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Distributional modelling and parsimony analysis of endemicity of *Senecio* in the Mediterranean-type climate area of Central Chile

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ABSTRACT

Aim Floristic blocks and areas of endemism resulting from a parsimony analysis of endemicity (PAE) using raw floristic data versus data generated from distributional modelling for 130 species in the genus *Senecio* Tourn. ex L. distributed in the Mediterranean-type climate area of central Chile were compared, and the results were used to identify conservation priorities for the flora of the region.

Location Central Chile, between 30° and 38° S.

Methods Using herbarium records, a species × area matrix consisting of presence/absence data was constructed from a $0.5° \times 0.5°$ grid. Distributional modelling techniques incorporating vegetation formations, elevation and the contagion index were used to interpolate floristic composition of poorly known areas. Parsimony analysis of endemicity was used to identify floristic blocks and areas of endemism.

Results Using the number of most parsimonious trees as an index, distributional modelling greatly optimized the results of the PAE analysis. Three floristic blocks and four areas of endemism were suggested based on the PAE results using potential distribution data not incorporating the contagion index, while four blocks and two areas of endemism were suggested from the PAE results using potential distribution data incorporating the contagion index. Floristic blocks for the northern coast, southern Andes, and northern/central Andes were found, with some blocks showing divisions within them representing distinct geographic subunits. Major breaks between and within floristic blocks were identified at 32.5°–33° S and 34.5°–35° S.

Main conclusions The floristic blocks identified with the distributional modelling and PAE correspond well to results from some previous studies and support hypothesized biogeographic divisions within Central Chile. The results were similar to those obtained from parallel analysis of the entire tree flora of central Chile. The vegetative formation-based distributional modelling produced robust and reproducible results when used along with PAE, especially when the contagion index was incorporated, and is a useful technique for area classification. The results demonstrate the utility of *Senecio* as an indicator genus for biogeography and conservation in southern South America.

Keywords

Parsimony analysis of endemicity, Central Chilean biodiversity hotspot, *Senecio*, biogeography, distributional modelling, contagion index, conservation.

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INTRODUCTION

A growing consensus of conservation biology is that the spatial configuration and size of protected areas should maximize the number and uniqueness of species protected, given that total area available for conservation is limited by the availability of non-arable and non-usable land for human habitation, and resources for acquiring and managing protected lands. Toward this end, a number of iterative algorithms have been developed (e.g. Kirkpatrick, 1983; Margules *et al.*, 1988; Vane-Wright *et al.*, 1991; Pressey *et al.*, 1994; Williams, 1995, 1996) allowing the selection and prioritization of areas for conservation. Parsimony Analysis of Endemicity (PAE) is another method that is useful for guiding conservation action (Posadas, 1996). PAE, originally developed by Rosen (1988), is a cladistic method that groups areas by their shared taxa according to the most parsimonious solution (Morrone & Crisci, 1995). The original PAE analysis has been modified to identify areas of endemism by using a system of quadrants as the units of analysis (Morrone, 1994a; Posadas, 1996; Linder, 2001; García-Barros *et al.*, 2002). PAE can also be used to identify floristic and faunistic areas or blocks within a region, represented as major clades in the cladogram (Mota *et al.*, 2002; Rojas-Soto *et al.*, 2003). Detection of major floristic or faunistic blocks provides a useful guide for distributing conservation actions across the landscape, while detection of areas of endemism is helpful for locating areas worthy of protection within the major blocks (Cavieres *et al.*, 2002).

Results obtained with the above-mentioned methods nevertheless will be affected strongly by the intensity and evenness of floristic and faunistic knowledge (e.g. Rojas-Soto *et al.*, 2003). When sampling is poor or spatially heterogeneous, predictions regarding priority areas and floristic and faunistic boundaries can be unreliable. Species accumulation curves are useful for indicating the degree to which areas are undersampled (Soberón & Llorente, 1993; Squeo *et al.*, 2001b); however this kind of analysis gives no concrete information about the taxa that have been overlooked. Distributional modelling (Scott *et al.*, 1993; Rojas-Soto *et al.*, 2003), in contrast, allows predictions regarding the presence of particular species that have not that been detected previously in an area. Distributional modelling has recently been used in conjunction with priority selection algorithms (Kiester *et al.*, 1996). In this paper, we compare the results of a parsimony analysis of endemicity of species of the genus *Senecio* Tourn. ex L. (Asteraceae, Senecioneae) in the Mediterranean-climate area of Central Chile based on raw floristic data with analyses based on two variants of distributional modelling. Up until now, distributional modelling has been used more in studies of animal species (see recent exceptions: Pliscoff, 2003; Rojas-Soto *et al.*, 2003). In particular, we were interested in determining to what extent distributional modelling optimized the results of PAE, as expressed by the number of most parsimonious trees.

Our study was motivated by the urgent need to make progress with the detection of priority areas for conservation in the Mediterranean-type climate area of central Chile. The Mediterranean zone of central Chile extends from 30° to 38° S (Van Hüsen, 1967). The area corresponds to a major part, and the most heavily populated sector, of the central Chilean Biodiversity Hotspot for Conservation Priority (Arroyo *et al.*, 1999; Myers *et al.*, 2000). The five Mediterranean-type climate areas of the world, when considered together, are known to contain a total of around 48,250 plant species (*c.* 20% of the world total) on less than 5% of land area (Cowling *et al.*, 1996). Present information suggests that around 3160 plant species (including infraspecific taxa) occur in central Chile, of which just over one-half are endemic to Chile and close to one-third are entirely restricted to the Mediterranean-area *per se* (Arroyo *et al.*, 2002; M.T.K. Arroyo *et al.*, unpubl. data; see also Arroyo *et al.*, 1995). This density of endemic species is the highest in all of the Southern Cone. Many endemic species in the Mediterranean-climate area of central Chile have limited ranges leaving them vulnerable to extinction. Such vulnerability has been exacerbated in the past 20 years by the rampant expansion of plantation forestry, drip-fed orchards developed on steep slopes, and urbanization (Arroyo *et al.*, 1999, 2003). Identifying areas with concentrations of these endemic species is critical for determining conservation priorities within the region (Cavieres *et al.*, 2001). The high species richness and many endemic species in the Mediterranean-type area, coupled with a huge imbalance in the amount of land protected in different ecoregions of Chile (Arroyo & Cavieres, 1997), where less than 5% of the Mediterranean-type area is protected in contrast with around 40% of the southern forests, make it a high priority area for conservation efforts within Chile and all of South America.

We chose to analyse species of the genus *Senecio* for the following reasons: *Senecio* is the largest genus of plants in Chile and in the Mediterranean-type climate region. It has around 220 native species (not counting infraspecific taxa) in continental Chile (Marticorena, 1990) of which no fewer than 134 species (not counting infraspecific taxa) are found in the Mediterranean-type climate area. It is widely distributed in many different vegetation types, and contains a variety of life-forms. Thus *Senecio* has the potential to serve as indicator genus for the flora of the entire central Chilean area. The taxonomy of *Senecio*, unlike in many other genera in central Chile, is relatively stable, thanks to the early taxonomic work of Cabrera (1949), and few specimens in herbaria are without identification at the species level. Finally, one of us (Pliscoff, 2003) has just completed a similar analysis for the entire tree flora of central Chile. Thus it was of interest to determine to what degree results pertaining to a particular life-form and a taxonomic group agree in terms of floristic block boundaries and areas of endemism.

METHODS

Data base and matrix construction

A data base of 2670 records for 134 native species of *Senecio* from 956 localities in Central Chile (Fig. 1) was constructed
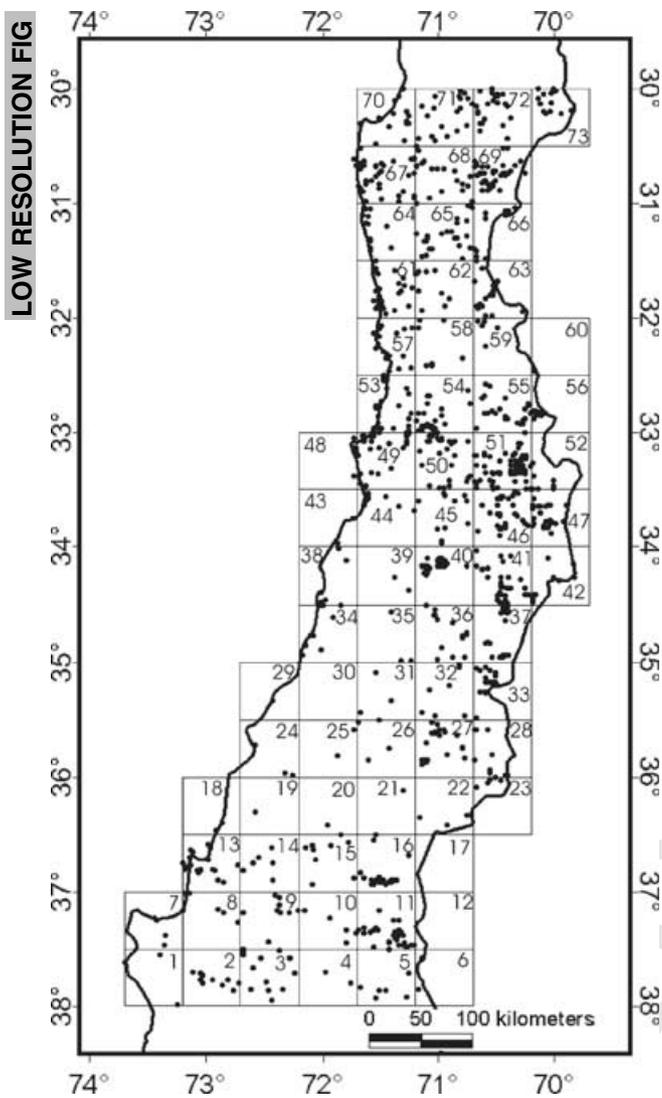
Figure 1 Map of central Chile showing locations of *Senecio* records from data base and quadrants used in analysis.

from various sources, principally the Universidad de Concepción Herbarium (CONC) and the Museo Nacional de Historia Natural Herbarium (SGO), Santiago, Chile and electronic, specimen-based data bases which contained records from CONC, SGO and many other herbaria outside of Chile. These data bases contain georeferences taken in the field as well as georeferences retroactively obtained to the minute level using place names. Records were also collected from published sources (Cabrera, 1949; Correa, 1971) and from recent field collection efforts by the authors, with voucher specimens from fieldwork deposited in CONC and SGO. Herbarium specimens from SGO and CONC showing discrepancies from known distributions were examined to check for misidentifications. Records from electronic data bases held in herbaria outside Chile showing such discrepancies were checked for possible georeferencing errors. Duplicate records and those showing obvious errors were eliminated before proceeding with the analysis. Since the identification and status of many subspecies

within the genus remain somewhat uncertain and because many records in the data base were only identified to species level, analysis was performed at the species level only. This may have decreased the potential to define area relationships in some cases (Morrone & Escalante, 2002) but we considered this option better than using subspecies with dubious identifications. Species definitions followed Cabrera (1949), and all identifications of new field specimens were confirmed at the Universidad de Concepción herbarium before adding them to the data base.

The study area was divided into 73 quadrants based on a $0.5° \times 0.5°$ geographic latitude/longitude grid. Morrone & Escalante (2002) found that the PAE results were more resolved with 1° quadrants than with 0.5° quadrants using data from raw point species records for Mexico; however, Rojas-Soto *et al.* (2003) obtained a well-resolved cladogram using 0.5° quadrants and distributional modelling for the Baja California peninsula. Based on these results, and the fact that a 1° grid would be only two quadrants wide for most of Chile and would have combined high alpine and lowland areas into the same quadrants, the smaller grid size of 0.5° was chosen. This last scale is more useful for conservation purposes. Linder (2001) was able to delineate areas of endemism with 0.25° quadrants for the Cape Floristic Region using both phenetic and parsimony analyses of the family Restionaceae, presumably because of better sampling of the Cape Region flora. This type of fine-scale analysis is highly desirable but is not possible at present for Central Chile, since inadequate sampling would likely create a large number of false species absences with such small quadrants. Grid placement maximized the land area within each quadrant as best as possible. The areas were numbered from southwest to northeast. Seventy-one of 73 quadrants had at least one point record for *Senecio*. Using the grid and data base records, a species × area matrix was constructed using the ArcView Spatial Analyst [Environmental Systems Research Institute (ESRI), 1999]. Species present in a quadrant were recorded as 1 for that quadrant, while species absent from the quadrant were recorded as 0.

Distributional modelling

Two different distributional modelling techniques (modified from Pliscoff, 2003) were used to generate the potential distribution of each species. In the first, the northern and southern latitudinal limits of each species were determined from the data base records. Digital maps of the vegetative formations of Gajardo (1993) and elevation ranges for each species were used to create the potential distribution of each species. A constant elevational range could not be used for each species, since there is a tendency for the upper and lower elevational limits of a species to decline with increasing latitude within Central Chile. Instead, graphs of elevation vs. latitude were constructed for each species to determine the upper and lower elevational limits for each 0.5° interval of latitude. If the graph of elevation vs. latitude for a species did not show a negative trend, constant values from the lowest and highest observed

elevations were used as the limits for the species; this lack of a negative trend in elevation with latitude was generally only seen in species with very small latitudinal ranges. The potential elevational range for the species was mapped for each 0.5° of latitude, and the vegetative formations that contained point records for the species were identified. If a quadrant was within the latitudinal limits of a species and contained an area where the selected vegetative formations overlapped with the potential elevational range of the species, then the species was recorded as present in the quadrant.

In the second distributional modelling variant, potential species distributions were determined as above but with an additional constraint: the contagion index was employed to limit the potential distribution to quadrants which had a certain level of connectivity to areas where the species had been collected. The contagion index measures the spatial aggregation of quadrants from which a species has been collected [1] (O'Neill *et al.*, 1988; Araujo & Williams, 2000) by taking a weighted average of neighbouring quadrants around a central quadrant. It is calculated using the following formula:

$$\text{Contagion} = \left(\frac{\sum_{b=1}^{k_a} w_{ab} y_b}{\sum_{b=1}^{k_a} w_{ab}} \right) \times 100,$$

where contagion is a weighted average of presence/absence of a species in k_a quadrants around a central cell y_a and w_{ab} is the weight given to quadrant y_b, calculated as $w_{ab} = 1/d_{ab}$, where d_{ab} is the distance between quadrants y_a and y_b (from

Araujo & Williams, 2000; Araujo *et al.*, 2002). Each neighbouring quadrant y_b has a value of 1 if a species has a point record within the quadrant, and 0 if the species had not been collected from the quadrant. The contagion index was calculated using a two-cell neighbourhood around each quadrant, and parts of the neighbourhood which fell outside the boundaries of the grid were not included in the calculation. A histogram of the resulting index values was generated, and a value of 0.23 (75th percentile) was used as the minimum value for possible species presence (following L. Cavieres, pers. comm.). The potential distributions generated using the latitudinal and elevational limits and vegetative formations were then constrained to those quadrants with index values greater than or equal to 0.23. All quadrants from which a species had been collected were recorded as having the species present, regardless of their contagion index value. The distributions generated using this method were therefore subsets of those generated using modelling without the contagion index. A possible advantage of incorporating the contagion index is that it will not record a species as present across large gaps between point records (Fig. 2).

Following the first distributional modelling technique, four species were recorded as present in only one quadrant and were eliminated from further analysis since they were not parsimony informative, leaving a total of 130 species. In the matrix constructed from the raw data and in the matrix constructed using the contagion index, 20 species were eliminated from the analysis as parsimony-uninformative,
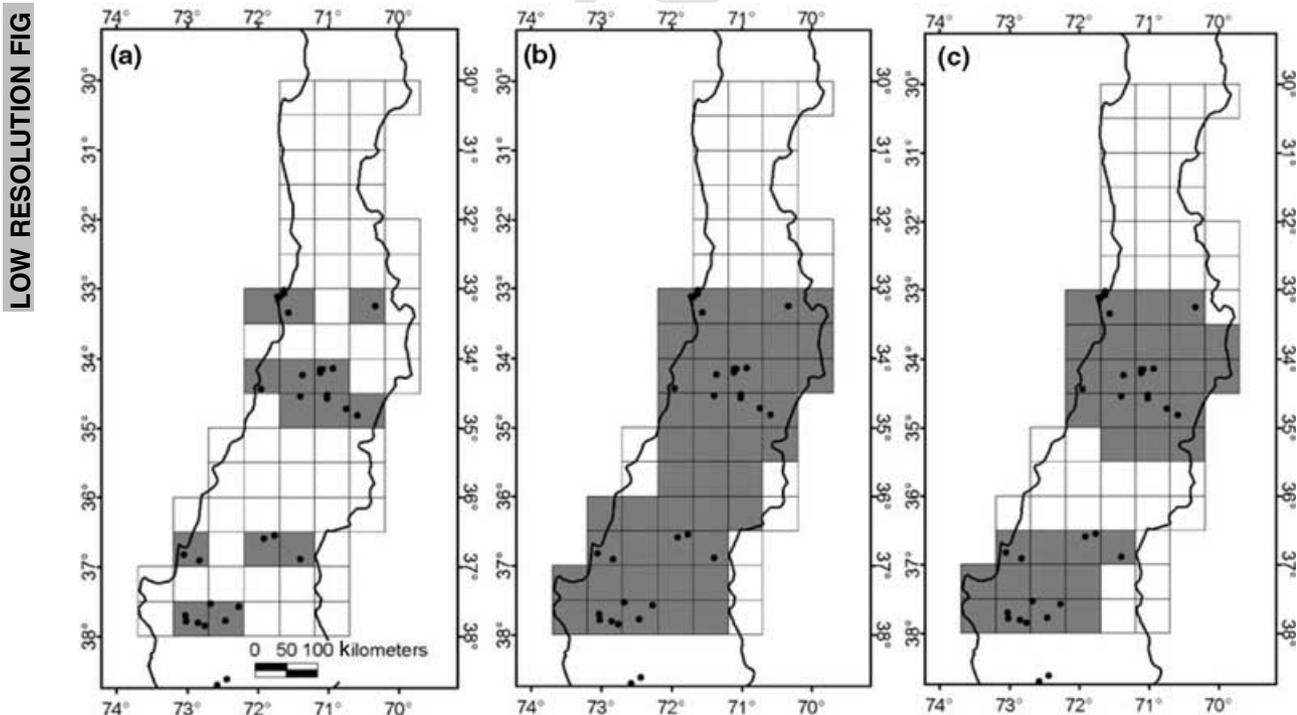
[10] **Figure 2** Distribution of *Senecio arnicoides* Hook. et Arn. from (a) point records from data base, (b) distributional modelling without contagion index and (c) distributional modelling with contagion index. Both distributional modelling methods make the distribution more continuous, but the contagion index prevents the distribution from being extended across the large collecting gap from 35.5° to 36.5° S.

leaving a total of 114 species. Most of these species had only a single locality within the study area with more records just outside the limits of the study area; hence they were included in the first potential distribution matrix but not in the matrix from the raw data or the potential distribution matrix incorporating the contagion index.

Parsimony analysis

Parsimony analysis of endemicity was performed with the program NONA 2.0 (Goloboff, 1997) using the heuristic search option and randomizing the entering order of the quadrants 100 times. A hypothetical area with all species absent was used as the outgroup (Morrone, 1994a). This procedure was performed with the matrices constructed from the raw distribution data and from both sets of potential distribution results. The strict consensus tree was constructed from the resulting most parsimonious cladograms, and was used to identify floristic blocks and areas of endemism. The main clades of the consensus tree were interpreted as floristic blocks (Mota *et al.*, 2002; Pliscoff, 2003), provided that they shared at least four species, which may also have been found in other areas. Areas of endemism were identified as terminal portions of the cladogram that shared endemic species or subendemic species whose ranges extended outside the limits of the study area. Finally, localities of species records from the data base were compared with the floristic blocks and areas of endemism to compile a list of endemic and subendemic species found within these areas.

RESULTS

All 73 quadrants had at least one species recorded as present after both distributional modelling analyses. Large increases in species richness were observed for isolated areas of the Andes, presumably because of lack of collection effort due to difficulty of access, and in the coast and central valley of the southern part of the Mediterranean zone, which has largely been transformed to agricultural land and so has been less well collected historically because of very early transformation. Species richness of each quadrant before and after distributional modelling is shown in Fig. 3. A total of 122 of 134 species had wider distributions after distributional modelling without the contagion index compared with the raw distribution data, with the other 12 species distributions remaining unchanged; with the contagion index, 88 of 120 species had wider potential distributions compared with their distributions from the raw data. More widely distributed species generally showed a smaller increase in distribution than narrowly distributed species.

The PAE generated 6912 equally parsimonious trees using the matrix from the raw distribution data ($L = 441$, Ci = 25, Ri = 53). The strict consensus tree was largely unresolved, showing five clades with four or more areas (Fig. 4). From the matrix produced by distributional modelling without the contagion index, PAE produced 720 equally parsimonious cladograms ($L = 462$, Ci = 28, Ri = 77). The consensus tree had three main clades, which represent major floristic blocks of Central Chile (Fig. 5). The first block represents the Andes

LOW RESOLUTION FIG
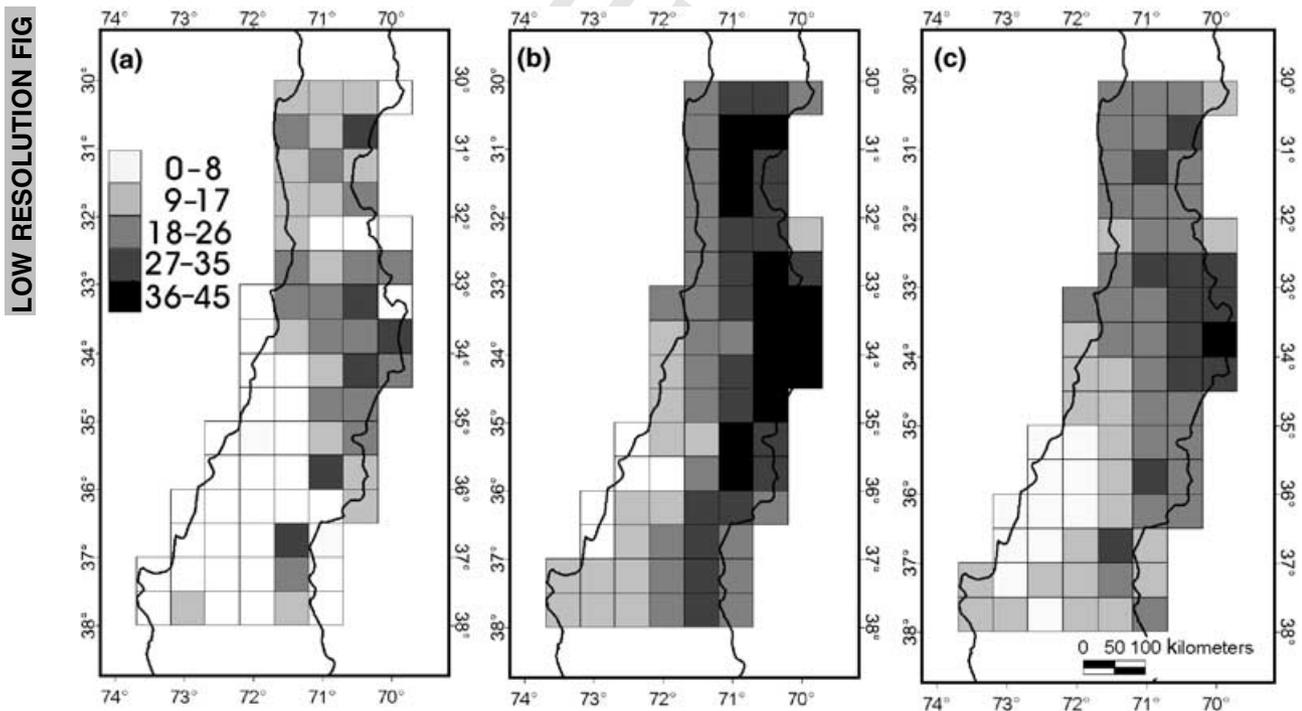
10 **Figure 3** Species richness for each quadrant from (a) raw floristic data, (b) potential distribution data without contagion index and (c) potential distribution data with contagion index.

LOW RESOLUTION FIG
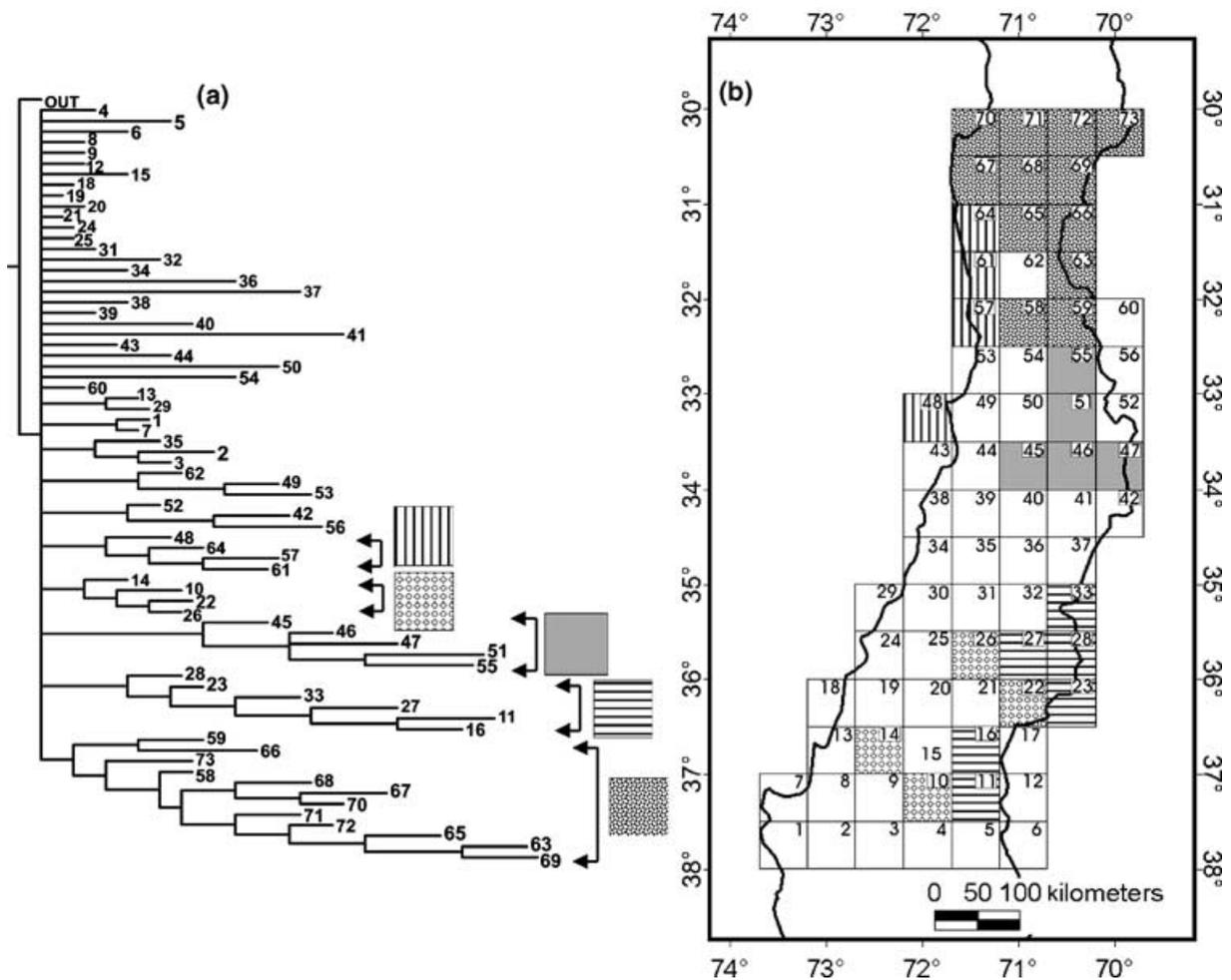
10 Figure 4 (a) Phylogram of consensus tree from raw point data showing floristic units. (b) Map of floristic units from cladogram. Most units contain few quadrants but show some geographic structure, with a large unit in the north, two smaller Andean units in the central and south, a north coast unit, and a south coast/central valley unit.

and parts of the Central Valley from 30° to 35° S, and is divided into two subunits separated by the 32.5° S parallel. The second block represents the coast and Coastal Cordillera from 30° to 35° S. It is divided into two subunits as well, with the first representing the coast from 30° to 32.5° S and the coast from 33.5° to 34.5° S, and the second representing the coast from 32.5° to 33.5° and the higher parts of the Coastal Cordillera from 33° to 35° S. The third block represents the Andes south of 35° S. Blocks two and three are joined in a larger but poorly-defined clade, as these areas have few species in common, and thus were considered as separate rather than part of a single larger block. This larger block also included a number of quadrants from the southern coast which did not fit into any floristic block and did not form a distinct clade of their own. The placement of these southern coastal quadrants in this clade may have been responsible for the inclusion of the north coast and southern Andes quadrants in the same clade, since the southern coastal quadrants probably have some floristic similarity to both areas.

The PAE using the matrix from distributional modelling with the contagion index produced 144 equally parsimonious cladograms ($L = 387$, $Ci = 29$, $Ri = 73$). The consensus tree had four main clades representing major floristic blocks (Fig. 6). The first block was similar to the northern/central Andes block described above, but also included parts of the coastal Cordillera and coast from 32.5° to 34.5° S. It was divided into the same two geographic subunits described above, with slightly different boundaries. The second block represents the coast from 30° to 32.5° S, plus one coastal quadrant further south. The third block represents the Andes from 34.5° to 36.5° S, and the fourth block represents the Andes from 36.5° to 38° S. The quadrants on the southern coast still did not form a distinct clade, but once again were grouped with the clades representing the southern Andes.

The level of resolution in the results using the raw floristic data did not allow the identification of any areas of endemism. From the PAE results from the potential distribution matrix without contagion index, four areas of endemism were identified. Within the north-central Andes block, three areas

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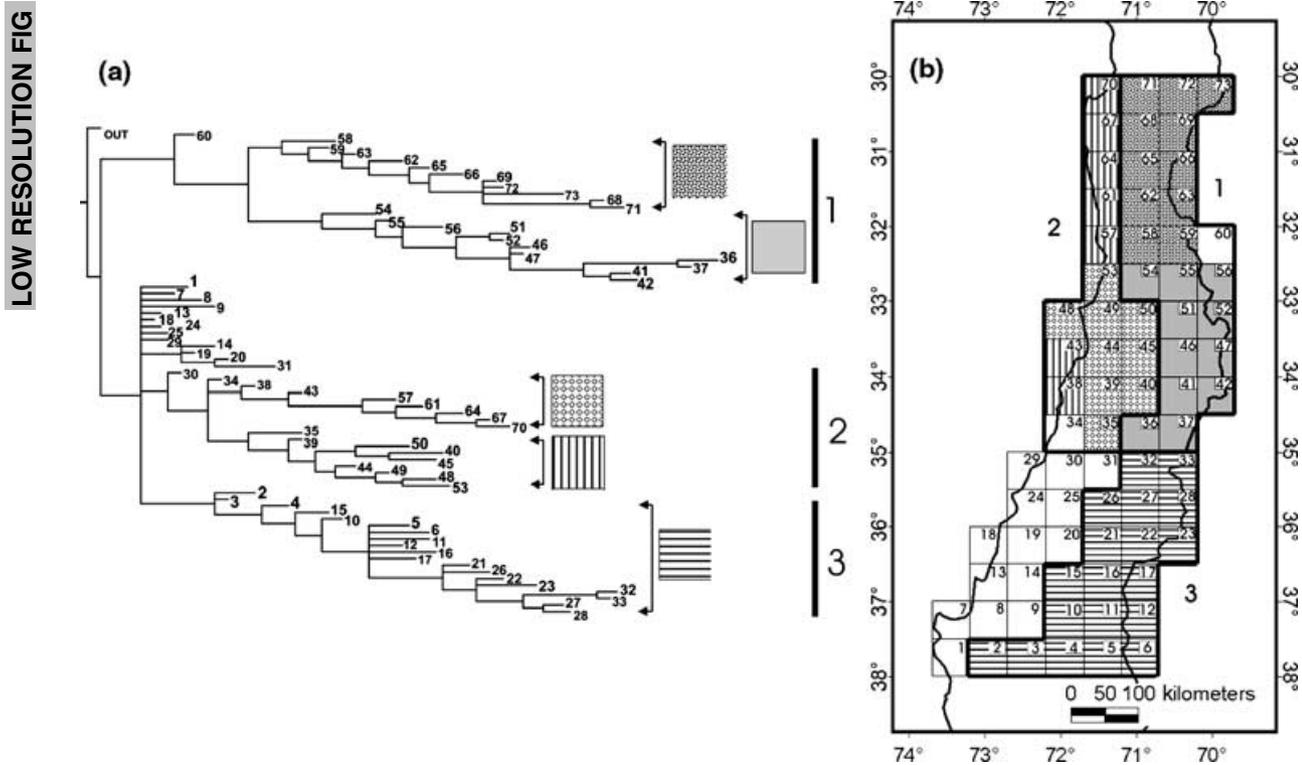
10 Figure 5 (a) Phylogram of consensus tree for PAE results from potential distribution matrix without contagion index. Floristic blocks are numbered and subunits are indicated by shaded squares. (b) Floristic blocks identified from PAE using potential distribution matrix without contagion index. Block 1 represents the northern/central Andes, block 2 is the northern/central coast, and block 3 is the southern Andes. Blocks are outlined in black and subunits are indicated by differences in shading. Quadrants within floristic blocks but which do not belong within any subunit are not shaded.

were identified (Fig. 7). The first comprises the area from 30° to 31° S and is defined by the presence of *Senecio portulacoides* Remy and *S. rivularis* Remy. The second area comprises the area from 32.5° to 35.5° S and is defined by *S. pentaphyllus* Phil. and *S. santiagoensis* OK. The third comprises the Andes from 34.5° to 35° S and is defined by *S. espinosae* Cabr. and *S. landbeckii* Phil. The fourth area represents the coast from 30° of 32.5° S, with the exception of quadrant 64, and is defined by *S. aristianus* Remy and *S. isernii* Phil. It should be noted that there is a single record of *S. isernii* from the coast north of the study area, and thus this species is subendemic to the area of endemism rather than strictly endemic. From the PAE results using the potential distribution matrix with the contagion index, two areas of endemism were identified. The first is identical to the area from 30° to 31° S described above and is defined by the same species. The second is located in the southern Andes from 35.5° to 36.5° S and is defined by *S. talquinus* Phil. and *S. leucophyton* Phil. Species endemic or subendemic to these areas of endemism are listed in Table 3.

DISCUSSION

The PAE results from both sets of potential distribution data were far better resolved compared with the results obtained when only the raw distribution data was employed. The

potential distribution matrix using the contagion index produced the most parsimonious tree and by far the lowest number of trees. The different number of species used in the two analyses might have affected this to some degree; however, it also seems to indicate that the distributional modelling without the contagion index probably overestimates species distributions, most notably across large collection gaps. The same species were used with the raw distribution data and the second modelling variant, so the lower number of trees for the PAE using the second potential distribution matrix indicates that potential distribution data does give more parsimonious results than the raw distribution data. The consensus tree generated from the potential distribution data using the contagion index also identified a division within the southern Andes that did not appear in the results without the contagion index. This may indicate that the modelling procedure without the index blurs some biogeographic boundaries by expanding species distributions across these boundaries.

Both distributional modelling methods probably overestimate the distributions of many species, as neither accounts for factors such as local extinction and geographic barriers that would prevent a species from occupying part of its potential distribution (Rojas-Soto *et al.*, 2003). This may have obscured some area relationships which would otherwise have been detected, but is clearly a better alternative than using the point
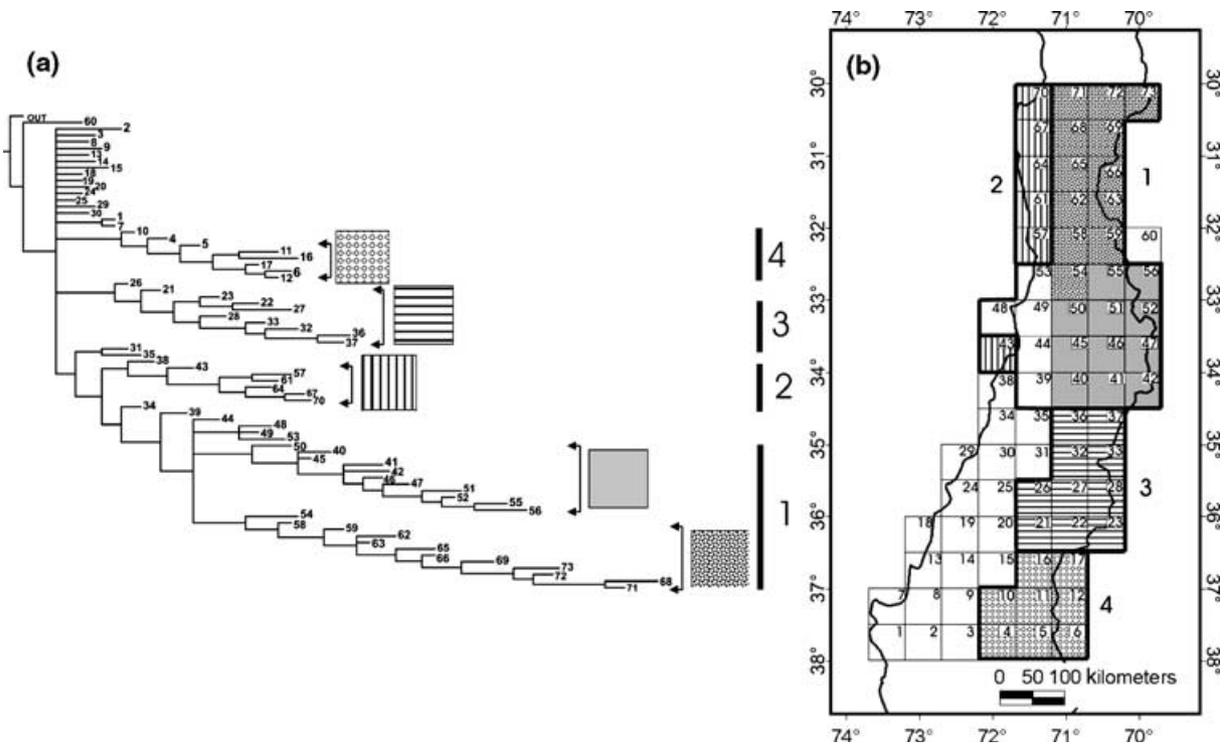
Figure 6 (a) Strict consensus tree for PAE results from potential distribution matrix with contagion index. Branch lengths are proportional to number of steps in cladogram. Floristic blocks are numbered and subunits are indicated by shaded squares. (b) Floristic blocks identified from PAE using potential distribution matrix including contagion index. Blocks are outlined in black and subunits are indicated by differences in shading. Quadrants within floristic blocks but which do not belong within any subunit are not shaded.

data alone. Fieldwork over the past 4 years in the reserves of Central Chile led by one of us (M.T.K.A.) increased the number of species present by an average of 3.78 ± 0.97 species (mean ± SE) per quadrant visited. The number of species present in one particularly under-collected quadrant (no. 40) increased from two to 13, and four quadrants had 10 or more new species recorded as present. The large increase in species richness for many areas based on this fieldwork demonstrates that there are probably many false absences in the raw data. These false absences result in decreased resolution when PAE is used with the raw data, making distributional modelling a very useful tool in this type of analysis. The potential distribution matrices produced much more resolved and therefore more useful trees, while the results from the raw data showed hardly any resolution at all and only identified one large geographical unit consisting of the northern part of Central Chile. Even this unit contained both coastal and Andean areas and is thus of limited biogeographical meaning, assuming that the separation of high and low areas of Central Chile found in previous studies is real.

The lack of structure within the cladograms for the southern coast and southern central valley probably results from the highly disturbed nature of these areas. The vegetation in these areas is highly fragmented and has mostly been converted to other uses (Armesto *et al.*, 1998). Additionally, these areas have been in a transformed state for many years, with the result that there are few recent collections from many of these areas

outside of protected reserves. This means that the species composition after distributional modelling probably reflects the actual historic species composition less well than in other areas; this may account for the lack of a clearly defined southern coast clade. These same areas, moreover, experienced population expansions and contractions, and probably much local extinction during the Pleistocene (Villagrán & Hinojosa, 1997), such that the present-day flora contains a mixture of phytogeographic elements. Finally, these areas have fewer species of *Senecio* than the rest of Central Chile, and would therefore be expected to be less well resolved in the cladogram. The distributional modelling thus appears to be highly affected by the quality and quantity of data available for a particular region. This is not surprising, as sample size has been shown to affect the accuracy of modelled species distributions (Stockwell & Peterson, 2002). Although it is possible that the modelling procedure simply mapped species distributions to fit within existing vegetation zone boundaries, this does not appear to be the case. The floristic block boundaries cut across boundaries for vegetation zones and therefore appear to represent distinct units from the vegetative formations.
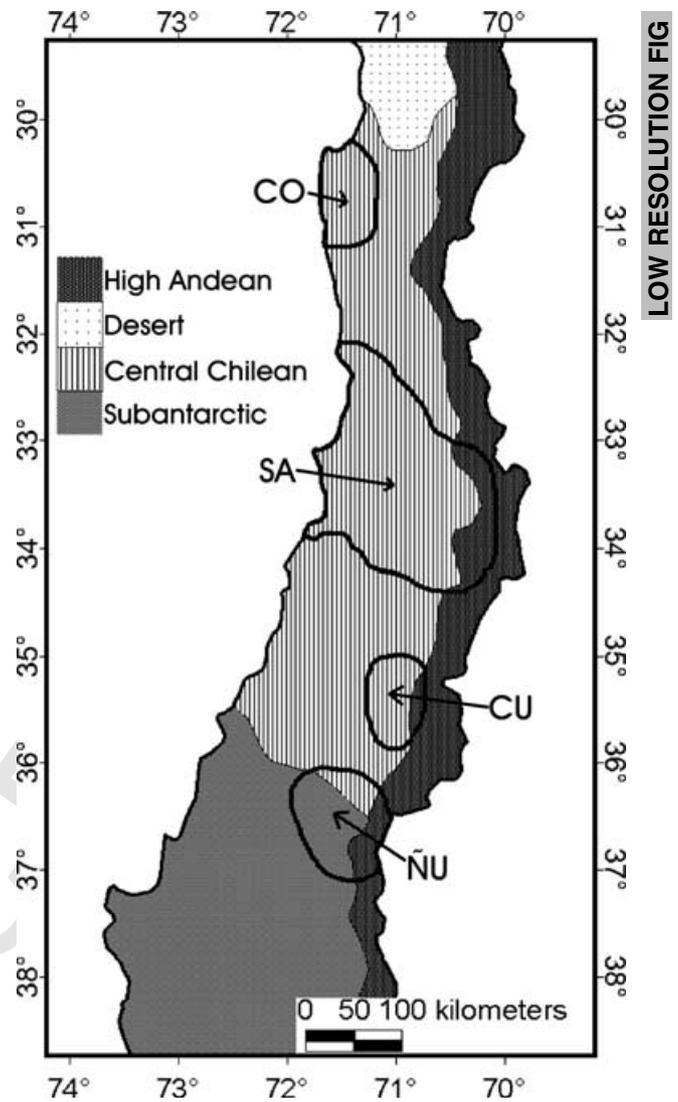
Biogeography

Several previous studies (some with conflicting results) have identified biogeographical divisions within central Chile, and thus is it of interest to compare our results. Cabrera & Willink

LOW RESOLUTION FIG

LOW RESOLUTION FIG
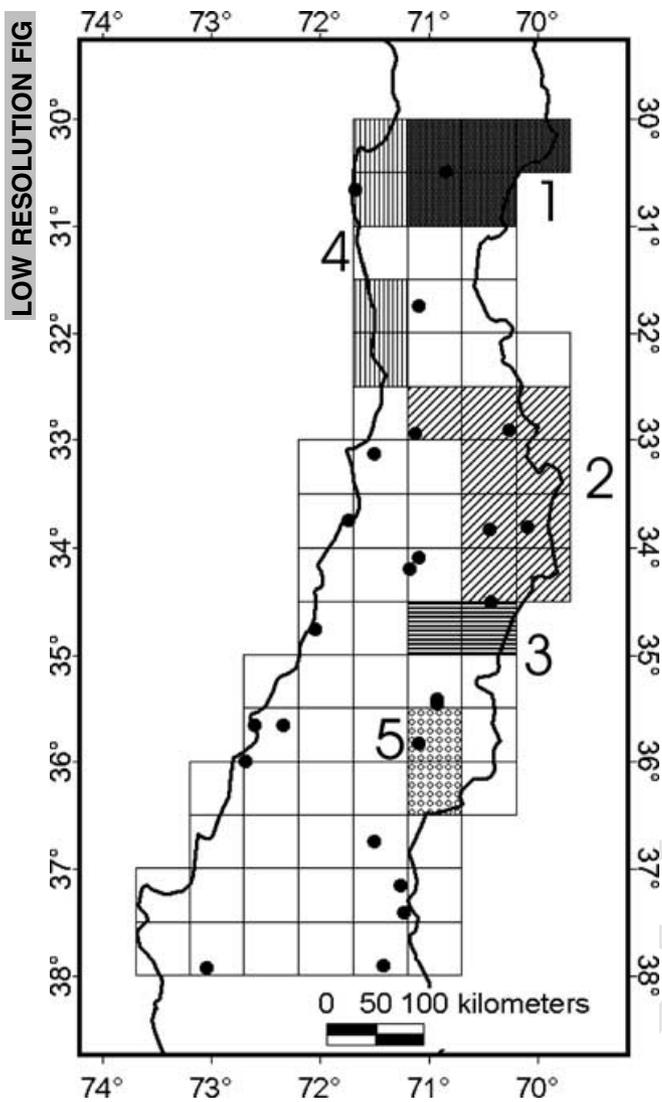
Figure 7 Areas of endemism identified from PAE with distributional modelling. Areas are defined by the following species: 1 (northern Andes): *S. portulacoides* Remy, *S. rivularis* Remy; 2 (Andes of Santiago): *S. pentaphyllus* Phil., *S. santiagoensis* OK.; 3 (Andes south of Santiago): *S. espinosae* Cabr., *S. landbeckii* Phil.; 4 (north coast): *S. aristianus* Remy, *S. isernii* Phil.; 5 (Andes of Talca): *S. leucophyton* Phil., *S. talquinus* Phil. The first four areas were identified from the potential distribution data without the contagion index, and the first and last areas were identified from the results with the contagion index. Locations of parks and reserves are indicated by black dots.

Figure 8 Biogeographic classifications of Cabrera & Willink (1973) and Morrone *et al.* (1997). Cabrera and Willinck's provinces are shown as shaded areas, and Morrone *et al.*'s provinces are outlined in black (CO, Coquimbo; SA, Santiago; CU, Curicó; ÑU, Ñuble).

(1973), based on physiognomic and floristic dominants, divided Central Chile into the Chilean, High Andean and Subantarctic provinces, with the latter two extending beyond Central Chile (Fig. 8). The break between the Chilean and Subantarctic provinces was placed at 35° S, with High Andean province defined as all regions above roughly 3500 m at 30° S and 2000 m at 40° S. Morrone (1994b) used a single area for Central Chile from 32° to 37° S, with the area north of 32° S defined as part of the Puna province and the area south of

37° S placed in the Subantarctic province. Within the northern part of central Chile alone (extending south to 32° S), an effort to determine conservation priorities for the flora using PAE revealed three main geographic zones and four subareas, with major divisions between the Andes, coast, and the region between the two cordilleras (Cavieres *et al.*, 2001). Morrone *et al.* (1997) later divided Central Chile into four units using cladistic analysis techniques based on a total of 67 species in 24 plant and arthropod genera: Coquimbo (30°–31° S), Santiago (32°–34° S), Curico (35°–36° S) and Ñuble (36°–37° S) (Fig. 8). Coquimbo and Santiago were found to represent the true Central Chilean subregion, whereas Curico and Ñuble were found to be part of the Subantarctic subregion. Morrone (2000, 2001) confirmed this division between subregions, placing the Coquimbo and Santiago

provinces in the Central Chilean subregion (30°–34° S) and the Maule province (34°–37° S) in the Subantarctic subregion. Pliscoff (2003) identified three floristic blocks for Central Chile (32°–38° S) using a combination of distributional modelling and PAE based on tree species. The coast was classified into two separate areas with a division at 34° S and the Andes were classified as a single area.

The division between floristic blocks at 34.5°–35° S resulting from both distributional modelling variants corresponds approximately to the break between the Chilean and Subantarctic provinces (Cabrera & Willink, 1973; Morrone *et al.*, 1997; Morrone, 2000, 2001). The *Senecio* results thus support this major biogeographic boundary within Central Chile. The division between the coastal and Andean blocks in the north and central parts of the Mediterranean zone does not correspond to the division between Cabrera and Willink's Chilean and High Andean provinces, since their High Andean province includes only the highest areas of the Andes. Our Andean block extends downward of Cabrera and Willink's High Andean province in that it contains extensions of mid-high altitude Mediterranean vegetation. This last result suggests that floristic boundaries in central Chile do not always correspond with physiognomic boundaries (used principally by Cabrera & Willink, 1973). This is not surprising given the 'porous' nature of the Mediterranean area treeline, permitting many species to occur both above and below treeline. The northern boundary of the Santiago district identified by Morrone *et al.* (1997) corresponds roughly to the division within the floristic blocks at 32.5° S identified from *Senecio*, but the split in the cladogram of Morrone *et al.* (1997) between the Coquimbo and Santiago districts at 31° S is not seen as a major division in any of the cladograms from *Senecio*. The *Senecio* results incorporating the contagion index identify two floristic blocks in the Andes of southern Central Chile, but the boundaries do not correspond exactly to those of the Curico and Ñuble districts of Morrone *et al.* (1997). The *Senecio* results without the contagion index show only a single floristic block for this area, which partially corresponds to the Maule province of Morrone (2001). The *Senecio* results delineate a distinct coastal floristic block not previously identified by Cabrera & Willink (1973) or Morrone *et al.* (1997).

The floristic blocks identified from the potential distribution data index correspond closely to those identified from a similar study (including distributional modelling) of 83 tree species found in Central Chile (Pliscoff, 2003). Both studies show a north coast block, extending south to 34° S for the trees and 34.5°–35° S for *Senecio*, which includes the highest areas of the Coastal Range in the tree study. The placement of these high areas differs between the two distributional modelling variants for *Senecio*; they are located in the coastal block in the first variant, as in the tree study, but are placed within the Andean block in the second variant. The distributional modelling procedure used in the tree study was the same as the first modelling variant of this study, so this difference appears to be a result of the use of the contagion index in the second

modelling variant. From these results, it is unclear which floristic block these Coastal Range quadrants should be placed in, but it seems likely that they would fall within the coastal block. It is also possible that these Coastal Range quadrants contain a mix of species from both the Andean and Coastal floristic elements, and cannot be placed within one of the floristic blocks. The tree study shows a division between the floristic blocks of the Andes and the southern coast, which appears in the *Senecio* results as a separation between the southern Andes blocks and the coastal quadrants which do not form a clade. The tree results also have a southern Andean block extending from 34.5° to 38° S, which matches well to the divisions between Andean blocks seen in both sets of results from *Senecio*. The tree study does not extend north of 32° S or into the highest regions of the Andes due to the lack of tree species in these areas, so results cannot be compared for these regions.

The good correspondence between the results of the *Senecio* and tree studies, as well as partial correspondence with major biogeographic breaks in previous results (Cabrera & Willink, 1973; Morrone *et al.*, 1997), seems to indicate that the emerging floristic blocks are robust and represent actual biogeographic units, since analyses using two different criteria (taxon vs. life form) produced similar results. It would be useful to compare these results to those of further studies utilizing different methods such as track analysis or different types of models, since the similarity in methods between this study and that of Pliscoff (2003) could force a bias in the results. The floristic blocks from the *Senecio* results also include a large number of endemic or subendemic species (Table 1), showing that the method succeeded in identifying areas of high endemism. In terms of endemic species, modelling without the contagion index performed the best because it delineated a coastal floristic block with many endemics, while modelling with the contagion index showed a coastal block that excluded parts of the distributions of many of these species. Despite slight differences in the placement of east–west boundaries, the results from the tree study and the first modelling variant in our study have revealed strong floristic separations between the Coast Range and inland Andean Cordillera, not previously detected in other studies. The separation between the Coast Range and Andean Range is not unexpected. The Coast Range is older geologically, and served as a refugium during the Pleistocene (e.g. Arroyo *et al.*, 1995; Villagrán & Hinojosa, 1997).

Conservation priorities

On the whole, the northern Andes subunit and the north coast floristic block have much less of their area protected than central Andean subunit or the two southern Andean blocks (Table 2). Similar results were obtained by Pliscoff (2003). These results show a serious imbalance in the distribution of protected areas within the Chilean National System of Protected Areas (SNASPE) that needs to be addressed. The floristic blocks identified from the potential distribution data

Table 1 Species endemic or subendemic to floristic blocks delineated in results from both sets of potential distribution data.

Floristic block	Modelling with contagion	Modelling without contagion
Northern/Central Andes	*S. bustillosianus, S. davilae, S. debilis, S. donianus** (ME, SJ), *S. elquiensis*, S. garaventae, S. grandjotii** (ME), *S. hickenii*, S. illapelensis, S. jaffuelii, S. jilesii, S. jungei, S. laetevirens** (ME), *S. looseri** (ME, SJ), *S. lorentziella**(ME, SJ), *S. mapuche, S. micropifolius, S. minutifolius*, S. obtectus** (ME), *S. oreinus** (ME), *S. otaeguianus, S. pentaphyllus, S. pissisii** (SJ), *S. portulacoides*, S. pubescens, S. tripinnatifidus, S. rivularis, S. santiagoensis S. werdermannii** (ME)	*S. aspericaulis** (ME, NE), *S. bustillosianus, S. davilae, S. donianus** (ME, SJ), *S. elquiensis*, S. espinosae, S. grandjotii** (ME), *S. hickenii*, S. illapelensis, S. jilesii, S. jungei, S. laetevirens** (ME), *S. landbeckii, S. looseri** (ME), *S. lorentziella**(ME, SJ), *S. micropifolius, S. obtectus** (ME), *S. oreinus** (ME), *S. pentaphyllus, S. pissisii** (SJ), *S. portulacoides*, S. pubescens, S. tripinnatifidus, S. rivularis, S. santiagoensis S. werdermannii** (ME)
North Coast	*S. aristianus, S. coquimbensis*, S. isernii*, S. jacobeiformis*, S. munnozii*	*S. aristianus, S. coquimbensis*, S. glabratus, S. hirsutulus, S. illinitus, S. isernii*, S. jacobeiformis*, S. munnozii, S. otaeguianus, S. paucidentatus*, S. viscosissimus*
Southern Andes 1	*S. barrosianus*, S. espinosae, S. landbeckii, S. leucophyton** (NE), *S. linaresensis, S. maulinus, S. pycnanthus, S. schoenemannii, S. talquinus*	*S. leucophyton** (NE), *S. linaresensis, S. maulinus, S. nublensis, S. pycnanthus, S. schoenemannii, S. scopulorum, S. subpubescens, S. talquinus*
Southern Andes 2	*S. nublensis, S. phylicifolius*, S. scopulorum*	

Subendemic species are indicated by an asterisk (*), and Andean species whose distributions extend into Argentina are listed with the Argentine province in which they are found (ME, Mendoza; NE, Neuquen; SJ, San Juan).

Table 2 Total protected area within Chilean system of parks and reserves for each of five floristic blocks and subunits identified from PAE results using potential distribution data.

Floristic block or subunit	Protected area (ha)	
	Modelling without contagion	Modelling with contagion
Northern Andes	4357	12357
North Coast	29152	10479
Central Andes	68251	57536
Southern Andes (34.5°–36.5° S)	118797	29900
Southern Andes (36.5°–38° S)		101191

Source for protected areas: Corporación Nacional Forestal (CONAF) (http://www.conaf.cl).

each have a number of endemic or subendemic species (Table 1). Many of the subendemic species have records from slightly outside the study area, including many Andean species whose distributions extend into neighbouring portions of Argentina. The large number of endemic or subendemic species in the northern and central Andes of Central Chile, along with the relatively low degree of protection of this area within SNASPE, highlights the need to establish reserves within the region.

The areas of endemism located within the floristic blocks represent some of the most important targets for conservation efforts, as they contain species with narrow ranges that are not found elsewhere (Table 3). The area of endemism in the Andes of northern Central Chile appeared in the results from both potential distribution matrices, and can thus be identified as a conservation priority. Part of this area of endemism was identified by Cavieres et al. (2001) although it was defined by

different species. This area of endemism contains a mere 128 ha of protected land in a single small reserve (Table 3, Fig. 7) and thus should be a primary target of efforts to preserve its unique biodiversity. The northern coast area of endemism identified in the results without the contagion index also corresponds partially to a coastal area of endemism identified by Cavieres et al. (2001). This area contains two endangered endemic species, *S. coquimbensis* Phil. and *S. munnozii* Cabrera, as well as several species identified as vulnerable (Squeo et al., 2001a). The other Andean areas of endemism have more protected area than the northern Andes area (Table 3).

CONCLUSIONS

Parsimony analysis of endemicity with distributional modelling is a useful tool in delineating biogeographic boundaries, and for setting the framework for making conservation decisions. It has only begun to be used in South America, where it is probably more urgently needed than in other areas of the world given the poorer representation of documented systematic collections in general. Aside from its use in Mexico (Luna et al., 1999; Morrone & Escalante, 2002; Rojas-Soto et al., 2003), Spain (García-Barros et al., 2002; Mota et al., 2002) and South Africa (Morrone, 1994b; Linder, 2001) it has scarcely been applied to other parts of the world where it might be very useful for both biogeographic and conservation purposes. The contagion index increases the power of distributional modelling by restricting potential species distributions to areas close to point records and should be employed further in biogeographical studies of relatively well-collected species. The correspondence between these results and those from studies using many different genera of trees show that

Table 3 Endemic species and amount of protected area within each area of endemism.

Area of endemism	Endemic or subendemic species	Protected area (ha)
Northern Andes	*S. rivularis, S pubescens***, *S. portulacoides**, *S. jilesii**, *S. elquiensis**	128
Andes of Santiago	*S. santiagoensis, S. pentaphyllus, S. davilae, S. bustillosianus***, *S. debilis**, *S. grandjottii** (ME), *S. laetevirens** (ME), *S. lorentziella** (ME, SJ), *S. obtectus** (ME), *S. werdermannii** (ME)	55957
Andes south of Santiago	*S. landbeckii, S. espinosae*	12294
North Coast	*S. aristianus, S. munnozii, S. coquimbensis***, *S. isernii**, *S. jacobeiformis**, *S. hirsutulus**	9959
Andes of Talca	*S. talquinus, S. schoenemannii, S. linaresensis, S. pycnanthus**, *S. leucophyton** (NE)	12580

Subendemic species are indicated by an asterisk (*), and species that are very nearly endemic to these areas but have records less than 0.1° outside the area boundaries are indicated by a double asterisk (**).

Species whose distributions extend into Argentina are listed with the Argentine province in which they occur (ME, Mendoza; NE, Neuquen; SJ, San Juan).

Senecio has the potential to be an indicator genus for the biogeography and conservation of the flora of southern South America. It would be useful to repeat the kinds of analyses carried out here for *Senecio* in other biogeographic regions of southern South America as a first step toward detecting floristic blocks, and eventually repeat the *Senecio* analysis for central Chile using the entire flora in order to further test the validity of the floristic blocks detected here on the basis of a single large genus.

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Insert hyphen	(As above)	(hy)
Start new paragraph	⌐	⌐
No new paragraph	⌒	⌒
Transpose	⊔⌐	⊔⌐
Close up	linking ⊃ letters	⊃
Insert space between letters	⋏ between letters affected	#
Insert space between words	⋏ between words affected	#
Reduce space between letters	⋏ between letters affected	⊤
Reduce space between words	⋏ between words affected	⊤