Biodivers Conserv (2007) 16:2627–2648
DOI 10.1007/s10531-006-9073-2

ORIGINAL PAPER

Distribution patterns of flora and fauna in southern Chilean Coastal rain forests: Integrating Natural History and GIS

**Cecilia Smith-Ramírez · Iván Díaz · Patricio Pliscoff ·
Claudio Valdovinos · Marco A. Méndez ·
Juan Larraín · Horacio Samaniego**

Received: 17 August 2005 / Accepted: 19 May 2006 / Published online: 27 October 2006

Abstract Knowledge of species richness centers is necessary for the design of conservation areas. In this study, we present a GIS analysis of two years of field data on animal and plant diversity distributions in evergreen, coastal rain forests of southern Chile (39°30′–41°25′ S). Despite their high endemism, these forests have remained largely unprotected. Field records were complemented with data from museum collections and scientific literature. We used selected environmental variables (evapotranspiration, altitude) and, in some cases, forest types as predictors of species distributions. Our study focused on the distribution of forest bryophytes, vascular plants, soil invertebrates, amphibians and birds. We generated distributional maps for each taxa based on their field records in the study area, comple-

---

C. Smith-Ramírez (✉)
Center for Advanced Studies in Ecology and Biodiversity (CASEB), P. Universidad Católica and Fundación Senda Darwin (FSD), 1220, Valdivia, Chile
e-mail: csmith@willnet.cl

I. Díaz
Department of Wildlife Ecology and Conservation, University of Florida and FSD, Gainesville, FL, USA

P. Pliscoff
FSD, Roman Díaz 390, dpto. 902, Providencia, Santiago, Chile

C. Valdovinos
Center of Environmental Sciences (EULA-Chile), University of Concepcion, Concepcion, Chile

M. A. Méndez
Laboratorio de Bioinformática y Expresión Génica (INTA-Universidad de Chile), Santiago, Chile

H. Samaniego
Department of Biology, University of New Mexico, Albuquerque, NM, USA

J. Larraín
FSD, Departamento de Botánica, Universidad de Concepcion, Concepcion Chile

mented by natural history information, except in the case of bryophytes and soil invertebrates. In general, species richness was lower at 600 m elevation or above for all the taxa studied. Species richness tends to increase in the northern sector of the study area. We observed a greater richness of vascular plants near rivers and streams, and noted important floristic differences between west and east-facing slopes of the Coastal Range, with more species in the oriental side. Because species in high altitude forests are not a subset of those found at lower elevations, we propose that conservation strategies should prioritize the protection of the entire altitudinal gradient of the southern Coastal Range, especially in the more diverse oriental and northern sectors.

Keywords Amphibian distributions · Arthropod distributions · Bird distributions · Bryophyte distributions · Hotspots · Vascular plant distribution

Introduction

Basic knowledge of species richness patterns and species distributions within a region is a necessary starting point to predict species extinction under habitat loss, to understand the potential impacts of future climate change on biodiversity, as well as to prioritize conservation efforts and designing conservation areas (Margules and Pressey 2000; Currie 2001; Tognelli and Kelt 2004; Meffe and Caroll 1997; Groves 2003). For many species, distribution data at the necessary spatial resolutions are largely lacking because of biased sampling efforts concentrated in the most accessible areas, or on the best known taxa. Surveys of remote, underexplored territories are usually expensive and logistically difficult. Therefore, to generate complete maps of species distributions in poorly sampled or unexplored areas, it may be necessary to extrapolate, using algorithms to estimate species distribution models (Scott et al. 1993; Moravec 1998; Peterson et al. 1999; Stockwell and Peters 1999; Guisan and Zimmermann 2000; Guisan and Hofer 2003; Ferrier 2002). Several studies have argued that species diversity hotspots cannot always be aggregated combining different groups of organisms because of disparity of species richness patterns of different taxa (Prendergast et al. 1993; Gaston 1996; Kerr and Packer 1997).

For modeling species distributions at regional or local scales, some environmental variables have proved more useful than others (Currie 1991; Kerr et al. 2000; Rahbek and Graves 2001; Faith 2003; Currie et al. 2004). Most frequently, species richness patterns have been predicted considering one or more of the following environmental variables: latitude (or geographic position along a north–south axis), altitude, available energy, habitat heterogeneity and contemporary climatic variables (Araujo et al. 2001, 2003; Tognelli and Douglas 2004; Currie et al. 2004). These variables do not influence every taxa in the same way. For example, climatic variables appear to have a greater effect on amphibian species distributions and richness than latitude (Parris 2004). Likewise, soil type and forest cover explain a large portion of the variance in the distribution of bryophytes in Belgium (Vanderpoorten and Engels 2002). Available energy (measured as evapotranspiration or productivity) explained large-scale patterns of species richness in many groups of plants and animals. (Currie 1991;

Currie et al. 2004). The relationship between climatic variables and species richness patterns of terrestrial birds was discussed by Rahbek and Graves (2001).

Temperate rainforests of southern South America are recognized as a global biodiversity hotspot because of their highly endemic and endangered biota (Olson and Dinerstein 1998; Myers et al. 2000). Chilean Coastal Range forests have been particularly recognized as important centers of biodiversity and a priority area for conservation. A relevant argument for conservation is that the coastal range of south-central Chile served as a major refuge for the rainforest biota during the Quaternary glaciations, when the Andes and most of the Chilean Central Valley were covered by glaciers (Villagrán and Hinojosa 1997). As a consequence of this history, most of the Chilean rain forest endemics are largely restricted to the Coastal Range of south-central Chile (Villagrán et al. 1998; Smith-Ramírez 2004).

The almost complete extirpation of forests in the Chilean central valley to open areas for agriculture and cattle ranching since the European settlement isolated coastal rainforests from native forests remaining at upper elevations in the Andean mountains. The isolation of coastal rain forests has increased in the last decades as large portions of coastal forests have been replaced by pastures and extensive commercial plantations of *Pinus radiata* and *Eucalyptus* sp (Lara & Veblen 1993). Presently, nearly 1 million hectares of forestry plantations are found on the Coastal Range (CONAF-CONAMA-BIRF 1997), but only around 400,000 ha of continuous old-growth forest remain relatively undisturbed (Smith-Ramírez 2004). These old-growth forests are most of the time located in remote, inaccessible areas and include a small portion of the nearly vanished lowland forests which occur below 400 m. Because current threats to these last remains of vulnerable coastal forests are increasing (Smith-Ramírez 2004), it has become critical to recognize and communicate their biological importance and to define priority areas for biodiversity conservation.

In this study, we present the results of a rapid assessment of the biological diversity in these last tracts of continuous forest in the continental Coastal Range of southern Chile (Fig. 1). The complete checklist of species recorded in the surveys was published elsewhere (Smith-Ramírez et al. 2005). The objective of this paper was to use the results of this field survey and available data from biological collections to model species distributions and richness patterns for different components of the biota in these threatened forests. Additionally, we define the location of current hotspots of species richness to guide future conservation efforts.

Methods

Study area

We surveyed remaining native forests in the Coastal Range from the Lingue river in the north (39°30′ S; Valdivia province) to the Llico river in the south (41°25′ S; Llanquihue province), and from the eastern foothills of the coastal range in the Central Valley (elevations above 120 m) to the Pacific coastline to the west (Fig. 1). The area explored 400,000 ha was composed primarily of old-growth, evergreen rain forests, including also smaller areas of second-growth forests and, to a lesser extent, the boundaries between forests and grasslands, wetlands, Magellanic tundra and coastline.

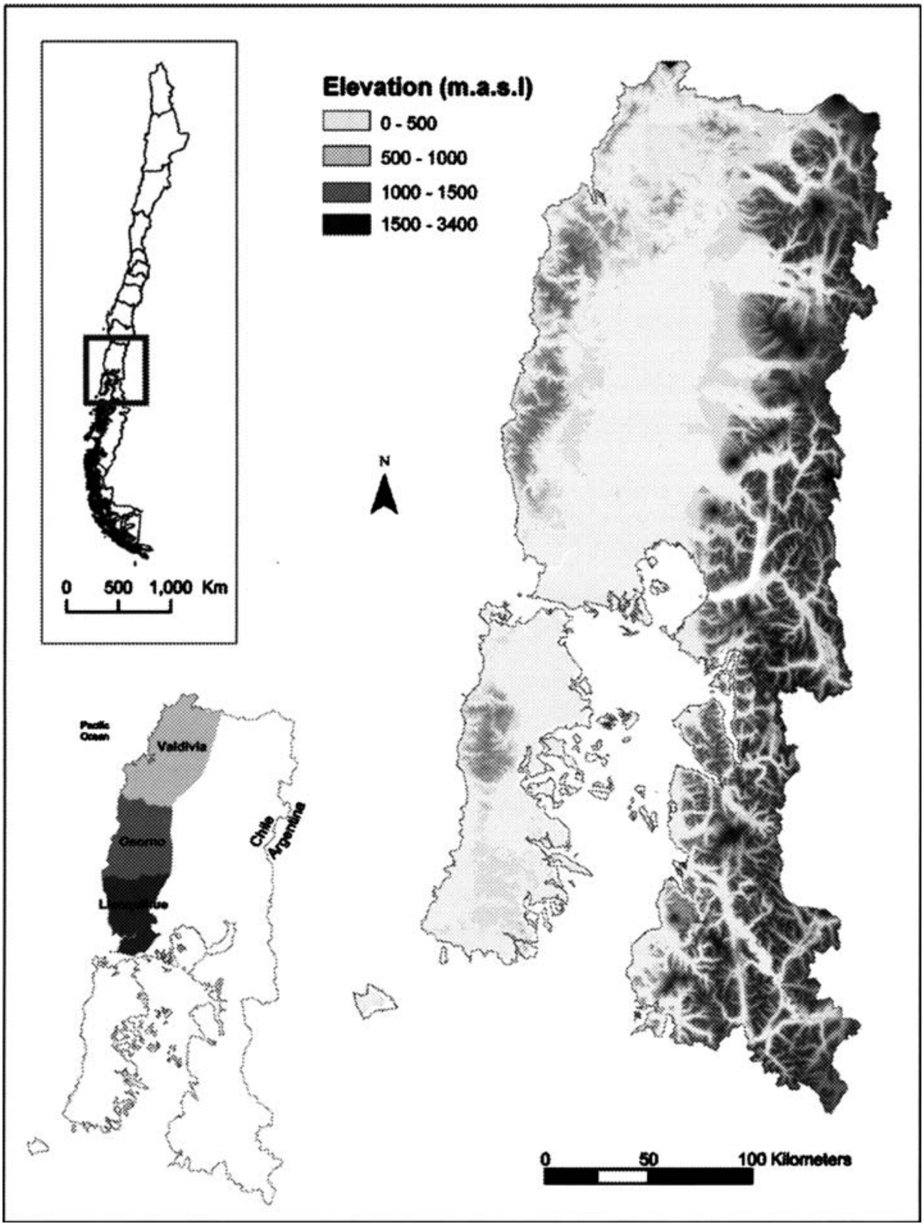


Fig. 1 Elevation map of the study area showing the three administrative provinces that subdivide the territory of the southern Chilean Coastal Range: Valdivia, Osorno and Llanquihue

The Coastal Range is characterized by highly eroded, rounded hills underlied by a micaschist bedrock of Paleozoic origin. The tallest hill in this mountain chain reaches an altitude of 1050 m. The climate is wet-temperate, with a strong oceanic influence, an average of 2000 mm of annual rainfall, which may surpass 5000 mm per year at higher elevations. There are different forest and vegetation types dominating across the altitudinal gradient and on the eastern and western slopes of the mountain range (Luebert and Pliscoff 2004).

At lower elevation on the eastern side, farms, pastures and disturbed scrublands dominate the landscape. Nonetheless, remnant patches of deciduous *Nothofagus obliqua* (Nothofagaceae) forests still exist between 120 m and 300 m elevation. At mid elevations (200–600 m), the slopes are covered by continuous evergreen broadleaved forests, composed mainly of *Drimys winteri* (Winteraceae), *Aextoxicon punctatum* (in the endemic family Aextoxicaceae), *Eucryphia cordifolia* (Eucryphiaceae), *Laurelia sempervirens* (Lauraceae) and several species of Myrtaceae. Above 600 m, the forest becomes dominated by homogeneous stands of *Nothofagus dombeyi, N. nitida* and *N. betuloides* and species of Podocarpaceae. Further up (700 m), the long-lived conifers *Fitzroya cupressoides* and *Pilgerodendron uviferum* (both Cupressaceae) dominate the landscape, forming a mosaic of patches intermixed with a treeless Magellanic tundra (see Ruthsatz & Villagrán 1991).

On the western side of the Coastal Range, the altitudinal vegetation belts are similar; however, evergreen forests begin at the coastline and dominance by *Aextoxicon* is greater at lower elevations, forming mono specific stands below 100 m. At the coastline the forest is bordered by dense thickets of native shrubs (e.g., *Escallonia, Fuchsia*)

Major anthropogenic impacts on coastal rainforests are human-set fires, and clearing of land for forestry plantations and agriculture. In addition, coastal forests are subjected to natural treefalls due to windstorms (Armesto et al. 1996). From these factors, human-set fire is the most destructive, significantly reducing the extent of remaining native forests. Fires have affected annually up to 10,000 ha of forests in the study area (National Forestry data (CONAF), data from 1982 to 1998).

Biological surveys

Field surveys considered only those groups of plants and animals that we were most familiar with. We sampled bryophytes, vascular plants (pteridophytes, coniferophytes, and anthophytes), selected invertebrate groups (with an emphasis on land mollusks), amphibians, and land birds.

Species richness patterns for particular sites and taxonomic groups were assessed during rapid surveys of biodiversity conducted during 25 days in March 2000, 12 days in November 2001 and 12 days in January 2002. Rapid biodiversity assessment (http://www.biodiversityscience.org) is a plot-less sampling methodology that seeks to obtain new biological data from large unexplored areas to be of immediate use for conservation. Variations on this 'checklisting', rapid assessment or ad hoc approaches are widely used (e.g. Conservation International's Rapid Assessment Program, Schulenberg et al. 1999). With this method, controls of sampling effort (which other methodologies do by fixing plot area or the number of trees) are minimal. However, one advantage of this rapid method is that it is possible to complement the original data with information from other published checklists and available biological collections The most relevant information obtained with this methodology is "what species is recorded in what place". Additional advantages have been highlighted by Droege et al. (1998). Rapid plot-less surveys have been applied to monitoring of plants and animals, and assessment of tree diversity

(Gordon et al. 2004; Hawthorne and Abu-Juam 1995). In an analysis of different quantitative methods to estimate tree species richness in a montane forest in Mexico, a rapid plot-less assessment was the most efficient method, over some plot-based methods (Gordon 2005).

At each sampling location, the assessment team surveyed a large, pre-defined area of forest, starting at its perimeter and progressing inwards in concentric circles, recording every new species of each taxa of interest, until the team decided subjectively that no new species were likely to appear. We collected and/or recorded the presence of all the plant and animal vertebrate species observed in the surveys, except for mammals. For logistical reasons, sampling of mammals was incompatible with rapid survey methods because mammal assessments require the use trapping equipment for several days at one site. Invertebrates were sampled with an emphasis on macro-invertebrates and land mollusks. Complete listings of species and sampling locations can be found in Díaz (2005), Larraín (2005), Méndez et al. (2005), Smith-Ramírez et al. (2005) and Valdovinos et al. (2005).

We collected specimens and conducted bird observations in all four forest types defined for the area: evergreen Olivillo-Tique (*Aextoxicon punctatum*) rainforest distributed mainly between 0 m and 100 m elevation; mixed angiosperm-conifer, evergreen forest occurring between 100 m and 600 m; Alerce (*Fitzroya cupressoides*) forest occurring above 700 m ; Coigue de Magallanes and Coigue de Chiloé (*Nothofagus betuloides* and *N. nitida*, respectively) forests occurring between 700 m and 800 m; and remnants of winter-deciduous Roble-Pellin (*Nothofagus obliqua*) forests located between < 120 m and 300 m, restricted to the eastern slopes of the Coastal Range. Three other non-forest habitats present at different altitudes in the study area were also sampled: Magellanic tundra above 800 m, secondary shrublands, and grasslands (low vegetation dominated by Juncaceae and Ciperaceae). Evergreen broad-leaved forests cover nearly 50% of the forested landscape, followed by conifer-dominated alerce forest (32%). Alerce forests have a greater cover in the Llanquihue province, southern portion of the Coastal Range (Fig. 1).

Sampling of bryophytes

We recorded and collected specimens from nine sampling locations in the Coastal Range. New species were added by visual inspection of the ground along forest trails, logs, living tree trunks, branches, and leaves, shrubs, rocks, as well as open areas such as cliffs and wetlands. We surveyed all microhabitats favorable for the growth of bryophytes in each sampling location (except for tree canopies). Mosses were identified using available taxonomic keys and by comparison with specimens stored at the Chilean Museum of Natural History (MNHN). Some specimens were identified to genera only, and affinity to some genera is reported for several species to avoid incorrect identification. Specimens were deposited at the Patricio Sánchez Flora and Fauna Collection in the Ecology Department at Pontificia Universidad Católica de Chile.

In addition, our records included data on the distribution of 125 moss specimens from the MNHN. Furthermore, species cited in previous explorations of the area by Krause (Lorentz 1866), Hosseus (Herzog and Hosseus 1938) and Deguchi (Deguchi 1991a, b, Reimer 1926; He 1998) were also added to our sample.

Vascular plants

We collected specimens of vascular plant species from 16 sites in the Coastal Range during the summer of 2000 and during the spring and summer of 2001 and 2002, respectively. Plants were collected from forests, marshes, coastline and tundra. We made an effort to record all plant species that were present along traveling paths, spending similar amounts of minimal time in each locality. Voucher specimens are deposited in the herbaria of the Universidad de Concepción (CONC), where doubtful samples were identified to species with the assistance of experts (Smith-Ramírez et al. 2005).

We complemented our field data with information about plant distributions and habitat use derived from an extensive review of published papers and monographs, including unpublished student theses, and additional collections (Ramírez and Riveros 1975; Ardiles 1977; Godoy et al. 1981; Mora 1986; Labbe 1989; Vásquez 1994; Lépez 1998; Ramírez 2005), particularly the Database of the Chilean Flora stored at Universidad de Concepción, Chile. Our data on the distribution of vascular plants generated during the first year of sampling (2000) showed that most plant species occupied specific altitudinal ranges (see Villagrán et al. 1986, for description of a similar altitudinal gradient in Chiloé Island). Based on these results, we predicted the presence of plant species within areas not sampled. During 2001 and 2002, we surveyed additional localities across the environmental gradient providing an informal test of our predicted distributions by altitude.

Sampling of invertebrates

We collected soil, arboreal and freshwater macroinvertebrates (>5 mm), with a particular emphasis in mollusks. In each sampling location, six samples of litter and soil were collected using a PVC core (area 0.1 m^2, depth 10 mm). Samples were analyzed in the laboratory using Berlese funnels and a stereomicroscope and inspected for micro-mollusks. Arthropods <5 mm were collected using sweeping traps along forest trails, stopping every 10–30 min for an exhaustive search of the area (ca. 60 m^2). We did not use traps to catch arthropods. Specimens were identified and deposited in the EULA-Chile Centre, University of Concepción. Flying insects were not considered.

The scientific literature about the natural history of mollusks was reviewed by Valdovinos and Stuardo (1988, 1989) and Valdovinos (1989, 1999). As for other taxonomic groups, this information was integrated into our database of species distributions. In two later surveys (2001 and 2002), additional collections in sites not surveyed in the first year were used to test our initial predictions about species distribution in the area. Our data indicated that altitude was the best predictor of the presence of different species of land and freshwater macro invertebrates (>5 mm). For land mollusks, altitude and evapotranspiration rates were the best predictors of distribution and species richness.

Sampling of amphibians

Amphibians were recorded or captured in the forest understory, forest margins, grasslands, scrublands and riparian vegetation along edges of streams and rivers. We collected three specimens per species whenever possible. For each collection, GPS coordinates were recorded. Specimens were identified at the Laboratorio de Zoología, Fac. de Ciencias, Universidad de Chile, using morphological and kariological characters. Collected specimens were deposited in the Herpetological Collection of the Departamento de Biología Celular y Genética de la Universidad de Chile (DBGUCH) and in the Patricio Sánchez Flora and Fauna Collection in the Ecology Department at Pontificia Universidad Católica de Chile.

Amphibian surveys were complemented with published data from the same or nearby areas (Veloso and Navarro 1988; Formas 1979, 1992, 1995; Formas and Vera 1982; Ortiz et al. 1990).

Sampling of forest birds

During March of 2000, we surveyed birds along east–west, in 100–50 m long transects and at fixed points in different forest types. Transects were surveyed every morning during 1–5 consecutive days, recording altitude, forest type and habitat where each bird was observed or heard. Playbacks of recorded bird songs were used to assist in bird surveys. We concentrated our sampling efforts in forested areas, but also recorded birds observed along the coastline and in wetlands. Birds commonly found in open pastures and human residence areas were not included.

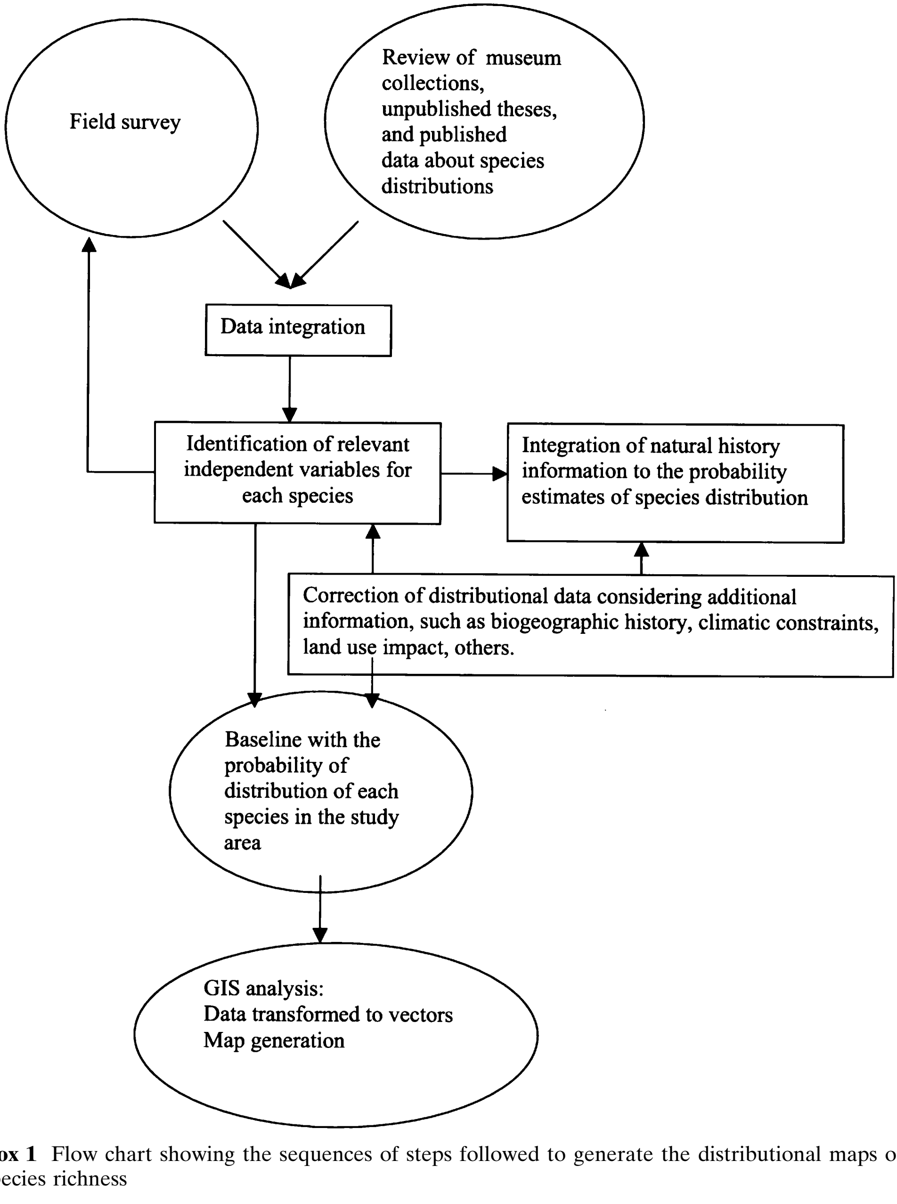
Information from our field surveys was complemented with data on bird distributions in the same area reported by Erazo (1984a, b), and Valverde et al. (1997). Additional information on habitat use by birds was obtained from Goodall et al. (1946), Willson et al. (2004) and Díaz et al. (2005).

Data analysis

Using GIS (Arcview 3.3), we recorded the location coordinates of each individual plant or animal observed and/or collected. For each record, we noted its associated environmental variables such as altitude (for vascular plants, amphibians and land mollusks), evapotranspiration rates (for amphibians and land mollusks) and forest and vegetation type (for birds). Published information on the natural history and distribution of each species recorded was useful for modeling species distributions across non-sampled landscape. For instance, the distribution of successional species or those associated with forest edges was extrapolated to all sites with successional cover and forest edges identified from SIG images.

Forest and vegetation cover types were obtained from the Native Vegetation Survey (CONAF-CONAMA-BIRF 1997). We obtained the evapotranspiration (energy layer) from average NDVI (Myneni et al. 1998, 2002; Turner et al. 2003, http://www.daac.gsfc.nasa.gov/avhrr/global8 km) for the area, associating average values of evapotranspiration with sampling locations. GIS was used to extrapolate species presence to areas not directly sampled.

We generated maps showing the predicted distribution of species richness for each taxonomic group within the study area (except by bryophytes and invertebrates-except mollusks), based field surveys and data from the literature (Box 1). The process of extrapolating point data (collection sites and database records) to continuous surfaces was accomplished as follows. First, all environmental variables were transformed from Raster format into vectors using the Spatial Analyst module in Arcview 3.3. For vascular plants, species richness values were extrapolated to each 100-m altitudinal range obtained from the DEM. In the case of amphibians,



Box 1 Flow chart showing the sequences of steps followed to generate the distributional maps of species richness

maximum species richness was defined for areas below and above 200 m, and then extrapolated using the NDVI values for the same areas. Finally, for land mollusks and birds, species richness values were extrapolated using different land use categories recognizable in the GIS image and their cover throughout the study area. To do this, GIS software Arcview 3.3 was used to relate the point samples with environmental variables using the geoprocessing module and the "assign data by location" command.

Once each point was related to the variable, an SQL command was used to extrapolate environmental variables to other polygons.

Given the latitudinal extent of the territory studied, spanning two degrees of latitude, the altitudinal range of species may differ between northern and southern sectors of the study area. One notable case was the tree *Fitzroya cupressoides* which occupied a very different altitudinal range in these provinces. In Valdivia it is distributed above 600 m, further south, in Osorno, it is found from 300 m elevation, and in Llanquihue, the southernmost province it may be found from 80 m elevation. For such cases, we used a mean altitude range to model the distribution of the species in the three provinces. In the case of *F. cupressoides* we predicted its presence mainly above 400 m. The occasional presence of a species at altitudes different from its main range as predicted by the model was not considered. One additional caveat is that for rare species, such as the vine, *Berberidopsis corallina* or the mollusk *Phyllocaullis araucanus*, among others, the distribution model has greater uncertainty than for common species.

We did not generate distributional maps for bryophytes and invertebrates (except mollusks) because we lacked information to extrapolate to non-sampled areas. For these we only present relationships between species richness and elevation.

Results

Species richness patterns

Bryophytes

We recorded 153 species and three varieties corresponding to 82 genera and 38 families of bryophytes. Most of their diversity occurs in low and mid elevation Coastal eRange forests and most species were found in the forest interior compared to margins or open areas (Fig. 2).

Vascular plants

The field survey complemented by subsequent review of collections and museum database, yielded a total of 577 vascular plant species for the study area, from 258 genera and 129 families. From these, 56 species are pteridophytes, eight gymnosperms, and 512 flowering plants. Historical maps of plant species distributions, assuming continuous forest cover (Figs. 3–5) suggested three major determinants of

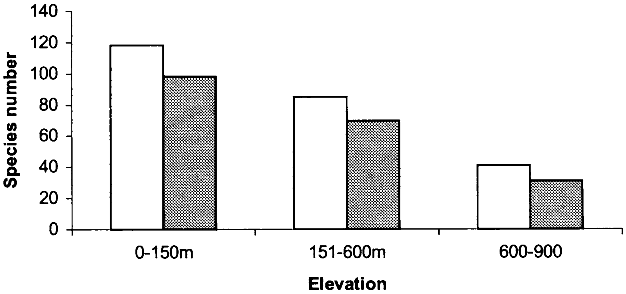


Fig. 2 Number of bryophyte species (white) and macro-invertebrates, except for land mollusks (grey), in three elevation zones of the southern Costal Range

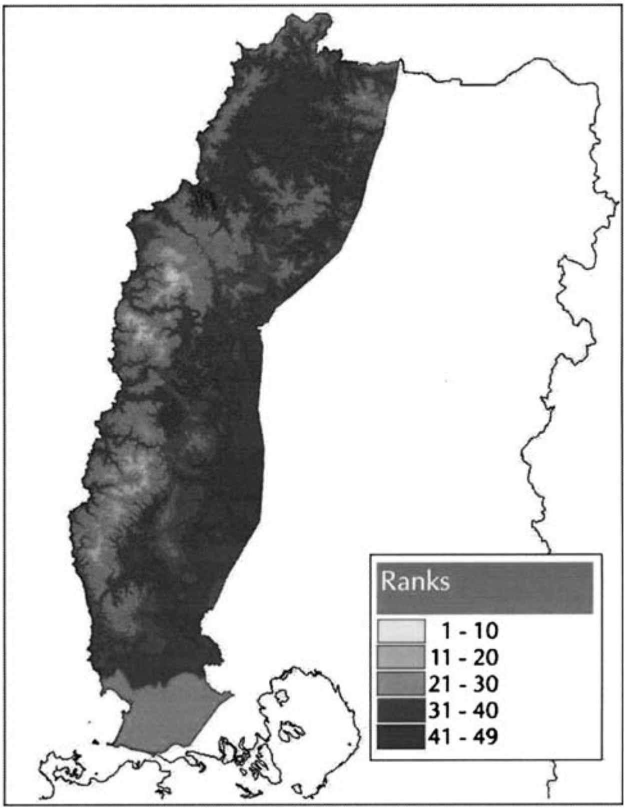


Fig. 3 Historical distribution (based on pre-settlement continuous forest cover) of species richness of Pteridophytes in the Coastal Range of Valdivia, Osorno and Llanquihue provinces, Chilean Lake District. The color gradation shows the changes in species richness across the latitudinal and altitudinal gradients

plant species richness: (1) Topography-most notably elevation and to a lesser extent the east or west orientation of slopes, (2) the presence of rivers, and (3) latitude.

Higher plant species richness was found at lower elevations on Pacific and eastern sides of the Coastal Range. In areas along beaches and near the coastline, we found a floristic assemblage of cosmopolitan and endemic species which are not present on the eastern side of the range. Examples of Cosmopolitan species are: *Ambrosia chamissonis* and *Euphorbia portulacoides;* examples endemic species are: *Arachnites uniflora* and *Lobelia anceps*. On the ocean-facing slopes we found some endemics that do not occur on the eastern slopes, such as *Dioscorea brachybothrya, Azara integrifolia, Maytenus boaria* and *Laurelia sempervirens*. At higher elevations, 700–1050 m, south of the Valdivia River, floristic richness decreases with respect to lower elevations. At higher elevations there are fewer than 60 plant species (Figs. 3–5). Burned forests of *F. cupressoides, Nothofagus betuloides* and mixed forests of Podocarpaceae and *Nothofagus* species prevail in this high altitude belt. In the open moorlands of the summits of the Coastal Range, mosses of the genus *Sphagnum* are the dominant species.

Dominance by different tree species varies between eastern and western sides of the Coastal Range, depending on elevation. For example, the North Patagonian

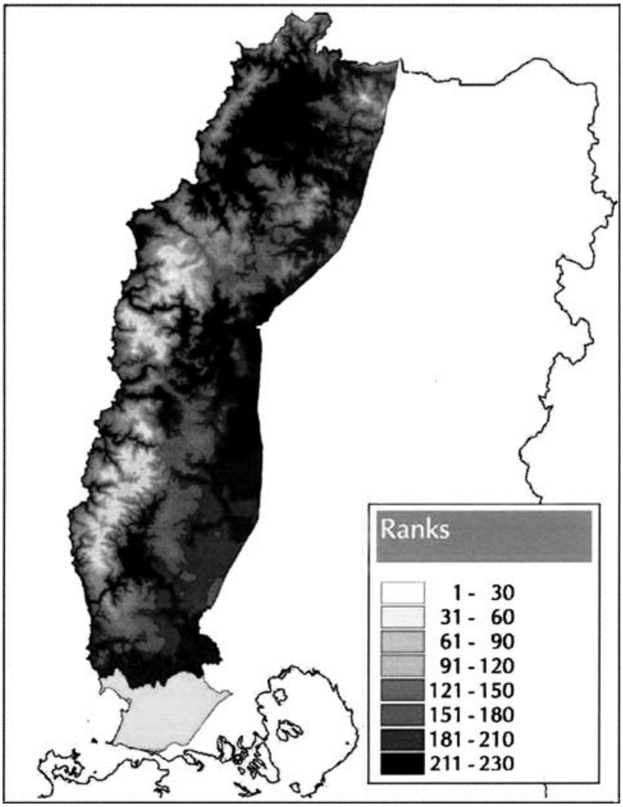


Fig. 4 Historical distribution (based on pre-settlement continuous forest cover) of species richness of angiosperms and gymnosperms in the Coastal Range of Valdivia, Osorno and Llanquihue provinces, in the Lake District of southern Chile. The colour gradation shows the trends in species richness across the latitudinal and altitudinal gradients

forest, dominated by two species of Podocarpaceae and *Nothofagus nitida*, extends to near sea level in the ocean-facing slopes, but is restricted to elevations above 400 m on the eastern slopes. Likewise, conifer forests dominated by *Fitzroya cupressoides* occur at 80 m elevation in the Llanquihue province and in the southern part of the Osorno province, but on the eastern slopes of the range *Fitzroya* forests occur above 700 m.

Localities of high vascular plant diversity were associated with the presence of major rivers, such as Bueno, Hueyelhue and Llico. A rich assemblage of vascular plants is found in the wet-mesic areas along river banks flowing across the Costal Range from the Central Valley. The tree *Laurelia sempervirens* was found only north of Valdivia along the coast, but it also occurs in the Bueno river delta. Similarily, the vine, *Lapageria rosea* was restricted to coastal areas south of 40°40′ S. *Peumus boldus*, on the other hand, occurred only in remnant forest patches in the Central Valley and in riparian strips, particularly along the Bueno River.

A major trend in the distribution of floristic richness is related to latitude. Significantly higher plant species richness was present in the northern areas of the Valdivia province. Here, the Valdivia River becomes the southern limit for a

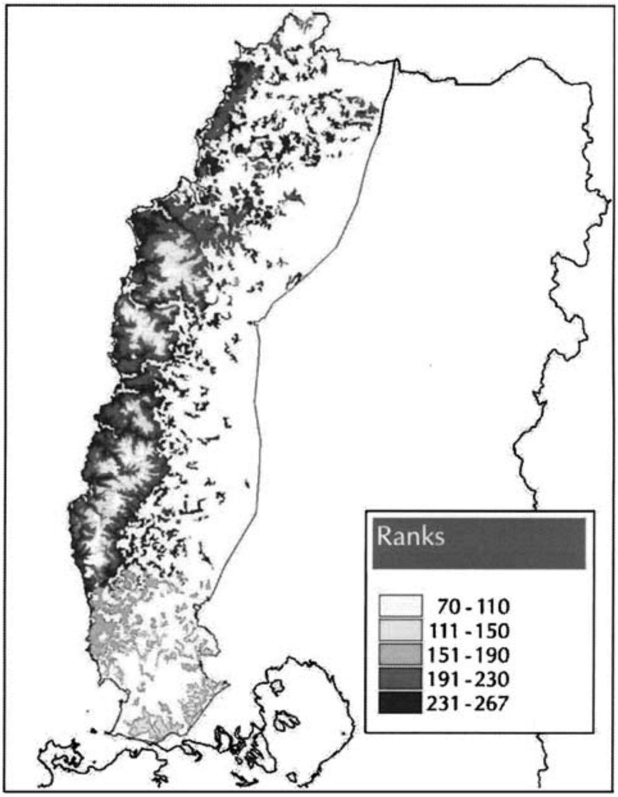


Fig. 5 Current distribution of species richness of angiosperms, gymnosperms and pteridophytes, showing present-day land use in the Coastal Range of the Valdivia, Osorno and Llanquihue provinces, Chilean Lake District. The colour gradations show the trends in species richness across the latitudinal and altitudinal gradients

number of vascular plants that inhabit the Coastal Range. Examples are *Luma chequen, Rhamnus diffusus, Jovellana violacea* and *J. punctata* (Figs. 3, 4). Higher species richness north of the Valdivia River can be explained, in part, by the lower elevations of the coastal range (the highest point is Oncol at 600 m), which allow the penetration of lowland species from the Central Valley.

An exception to the general pattern of species richness occurs in the southern portions of the Llanquihue province. In this lowland area, the low species richness could be explained by the effects of the last glaciation (maximum 18,000 years ago) that left behind poorly developed soils, with a thin organic layer and limited drainage. Species richness here is similar to that found at elevations between 700 m and 900 m further north in the Coastal Range. The presence of *Fitzroya cupressoides* and its companion species at low elevations (<100 m) in the southern portion of the Llanquihue province documents this historical pattern.

Invertebrates

We sampled 57 Coastal Range sites and recorded 153 morphospecies of macroinvertebrates (>5 mm), from which 47 are freshwater taxa (Insecta $N = 25$, Mollusca

$N = 13$, Crustacea $N = 5$, Annelida $N = 2$, Platyhelmintes $N = 1$, Aschelmintes $N = 1$), and 98 taxa are terrestrial (Insecta $N = 49$, Chelicerata $N = 18$, Mollusca $N = 14$, Miriapoda $N = 8$, Crustacea $N = 3$, Annelida $N = 3$, Platyhelmintes $N = 3$, Onychophora $N = 1$). Due to the poor knowledge of invertebrate taxonomy for the area, most of the morphospecies could only be identified to order or family level. One exception was land mollusks, which could be identified to genera or species (Valdovinos et al. 2005). The attitudinal distribution of soil invertebrates, excluding land mollusks, is shown in Fig. 2.

Land mollusks

Among freshwater mollusks were recorded two species of bivalves (Hiriidae $N = 1$, Sphaeriidae $N = 1$) and 11 gastropods (Chilinidae $N = 5$, Amnicolidae $N = 2$, Physidae $N = 1$, Lymnaeidae $N = 1$, Planorbidae $N = 1$, Ancylidae $N = 1$), all of them native. Soil gastropods were 14 native species (Charopidae $N = 7$, Veronicellidae $N = 2$, Bulimulidae $N = 2$, Succineidae $N = 1$, Helicodiscidae $N = 1$, Macrocyclidae $N = 1$). Of these species, 63% are restricted to 39°30′–41°30′ S, while 37% are only found south of 38° S.

Native land mollusks, whether they live in the soil or in water, use very specific microhabitats. They are highly sensitive to changes in humidity, temperature, illumination and food type. Native land mollusks have limited capacity for dispersal, due to their small size, and poor mobility, often showing low local population densities (e.g. Veronicellidae, Macrocyclidae and Bulimulidae 1–3 ind. 50 m^{-2}; Charopidae and Helicodiscidae 1–3 ind. m^{-2}). All native species of land mollusks in the study area were restricted to forest interior, occurring either in humus (e.g. Charopidae and Helicodiscidae), soils (e.g. Veronicellidae and Macrocyclidae) or on shrubs and trees (e.g. Bulimulidae). Freshwater species are generally restricted to cold (<10°C), highly oxygenated water (>70% saturation), with low turbidity (<1 UTN) (examples include Chilinidae, Ancylidae, Amnicolidae, Sphaeriidae and Hyriidae.) The gastropod, *Plectostylus vagabondiae*, is restricted to coastal forests of *Aextoxicon punctatum*, at elevations below 100 m. Few native species such as Lymnaeidae, Physidae and Planorbidae have the capacity to tolerate variations in water temperature and quality.

The species richness pattern for land mollusks tends to resemble that of vascular plants, with greater species richness at lower elevations on both sides of the Coastal Range, and decreasing in diversity at higher elevations (Fig. 5). Other invertebrates studied exhibited a similar pattern (Figs. 3, 4). Above 600 m, we recorded less than half the number of macro-invertebrate species that were observed below 150 m (Fig. 3)

Amphibians

We found 13 amphibian species, belonging to eight genera (*Alsodes, Batrachyla, Insuetophrynus, Eupsophus, Pleurodema, Caudiverbera, Hylorina* and *Rhinoderma*) and two families (Leptodactylidae and Rhinodermatidae).

In the field survey, we recorded a total of 192 individuals, representing nearly all the species potentially present in the area, with the exception of *Bufo rubropunctatus* and *Telmatobufo australis*, two rare species. Amphibians are amply distributed in this region of Chile, with a peak in number of species around 40° latitude. However, the greatest diversity of amphibian species was found in low elevation forests. Above 200 m, there was a remarkable drop in amphibian species diversity (Figs. 6, 7).

Birds

Overall, we recorded 1204 individuals, belonging to 36 species, 33 genera and 18 families. In the limited area surveyed, we observed 12 of the 13 bird species endemic to South American temperate rainforests, and 26 of the 29 species restricted to the southern cone of South America. A larger number of bird species were recorded in old-growth, evergreen rainforests located at low and mid elevations, with around 30 bird species in each altitudinal belt. The lowest number of bird species was observed in fragmented forest patches surrounded by an agricultural matrix, with around 17 bird species.

The most frequently detected species was the Chucao tapaculo (*Scelorchilus rubecula*), an endemic understory bird that presented a loud call and a friendly behavior toward humans. The next most abundant species were the summer visitors: White-crested Elaenia (*Elaenia albiceps*), Green-backed Firecrown hummingbird (*Sephanoides sephaniodes*), the Chilean Pigeon (*Columba araucana*) and the

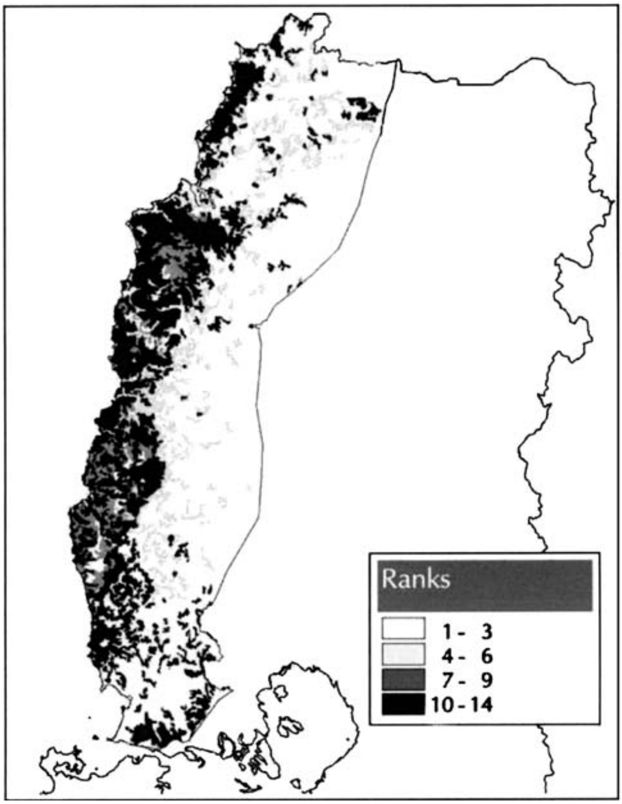


Fig. 6 Current distribution of species richness of land mollusks in the Coastal Range of Valdivia, Osorno and Llanquihue provinces, Chilean Lake District. The colour gradation shows the trends in species richness across the latitudinal and altitudinal gradients

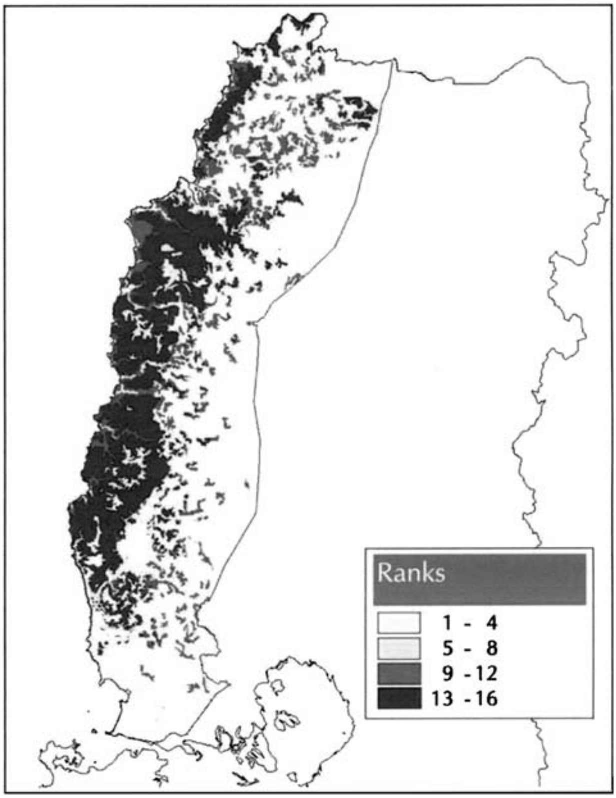


Fig. 7 Current distribution of amphibian species richness in the Coastal Range of Valdivia, Osorno and Llanquihue provinces, Chilean Lake District. The colour gradation shows the changes in species richness across the latitudinal and altitudinal gradients

Thorn-tailed Rayadito (*Aphrastura spinicauda*). Some of these are also the most common species in secondgrowth forests in Chiloé Island (Rozzi et al. 1996; Armesto et al. 1996). The less detected species were those with large home ranges, such as raptors and the large Magellanic Woodpecker. Forest species were absent from non forested areas.

Discussion

Studies that model species distributions are limited by the quality of field data and published information that can be used to extrapolate presence of species between sampling points, and by the type and number of assumptions made about species distributions. Problems occur when extrapolations are used to create statistical models correlated with a set of environmental variables (Ferrier 2002; Peterson et al. 2002; Araujo et al. 2003). In this study, major uncertainties are due to environmental descriptor variables, such altitudinal ranges, evapotranspiration, and forest type to which species were assigned. It is known that patterns of species richness, especially at local scales, respond to a wide variety of processes. Our analysis integrates field and published information to propose potential distribution maps of species of different taxonomic groups. This approach, using both knowledge of natural history of each species and GIS, is a more powerful tool than mapping species distributions from records associated with a grid of quadrants (Pliscoff 2003; Stockwell and Peterson 2003). Quadrants produce many artifacts in the resulting distribution ranges and patterns are strongly dependent on the number of collections available. Nevertheless, our method is limited in that it requires high quality information about the natural history of each species. Probably, for some tropical areas with thousands species in one hectare this is not feasible. However, it works reasonably well for the Chilean temperate forests, with fewer species per hectare.

The analysis of biodiversity distribution in this Chilean coastal forest, showed a trend towards higher species richness in mid and low elevation forests than in higher elevations for all the taxonomic groups studied. The area of forest in each altitudinal zone is greatest at mid elevations (150–600 m), and significantly lower at higher and lower elevations in the Coastal Range for the three provinces studied (Fig. 8, 9). Extensive lowland forests have nearly disappeared due to human land use. In addition, high altitude conifer forests in the Coastal Range have been severely disturbed by human-set fires and intensive logging, resulting in high ecosystem degradation (Cortes 1990). The presence of higher species richness in lowland forests has been reported in other regions where forests are less disturbed (Bachman et al. 2004). In the case of the Chilean Coastal Range, species richness for different groups was greater in lowland areas, but because of past human land use, the greatest area covered by forest occurs at mid elevations (Fig. 9).

In the southern sector of the study area, in Llanquihue province (Fig. 1), plant species richness drops notoriously (Fig. 5), which can be attributed to the fact that this area was directly affected by the advance of Llanquihue glaciar, which retrieved 18–12,000 years ago. Soils in this area are very shallow or non-existent. A notable feature of this place is that at low altitude, around 50 m, species composition is similar to ecosystems found on the summits of the Coastal Range further north (Smith-Ramírez et al. 2005).

The composition of plant and animal assemblages in montane habitats is very different from the lowlands. Most bird species, however, are distributed across all elevations, and are probably more limited by food than by climatic stress. For example, the Magellanic woodpecker, *Campephilus magellanicus* is more frequently found between 600 m and 800 m, where it can eat larvae found in old *Nothofagus* trees or snags. By contrast, *Elaenia albiceps*, an omnivorous bird species, can be found throughout the elevation gradient, habitats and across all forest types,, with the exception of moss-dominated bogs.

A comparison of historic reconstructions of species richness patterns (Figs. 3, 4) with the present day map for species richness of vascular plants (Fig. 5) reveals that the richest habitats, on the lower eastern slopes of the Coastal Range, have already been lost for conservation purposes. The remaining forest habitats on the eastern slopes have medium to low species richness. At present, second-growth forests with medium to low species richness represent the largest remaining forest cover in the region studied. Nevertheless, small remnant forests should be considered valuable areas for conservation, especially where public reserves are lacking (Smith-Ramírez 2004).

As a conservation strategy based on the current patterns of species richness, we recommend a reserve design that includes the entire elevation gradient, and especially lowland areas on both sides of the Coastal Range. Although areas on the eastern side of the Coastal Range are more degraded than areas on the western side, it is still possible and necessary to find small remnant forests worth of conservation.

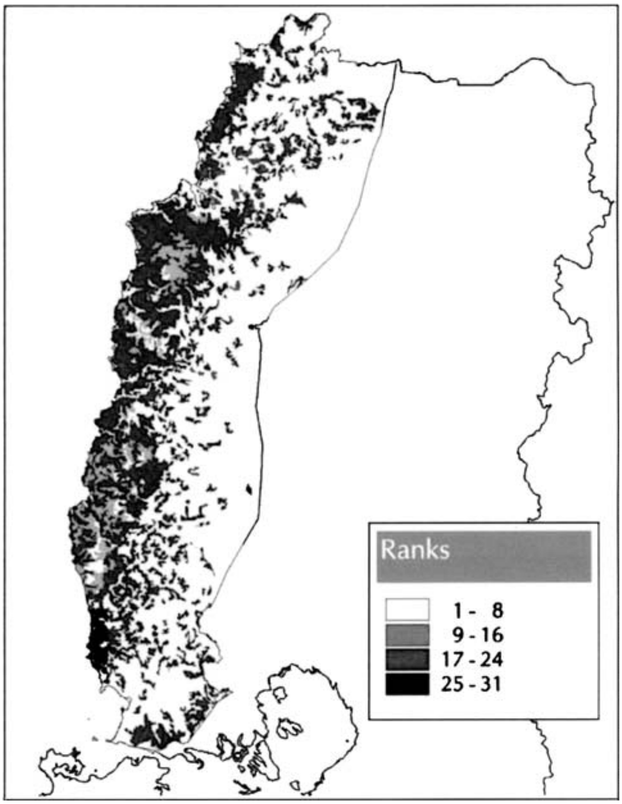


Fig. 8 Current distribution of bird species richness in the Coastal Range of Valdivia, Osorno and Llanquihue provinces, Chilean Lake District. The colour gradation shows the trends in species richness across the latitudinal and altitudinal gradients

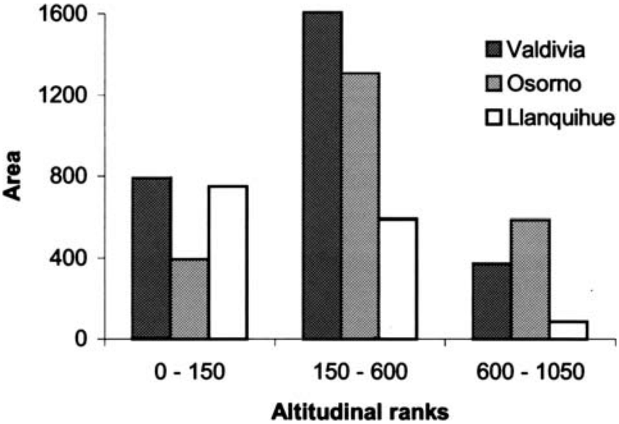


Fig. 9 Area of land (km^2) with forest cover in three altitudinal ranges compared in the Coastal range of Valdivia, Osorno and Llanquihue provinces, Chilean Lake District

Acknowledgements This work was supported by WWF grants FC11 and FC49, National Science Conservation, Proyecto Nücleo Milenio No. P99-103FICM, Fondecyt-Fondap 1501-0001 (to CASEB), BBVA Foundation and Biocores project funded by INCO-DC program IV under contract ICA 4-CT-2001-10095. We are grateful to Ek del Val, Juan Armesto and Pablo Necochea for assistance with the English version.

References

Araujo MB, Humphries CJ, Densham PJ, Lampinen,R., Hagemeijer WJM, Mitchell-Jones AJ, Gasc JP (2001) Would environmental diversity be a good surrogate for species diversity? Ecography 24:103–110

Araujo MB, Densham PJ, Humphries CJ (2003) Predicting species diversity with ED: the quest for evidence. Ecography 26:380–384

Ardiles R (1977) Contribución al estudio del bosque nativo perennifolio de la Cordillera de la Costa, en tres niveles altitudinales. Thesis de Ingeniero Forestal, Facultad de Ingeniería Forestal, Universidad Austral de Chile, Valdivia

Armesto JJ, Aravena JC, Villagrán C, Pérez C, Parker GG (1996) Bosques templados de la Cordillera de la Costa. In: Armesto JJ, Villagrán C, Arroyo MTK (eds) Ecología de los bosques nativos de Chile, Editorial Universitaria, Santiago, Chile, 199–213

CONAF-CONAMA-BIRF (1997) Catastro y evaluación de los recursos vegetacionales nativos de Chile. Informe Nacional con Variables Ambientales. CONAMA, Santiago

Bachman S, Baker WJ, Brummitt N, Dransfield J, Moat J (2004) Elevational gradients, area and tropical island diversity: an example from the palms of New Guinea. Ecography 27:299–310

Cortés M (1990) Estructura y dinámica de los bosques de alerce (*Fitzroya cupressoides* (Mol.) Johnston) en la cordillera de la Costa de la Provincia de Valdivia. Tesis de Ingeniero Forestal, Facultad de Ciencias Forestales. Universidad Austral de Chile, Valdivia

Currie DJ (1991) Energy and large-scale patterns of animal species and plant species richness. Am Nat 137:27–49

Currie DJ (2001) Projected effects of climate change on patterns of vertebrate and tree species richness in the conterminous United States. Ecosystems 4:216–225

Currie DJ, Mittelbach GG, Cornell HV, Field R, Guégan J-F, Hawkins BA, Kaufman DM, Kerr JT, Oberdorff T, O'Brien EM, Turner JRG (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecol Lett 7:1121–1134

Deguchi H (1991a) A list of Moss Collection made during the Expeditions to Chile in 1981 and 1987 (1). Bull Natn Sci Mus Tokyo Ser B 17:15–34

Deguchi H (199lb) A list of Moss Collection made during the Expeditions to Chile in 1981 and 1987 (2). Bull Natn Sci Mus Tokyo Ser B 17:67–83

Díaz I (2005) Historia natural, diversidad y conservación de las aves en bosques de la Cordillera de la Costa de la Región de Los Lagos, Chile. In: Smith-Ramírez C, Armesto JJ, Valdovinos C (eds) Historia, Biodiversidad y Ecologia de los bosques de la Cordillera de la Costa de Chile. Editorial Universitaria, Santiago, Chile

Droege S, Cyr A, Larivée J (1998) Checklists: an under-used tool for the inventory and monitoring of plants and animals. Conservation Biology 12:1134–1138

Erazo S (1984a) Estudio de la ornitocenosis en un rodal de Olivillo, Valdivia, Chile. Tesis Magíster. Universidad Austral de Chile, Valdivia

Erazo S (1984b) Análisis de censos de la avifauna realizados en un rodal boscoso de olivillo, Valdivia, Chile, X Región. Revista Geográfica de Valparaíso (Chile) 15:49–71

Faith DP (2003) Environmental diversity (ED) as surrograte information for species-level biodiversity. Ecography 26:374–379

Ferrier S (2002) Mapping spatial pattern in biodiversity for regional conservation planning: where to from here?. Syst Biol 42:331–363

Formas JR (1979) La herpetofauna de los bosques temperados de Sudamerica. In: Duellman W (ed) The South American herpetofauna: its origin, evolution and dispersal. Museum of Natural History, University of Kansas, Monograph 7:341–369

Formas JR (1992) The tadpole of *Eupsophus vertebralis* (Anura: Leptodactylidae). Herpetologica 48:115–119

Formas JR (1995) *Anfibios*. In: Simonetti JA, MTK Arroyo, AE Spotorno, E Lozada (eds) Diversidad biológica de Chile. Comite Nacional de Diversidad Biologica. CONICYT, Santiago, pp 314–325

Formas JR, Vera MI (1982) The status of two Chilean frogs of the genus *Eupsophus* (Anura: leptodactylidae). Proc Biol Soc Washington 95:668–693

Gaston G (1996) Species richness: measure and measurements. In: Gaston KJ (eds) Biodiversity. A biology of numbers and differences. Blackwell Science Ltd., Oxford, pp 77–113

Godoy R, Ramírez C, Figueroa H, Hauenstein E (1981) Estudios ecosociológicos en Pteridófitos de comunidades boscosas valdivianas, Chile. Bosque 4:12–24

Goodall JD, Johnson AW, Philippi RA (1946) Las ayes de Chile, su conocimiento y sus costumbres. Platt establecimientos Gráficos, Buenos Aires

Gordon JE, Hawthorne WD, Reyes-García A, Sandoval G, Barrance AJ (2004) Assessing landscapes: a case study of tree and shrub diversity in the seasonally dry tropical forests of Oaxaca, Mexico and southern Honduras. Biol Conserv 117:429–442

Gordon J (2005) Biodiversity Conservation and Non-Governmental Organisations in Oaxaca, Mexico. Ph.D. Thesis, Durham University, UK

Groves CR (2003) Drafting a Conservation Blueprint. Island Press

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. Ecol Model 135:147–186

Guisan A, Hofer U (2003) Predicting reptile distributions at mesoscale: relation to climate and topography. J Biogeogr 30:1233–1243

He S (1998) A checklist of the mosses of Chile. J Hattori Bot Lab 85:103–189

Hawthorne WD, Abu-Juam M (1995) Forest protection in Ghana. IUCN, Gland, Switzerland and Cambridge, UK

Herzog T, Hosseus C (1938) Contribución al conocimiento de la Flora Briófita del sur de Chile. Archivos de la Escuela de Farmacia de la Facultad de Ciencias Medicas de Córdoba 7:3–95

Kerr JT, Sugar A, Packer L (2000) Indicator taxa, rapid biodiversity assessment, and nestedness in an endangered ecosystem. Conserv Biol 14:1726–1734

Kerr JT, Packer L (1997) Habitat heterogeneity as a determinant of mammal species richness patterns in high-energy regions. Nature 385:252–254

Larraín J (2005) Musgos de la Cordillera de la Costa de Valdivia, Osorno y Llanquihue: consideraciones ecólogicas y lista de especies. In: Smith-Ramírez C, Armesto JJ, Valdovinos C (eds) Historia, Biodiversidad y Ecologia de los bosques de la Cordillera de la Costa de Chile. Editorial Universitaria. Santiago, Chile

Labbe S (1989) Estudio fitosociológico estadístico de los bosques de boldo de la cuenca del río Bueno (Chile). Thesis de Ingeniero Forestal. Universidad Austral de Chile, Valdivia, Chile

Lépez P (1998) Estudio fitosociológico del Parque Oncol (Valdivia, Chile). Thesis de Ingeniero Forestal. Universidad Austral de Chile, Valdivia, Chile

Lorentz PG (1866) Musci frondosi in Chile prope Valdiviam et prope Corral lecti per Dr. Krause. Botanische Zeitung (Berlin) 24:185–189

Luebert F, Pliscoff P (2005) Bioclimas de la Cordillera de la Costa del centro-sur de Chile. In: Smith-Ramírez C, Armesto JJ, Valdovinos C (eds) Historia, Biodiversidad y Ecologia de los bosques de la Cordillera de la Costa de Chile. Editorial Universitaria, Santiago, Chile

Margules CR, Pressey RL (2000) Systematic conservation planning. Nature 405:243–253

Meffe C, Caroll R (1997) Principles of conservation biology, 2nd ed. Sinauer Associates, Sunderland, Massachussetts

Méndez M, Soto E, Torres-Pérez F, Veloso A (2005) Anfibios y reptiles de los bosques de la Cordillera de la Costa (X Région, Chile). In: Smith-Ramírez C, Armesto JJ, Valdovinos C (eds) Historia, Biodiversidad y Ecologia de los bosques de la Cordillera de la Costa de Chile. Editorial Universitaria. Santiago Chile

Mora A (1986) Estudios fitosociólogicos en el bosque de olivillo (LapagerioAextoxiconetum) de la Decima región de Chile. Thesis de Ingeniero Forestal, Universidad Austral de Chile, Valdivia, Chile

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Myneni RB, Hoffman J, Glassy Y, Zhang PV, Nemani R, Running S, Privette JL et al (2002) Global products of vegetation leaf area and fraction absorbed PAR from year one of MODIS data. Remote Sensing Environ 83:214–231

Moravec J (1998) Reconstructed natural versus potential natural vegetation in vegetation mapping: a discussion of concepts. Appl Veg Sci 1:173–176

Olson D, Dinerstein E (1998) The global 200: a representation approach to conserving the earth's most biologically valuable ecoregions. Conserv Biol 12:502–515

Ortiz JC, Troncoso JF, Ibarra-Vidal H, Nuñez H (1990) Lista sistemática, distribución, estados de conservación y clave para los herpetozoos de la VIII Región, Chile. Comunicaciones Museo Regional Concepción (Chile) 4:31–43

Parris K (2004) Environmental and spatial variables influence the composition of frog assemblages in sub-tropical eastern Australia. Ecography 27:392–400

Peterson AT, Soberón J, Sánchez-Cordero V (1999) Conservatism of ecological niches in evolutionary time. Science 285:1265–1267

Peterson AT, Ortega-Huerta MA, Bartley J, Sánchez-Cordero V, Soberon JM, Buddemeier RH, Stockwell RB (2002) Future projections for Mexican faunas under global climate change scenarios. Nature 416:626–629

Pliscoff P (2003) Priorización de áreas para fortalecer la conservación de la flora arbórea nativa en la zona mediterránea de Chile. MS Tesis, Facultad de Ciencias, Universidad de Chile, Santiago

Prendergast JR, Wood SN, Lawton JH, Evershaur BC (1993) Correcting for variation in recording effort in analyses of diversity hotspots. Biodiv Lett 1:39–53

Rahbek C, Graves GR (2001) Multiscale assessment of patterns of avian species richness. Proc Natl Acad Sci USA 98:4534–4539

Ramírez C, Riveros M (1975) Los alerzales de la cordillera Pelada: flora y fitosociología. Medio Ambiente 1:3–13

Ramírez C (2005) Asociaciones vegetales de la Cordillera de la Costa de la Region de Los Lagos. In: Smith-Ramírez C, Armesto JJ, Valdovinos C (eds) Historia, Biodiversidad y Ecología de los bosques de la Cordillera de la Costa de Chile. Editorial Universitaria, Santiago, Chile

Reimers H (1926) Beitrage zur Bryophytenflora Sudamerilcas. I. Die von Pater A, Hollermeyer in Chile 1918/1923 gessammelten Leber-and Laubmoose. Hedwigia 66:27–75

Rozzi R, Martínez D, Willson MF, Sabag C (1996) La avifauna de los bosques templados de Sudamérica. In: Armesto JJ, Villagrán C, Arroyo MTK (eds) Ecología de los bosques nativos de Chile, Editorial Universitaria, Santiago, Chile, 135–152

Schulenberg TS, Short CA, Stephenson PJ (eds) (1999) A biological assessment of Parc National de la Marahoué, Côte d'ivoire. Vol. RAP Working Papers 13. Conservation International, Washington

Scott JM, Davis FW, Csuti BR, Noss B, Butterfield C, Groves H, Anderson Caicco S, D'Erchia F, Edwards TC, Ulliman J, Wright RG (1993) Gap analysis: a geographic approach to protection of biological diversity. Wildlife Monogr 123:1–41

Smith-Ramírez C (2004) The Chilean Coastal Range: A Vanishing Center of Biodiversity and Endemism in Southern Temperate Rain Forests. Biodiv Conserv 13:373–393

Smith-Ramírez C, Pliscoff P, Teillier S, Barrera E (2005) Patrones de riqueza y distribución de la flora vascular en la Cordillera de la Costa de Valdivia, Osorno y Llanquihue, Chile. In: Smith-Ramírez C, Armesto J, Valdovinos C (eds) Historia, Biodiversidad y Ecología de los bosques de la Cordillera de la Costa de Chile. Editorial Universitaria, Santiago, Chile

Stockwell D, Peters D (1999) The GARP modelling system: problems and solutions to automated spatial prediction. Int J Geogr Inform Sci 13:143–158

Stockwell DRB, Peterson AT (2003) Comparison of resolution of methods used in mapping biodiversity patterns from point occurrence data. Ecol Indicators 3:213–221

Tognelli M, Douglas K (2004) Analysis of determinants of mammalian species richness in South America using spatial autoregressive models. Ecography 27:427–436

Turner W, Spector S, Gardiner N, Fladeland M, Sterling E, Steininger M (2003) Remote sensing for biodiversity science and conservation. Trends Ecol Evol 18:306–314

Valdovinos C (1989) Catálogo de los moluscos terrestres y dulceacuícolas de la Cordillera de Nahuelbuta y areas adyacentes. Comunicaciones del Museo Regional de Concepción 3:7–14

Valdovinos C (1999) Biodiversidad de moluscos chilenos: base de datos taxonómica y distribucional. Gayana Zoologiá 63:111–164

Valdovinos C, Stuardo J (1988) Morfologia, sistemática y distribución del genero *Plectostylus* Beck (1837) (Pulmonata: Bulimulidae). Gayana Zoología 52:115–195

Valdovinos C, Stuardo J (1989) *Austrodiscus solemi spec. nov*. (Pulmonata: Endodontidae) un nuevo gastrópodo humícola de Chile. Boletín de la Sociedad de Biología de Concepción, Chile 60:239–245

Valdovinos C, Olmos V, Moya C (2005) Moluscos terrestres y dulceacuícolas del la Cordillera de la Costa. In: Smith-Ramírez C, Armesto J, Valdovinos C (eds) Historia, Biodiversidad y Ecologia de los bosques de la Cordillera de la Costa de Chile. Editorial Universitaria, Santiago, Chile

Valverde V, Lagos V, Díaz I (1997) Catastro de vertebrados terrestres. Plan de ordenación forestal, Reserva Nacional Valdivia. Documento Técnico, CONAF, Santiago

Vanderpoorten A, Engels P (2002) The effects of environmental variation on bryophytes at a regional scale. Ecography 25:513–522

Vásquez R (1994) Estudio de la flora y vegetacion boscosa potencial de la cordillera pelada (Valdivia, Chile). Thesis of Forestry, Universidad Austral de Chile,Valdivia, Chile

Veloso A, Navarro J (1988) Lista sistematica y distribucion de anfibios y reptiles de Chile. Bolletino del Museo Regionale di Scienzie Naturali, Torino 6:481–539

Villagrán C, Armesto JJ, Leiva R (1986) Recolonización postglacial de Chiloé insular. Evidencias basadas en la distribución geográfica y los modos de dispersión de la flora. Revista Chilena de Historia Natural 59:19–39

Villagrán C, Le-Quesne C, Aravena JC, Jiménez H, Hinojosa F (1998) El rol de los cambios de clima del Cuaternario en la distribución actual de la vegetacion de Chile central-sur. Bamberger Geographische Schriften 15:227–242

Willson MF, De Santo TL, Sabag C, Armesto JJ (1994) Avian communities of fragmented south temperate rainforest in Chile Conserv Biol 8:508–520