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Spatial methodologies in historical biogeography of islands

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The study of insular biotas has influenced biology for a considerable period of time. The uniqueness of many biotic assemblages on islands or isolated ecosystems (e.g. mountaintops, caves or lakes), which act as habitat islands has prompted the development of biological fields such as evolutionary biology and ecology.

It is well known that the ideas of Darwin and Wallace on evolution were rooted in a historical approach to the geographical distribution of organisms (Crisci & Katinas, 2009). As Darwin himself put it: ‘In considering the distribution of organic beings over the face of the globe, the first great fact which strikes us is, that neither the similarity nor the dissimilarity of the inhabitants of various regions can be accounted for by their climatal and other physical conditions’ (Darwin, 1859: 346, quoted in Crisci & Katinas, 2009). Notably, the experiences of Darwin on the Galapagos and Wallace in the East Indies profoundly influenced their thinking (Brown & Lomolino, 1998) through the observed patterns of organism distributions in those archipelagos. So, island biogeography has been the root of major paradigm shifts which affect the entire field of biology.

Heaney (2007) postulates that current island biogeographic research is framed in two opposite paradigms that have existed side by side during the last four decades. These two paradigms are MacArthur and Wilson’s (1963, 1967) equilibrium theory of island biogeography, and vicariance biogeography (Nelson & Platnick, 1981). Alternatively, equilibrium theory and vicariance biogeography may be better placed as two different approaches to biogeography: ecology vs history (see Crisci *et al.*, 2003).

While MacArthur and Wilson’s (1963, 1967) equilibrium theory is an approach to ecological biogeography, vicariance biogeography is an approach to historical biogeography. Ecological and historical biogeography are two research traditions

which have been distinguished since the early nineteenth century (de Candolle, 1820, as 'stations' and 'habitations', respectively). Each subdiscipline uses different epistemological approaches in addition to focusing on different spatio-temporal scales – i.e. evolutionary processes occurring over millions of years on a large, often global, scale in historical biogeography versus ecological processes occurring over a short temporal and small spatial scale in ecological biogeography (Myers & Giller, 1988; Crisci *et al.*, 2006).

Within a historical biogeographic framework, the emergence of phylogenetic and molecular systematics over the past years has been widely employed to infer evolutionary and biogeographic hypotheses on islands. For example, molecular information has been applied to study colonisation scenarios in such well-known islands and archipelagos as Hawaii (Desalle, 1995; Baldwin & Robichaux, 1995), Macaronesia (Helfgott *et al.*, 2000; Francisco-Ortega *et al.*, 1997), Caribbean islands (Calsbeek & Smith, 2003; Vidal *et al.*, 2008) and Madagascar (Yoder & Nowak, 2006).

Historical biogeographic, non-phylogeny-based, approaches exist which are also important tools for providing testable hypotheses to explain the spatial arrangement of island and continental organisms. To Darwin, the distribution of organisms was sufficiently historically informative that it became central in his evolutionary theory. This belief prevailed until the arrival of modern methods of phylogenetic reconstruction, especially those using molecular data. Hence, the empirical data on geographical distribution of organisms that were so useful to Darwin and others are in many current analyses considered historically uninformative if they are not combined with a phylogenetic analysis. Thus, geographical distributions become informative, understandable and comparable only when combined with a genealogical hypothesis and expressed in an area cladogram. The construction of area cladograms assumes that the nodes of the cladograms, with their information about relationships among taxa, are the medium through which geographical distributions are conveyed in a historically informative way.

There are, however, authors who support the idea that the geographical distribution of organisms, in itself, is historically informative. Craw *et al.* (1999) stressed that many aspects of current distribution (geographical structure, distributional limits, spatial geometry, boundaries and range, etc.) are potentially informative of evolutionary aspects. They emphasised the importance of the spatial or geographical dimension of life's diversity in the study of biogeography. This attempt is based on the panbiogeographical approach of Croizat (1958, 1964). Another method that focuses on the distribution of organisms is parsimony analysis of endemism or PAE (Rosen, 1988), which classifies areas (or localities or quadrats) according to their shared taxa, resulting in a hierarchical classification of the geographical units. According to Rosen (1988) parsimony analysis of endemism generates historical

(hence geological) hypotheses even from modern distributions (Crisci & Katinas, 2009).

In the last few years, there has been an extraordinary development of what is called 'spatial thinking' (National Research Council, 2006). Spatial thinking is not a content-based discipline in the way that physics, biology or economics are disciplines: it is not a stand-alone subject in its own right. It is a way of thinking that permeates those disciplines and virtually all subject matter disciplines. Spatial thinking is one form of thinking based on three elements: concepts of space, tools of representation and processes of reasoning. It is the concept of space that makes spatial thinking a distinctive form of thinking. By understanding the meaning of space, its properties (e.g. dimensionality, continuity, proximity and separation) can be used as a vehicle for structuring problems, finding answers and expressing solutions. Expressing relationships within spatial structures (e.g. maps) enables perception, recognition and analysis of the static and, via transformations, the dynamic properties of objects and the relationships between objects. This is clearly the way that Darwin, through the analysis of geographic distribution of South American living and fossil organisms, justified the reality of biological evolution, and established natural selection as the promoting process of evolution. It is also the underlying philosophy of panbiogeography and PAE. These two approaches can be referred to as 'spatial methodologies'.

In this chapter we will briefly describe parsimony analysis of endemism (PAE) and panbiogeography track compatibility analysis; and present examples of their application to insular systems of southern South America, including habitat and continental and oceanic island systems.

Parsimony analysis of endemism

Parsimony analysis of endemism or PAE is a tool of historical biogeography that allows discovery of the natural patterns of organism distribution (Rosen, 1988; Rosen & Smith, 1988). PAE classifies geographic units (e.g. localities, quadrats or areas) according to their shared taxa by means of the most parsimonious solution (parsimony criterion) (Crisci *et al.*, 2003). PAE is one of the most widely applied techniques described in the historical biogeographic literature (Posadas & Donato, 2007). PAE was developed based on an analogy between systematics and biogeography. This analogy is established on the basis that taxa distribution in geographical units is analogous to character distribution in taxa. For example, one character could be unique to a taxon (autapomorphy) or it could be shared by two or more taxa; similarly, one taxon could be unique to one locality or it could inhabit two or more localities. Then, it is possible to proceed to analyse distributional data of taxa using the same methodological tools as to analyse character distribution among

taxa. Rosen (1988) proposed that parsimony analysis, as in cladistic systematics, could be usefully applied to the distribution of taxa. Thus, PAE application consists in the construction of a data matrix in which terminals are represented by area units and characters are represented by the presence (scored with 1) or absence (scored with 0) of taxa. The data matrix is then analysed using a parsimony algorithm resulting in an area cladogram, which reflects relationships between the area units considered.

PAE has been criticised because it ignores cladistic relationships among taxa, considering only their distributions (Humphries, 1989). Garzón-Orduña *et al.* (2008), by comparing PAE results with that of other historical biogeographical methodologies (e.g. Brooks parsimony analysis and dispersal-vicariance analysis), concluded that PAE aims to describe but does not explain the current distribution of organisms in terms of historical biogeography. These authors disregard PAE as a historical biogeographical method. They propose that PAE is a useful tool in other biogeographical or ecological analyses for exploring the distribution of taxa or for establishing hypotheses of primary homology between areas. Nonetheless, the search for primary homology between areas is a necessary first step in historical biogeography. According to Rosen (1988), a PAE cladogram represents a hypothesis of contemporaneous ecological conditions, where sister localities are then those that are most closely related ecologically. In addition, PAE cladograms represent schemes of successive emergences of biotas, that is, relative recency of biotic interchange between sister localities or, conversely, historical sequences of biotic divergences and isolations.

Panbiogeography track compatibility analysis

Panbiogeography is an approach to historical biogeography that focuses on the role of place in the history of life. It was originally proposed by Léon Croizat (1952, 1958, 1964, 1981). Panbiogeographers acknowledge that an understanding of locality is a fundamental precondition to any adequate analysis of the patterns and processes of evolutionary change (Crisci *et al.*, 2003).

Croizat (1964) posed the idea that barriers evolve together with biotas when he postulated that 'earth and life evolve together'. From this seminal statement grew the concept of panbiogeography. Croizat's method was basically graphic, consisting of plotting distributions of organisms on maps and connecting the disjunct distribution areas (or collection localities) together with lines called tracks. If superimposing of individual tracks of unrelated groups of organisms showed coincidence, the resulting summary lines were considered generalised tracks. According to panbiogeographic thinking, generalised tracks indicate the preexistence of ancestral biotas, which subsequently become fragmented by tectonic and/or climatic

change. Intersection of two or more generalised tracks in a given area results in a panbiogeographic node. A node is interpreted as a composite area in which different ancestral biotic and geologic fragments interrelate in space-time. Generalised tracks commonly stretch across the major oceanic barriers (e.g. between New Zealand and South America through the Pacific Ocean). Croizat thus developed the concept of considering the ocean basins, not continents, as the major focus for biogeographic attention (Keast, 1991).

Several authors developed quantitative approaches to panbiogeography. Probably the most accepted one has been the track compatibility analysis developed by Craw (1988, 1989). Craw's method is based on the concept of distributional compatibility. In track compatibility analysis, two or more individual tracks are considered compatible with each other when tracks are either included within or replicated by one another (Crisci *et al.*, 2003; Katinas *et al.*, 2004). Thus, in panbiogeography, compatibility is applied in a more restricted way compared with its original use in taxonomy (see Meacham, 1984).

A data matrix of areas vs tracks is constructed to apply track compatibility analysis. In this matrix an entry is 1 if the track is present in the area and 0 if it is absent. The matrix is analysed by means of a compatibility algorithm to find the largest cliques of compatible tracks. If more than one large clique or several cliques of considerable size are found, it could be hypothesised that: (1) several generalised tracks link the localities or distribution areas in different ways, or (2) those tracks common to all the largest cliques can be identified as a generalised track (Craw, 1989). According to the first hypothesis, a given locality or distribution area could be part of more than one generalised track, which is not allowed in the second hypothesis.

Example 1: Tierra del Fuego

The Antarctic is a continental mass which is isolated from the other continents by a wide oceanic belt (from $c.66^{\circ}$ S to 40° S). The subantarctic islands, southern New Zealand and Tierra del Fuego are the only terrestrial areas that penetrate this oceanic zone.

The Tierra del Fuego archipelago constitutes the southernmost tip of Patagonia in South America. It has a surface area of 66 000 km². From a biogeographic viewpoint, Tierra del Fuego belongs to the Subantarctic subregion of the Andean region (Morrone, 2001). However, floristically, southern South America (including Tierra del Fuego) has been a controversial area belonging either to the Antarctic or to the Neotropical floristic kingdoms (Tuhkanen *et al.*, 1990).

The archipelago is characterised by the presence of the Andean cordillera, which generates a remarkable topographic and climatic gradient over short distances.

Thus, the phytogeographical zones of the archipelago form a gradient of vegetation formation from semiarid steppes (northeast) to the extremely humid Magellanic forest and oceanic heath in the west and south (Niemelä, 1990). In southeastern Patagonia and northern Tierra del Fuego the Antarctic floristic element of moist and cool climatic conditions (as cushion plants and soft herbs) is mixed with spiny dwarf shrubs, annual grasses and tussocks (typical of Patagonian semiarid flora). Such mixing constitutes a transitional belt of humid steppe, the sub-Andean floristic province described by Cabrera (1978). According to Tuhkanen *et al.* (1990), several Antarctic genera are conspicuous in this area (e.g. *Acaena*, *Nothofagus*), representing the ancient Gondwanan flora. These Antarctic elements occupied southern South America, New Zealand and Tasmania, and fossil evidence of their presence has been found in the Kerguelen Islands and Antarctic Peninsula. Summarising, the flora of Tierra del Fuego could be interpreted as an extension of that of southern South America and it shows connection with other austral areas, including the subantarctic islands.

The subantarctic islands (Fig. 3.1) form a loose ring within the latitudinal belt of 54° to 48° S clustered around the major climatic and oceanic boundary, the Antarctic Polar Frontal Zone (Whinan *et al.*, 2005). The main islands of this group are: Islas Malvinas (Falkland Islands), South Georgia, Diego Ramírez, Tristan da Cunha–Gough in the South Atlantic Ocean; Macquarie, Campbell, Auckland and Chatham in the South Pacific Ocean; and Marion, Crozet, Prince Edward, Amsterdam, Kerguelen and Heard in the South Indian Ocean. Bergstrom and Chown (1999) classified subantarctic islands into two groups according to their history: older islands with a continental origin (e.g. Islas Malvinas, South Georgia, Campbell and Auckland); and younger islands, of volcanic origin (e.g. most of the subantarctic islands of the Indian Ocean).

The objective of this analysis is to apply a spatial-based biogeographic methodology to infer the relationships of the flora of Tierra del Fuego with that of other areas, especially subantarctic islands.

Material and methods

Delimitation of areas

We included all areas that share vascular plant species with Tierra del Fuego. A total of 20 areas were considered, which included continental areas and islands. Among the continental areas are North America, Eurasia, Africa, the Antarctic Peninsula, South East Australia and South America. The latter was divided in its main biogeographic components, Andean and Neotropical regions, since South America is a hybrid area according to previous studies (e.g. Crisci *et al.*, 1991; Katinas *et al.*, 1999). Among islands, we included the subantarctic group and other islands. In the

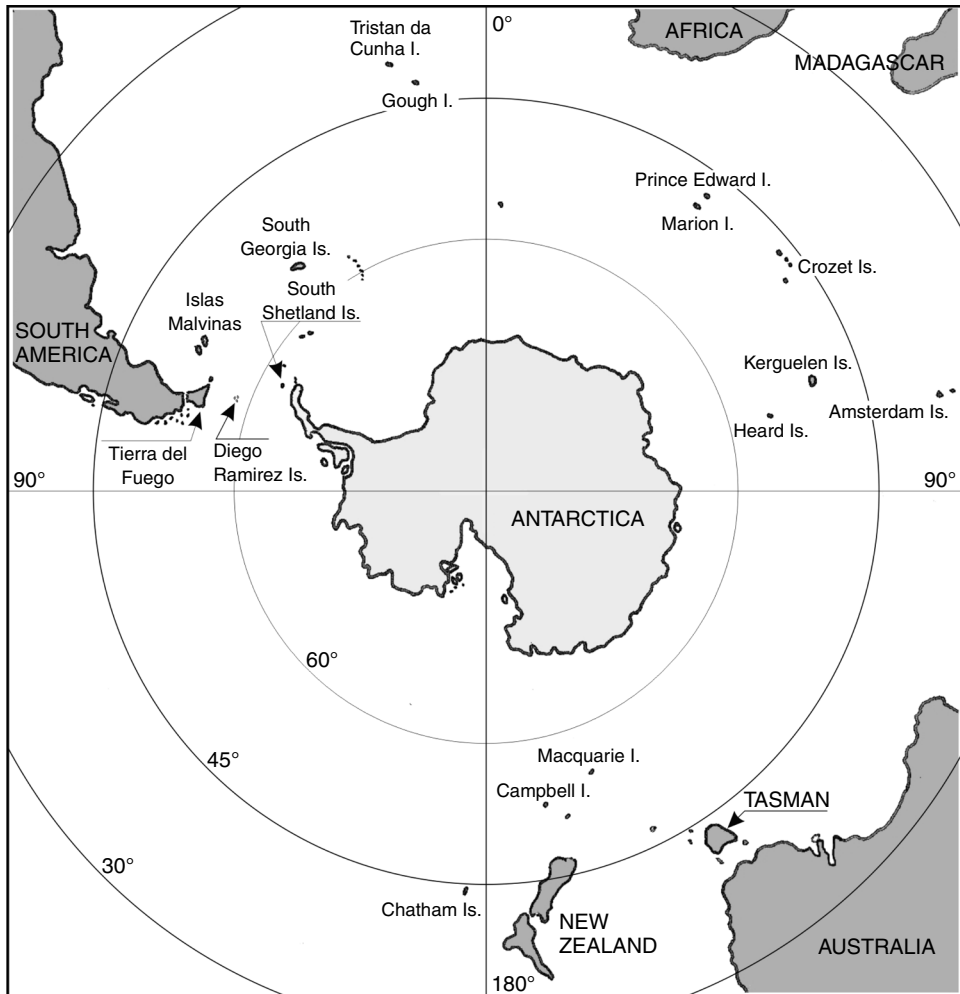


Figure 3.1 Map showing the main areas considered in the parsimony analysis of endemism of Tierra del Fuego's flora.

first group we included Islas Malvinas, South Georgia, Diego Ramírez, Tristan da Cunha–Gough, Crozet–Prince Edward–Marion, Kerguelen–Heard–Amsterdam, Macquarie–Campbell, Chatham and New Zealand. In the second group we included Islas Juan Fernández and Tasmania.

Selection of taxa

Distributional data of the 386 species and infraspecific taxa of vascular plants inhabiting Tierra del Fuego were considered. Data were taken from *Flora of Tierra del Fuego* (Moore, 1983). Nomenclatural changes and current systematic status of each taxon were checked with recent literature (e.g. Zuloaga *et al.*, 2008). The

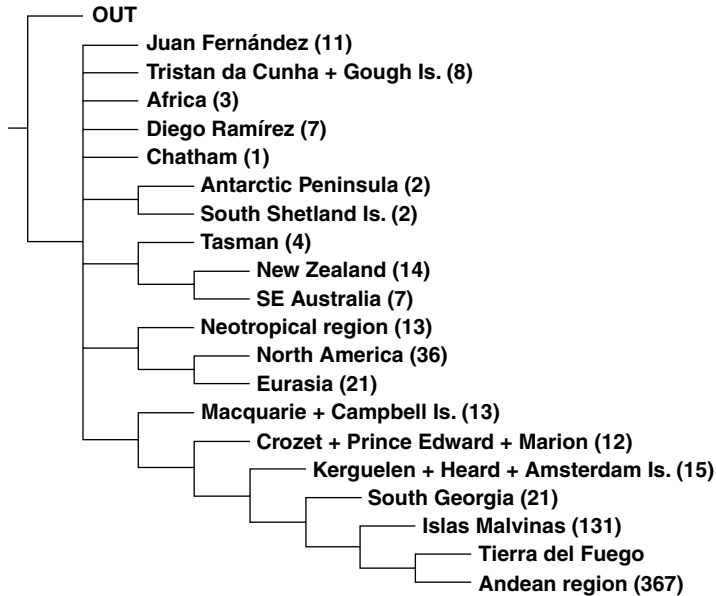


Figure 3.2 Strict consensus cladogram resulting from parsimony analysis of endemism applied to the flora from Tierra del Fuego. Numbers indicate the quantity of species in each area also present in Tierra del Fuego.

distribution of each taxon beyond Tierra del Fuego was confirmed from the literature in checklists, floristic treatments and revisionary studies (e.g. Dawson, 1958; Greene & Groves, 1963; Lindsay, 1971; Allison & Smith, 1973; Meurk *et al.*, 1994; Convey, 1996; Convey *et al.*, 2000; Bergstrom *et al.*, 2006). Adventitious, cultivated and naturalised species were excluded from the analysis.

Parsimony analysis of endemism

A data matrix of 21 areas (the 20 aforementioned plus a hypothetical outgroup with all species absent) by 386 taxa (presence in a given area coded as 1 and absence as 0) was analysed using TNT ver. 1.1 (Goloboff *et al.*, 2003). An exhaustive search was applied using implicit enumeration option.

Results and discussion

Parsimony analysis of the data matrix yielded five equally most parsimonious cladograms ($L = 493$). The strict consensus cladogram is shown in Fig. 3.2. Since our analysis focuses on Tierra del Fuego archipelago relationships, the main group of interest in our results is that containing Tierra del Fuego. The archipelago is part of a pectinate clade which contains a continental Andean region and several sub-antarctic islands. The most basal area of this clade is occupied by the South Pacific

Campbell and Macquarie islands, which share 13 plant species with Tierra del Fuego. The next two groups of islands in the clade are the South Indian Ocean subantarctic islands: first, the group composed of Crozet, Prince Edward and Marion islands (sharing 12 plant species with Tierra del Fuego); second, the group containing Kerguelen, Heard and Amsterdam islands (this group shares 15 plant species with Tierra del Fuego). Then, the South Atlantic subantarctic islands are depicted in the cladogram: first, South Georgia (which shares 21 species with Tierra del Fuego), followed by Islas Malvinas (131 species in common with Tierra del Fuego). The Andean region and Tierra del Fuego are sister areas with 367 species in common, of the 386 considered. The relationships of Tierra del Fuego's flora can be summarised as follows: (Pacific Ocean subantarctic islands (Indian Ocean subantarctic islands (Atlantic Ocean subantarctic islands (continental Andean region, Tierra del Fuego))). This means that Tierra del Fuego flora shows a movement from West to East across the southern oceans to other subantarctic islands. This sequence is congruent with the direction of the Antarctic Circumpolar Current (West Wind Drift).

When considering the number of Tierra del Fuego's plant species present in the other areas according to the depiction sequence of the clade, we observed an increasing quantity of shared species in those areas more closely related to Tierra del Fuego (see Fig. 3.2). However, the number of Fuegian species in the other areas did not affect the topology of the cladogram, since distant areas such as North America, which has 35 species in common with Tierra del Fuego, appears in a separate clade (see Fig. 3.2).

The sister relation of Tierra del Fuego with the continental Andean region and the relationships of this pair with Islas Malvinas have been established for other taxonomic groups. Morrone (1998) found these same relationships when applying PAE to analyse the weevil fauna (Insecta: Coleoptera: Curculionidae) of subantarctic islands. In fact, as pointed out above, Tierra del Fuego's flora includes part of the Magellanic forest and moorland and the semiarid Patagonian steppe of southernmost South America. Also, the closest relation between Tierra del Fuego and the Andean region with Islas Malvinas is expected, since Islas Malvinas' flora is very similar to that of Tierra del Fuego, except for the lack of arboreal species and a diminished number of other species (Posadas, 2008). Posadas and Morrone (2004) have hypothesised that the geographical isolation of Islas Malvinas from Tierra del Fuego was broken more than once during sea-level changes in Tertiary and Quaternary times. The link of Tierra del Fuego flora with other subantarctic islands following the sequence South Atlantic–South Indian–South Pacific Ocean, in accordance with the Antarctic Circumpolar Current, could indicate a transoceanic dispersal origin. However, it is important to note that the final breakup of southern South America and the Antarctic Peninsula occurred around 30 million years ago

(Ma). This created the Drake Passage and generated the Antarctic Circumpolar Current (Ortiz-Jaureguizar & Cladera, 2006), which led to climatic changes in Antarctica, accompanying the marked fall in marine temperatures (Zachos *et al.*, 2001). By this time, most of the ‘younger’ subantarctic islands had already emerged. For example, the Kerguelen Plateau, in which the Kerguelen, Heard and McDonald archipelagos are placed, is dated as older than 110 Ma (Duncan, 2002). The Kerguelen archipelago exhibits volcanism dated from 29 Ma to the Pleistocene (Wallace *et al.*, 2002). Thus, an alternative hypothesis to long-distance dispersal must be considered: at least part of the flora of subantarctic islands could belong to a widespread Antarctic-subantarctic flora fragmented by tectonic and climatic events. Antarctica could hold the key to testing these alternative hypotheses through its fossil record.

These two hypotheses require testing through new geological, palaeontological and phylogenetic information.

Example 2: the Tandilia and Ventania mountain ranges

Since Darwin’s journey in Argentina in 1835 the geology of Tandilia and Ventania and their inhabiting biota have attracted several generations of geologists and biologists (Crisci *et al.*, 2001). Tandilia and Ventania are the only systems of mountain ranges situated in a grassy steppe or ‘pampas’ in the political province of Buenos Aires, in central eastern Argentina. The pampas are a plain situated at sea level, or even below sea level (e.g. the big depression of the Salado river), with the exception of two major systems of mountain ranges or ‘sierras’, namely Tandilia and Ventania. From a geological point of view the two areas do not appear to be closely related. Tandilia (500 m high), in the southeast of Buenos Aires province, originated in the Proterozoic Age, being the oldest nucleus in Argentina (2200 Ma). Ventania (900–1000 m high) is located in the southwest of the province and has a more recent origin dating from the Palaeozoic (490 Ma). Gondwanaland and pre-Gondwanaland events seem to have played a major role in the building of these mountain ranges.

Biologically, Tandilia and Ventania exhibit a high taxon diversity and endemism. These mountain ranges not only have a characteristic petrophilous flora, but are the only regions in the province with endemic plant taxa. Within the diverse plant families inhabiting Tandilia and Ventania, Asteraceae hold second place (after Poaceae, the grass family). Approximately 30% of the Asteraceae known in Buenos Aires province occur in Ventania and Tandilia. In addition, there are four species of Asteraceae endemic to Tandilia, three species and two varieties endemic to Ventania, and one species endemic to both. Based on their

particular biodiversity, and isolation within grassy ecosystems, these ranges are considered orographic islands (Kristensen & Frangi, 1995) or habitat islands. According to MacArthur (1984), the chief difference between habitat islands on the mainland and oceanic islands is that the latter exist in a vacuum insofar as land birds or insects are concerned whereas mainland islands are adjacent to other habitats filled with birds and insects. Consequently, provided that the mainland islands are not too different from their surroundings, birds from the surrounding areas are able to migrate onto mainland islands more frequently and with more success than for immigration onto oceanic islands. Crisci *et al.* (2001) wondered if the same principle could be applied to plants, exemplified by Asteraceae.

A parsimony analysis of endemism and a track compatibility analysis were carried out (Crisci *et al.*, 2001) to seek historical explanations for the high diversity and endemism of Asteraceae in these island-like mountain ranges and the relationships of the biota inhabiting Tandilia and Ventania with other areas.

Material and methods

Delimitation of areas

Thirteen areas were delimited for this study on the basis of several overlapping taxon distributions and phytogeographical and geological criteria: Central Chile (CC), Central and North America (CNA), Chaco (CHA), Mahuidas (MA), northern Andes (NA), Pampa (PAM), Patagonia (PAT), Sierras Pampeanas (SPA), Sierras Subandinas (SA), southern Brazil (SB), Tandilia (TA), Uruguay (UR) and Ventania (VE). Mahuidas, Pampeanas and Subandinas are mountain ranges west of Tandilia and Ventania.

Selection of taxa

Distributional data of the 112 species and infraspecific taxa of Asteraceae inhabiting Tandilia and Ventania were analysed. Data were obtained from the labels of specimens (*c.*2500, correctly identified prior to data extraction) at the Herbarium of La Plata, Argentina (LP) and from the literature (checklists, floristic treatments and revisionary studies). Adventitious, cultivated, naturalised and cosmopolitan species were excluded from the analysis.

Track compatibility analysis

Distributions of the 112 taxa were plotted on maps and their separate distribution localities were connected with lines (individual tracks) according to their geographic proximity. The constructed data matrix (13 areas × 112 tracks) was analysed using SECANT 2.2 (Salisbury, 1999).

Parsimony analysis of endemicity

The same areas and matrix used in the track compatibility analysis were used and analysed for PAE, using PAUP* version 4.0 beta 2 (Swofford, 1999) and applying the branch-and-bound option. A strict consensus tree was constructed based on the results generated from PAUP*. The cladogram was rooted with a hypothetical area coded all zeros.

Results

Track compatibility analysis

Analysis of the data matrix resulted in four largest cliques (generalised tracks) of 30 individual tracks each (Fig. 3.3A–D). The intersection of 27 individual tracks common to the four largest cliques is identified as the fifth clique or generalised track (Fig. 3.3E). In this way, six individual tracks are combined in groups of three with the 27 individual tracks to form the four cliques of 30 individual tracks. The main distributional pattern obtained connects Tandilia and Ventania with southern Brazil, Pampa, Uruguay and Sierras Pampeanas.

Parsimony analysis of endemicity

Analysis of the data matrix generated four area cladograms (Fig. 3.4A–D). The strict consensus of the four trees (Fig. 3.4E) shows the following area relationships:

(Mahuidas (Patagonia (Chile (Sierras Subandinas (Sierras Pampeanas (Ventania (Pampa (southern Brazil-Tandilia-Uruguay)))))))).

Comparison of methods

Comparison of the results obtained applying track compatibility analysis and parsimony analysis of endemicity to the areas under study shows a coincidence in the relationships of Sierras Pampeanas (SPA), Ventania (VE), Pampa (PAM), southern Brazil (SB), Tandilia (TA) and Uruguay (UR). The areas relationship PAM-SB-SPA-TA-UR-VE forms a main distributional pattern strongly supported by the two approaches, and represented in Fig. 3.5 as a generalised track. Both methods show that Tandilia is more closely related to Uruguay, southern Brazil and Pampa than to Ventania or other austral areas. In addition, PAE and track compatibility analysis resulted in different relationships of the remaining areas with the main distributional pattern or generalised track.

Discussion

The main distributional pattern connecting Tandilia and Ventania with southern Brazil, Pampa, Uruguay and Sierras Pampeanas agrees with the previous

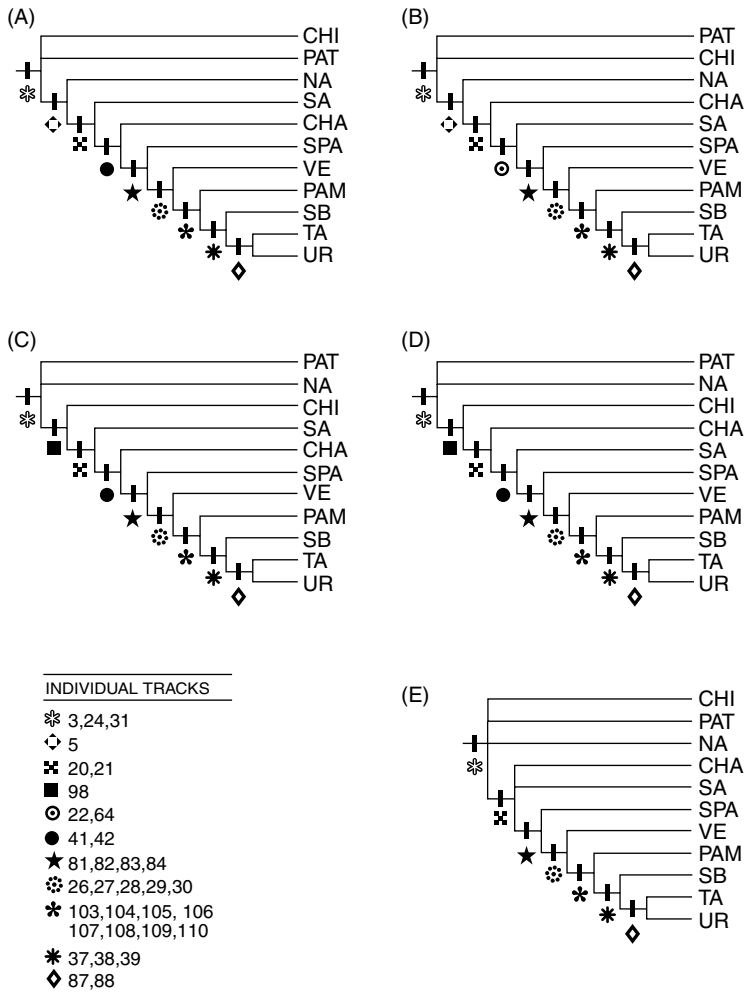


Figure 3.3 Largest cliques resulting from track compatibility analysis of Asteraceae from Tandilia and Ventania. A–D: Four largest cliques (generalised tracks) of 30 individual tracks each. E: Intersection of 27 individual tracks common to the four largest cliques. Abbreviations as in text. Each number corresponds to a taxon name as cited in the original list of taxa (see Crisci *et al.*, 2001).

hypothesis. A biotic migratorial route from the Andes to Brazil, through Sierras Pampeanas, the sierras of Buenos Aires, the sierras of Uruguay and Planalto and the sierras of Brazil was postulated many years ago (e.g. Hicken, 1918–1919). Frenguelli (1950) gave the name of peripampasic orogenic arc (‘arco peripam-pásico serrano’) to a biotic corridor constituting Sierras Pampeanas, Mahuidas and Tandilia. De la Sota (1967) concluded that the pteridological flora of Tandilia and Ventania have four origins – Austral-Antarctic, Andean-Pampean, Austrobrazilian and endemic – and that these mountain ranges constitutes an

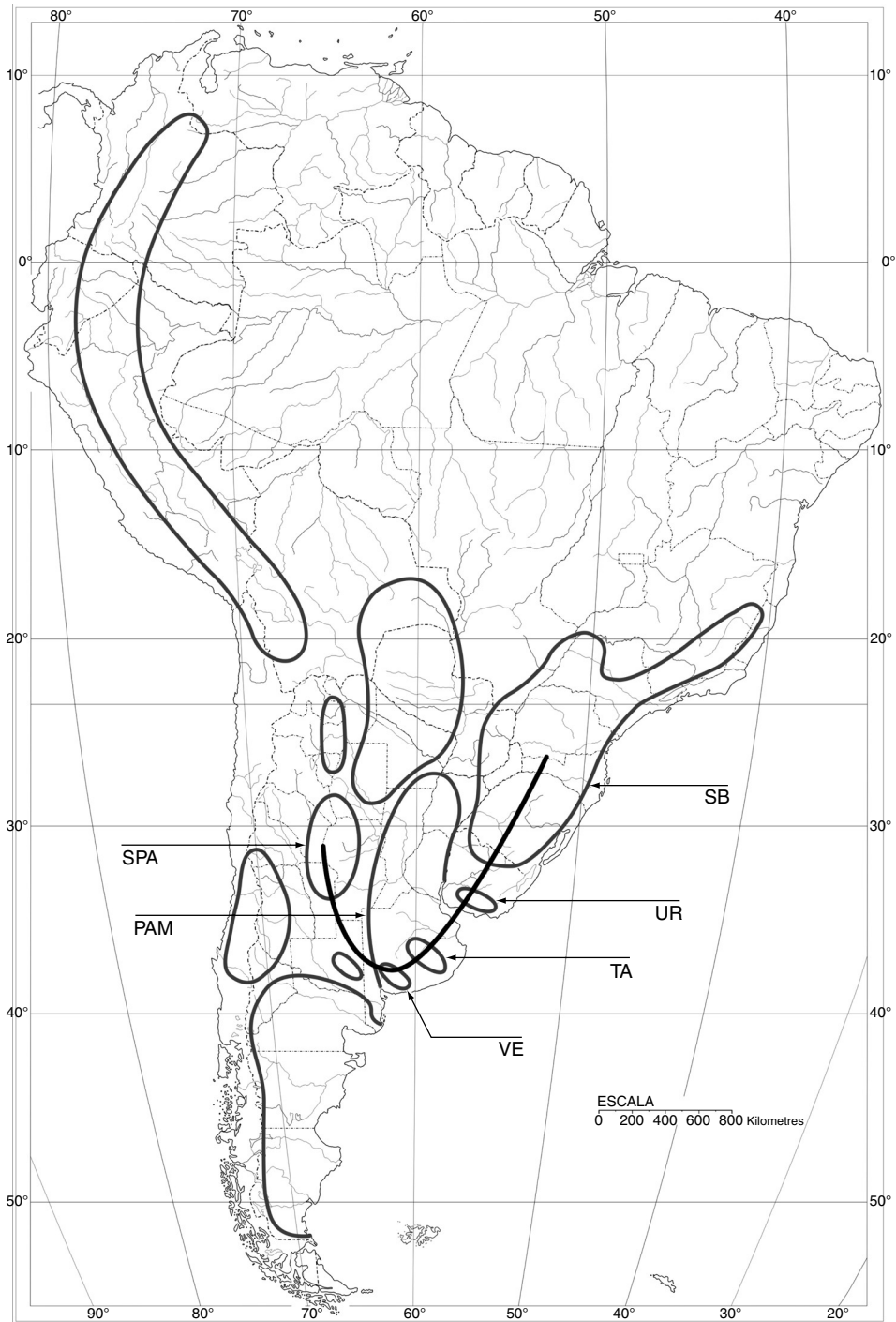


Figure 3.5 Map showing the main distributional pattern of Asteraceae from Tandilia and Ventania represented as a generalised track according to track compatibility analysis and parsimony analysis of endemity. Abbreviations as in text. Modified from Crisci *et al.* (2001).

intermediate orophilous station on a migratorial route. Therefore, the study of different plant and animal taxa inhabiting Tandilia and Ventania, including this example of Asteraceae, coincide with the idea of these mountain ranges being part of a biotic corridor.

The relationships of the Asteraceae inhabiting Tandilia with Uruguay and southern Brazil rather than with Ventania coincide with the different origins of these mountain ranges. Tandilia was a part of the Rio de la Plata craton together with northeastern Argentina, east Paraguay, Uruguay and southeast Brazil. Ventania, on the other hand, was the result of the collision of a Patagonian block that drifted from the south. The family Asteraceae was hypothesised to have originated in southern South America during the Oligocene (Stuessy *et al.*, 1996), long before Tandilia and Ventania were raised. The uplift of the Andes and the Pleistocene glaciations may have significantly affected the evolution of this family in South America. The former event resulted in drier climatic conditions beginning in the Miocene (25.5 Ma) and in additional uplift of several mountain systems. The Quaternary glaciations resulted in dry and wet cycles that caused fragmentation and differentiation of populations (Simpson Vuilleumier, 1971; Simpson, 1975). The main distributional pattern found in this study and the high endemism of Asteraceae now found in Tandilia and Ventania could be explained by these two events that resulted in eventual fragmentation of populations in more elevated regions, restricted now to rocky and loose soils.

Conclusions

The two examples presented here, applying PAE and panbiogeography, illustrate the importance of geographic information as spatial data to infer the biogeographic history of organisms. The use of phylogenies in most historical biogeographic studies, which has become mandatory in the last years, has obscured the great relevance of the use of space information on biogeography.

Biogeography is fundamentally based in spatial thinking and it would be an error to disregard spatial information as visualised by spatial thinking, i.e. the use of space as a framework for scientific understanding of the nature, structure and function of evolutionary phenomena. Panbiogeography and PAE are historical biogeographic approaches which apply spatial thinking, since both of them use the spatial information of taxa as the main source to uncover their distributional histories.

Islands (oceanic, continental or habitat islands) are perfect subjects for biogeographical analysis, since they have clear limits which separate each from its surrounding areas. Their isolation generates questions about the relationship of their biotas, questions which can only be answered in terms of spatial thinking.

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