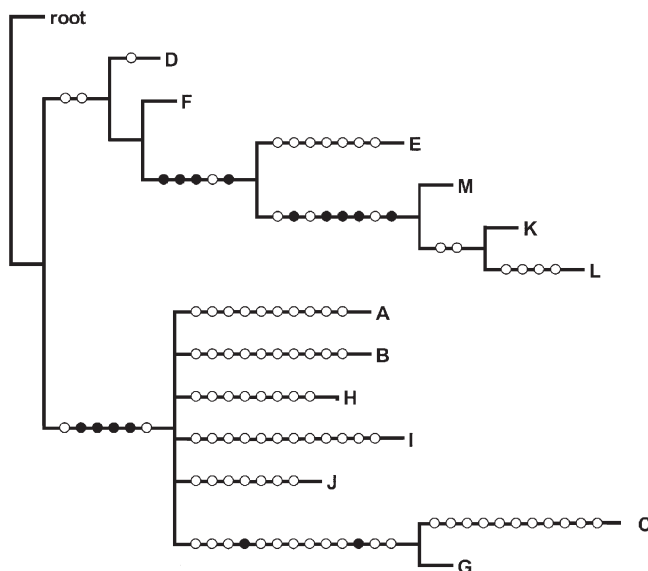


Fig. 3. General area cladogram. Areas A–M as in Fig. 1.

The cladistic biogeographic analysis corroborates the transitional character of the provinces assigned to the South American Transition Zone, because they do not constitute a monophyletic group, with some provinces related to the Andean region and others to the Neotropical region. The existence of a single, clear “tropical line” separating the Neotropical and Andean regions has been questioned by Rapoport (1968), Ruggiero & Ezcurra (2003) and Morrone (2004a, 2006). According to these authors, there is evidently a wide area with several “lines”, according to the different taxa analyzed. The two main clades of our general area cladogram allow drawing one of such boundaries between both regions, going from northern Chile to southern Argentina.

The panbiogeographic and cladistic biogeographic analyses represent the most basic steps of an evolutionary biogeographic analysis (Morrone, 2009). Future phylogeographic and molecular clock studies should incorporate a time perspective, by establishing when the different cenocrons (sets of taxa that share the same biogeographic history) assembled in the South American Transition Zone.

ACKNOWLEDGEMENTS

This work was supported by CONICET (Argentina) to E. Urtubey, FWF (Austria, grant number P1844b-B03) to T.F. Stuessy, a Juan de la Cierva postdoctoral fellowship (co-financed by the Spanish Ministerio de Educación y Ciencia and the European Social Fund) to K. Tremetsberger, and DGAPA-UNAM (Mexico) to J.J. Morrone.

LITERATURE CITED

- Abrahamovich, A., Díaz, N.B. & Morrone, J.J. 2004. Distributional patterns of the Neotropical and Andean species of the genus *Bombus* (Hymenoptera: Apidae). *Acta Zool. Mex.*, n.s., 20: 99–117.
- Anderberg, A.A. & Freire, S.E. 1991. A cladistic and biogeographic analysis of the *Lucilia* group (Asteraceae, Gnaphalieae). *Bot. J. Linn. Soc.* 106: 173–198.
- Berry, P.E. 1982. The systematics and evolution of *Fuchsia* sect. *Fuchsia* (Onagraceae). *Ann. Missouri Bot. Gard.* 69: 1–198.
- Cabrera, A.L. 1963. *Compositae*. Flora de la provincia de Buenos Aires 6. Buenos Aires: Colección Científica del INTA.
- Cabrera, A.L. 1971. *Compositae*. Flora Patagónica 7. Buenos Aires: Colección Científica del INTA.
- Cabrera, A.L. 1974. *Compositae*. Flora ilustrada de Entre Ríos 6. Buenos Aires: Colección Científica del INTA.
- Cabrera, A.L. 1978. *Compositae*. Flora de la Provincia de Jujuy 10. Buenos Aires: Colección Científica del INTA.
- Contreras-Medina, R., Luna, I. & Morrone, J.J. 2007. Gymnosperms and cladistic biogeography of the Mexican Transition Zone. *Taxon* 56: 905–915.
- Craw, R.C., Grehan, J.R. & Heads, M.J. 1999. *Panbiogeography: Tracking the history of life*. Oxford: Oxford Univ. Press.
- Ezcurra, C. 2002. Phylogeny, morphology, and biogeography of *Chuquiraga*, an Andean-Patagonian genus of Asteraceae-Barnadesioideae. *Bot. Rev.* 68: 153–170.
- García-Barros, E. 2003. Mariposas endémicas de la región Paleártica Occidental: Patrones de distribución y su análisis mediante parsimonia (Lepidoptera, Papilionoidea). *Graellsia* 59: 233–258.
- García-Barros, E., Gurrea, P., Luciani, M.J., Martín Cano, J., Munguira, M.L., Moreno, J.C., Sainz, H., Sanz, M.J. & Simón,

- J.C. 2002. Parsimony analysis of endemism and its application to animal and plant distributions in the Ibero-Balearic region (western Mediterranean). *J. Biogeogr.* 29: 109–124.
- Goloboff, P.** 1993. NONA, version 2. Tucumán, Argentina: published by the author. <http://www.cladistics.com/aboutNona.htm>.
- Gregory-Wodzicki, K.M.** 2000. Uplift history of the Central and Northern Andes: A review. *Bull. Geol. Soc. Amer.* 112: 1091–1105.
- Katinas, L., Morrone, J.J. & Crisci, J.V.** 1999. Track analysis reveals the composite nature of the Andean biota. *Austral. Syst. Bot.* 47: 111–130.
- Humphries, C.J. & Parenti, L.R.** 1999. *Cladistic biogeography: Interpreting patterns of plant and animal distributions*, 2nd ed. New York: Oxford Univ. Press.
- Jeffrey, C.** 2007. Introduction with key to tribes. Pp. 59–81 in: Kadereit, J.W. & Jeffrey, C. (eds.), *The families and genera of vascular plants*, vol. 8, *Flowering Plants; Eudicots; Asterales*. Berlin: Springer.
- Luna Vega, I., Alcántara Ayala, O., Morrone, J.J. & Espinosa Organista, D.** 2000. Track analysis and conservation priorities in the cloud forests of Hidalgo, Mexico. *Diversity Distrib.* 6: 137–143.
- Morrone, J.J.** 1994. On the identification of areas of endemism. *Syst. Biol.* 43: 438–441.
- Morrone, J.J.** 2001a. Toward a formal definition of the Paramo-Punan subregion and its provinces. *Revista Mus. Argent. Ci. Nat.*, n.s., 3: 1–12.
- Morrone, J.J.** 2001b. *Biogeografía de América Latina y el Caribe*. M&T-Manuales & Tesis SEA, vol. 3. Zaragoza: Sociedad Entomológica Aragonesa.
- Morrone, J.J.** 2004a. La zona de transición Sudamericana: Caracterización y relevancia evolutiva. *Acta Entomol. Chilena* 28: 41–50.
- Morrone, J.J.** 2004b. Panbiogeografía, componentes bióticos y zonas de transición. *Revista Brasil. Entomol.* 48: 149–162.
- Morrone, J.J.** 2006. Biogeographic areas and transition zones of Latin America and the Caribbean Islands, based on panbiogeographic and cladistic analyses of the entomofauna. *Annual Rev. Entomol.* 51: 467–494.
- Morrone, J.J.** 2009. *Evolutionary biogeography: An integrative approach with case studies*. New York: Columbia Univ. Press.
- Morrone, J.J. & Carpenter, J.M.** 1994. In search of a method for cladistic biogeography: An empirical comparison of component analysis, Brooks parsimony analysis, and three-area statements. *Cladistics* 10: 99–153.
- Nelson, G. & Ladiges, P.Y.** 1995. TASS. New York and Melbourne: Published by the authors.
- Nixon, K.C.** 1999. WinClada, version 0.9.99. Ithaca, New York: published by the author. <http://www.cladistics.com/aboutWinc.htm>.
- Rapoport, E.H.** 1968. Algunos problemas biogeográficos del Nuevo Mundo con especial referencia a la región Neotropical. Pp. 55–110 in: Delamare Deboutville, R. & Rapoport, E.H. (eds.), *Biologie de l'Amérique Australe*, vol. 4. Paris: CNRS.
- Rosen, B.R.** 1988. From fossils to earth history: Applied historical biogeography. Pp. 437–481 in: Myers, A.A. & Giller, P.S. (eds.), *Analytical biogeography: An integrated approach to the study of animal and plant distributions*. London, New York: Chapman and Hall.
- Ruggiero, A. & Ezcurra, C.** 2003. Regiones y transiciones biogeográficas: Complementariedad de los análisis en biogeografía histórica y ecológica. Pp. 141–154 in: Morrone, J.J. & Llorente, J. (eds.), *Una perspectiva latinoamericana de la biogeografía*. Mexico: Las Prensas de Ciencias, UNAM.
- Stuessy, T.F., Sang, T. & DeVore, M.L.** 1996. Phylogeny and biogeography of the subfamily Barnadesioideae with implications for early evolution of the Compositae. Pp. 463–490 in: Hind, D.J.N. & Beentje, H. (ed.), *Proceedings of the International Compositae Conference, Kew, 1994*, vol. 1, *Compositae: Systematics*. Kew: Royal Botanic Gardens.
- Stuessy, T.F., Urtubey, E. & Grünstäudl, M.** 2009. Barnadesieae (Barnadesioideae). Pp. 215–228 in: Funk, V., Susanna, A., Stuessy, T.F. & Bayer, R. (eds.), *Systematics, evolution and biogeography of Compositae*. Vienna: IAPT.
- Taylor, D.W.** 1991. Paleobiogeographic relationships of Andean angiosperms of Cretaceous to Pliocene age. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 88: 69–84.
- Taylor, D.W.** 1995. Cretaceous to Tertiary geologic and angiosperm paleobiogeographic history of the Andes. Pp. 3–9 in: Churchill, S.P. (ed.), *Biodiversity and conservation of Neotropical montane forests*. Bronx, New York: The New York Botanical Garden.
- Tremetsberger, K., Stuessy, T.F., Kadlec, G., Urtubey, E., Baeza, C.M., Beck, S.G., Valdebenito, H.A., Ruas, C de F. & Matzenbacher, N.I.** 2006. AFLP phylogeny of South American species of *Hypochaeris* (Asteraceae, Lactuceae). *Syst. Bot.* 31: 610–626.
- Urtubey, E.** 1999. Revisión del género *Barnadesia* (Asteraceae, Barnadesioideae). *Ann. Missouri Bot. Gard.* 86: 57–117.
- Urtubey, E. & Stuessy, T.F.** 2001. New hypotheses of phylogenetic relationships in Barnadesioideae (Asteraceae) based on morphology. *Taxon* 50: 1043–1066.