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Extinction debt in a biodiversity hotspot: the case of the Chilean Winter Rainfall-Valdivian Forests

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Abstract
Habitat fragmentation has become a major concern of conservation because of negative influences on plant species declines and extinctions. However, local extinction of species can occur with a temporal delay following habitat fragmentation, which is termed extinction debt. Many studies about extinction debt rely on community equilibrium from relationships between species richness and habitat variables. We assumed that the distribution of many vascular plant species in the coastal range of south-central Chile is not in equilibrium with the present habitat distribution. The aim of this research is to quantify patterns of habitat loss and to detect extinction debt from relationships between the current richness of different assemblages of vascular plants (considering longevity and habitat specialization) and both past and current habitat variables. The results showed that native forests have been fragmented and reduced by 53%, with an annual deforestation rate of 1.99%, in the study area between 1979 and 2011. Current richness of plant species was mostly explained by past habitat area and connectivity. Past habitat variables explained best richness of long-lived specialist plants, which are characterized by restricted habitat specialization and slower population turnover. We also showed that habitat fragmentation has resulted in a significant reduction in long-lived plant species' "dwelling patch sizes (DPS)" between 1979 and 2011. Our analyses provide the first evidence of predicted future losses of plant species in a South American temperate biodiversity hotspot. Consequently, an unknown proportion of the plants in the study area will become extinct if no targeted restoration and conservation action is taken in the near future.

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Introduction

Habitat fragmentation has become a major research theme in conservation biology (Fazey et al. 2005; Haila 2002) as one of the main threats to biodiversity [Convention on Biological Diversity (CBD) Secretariat 2001]. Habitat fragmentation is associated with a reduction of habitat area and increased isolation of remaining habitats (Laurance et al. 2002; Loreau et al. 2001), and leads to species declines and extinctions (Lienert 2004; Ouborg et al. 2006; Young et al. 1996; Young and Clarke 2000). Species extinction associated with habitat fragmentation begins as a result of deterministic and stochastic threatening processes, which are exogenous (Bennett et al. 2003; Fischer and Lindenmayer 2007). Although a large proportion of exogenous extinctions typically occur almost immediately, endogenous threatening processes can cause local extinction for many years due to demographic, genetic or environmental variability in an isolated small population (Lindenmayer and Fischer 2006). This means

local extinction of individual species is often characterized by considerable time-lags (relaxation time) following habitat fragmentation because species do not always respond instantly to habitat changes (Dullinger et al. 2012, 2013; Gilbert and Levine 2013; Kuussaari et al. 2009). This is known as extinction debt (time-delayed extinction), i.e., future extinction of species due to events in the past (Tilman et al. 1994). Extinction debt implies that, although the species are still present, the conditions for species' persistence are no longer met (Hanski and Ovaskainen 2002; Tilman et al. 1994).

Over the last two decades, many studies have attempted to understand extinction debt and predict the extinction proneness of species and length of relaxation times. The following four factors regards extinction debt have been reliable to date (Kuussaari et al. 2009; Lindenmayer and Fischer 2006). First, Lindborg (2007) showed that species vary in their sensitivity to habitat fragmentation depending on life history traits. It has been suggested that species with short generation times and habitat specialization might be the most sensitive to habitat changes, and thus have the shortest relaxation time, although these predictions remain largely unconfirmed by empirical data (Allendorf and Hard 2009; Koh et al. 2004; Kuussaari et al. 2009). Secondly, species' responses to habitat fragmentation, in many cases, depend on the patch attributes (e.g., spatio-temporal configuration of habitat patches) (Lindborg and Eriksson 2004). In many studies on extinction debt, habitat patch size and connectivity are considered to be parts of a crucial spatial configuration (Cousins and Vanhoenacker 2011; Helm et al. 2006; Kolk and Naaf 2015; Piqueray et al. 2011). Thirdly, historical contingency can affect the results. For example, the time since the habitat was altered is crucial because of the possibility that extinction debt has already been paid via realized extinctions (Hanski 2000). Finally, the nature of the alteration, which refers to the spatial and temporal dynamics of landscape perturbation (e.g., perturbation frequency, size, intensity, and return interval), affects the time of extinction after the metapopulation falls below an extinction threshold (Ovaskainen and Hanski 2002, 2004; Turner 2010).

As knowledge of species richness in the past is rarely available, past and present habitat information can be mostly used to detect ongoing extinction debt from the relationships between current species richness and habitat variables (Lindborg and Eriksson 2004; Piessens and Hermy 2006; Ranius et al. 2008). Aside from the large number of studies undertaken in fragmented grasslands and temperate forests of Europe (Adriaens et al. 2006; Cousins et al. 2007; Gustavsson et al. 2007; Lindborg and Eriksson 2004; Öster et al. 2007), few researchers have explored the presence of extinction debt in the rest of the world (Vellend et al. 2006) and very little work has been done in the Southern Hemisphere's temperate forests. While the presence of an extinction debt has been largely tested in well-delimited areas, where natural cover (forests or grassland) has been relatively stable over the last couple of centuries (Lindborg 2007; Piqueray et al. 2011; Vellend et al. 2006), extinction debt in rapidly changing landscapes has been little studied (Piqueray et al. 2011). Thus, empirical studies that specifically examine potential extinction debt have been focused on species occupancy or richness at the community level (Cousins et al. 2007; Lindborg and Eriksson 2004), whereas identifying individual species at increased risk of extinction in the near future is rare (Piqueray et al. 2011). Because responses to habitat fragmentation are species dependent (Lindborg 2007; Mildén et al. 2007), identification of particular species at a high risk of extinction among groups of species that share a common set of life history traits is vital for developing appropriate conservation strategies.

The Chilean Coastal Range (CCR) has been identified as a center of biodiversity and endemism in the South American temperate rainforests (Armesto et al. 1998). Because of their geographic isolation, these rainforests are characterized by a highly endemic flora and fauna (Armesto et al. 1996), and are considered to be globally threatened ecosystems (Armesto et al. 1998; Myers et al. 2000). During the last few decades, native forests in the CCR were rapidly destroyed, fragmented and associated with small patches (< 100 ha) of native forest surrounded by exotic species plantations (Aguayo et al. 2009; Echeverria et al. 2006). Despite an ongoing trend of forest fragmentation and decline, this area still contains high species diversity and endemism among plants (Cavieres et al. 2005). Therefore, we assumed that the distribution of many vascular plant species in the CCR is in disequilibrium with the present habitat distribution (Grez et al. 2005; Wolodarsky-Franke and Herrera 2011). The recent deforestation and forest fragmentation of the CCR, with dramatic declines in patch area and connectivity, should provide an excellent model system to test for the presence of an extinction debt in a wide range of ecological traits.

Our objective was to evaluate relationships between the current richness of vascular plant species and spatial patterns of both the past and the current habitat in a rapidly changing biodiversity hotspot located in Chilean temperate forests. We tested the following hypotheses: (1) the current richness of vascular plant species is more related to patch size and connectivity of past habitat than current habitat; (2) the richness of short-lived plants, as well as long-lived plants, exhibits a temporal delay of response to habitat fragmentation in a rapidly changing landscape; and (3) long-lived species are more probable in smaller patches in 2011 compared to in 1979.

Materials and methods

Study site

The study was carried out in coastal temperate deciduous forest of *Nothofagus nervosa* and *Persea lingue,* with elevations ranging between 600 and 1000 m a.s.l. (Luebert and Pliscoff 2006) (Fig. 1). This is one of six vegetation formations (ecosystems) located in the Nahuelbuta Mountain Range (NMR) of the CCR (37°11′–38°45′S, 73°13′E). The range is located in a transition zone of two ecosystems: Mediterranean vegetation and temperate rainforest. This feature of the study area allows an increase in plant species richness compared to the rest of the Chilean temperate forests (Hinojosa and Villagrán 1997). There are 690 native vascular plant species growing on this mountain range, of which 265 are endemic (Wolodarsky-Franke and Herrera 2011). However, recent data suggest a pessimistic future for this globally important area. Many specialist plants including nine representative trees (e.g., *Myrceugenia pinifolia*, *Araucaria araucana*, *Pitavia punctata*, *Gomortega keule* and *Prumnopytis andina*) have been evaluated as threatened species by the International Union for Conservation of Nature (IUCN) (2017). The NMR's

landscape structure over the past 40 years has been highly dynamic, with reductions in native forest cover of 33.2% (Otavo and Echeverría 2017). Moreover, the high rate of native forest loss and turnover has been continuing (31.5% of native forest loss in unprotected areas between 1999 and 2008) (Altamirano et al. 2013) in a landscape where only 1.8% of the land is under protection (Wolodarsky-Franke and Herrera 2011). At present, the landscape is dominated by massive commercial plantations of exotic species of *Pinus radiate* and *Eucalyptus* spp., and large industrial plantation companies own most of the remaining native forests (Wolodarsky-Franke and Herrera 2011). Recognizing the continuing threats to this area of biologically important value, the NMR has been currently reported as a global conservation priority by The World Wildlife Fund (WWF), the IUCN, the World Resources Institute, and BirdLife International (Owen 2007).

Forest cover data

We obtained forest cover data from spring and summer Landsat satellite scenes (< 10% cloud cover) acquired from different sensors: 1979 (multi-spectral scanner; MSS) and 2011 (thematic mapper; TM), which had been pre-processed and classified by the Laboratory of Landscape Ecology,
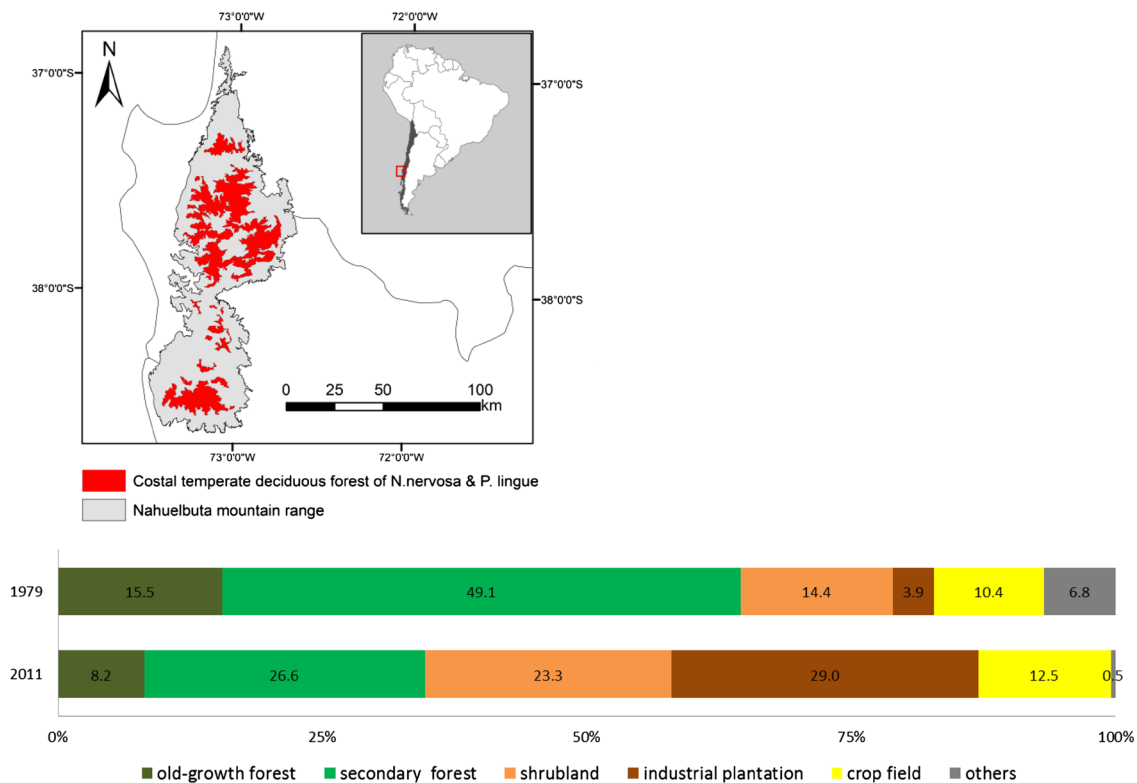

Fig. 1 Map of study area including the study ecosystem (costal temperate deciduous forest of *Nothofagus nervosa* and *Persea lingue*) and the major land cover types in 1979 and 2011

Table 1 Description of land cover types defined in the study area

Land cover type	Description
Old-growth/secondary forest	Vegetation with native tree species > 2-m height, > 25% canopy cover, including old-growth forests with species such as *Nothofagus nervosa*, *Araucaria araucana*, *Cryptocarya alba*, *Persea lingue, Gevuina avellana* and secondary forest with mainly *Nothofagus oblique* as the dominant species
Shrubland	Vegetation with native species < 2-m height, tree cover < 25%, and shrubland cover of 10–75%
Industrial plantation	Vegetation with planted exotic species such as *Pinus radiate* and *Eucalyptus* sp., including young and harvested plantations
Crop field	Crops of wheat, maize and vegetables. Also including annual and semi-annual pastures
Urban areas	Land occupied by cities, industry and other anthropogenic surfaces
Open water	Land occupied by water bodies such as small lakes and ponds
Bare ground	Cleared land, rocks and river beds

University of Concepción through the Chilean National Fond for Scientific and Technological Development (FONDECYT) research project 1140531. Each image had been corrected geometrically, atmospherically, and topographically (Chander et al. 2009), with shadow-reduced hillshade correction (Reese and Olsson 2011). These resources were available to aid the image classification: Catastro, a geographic information system (GIS)-based data set of thematic maps derived from aerial photographs and satellite imagery [National Forest Corporation (CONAF) 1999], which provide detailed information on land use and forest types; (2) forest cover maps generated from aerial photograph between 1978 and 1987 (Lara et al. 1989) for the 1979 image classification; and (3) a set of 300 training sites used in the 2011 image classification. Owing to the availability of ground-based data sets, we used a supervised classification method (Echeverria et al. 2006; Otavo and Echeverría 2017) and generated 30 × 30-m raster land cover maps using Arc-GIS (ESRI). The statistical decision criterion of maximum likelihood was used in the supervised classification to assist in the classification of overlapping signatures, in which pixels were assigned to the class of highest probability. A minimum mapping unit of greater than five pixels was used in this study. This enabled differences in data quality produced by the resampling of the MSS images to be minimized (Echeverria et al. 2006). To increase the accuracy of the land cover classifications, we added calculated raster for the normalized difference vegetation index, simple ratio, soil-adjusted vegetation index and land surface water index (Huete 1988; Rouse et al. 1974). In the classification models, ridge regression was used to reduce collinearity among selected land use variables (Lesaffre and Marx 1993).

Apart from the land cover classification, a wholly independent verification data set was generated for an accuracy assessment of the classification results of each image. Importantly, the following sample points were used in the present study: (1) 300 training sites for 2011 image classification, (2) 452 verification points for the classification results of the 1979 image, and (3) 653 verification points for the classification results of the 2011 image. The data used for accuracy assessments of land cover classification based on MSS in 1979 were from aerial photograph-based land cover maps developed by Lara et al. (1989). The points were overlaid on the reference land cover maps and assigned to their respective classes. The accuracy of the land cover classification based on TM in 2011 was assessed between 2012 and 2013. Confusion matrices were constructed to compare the class identified for each sample point, with land cover derived from the satellite images. Overall agreement of the classification was 80.3% for the 1979 MSS, and 82.4% for the 2011 TM (see Supplementary Appendix 1).

In the present study, the following land cover types were distinguished: old-growth forest, secondary forest, shrubland, industrial plantation with exotic species, crop field, urban areas, open water, bare ground and others (Table 1). These categories were based on the land cover types defined by Catastro (CONAF 1999). Furthermore, habitat maps were derived using two land cover types: secondary forest and old-growth forest. Both of these forests are dominated by tree species of height greater than 2 m and covered by at least 50% of forest (CONAF 1999) (Table 1).

Plant species richness

A total list of vascular plant species was completed by surveys from 46 sampling plots within 31 patches based on the land cover map in 2011 (Table 2). To ensure sampling independence, a minimum distance (1600 m; *z*-score

Table 2 Number of selected patches and sampling plots per patch size

Patch size (ha)	Number of selected patches	Number of sampling per patch
< 1	13	1
1–10	8	1
10–100	5	2
100–1000	5	3
Total	31	46

1.20, p-value 0.22) among fragments was calculated using Moran's I coefficient (Moran 1950), based on sample size. We randomly set up different numbers of sampling plots of 20×10 m (200 m^2) according to patch size and accessibility. Each plot was divided into eight contiguous subplots of 5×5 m, and the current occurrences of all vascular plant species (tree, shrub, herb, fern, climbing plant and epiphyte) were identified and recorded in each of these subplots during 2014–2015.

Many native trees in South American temperate forests have lifespans of more than 200 years (Donoso et al. 2006), so plant species were divided into two groups according to longevity (Comes and Kadereit 1998): long-lived species referred to as trees; and short-lived species referred to as herbs, ferns and climbers. Habitat specialization for long-lived species was classified by considering the following factors: (1) the type of species considered [endemic plants as specialists (Harrison 1999)]; (2) the number of habitat classes [specialists as species occurring in a few habitat classes, while generalists occurred in many habitat classes (Owens and Bennett 2000)]; and (3) local expert knowledge [an ability to determine which habitat is appropriate for which species (Gregory et al. 2005)]. The degree of habitat specialization was quantified as high, medium, and low (see Supplementary Appendix 2).

Analysis

The spatial patterns of habitat fragmentation were assessed using the following indices of FRAGSTATS (Echeverría et al. 2012; McGarigal et al. 2002; Nagendra et al. 2009): (1) patch density (number of habitat patches per 100 ha), (2) largest patch index (percentage of the landscape comprising the largest habitat patches), and (3) total edge length (kilometers). These indices provide information about the patterns of subdivision of forest patches, in which forest cover becomes disaggregated and isolated across the landscape (Forman and Godron 1986). The annual deforestation rate was calculated using the formula proposed by Puyravaud (2003):

$$P = \frac{100}{t_2 - t_1} \ln \frac{A_2}{A_1},$$

where A_1 and A_2 are the forest cover at times t_1 and t_2.

For 31 forest patches, the habitat patch size (hectares) was measured in GIS. In order to measure patch connectivity, we analyzed a simple proportional index—the proportion of old-growth forest and secondary forest—within a different buffer distance around each patch. This index has been recommended and implemented when habitat patches are oddly shaped and relatively close together (Winfree et al. 2005). Buffer distances of 100, 500 and 1500 m were chosen

to reflect the potential dispersal rates of different vascular plant species in temperate forests of South America (Donoso et al. 2006; García et al. 2009).

The relationship between plant species richness and patch variables was tested through regression analysis with a Poisson error distribution and log-link function. The dependent variables were species richness of (1) all vascular plants, (2) long-lived plants (trees), (3) long-lived specialist plants (specialist trees), and (4) short-lived plants (herbs, ferns and climbers). The independent variables were: (1) current patch size; (2) past patch size; (3) current connectivity, and (4) past connectivity.

In order to compare the maximum probability of the presence of a single long-lived species between 1979 and 2011, we also investigated changes in patch size over the study area using a Gaussian logit model (Lenoir et al. 2008; ter Braak and Looman 1986). Logistic regression is a generalized linear modeling technique using a logit link function computed with the log-likelihood expression of the Bernoulli distribution (presence/absence). We rewrote the model by defining it as a second-degree polynomial with a logarithmic link function (Jamil et al. 2014):

$$\text{Logit}(p) = b_0 + b_1 x + b_2 x^2,$$

where p is probability of presence, and x is patch size.

To track changes in species' "DPS", we compared the patch size information criterion between two periods. This parameter for DPS can be easily found by using the following formula (Ter Braak and Barendregt 1986; ter Braak and Looman 1986):

$$\text{DPS} = -\frac{b_1}{2b_2},$$

where b_1 and b_2 are the two coefficients of the Gaussian logit model using maximum likelihood. The DPS represents the habitat patch size at which the probability of presence reaches its maximum. All statistical analyses were made with open source software R (version 3.2.2).

Results

Habitat fragmentation and actual plant richness

Between 1979 and 2011, native forests were reduced by 53% in the study area (Fig. 1). In 1979, there were 4672 habitat patches covering an area of 115,132 ha with a mean patch size of 24.64 ha. By 2011, the mean patch size had declined to 1.44 ha, ranging from 0.09 to 5731 ha. During this period, habitat loss (old-growth forest plus secondary forest) occurred at a rate of 1.99% year^{-1} in the study area. The process of habitat fragmentation was accompanied by the loss of the largest forest patch, ranging from 43% in 1979

to 9.42% of the total area in 2011, while patch density and total edge increased between 1979 and 2011 (Table 3).

A total of 84 vascular plant species (36 trees, 17 shrubs, 19 herbs, five ferns, six climbing plants and one epiphyte) were identified in 31 habitat patches, with a mean richness of 14.77 per patch (SD 4.16; range 4–23) (Table 4). There were 36 long-lived species (7.97 per patch; SD 3.38), of which 18 species were specialists (3.161 per patch; SD 2.29). Mean richness of short-lived plants was 3.19 per patch (SD 1.76) (Table 4).

Influence of past habitat on plant species richness

The study patch size ranged between 0.09 ha and 628.65 ha in 2011 and between 1.8 ha and 15,077 ha in 1979. The linear regression models revealed significant relationships between the past patch size and the current richness of long-lived plants and long-lived specialist plants (Table 4). Richness for long-lived specialist plants was best explained by past patch size (Fig. 2). The current richness of plant assemblages could not be explained by the current patch size of the native forest.

The connectivity index of study patches varied between 0.015 (isolated) and 0.972 (connected) in 1979, and between 0.02 and 0.941 in 2011. A positive significant relationship was found between past connectivity and the richness of different plant assemblages, except in short-lived plants. This strengthened as the buffer distance increased. Likewise, the model for long-lived specialist plants with a 1500-m buffer was best explained by past connectivity (Table 5). Current connectivity had a mostly negative relationship with short-lived plant richness.

Changes in long-lived species' DPS

We computed the patch size of maximum probability of presence, also called here DPS, within each period for 27 long-lived species that were best described by a unimodal bell-shaped model. The DPSs of these species were reduced from 8063 to 145 ha during the study period (Supplementary Appendix 3). Species patch size reduction between 1979 and

Table 3 Changes in landscape pattern indices for the native forests in 1979 and 2011

	1979	2011
Total area (ha)	115,132	60,846
Number of patches	4672	42,094
Mean patch area (ha)	24.64	1.44
Patch density	4.05	69.18
Largest patch index (%)	43.72	9.42
Total edge (km)	9606	17,985

Table 4 Current richness of different assemblage of plant species

Plant assemblage	Richness		Patch size	
	n	Mean ± SD	Current F-value	Past F-value
All vascular plants	84	14.77 ± 4.16	0.051	2.371
Long-lived plants	36	7.97 ± 3.38	2.426	7.406*
Long-lived specialists	18	3.16 ± 2.29	3.160	11.650**
Short-lived plants	31	3.19 ± 1.75	1.505	1.786

n Species number, *Patch size* linear regression testing the relationship between the current and past patch size and current richness of plant species

*$P < 0.05$, **$P < 0.01$

2011 was statistically highly significant (mean difference in DPS was 7918 ha, 95% confidence interval for the mean was 4700.2, 11,136.1; Student's paired sample t-test, $t = 5.06$; $df = 26$; $P < 0.001$], amounting to an average of −267.5 ha per year. The current DPSs were found to be almost zero in seven long-lived specialists: *Araucaria araucana*, *Dasyphyllum diacanthoides*, *Drimys winteri*, *Nothofagus nervosa*, *Prumnopitys andina*, *Saxegothaea conspicua* and *Weinmannia trichosperma* (Fig. 3).

Discussion

Detection of extinction debt

In this study, current species richness is generally better explained by past patch size and connectivity than by current patch size and connectivity, except in short-lived plants. If past landscape patterns explain current species richness better than the current landscape pattern (Kuussaari et al.
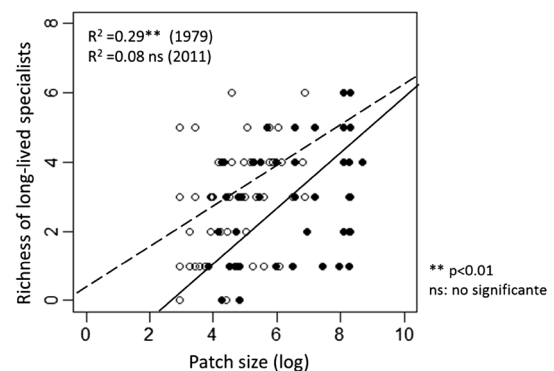

Fig. 2 Generalized linear model for current richness of long-lived specialist plants and patch size in 1979 (*solid line*, *solid symbols*) and 2011 (*dotted line*, *open symbols*)

Table 5 Multiple regression of current and past connectivity relationships on current richness (regression coefficients, F-values)

| Buffer distance (m; the focal patch included)	All plant spp.		Long-lived plants		Long-lived specialists		Short-lived plants	
	β	F	β	F	β	F	β	F
100								
Current	−1.63	0.18	1.10	0.53	0.20	0.10	−2.10	−2.10
Past	5.18	4.28*	4.78	6.25*	2.88	4.60*	0.38	0.38
R^2	0.14		0.19		0.14		0.11	
500								
Current	−5.75	1.29	−1.30	0.01	−1.32	0.09	−1.82	1.15
Past	6.06	5.01*	5.90	7.96*	3.38	5.25*	−0.53	0.19
R^2	0.18		0.22		0.16		0.05	
1500								
Current	−12.7	4.85*	−0.08	1.390	−4.22	0.84	−0.94	0.52
Past	8.82	4.83*	9.74	9.77**	6.69	9.87**	−1.98	1.12
R^2	0.26		0.29		0.28		0.06	

$*P < 0.05$, $**P < 0.01$
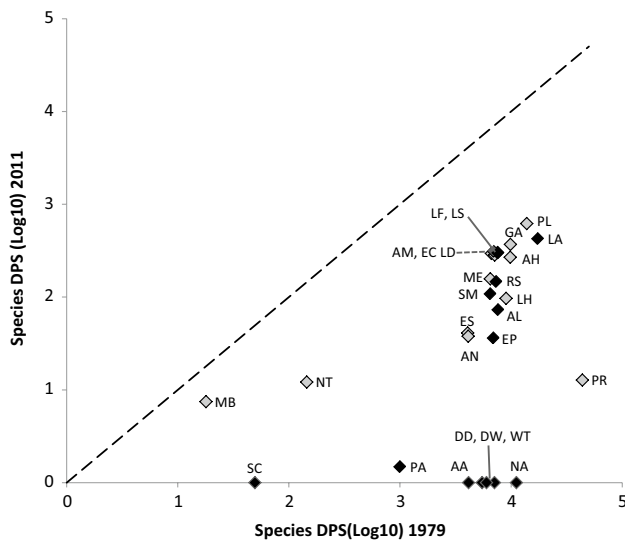
Fig. 3 Changes in optimum patch size (value at maximum probability of presence) of single long-lived species ($n = 27$) for 1979 and 2011. *Each point* represents one species; specialists are displayed as *black diamonds* and *solid line* ($n = 13$), whereas remnant species are displayed as *gray diamonds* and *dotted line* ($n = 14$). AA: *Araucaria araucana*, AH: *Aristotelia chilensis*, AL: *Amomyrtus luma*, AM: *Acacia melanoxylon*, AN: *Azara dentata*, DD: *Dasyphyllum diacanthoides*, DW: *Drimys winteri*, EC: *Eucryphia cordifolia*, EP: *Escallonia pulverulenta*, ES: *Acacia caven*, GA: *Gevuina avellana*, LA: *Luma apiculata*, LD: *Lomatia dentata*, LF: *Lomatia ferruginea*, LH: *Lomatia hirsuta*, LS: *Laurelia sempervirens*, NT: *Nothofagus antarctica*, MB: *Maytenus boaria*, ME: *Myrceugenia exsucca*, NA: *Nothofagus nervosa*, PA: *Prumnopitys andina*, PL: *Persea lingue*, PR: *Pinus radiate*, RS: *Rhaphithamnus spinosus*, SC: *Sophora cassioides*, SM: *Sophora cassioides*, WT: *Weinmannia trichosperma*

2009), this can be interpreted as evidence of an extinction debt. Consequently, an unknown proportion of the current vascular plants in the study area will become extinct.

Although particular organisms display different patterns of distribution to habitat fragmentation, species that share the same ecological properties may show similar, consistent patterns of changes (Dambrine et al. 1995). Studying richness within species groups that differ in their degree of habitat specialization may provide a more complete picture of the community-level consequences of habitat fragmentation than analyses focusing on total species richness (Brückmann et al. 2010; Reitalu et al. 2012). Species that have restricted ecological preferences (habitat specialists) are likely to be more strongly affected by habitat loss and fragmentation than species that have broader ecological tolerances and are able to occupy a wider range of habitats (generalists) (Devictor et al. 2008; Polus et al. 2007). Additionally, the response to habitat fragmentation in long-lived specialists is slower than in other species' groups in the same landscape (Krauss et al. 2010; Sang et al. 2010). Our results showed that long-lived specialist plants are best explained by past habitat area and connectivity (Tables 4, 5), and confirmed that the detection of extinction debt clearly depends on the longevity and habitat specialization of study species (Cousins and Vanhoenacker 2011; Reitalu et al. 2012).

In terms of relaxation time, a number of theoretical studies supported the finding that species richness in patches was negatively correlated with time since fragmentation (Helm et al. 2006; Kuussaari et al. 2009; Saunders et al. 1991). Extinction debts are more likely in those landscapes where large-scale habitat destruction has occurred recently (Cousins 2009). However, field observations indicate the limited applicability of the relaxation time for describing the effect of habitat fragmentation on risks of species extinctions, which varies in both space and time. In the temperate deciduous forests of Europe, for example, the extinction debt of forest plant species was found to persist for more than

a couple of centuries (Kolb and Diekmann 2005; Vellend et al. 2006), while other studies did not find any extinction debts over a similar period of time (Adriaens et al. 2006; Cousins et al. 2007). Likewise, studies from landscapes with a large amount of remaining natural areas supported the concept of an extinction debt, while highly fragmented landscapes did not provide any evidence of an extinction debt (Adriaens et al. 2006; Cousins 2009). We assumed that an extinction debt across a wider range of ecological traits may be identified in a rapidly changing landscape with a recent fragmentation history and relatively large amounts of remnant forest area. However, we did not detect any statistically robust effect of habitat configuration on the richness of short-lived plant species. This unpredictability of extinction debt of short-lived plants in the NMR may be explained by a combination of the following factors: (1) in southern Chile, alien herbaceous species are widely introduced by anthropogenic disturbances (logging and grazing) in understory layers (personal observation; Bustamante and Simonetti 2005; Pauchard and Alaback 2004; Braun and Vogt 2014); (2) in the study area, secondary forest occupied 77% of native forest area. These secondary forests with relatively open canopy may have changed microclimates (light, wind, soil moisture, etc.) that have often been linked to the performance of native herb species (Bierzychudek 1982; Matlack 1994; Grace and Tilman 1990); and (3) changes in plant reproduction and recruitment (flowering, seed production, etc.) of understory native species due to current abiotic and biotic alteration (personal observation; McKinney and Goodell 2010; Schemske et al. 1978; Ramirez and Armesto 1994).

Change of long-lived species' DPS during 1979–2011

To identify species which have current occurrences highly connected to past habitat and have not yet paid an extinction debt, we investigated changes in long-lived species' DPS over the study periods. Our results provided strong evidence that 27 long-lived species have already distributed into severely reduced patches in 2011 compared to 1979 (Fig. 3; Supplementary Appendix 3).

We showed that many long-lived specialist plants have experienced a notable decline in DPS over about 30 years (Fig. 3), and are more affected and threatened by habitat fragmentation. Among them, *A. araucana* and *P. andina* are vulnerable, and *S. conspicua* is near-threatened according to the IUCN Red List of Threatened Species (2015) (Supplementary Appendix 3). Although these specialist trees associated with small habitat patches seem to persist at present, their additional biological attributes that are directly linked to key threatening processes could act synergistically to elevate extinction risk and change this pattern quickly (Davies et al. 2004; Gaston et al. 1997; Lindenmayer and Fischer 2013; Valiente-Banuet et al. 2015). Two additional

attributes of concern are population size and dispersal ability. Piqueray et al. (2011) showed that it is likely that grassland specialist species which cannot maintain relatively large populations in small habitat patches require larger habitat patches. In the fragmented landscape of the CCR, several specialist trees were shown to have reduced population density in small habitats. For example, *W. trichosperma* shows a reduced germination rate as well as a lower seedling survival rate in small patches (Lusk and Pozo 2002). Echeverría et al. (2007) observed that the seedling abundance of *P. andina* was significantly related to only large forest patches. Poor dispersal ability might have another effect that increases the extinction risk which disrupts metapopulation functioning (Honnay et al. 1999; Jamoneau et al. 2011). Many previous studies suggested that specialist trees in our study area have traits associated with short-distance dispersal. For *N. nervosa*, fruit dispersal only reaches between 50 and 100 m per year (Donoso 1993), and the average distance of pollen dispersal is also very short (< 35 m) (Marchelli et al. 2012). *A. araucana* is known as a gravity-dispersed species with poor dispersal distance due to its seed size (2–4 cm long, 1–2 cm wide) and heavy weight (3.5–5.0 g) (González and Veblen 2006). Conversely, the population density and seed dispersal of shade-intolerant generalist trees (e.g., *P. lingue, G. avellana, El. Cordifolia, L. dentate*) are likely to benefit from forest edges in a fragmented habitat surrounded by plantations of exotic species (Bustamante and Simonetti 2005; Echeverría et al. 2007).

Value of small patches in rapidly changing landscapes

Despite strong evidence of the importance of large areas of native vegetation (Gaston and Spicer 2013; Rosenzweig 1995), according to mechanisms underlying the species-area relationship (Arrhenius 1921), extinction debt is proportionally higher in recently fragmented small patches than in historically fragmented large patches (Kuussaari et al. 2009). Patch-level extinction may occur faster in small patches than in large patches due to species' differences in susceptibility to disturbance between small and large patches (Sheil and Burslem 2003). Habitat fragmentation of Chilean temperate forests is associated with a rapid decrease in patch size (Echeverria et al. 2006). A high number of plant species were observed in small patches in the present study, which typically had shorter relaxation time. Although expanding the habitat area may be a straightforward solution to prevent future extinction of specialist species in the NMR, preserving or restoring large reserve areas is usually difficult because of the high costs involved.

In the CCR, a positive relationship between patch quality/connectivity and plant abundance/richness was reported in fragmented landscapes dominated by small patches

(Robledo-Arnuncio et al. 2014; Vergara et al. 2010). Similarly, Wulf and Kolk (2014) demonstrated that increasing the quality of small patches reaps more benefits than increasing patch area in the fragmented landscapes of Australia. Diamond (1975) found that if small patches of remnant habitats are widespread in the landscape, they might be a contributing factor to a relatively lower extinction debt or longer relaxation time by enhancing habitat connectivity. Likewise, configuring the spatial arrangement to minimize isolation may help to ensure that many of the species with extinction debts do not reach their extinction threshold in the long term (Paltto et al. 2006).

Bearing in mind the above, specific recommendations for the management of small habitat patches in the NMR should include (1) maintaining the current quality and quantity of old-growth forests, which are at risk of rapid decline and degradation of their structure without active management (15.5% of old-growth forest rate in 1979, declining to 8.2% in 2011); (2) restoring the habitat quality of secondary forests targeted for the redevelopment of old-growth attributes (Bauhus et al. 2009); (3) managing softened boundaries or creating buffers around ecologically sensitive areas to reduce the edge effect and enhance landscape connectivity (Lindenmayer and Fischer 2006; López-Barrera 2004); and (4) identifying and designing an adequate landscape configuration based on the remnant small patches to enhance specialist species' persistence and resilience because it is likely the current landscape configuration no longer supports these species' habitat requirements (Suding et al. 2004; Tambosi and Metzger 2013).

Suggestions for preventing future biodiversity loss in the NMR

Early detection of an extinction debt of long-lived specialist plants can be considered a benefit when beginning habitat restoration and conservation actions in adequate time in the area studied. However, as responses to habitat fragmentation are species dependent, conservation actions which target species groups are inadequate. Future monitoring plans of extinction dynamics must focus on single species of long-lived specialist plants rather than focusing on species richness or a set of species. In the fragmented landscapes of a biodiversity hotspot, it may be crucial to identify and prioritize the conservation of species that are prone to extinction over those that have no significant risk.

Finally, because a large portion of the study area is privately owned (Carruthers and Rodriguez 2009), participation and cooperation of the private sector is a key element to addressing biodiversity conservation goals in the NMR. Thus, it will be necessary to create appropriate conditions for the participation of all relevant stakeholders in the planning and implementation of conservation initiatives.

Conclusion

Our analyses provide the first evidence of the potential future loss of many vascular plant species in a South American temperate hotspot. However, as long as a species that is predicted to become extinct still persists, we believe that extinction debt provides new challenges and opportunities to current biodiversity conservation. However, this depends on valid timing because extinction debt payment is in progress and imposes an undefined deadline. Instead of waiting to launch large-scale conservation projects, we suggest the immediate implementation of local or small-scale restoration projects in order to mitigate the existing extinction debt.

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