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Increase in nonnative understorey vegetation cover after nonnative conifer removal and passive restoration

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Abstract Nonnative conifers are widespread in the southern hemisphere, where their use as plantation species has led to adverse ecosystem impacts sometimes intensified by invasion. Mechanical removal is a common strategy used to reduce or eliminate the negative impacts of nonnative conifers, and encourage native regeneration. However, a variety of factors may preclude active ecological restoration following removal. As a result, passive restoration – unassisted natural vegetation regeneration – is common following conifer removal. We asked, 'what is the response of understorey cover to removal of nonnative conifer stands followed by passive restoration?' We sampled understorey cover in three site types: two- to ten-year-old clearcuts, native forest and current plantations. We then grouped understorey species by origin (native/nonnative) and growth form, and compared proportion and per cent cover of these groups as well as of bare ground and litter between the three site types. For clearcuts, we also analysed the effect of time since clearcut on the studied variables. We found that clearcuts had a significantly higher average proportion of nonnative understorey vegetation cover than native forest sites, where nonnative vegetation was nearly absent. The understorey of clearcut sites also averaged more overall vegetation cover and more nonnative vegetation cover (in particular nonnative shrubs and herbaceous species) than either plantation or native forest sites. Notably, 99% of nonnative shrub cover in clearcuts was the invasive nonnative species Scotch broom (*Cytisus scoparius*). After ten years of passive recovery since clearcutting, the proportion of understorey vegetation cover that is native has not increased and remains far below the proportion observed in native forest sites. Reduced natural regeneration capacity of the native ecosystem, presence of invasive species in the surrounding landscape and land-use legacies from plantation forestry may inhibit native vegetation recovery and benefit opportunistic invasives, limiting the effectiveness of passive restoration in this context.

Abstract in Spanish is available with online material.

Key words: ecological restoration, Nonnative conifers, nonnative species removal, Patagonia, Scotch broom, vegetation regeneration.

INTRODUCTION

Nonnative vegetation removal has become a common element of ecological restoration as nonnative species are recognised for their potential to negatively impact biodiversity and ecosystem services (Ricciardi *et al.* 2013). Emphasis is often placed on the ecological impacts of *invasive* nonnative species both in the literature and in practice (Zavaleta 2002; Blackburn *et al.* 2011), though removal or eradication may be an important element of management for restoration regardless of a species' invasiveness in a given ecosystem (D'Antonio & Meyerson 2002; SER 2004). Removal of nonnative vegetation can be costly and generally carries a risk of unintended effects (Myers *et al.* 2000); thus, resources are often invested in areas of high ecological value, or in protected areas managed for ecological integrity (D'Antonio & Meyerson 2002). Successful reestablishment of native species is an important objective of ecological restoration activities (SER 2004; Ruiz-Jaén & Aide 2005), and achieving that goal requires forethought and follow-up to avoid inadvertent undesirable outcomes (Zavaleta *et al.* 2001; Clewell & McDonald 2009). Management objectives, ecological threats or socioeconomic values may lead to the decision to initiate nonnative species removal, and subsequent choices about if and how restoration should proceed (Zavaleta *et al.* 2001; Clewell & Aronson 2006).

Passive restoration (also referred to as natural regeneration or recovery) is defined here as reduction or elimination of components or processes causing degradation to an ecosystem, followed by otherwise

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unassisted natural regeneration (Rohr *et al.* 2018). Such techniques rely heavily on the natural successional processes of germination from soil seed banks, resprouting and seed dispersal for revegetation (McDonald *et al.* 2016) , and are commonly applied in forest restoration throughout the world, whether deliberately or by default (DellaSala *et al.* 2003; Holl & Aide 2011; Meli *et al.* 2017). Passive restoration has been praised as a means to achieve ecological restoration goals despite financial resource limitations, and has proven effective under favourable conditions, notably in the tropics (Chazdon 2008; Rey Benayas *et al.* 2008). Nonetheless, there have been numerous cases where natural recovery alone has been an insufficient means to restore degraded sites. Holl and Aide (2011) propose that the suitability of passive restoration techniques depends on the extent of degradation, a system's capacity for natural regeneration and the landscape context of a site. Both biotic (e.g. seed bank, seed dispersal mechanisms, invasive species and herbivory) and abiotic characteristics (e.g. changes in soil chemistry or compaction, climate and water availability) can influence successful outcomes (Rey Benayas *et al.* 2008; Holl & Aide 2011; Torres *et al.* 2018).

If degradation has pushed the system into an alternative stable state, or if the site has a limited natural capacity for recovery, there is evidence that passive restoration may be ineffective or even result in less favourable outcomes than inaction (Rey Benayas *et al.* 2008; Zahawi *et al.* 2014). In such situations, active restoration (i.e. continued intervention to assist recovery) may be required to achieve successful outcomes (Holl & Aide 2011; Rohr *et al.* 2018). Even with active restoration, it can be difficult to prevent recolonisation of the species targeted for removal (Myers *et al.* 2000; Zavaleta *et al.* 2001), and the spread of disturbance-adapted invasive plant species into newly disturbed areas (Hobbs & Huenneke 1992; Erskine Ogden & Rejmánek 2005; Hughes *et al.* 2012). Thus, removal of a nonnative species without active restoration to desired conditions does not necessarily result in regeneration of native vegetation (Zavaleta 2002; Flory & Clay 2009) and may have unforeseen effects, such as ecological release of invasive competitors (Mack & Lonsdale 2002; Kuebbing & Nuñez 2015).

Throughout the southern hemisphere, conifer tree species from North America, Europe and Asia are conspicuous nonnative species in regions where they have been used extensively in plantation forestry, beginning in southern Africa and Oceania in the 1800s, and more recently expanding in South America over the past century (Richardson 1998; Simberloff *et al.* 2010; Nuñez *et al.* 2017). In South Africa, New Zealand and Australia, where nonnative conifer forestry has a long-standing history, there have been documented costs to native biodiversity (Armstrong *et al.* 1998), disruptions to nutrient cycling (Scholes & Nowicki 1998) and alteration of hydrologic processes (Scott *et al.* 1998; Le Maitre *et al.* 2002). The same life-history characteristics that make a tree species well-suited to plantation forestry (e.g. rapid growth, tolerance of varied site conditions and high propagule pressure) are also often associated with high potential for invasion (Essl *et al.* 2010), increasing the risk that impacts to native ecosystem structure, function and services could be exacerbated (Richardson *et al.* 1994; Richardson 1998; Dodet & Collet 2012). The Patagonian region of southern South America has no native Pinaceae species and few native conifers. Nonnative conifer species were introduced to Patagonia for forestry experimentation in the early 20th century, and their use in large-scale plantation forestry across South America has increased in the past 50–60 years (Schlichter & Laclau 1998; Simberloff *et al.* 2010). Plantations and invasions in Patagonia have had similarly negative effects on biodiversity (Paritsis & Aizen 2008), water availability (Huber *et al.* 2008; Little *et al.* 2009), nutrient cycling (Oyarzun *et al.* 2007) and fire regimes (Veblen *et al.* 2008).

Concern regarding the expanding scale of nonnative conifer plantations, and the impacts of invasions into native ecosystems, has led to removal and control efforts in affected southern hemisphere regions, including Patagonia (Nuñez *et al.* 2017). Temperate forests in this region have been recognised for their unique conservation value (Rodriguez-Cabal *et al.* 2008), while at the same time, north-west Patagonia has a high and increasing rate of nonnative plants (Speziale & Ezcurra 2011). Over the past few decades, managers of protected areas in northern Patagonia, Argentina (e.g. Nahuel Huapi and Lago Puelo National Parks), have initiated removal of nonnative conifer stands planted in the early 1900s. Though plantation species have not been observed to invade temperate evergreen forests in this region (Simberloff *et al.* 2002), there are many documented cases of nonnative conifer invasions in southern South America (Richardson *et al.* 2008; Simberloff *et al.* 2010).

In Nahuel Huapi National Park, clearcut harvesting of select plantations began in 1989 and has continued intermittently until the present, with most removal occurring in the past decade (detailed in initial harvest agreement; APN 1988). In justifying removal, managers cite the negative impacts of nonnative conifer plantations elsewhere in the southern hemisphere and the threats posed to native ecosystems if the trees begin to spread following a time lag (Hourdequin 1999; Crooks 2005). Management directives, including the National Park Administration's (Administración de Parques Nacionales, APN) *Strategic Guidelines for Exotic Species Management* (APN 2007)

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and socioeconomic factors, undoubtedly influence decision-making as well. At most sites where trees have been removed, park managers have opted for passive restoration management, allowing vegetation to regenerate without additional intervention.

This study addresses vegetation recovery after removal of nonnative conifers (primarily *Pinus ponderosa* and *Pseudotsuga menziesii*) in Nahuel Huapi National Park in north-west Patagonia, Argentina. Sites that have been targeted for removal occur mainly in temperate evergreen mixed *Nothofagus*/*Austrocedrus* forests that occur in the central region of the park along a sharp west to east gradient from *Nothofagus*-dominated rain forest to xeric *Austrocedrus* woodlands and bunchgrass steppe (Veblen 1989a). We surveyed understorey vegetation in clearcut sites where passive restoration has been the primary post-removal management strategy. Prior to this study, the efficacy of passive restoration had not been examined in this ecosystem type, although a study (conducted in 1998) on establishment of native tree seedlings in some of the same clearcuts we surveyed demonstrated that successful restoration outcomes are difficult to achieve after nonnative conifer removal even with active restoration techniques (Hourdequin 1999). Our research goal was to learn whether tree removal and passive restoration management practices have promoted native forest recovery in this system over the short to medium term common to management plans and decision-making. We had two primary questions: (1) to determine the effects of clearcutting and passive restoration on vegetation, we asked 'Does understorey cover composition differ significantly between clearcut sites, current nonnative conifer plantations, and native forest?' and (2) to identify possible vegetation changes resulting from a longer recovery period, we asked 'Is the number of years since tree removal ("recovery time") a significant factor influencing the understorey cover of clearcut sites over the short to medium term?'

METHODS

Study area

Our study took place in Nahuel Huapi National Park (Parque Nacional Nahuel Huapi, PNNH), on Isla Victoria (40°58′09″S, 71°31′19″ W), a 3710-hectare island located in Nahuel Huapi Lake (Fig. 1). Established in 1934 and covering 703 000 hectares in Río Negro and Neuquén provinces, PNNH is both the oldest and largest national park in Argentina. Isla Victoria falls within the narrow band of South American temperate forests that runs north–south along the eastern edge of the Andean Cordillera. Evergreen *Nothofagus dombeyi*/*Austrocedrus chilensis* forest and matorral (local mixed shrubland) characteristic of cool temperate northern Patagonia dominate island vegetation (Veblen *et al.* 1996). Common sub-trees and shrubs include *Aristotelia chilensis*, *Dasyphyllum diacanthoides*, *Lomatia hirsuta*, *Luma apiculata*, *Maytenus boaria*, *Schinus patagonicus*, *Berberis buxifolia*, *Berberis darwinii*, *Gaultheria mucronata* and *Maytenus chubutensis*. In the native *Nothofagus*/*Austrocedrus* forests of PNNH, forest structure and regeneration are dependent on small-scale disturbances (i.e. treefall gaps) after which the dominant species are able to recolonise despite their limited seed dispersal ability (Kitzberger & Veblen 1999) and lack of a persistent seed bank (Raffaele & Gobbi 1996). In the event of a stand-destroying disturbance like wildfire (and in the absence of introduced nonnative species), *Nothofagus*/*Austrocedrus* forests are able to regenerate and mature over the course of 50 to 100 years, often after a period of dominance by native shrubs and sub-trees (Veblen & Lorenz 1987).

Over a 15-year span ending in 1940, approximately 63 hectares of Isla Victoria (1.7% of the island's total area) were planted with nonnative tree species from across the world, and these plantations persist in two areas of the island (Fig. 1) (Simberloff *et al.* 2002, 2003). Many of the introduced species that have thrived until the present are members of the *Pinaceae* family, most notably *Pinus ponderosa, Pinus contorta, Pinus sylvestris and Pseudotsuga menziesii*. These four species are also heavily represented in commercial forestry operations throughout Patagonia as a whole (Simberloff *et al.* 2010). Gradual removal of nonnative conifer stands on Isla Victoria has been implemented via mechanical clearcutting, with no supplemental chemical control of understorey vegetation.

Study design

Understorey cover composition is one important measure of vegetation regeneration (McLachlan & Bazely 2001). By sampling understorey cover in clearcut sites ranging from two to 10 years of recovery time, we obtained a snapshot of the results-to-date of current park management of nonnative conifers and passive restoration of native vegetation. Using information provided by PNNH managers and Google Earth historical imagery, we located all discernible clearcut sites on Isla Victoria. When mapped, the clearcuts were mostly clustered near the central developed part of the island (Puerto Anchorena), with a separate set of sites located to the north-west (Puerto Pampa) (Fig. 1). In the Puerto Anchorena area, sites were labelled according to their location in one of three geographic areas ('zones') commonly used by park staff to describe groups of clearcuts (Table 1, Fig. 1), though these zones were not differentiated in analysis. To assess understorey vegetation regeneration after nonnative conifer removal, we conducted sampling in all 17 clearcut sites identified on the island.

In order to compare understorey cover in clearcut sites to a historical baseline, we sampled five randomly selected current plantation sites located in areas representative of nonnative conifer stands on the island (generally dominated by either *Pseudotsuga menziesii* or *Pinus* spp.). Regardless of the species or mix of species, nonnative conifer plantations on Isla Victoria have had similar effects on native biodiversity including the near elimination of understorey vegetation (Paritsis & Aizen 2008) and were thus grouped into one category. We also sampled five native forest sites to

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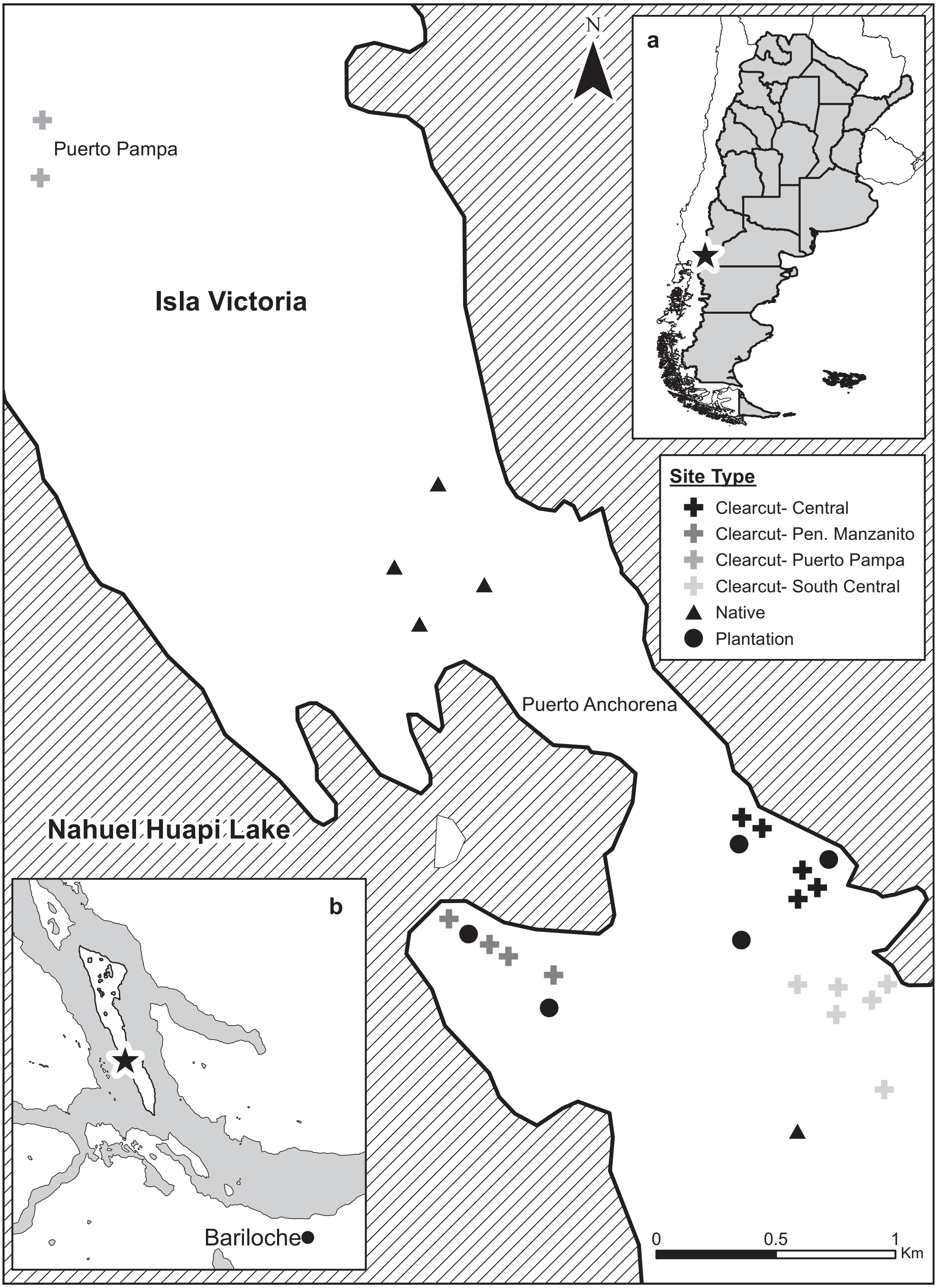

Fig. 1. Location of study sites on Isla Victoria. Clearcut sites are symbolised by crosses and are shaded according to their geographic cluster ('zone'). The upper right panel (a) shows the location of study site (star) in Argentina (shaded) within southern South America. The lower left panel (b) shows the location of the study site (star) on Isla Victoria, and Nahuel Huapi Lake (shaded) with the nearby city of San Carlos de Bariloche as a reference point.

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compare clearcut sites to a desired restoration outcome. Native and plantation sites were randomly selected using random compass bearings and pace counts within a two-kilometre radius from Puerto Anchorena to standardise propagule pressure and seed bank presence of native and nonnative species. Native sites represented common native forest types in the study area: presence of native trees and herbaceous vegetation and absence of common nonnative invasive species (e.g. *Cytisus scoparius, Juniperus communis, Rosa eglanteria and Cynoglossum creticum*).

Data collection

We conducted fieldwork during the austral summer of late 2015 and early 2016. In each of the 27 sites (clearcut = 17, current plantation = 5 and native forest = 5), we established six randomly placed 4-m^2 plots to survey understorey cover. In each plot, we recorded ocular estimates of per cent cover of every species less than three metres tall (the typical height of the tallest shrubs in clearcut sites). For species that accounted for less than one per cent of cover, a value of '<1' was recorded. In addition to understorey vegetation, we also recorded per cent cover of bare ground and litter.

Data analyses

To obtain a single cover value for each species in each site, we calculated the mean of cover estimates across the six plots sampled in each site prior to analysis. Before averaging, we changed cover values of < 1 in the database to 0.5 at the plot level. In most cases, species-specific cover data were combined into groups ('cover categories') based on origin (nonnative/native) and growth form (tree, shrub, herbaceous). These cover categories (e.g. 'nonnative trees') were created to facilitate the interpretation and management application of our results (category descriptions and calculations are found in Appendix S1). Per cent cover of herbaceous and woody litter was combined into a single 'litter' measurement for analysis.

When necessary, we transformed cover data via arcsine-square root to approximate normality. If transformed data were still unable to meet requisite assumptions, we used corresponding non-parametric tests on untransformed data. All analyses were run using R version 3.4.2 (R Development Core Team 2016).

To identify the effects of tree removal and passive restoration on understorey vegetation cover categories, we performed analyses of variance (ANOVAS) (total native cover, proportion native cover, proportion exotic cover, total litter cover and bare ground cover) or Kruskal–Wallis tests (native tree, shrub and herbaceous cover; nonnative tree, conifer and herbaceous cover) to compare cover across the three site types: clearcut, native forest and current plantation. Because we subjected the same data set to a number of different tests, we used a Bonferroni correction for our significance level, such that we accepted P-values of <0.007 as significant to avoid inflation of type 1 statistical error. When comparisons detected the presence of significant differences between the site types, we used Tukey's honestly significant difference (HSD) test (for ANOVAS) or Dunn's test (for Kruskal–Wallis) to determine which paired comparisons were significantly different at the $P < 0.05$ level.

We used a Wilcoxon rank-sum test to compare nonnative shrub cover in clearcut and native sites, excluding plantation sites due to complete absence of cover in this category. Because Scotch broom cover was only recorded in clearcut sites and absent in both native and plantation sites, we performed no analyses and only report mean per cent cover for each site type.

To assess the influence of recovery time on understory cover within the 17 clearcut sites, we performed simple linear regression (total native cover, proportion native cover, herbaceous cover, total nonnative cover, proportion nonnative cover, nonnative herbaceous cover, total vegetation cover and bare ground cover) or Spearman rank correlation analyses (native tree cover, native shrub cover, nonnative tree cover, nonnative shrub cover, Scotch broom cover). The number of years passed since tree removal ('recovery time') was used as the predictor variable, and cover categories were response variables. Additionally, we used an exploratory principal components analysis (PCA) to determine which sites were most similar to one another based on the combined per cent cover of individual species and non-vegetative cover types projected into a space defined by two principal components.

Table 1. Site characteristics of conifer plantation clearcuts on Isla Victoria. For each of the 17 clearcut sites sampled, geographic 'zone' (Fig. 1), unique name (Site ID), year of tree removal and site area (in hectares) are provided

Zone	Site ID	Year of Clearcut	Site Area (ha)
Centre (CN)	CN2006A	2006	0.104
	CN2006B	2006	0.184
	CN2009Bavg	2009	0.495
	CN2009Cavg	2009	0.519
	CN2010A	2010	0.163
Peninsula Manzanito (PM)	PM2012A	2012	0.127
	PM2012B	2012	0.11
	PM2013Ax	2013	0.19
	PM2013Bx	2013	0.11
South Central (SC)	SC2006A	2006	0.32
	SC2009Aavg	2009	1.337
	SC2010A	2010	0.386
	SC2010Bavg	2010	0.975
	SC2010C	2010	0.446
	SC2011Aavg	2011	0.659
Puerto Pampa (PP)	PP2011A	2011	1.953
	PP2011Ax	2011	0.217

RESULTS

Effects of clearcutting and passive restoration on understorey cover

Our analysis of per cent cover of all vegetation in the understorey revealed that the mean per cent cover of all understorey vegetation in clearcut sites was

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51.56% (±6.76 SE), significantly more total understorey vegetation cover than current plantation sites (Kruskal–Wallis chi-square = 13.24, *df* = 2, $P = 0.002$, pairwise Dunn's $P = 0.003$), and marginally non-significantly more cover than native forest sites (pairwise Dunn's $P = 0.086$) (Fig. 2). Clearcut sites (mean 31.85 ± 4.56% SE) and native forest sites (mean 53.3 ± 9.88% SE) also had significantly less litter cover than plantation sites (mean 102.13 ± 2.36% SE) (ANOVA $F = 39.87$, $df = 2{,}24$, $P < 0.0001$, both Tukey HSD $P < 0.0001$) (Fig. 2). With adjustments for multiple testing, there were no significant differences detected in bare ground cover between the three site types (ANOVA $F = 3.54$, $df = 2$, 24, $P = 0.045$) (Fig. 2).

Examining the breakdown of native and nonnative plants contributing to per cent cover of total vegetation, we found significantly greater proportions of nonnative vegetation (ANOVA $F = 31.31$, $df = 2{,}24$, $P < 0.0001$, both Tukey HSD $P < 0.0001$) and lower proportions of native vegetation (ANOVA $F = 38.52$, $df = 2{,}24$, $P < 0.0001$, both Tukey HSD $P < 0.0001$) in both clearcut (0.21 native and 0.75 nonnative) and current plantation (0.085 native and 0.851 nonnative) sites compared with native forest sites (0.96 native and 0.035 nonnative) (Fig. 3). Both clearcut and current plantation sites had more than twice as much nonnative understorey vegetation as native vegetation, whereas only 3.5% (± 1.9 SE) of the vegetation cover in the understorey of native forest sites was nonnative. Due to the differences in per cent cover of total vegetation between site types, the high proportion of nonnatives in the understorey of current plantation sites equates to only 5.35% (± 1.93 SE) of total cover, while the similar proportion of nonnative vegetation found in clearcut sites accounted for a much larger 42.41% (± 6.84 SE) of the understorey. Additionally, nonnative vegetation cover in clearcut sites was mostly composed of invasive nonnative herbaceous and shrub species, rather than the nonnative conifers targeted by removal efforts.

In nonnative vegetation cover categories based on growth form, we found that 22.12% (± 7.68 SE) of understorey cover in clearcuts was attributable to nonnative shrubs, and a full 99% of nonnative shrub cover in those sites was attributable to Scotch Broom (*C. scoparius*). In stark comparison, nonnative shrubs were absent in plantation sites, and only accounted for 0.083 (± 0.037 SE) in native forest, significantly less than the average cover of clearcuts (Wilcoxon $W = 81$, $p = 0.018$). Nonnative herbaceous plants accounted for another 18.47% (± 3.62 SE) of the understorey in clearcut sites, significantly more than native forest and current plantation sites which each averaged less than one per cent for nonnative herbaceous cover (Table 2). Unsurprisingly, current plantations had more nonnative (specifically nonnative conifer) tree cover in the understorey than the other two site types, though nonnative tree seedlings and saplings were also conspicuously present in clearcut sites (Table 2). For native growth form-based categories, we found that no individual category (trees, shrubs, herbaceous) covered more than 10% of the

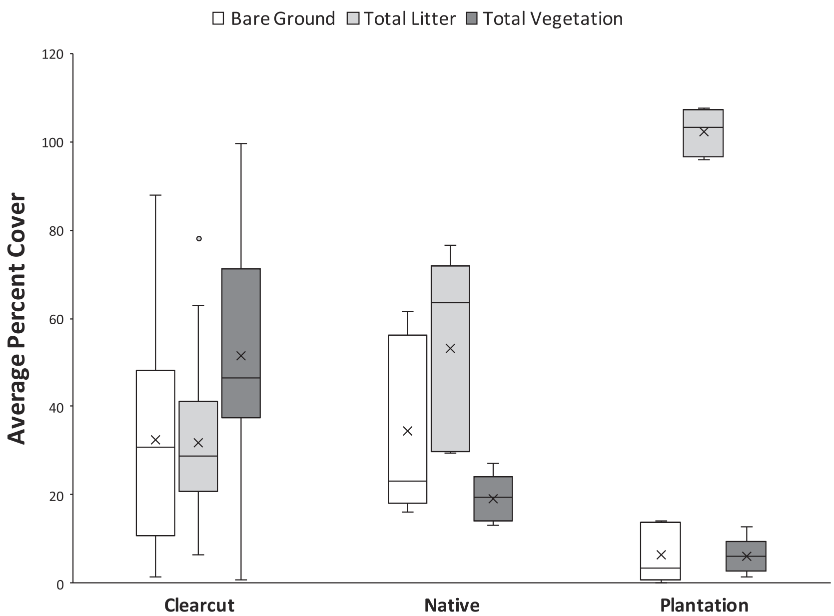

Fig. 2. Box plot displaying the mean (X) and distribution of per cent cover data for bare ground, total litter and total vegetation cover categories in clearcut, native forest and current plantation sites.

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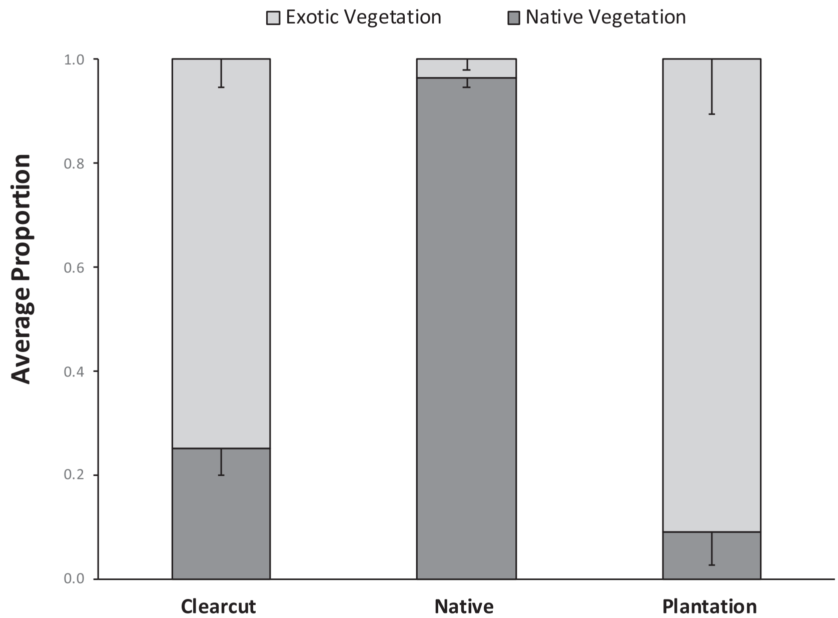

Fig. 3. Mean (± SE) proportion of native vs. nonnative species represented in the total understorey vegetation cover of clearcut, native forest and current plantation sites.

understorey in any site type. Nonetheless, there were significantly greater native tree cover and native shrub cover in native forest sites than in clearcut or plantation sites, and there was significantly less cover of native herbaceous plants in current plantations than in native forest or clearcut sites (Table 2).

Effects of recovery time on understorey cover in clearcut sites

Most cover categories analysed in clearcut sites were not correlated with the number of years passed since clearcutting (Table 3). Per cent cover of all native vegetation in the understorey did have a significant relationship to recovery time, though there was still a sizeable amount of variation left unexplained by recovery time alone ($n = 17$, Pearson's $P = 0.008$, $r^2 = 0.34$) (Fig. 4). As a subset of all native vegetation, per cent cover of native herbaceous plants had a similar relationship with recovery time ($n = 17$, Pearson's $P = 0.009$, $r^2 = 0.34$) (Table 3). Analysed as a proportion (using arcsine-square root-transformed data), native understorey cover was not correlated with recovery time ($n = 17$, Pearson's $P = 0.25$, $r^2 = 0.03$) (Fig. 4). Additionally, if average canopy cover of clearcuts (0% native or nonnative) and native sites (67% native and 0% nonnative) (M. Nuñez, unpubl. data, 2013) are combined with understorey composition to examine total native

Table 2. Mean (± SE) per cent cover of origin and growth form-based understorey vegetation categories in clearcut, native forest and current plantation sites

Cover Category	Clearcut	Native Forest	Plantation	*P*-value
Native Tree	0.06 ± 0.04^a	5.60 ± 1.20^b	0.47 ± 0.39^a	<0.001
Native Shrub	0.05 ± 0.04^a	3.73 ± 1.57^b	0.033 ± 0.033^a	<0.001
Native Herbaceous	7.57 ± 1.69^a	9.15 ± 1.42^a	0.033 ± 0.020^b	0.002
Nonnative Tree	1.82 ± 0.98^a	0.15 ± 0.13^a	5.33 ± 1.93^b	0.004
Nonnative Conifer	1.70 ± 0.92^a	0.13 ± 0.13^a	5.28 ± 1.96^b	0.004
Nonnative Shrub	22.12 ± 7.68^a	0.083 ± 0.037^b	0	*0.018
Scotch broom	21.82 ± 7.68	0	0	–
Nonnative Herbaceous	18.47 ± 3.62^a	0.37 ± 0.16^b	0.017 ± 0.017^b	<0.001

P-values without asterisks represent the results of Kruskal–Wallis tests ($df = 2$), all of which were significant at the $P \le 0.007$ level. Only two site types had nonnative shrub cover, and so the *P*-value reported is from a Wilcoxon rank-sum test, which we accept as significant at the $P \le 0.05$ level. Means with different superscript letters have significant pairwise differences between site types based on results from Dunn's or Wilcoxon tests. Nonnative conifer cover is a subset of nonnative tree cover, and Scotch broom cover is a subset of nonnative shrub cover. Clearcuts were the only site type where Scotch broom was observed, so only the means are reported.

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vegetation cover, even the oldest clearcuts exhibit <20% native cover, whereas native forest exhibits more than 80% cover, a stark difference (Fig. 4).

Across the 17 clearcut sites surveyed, per cent cover varied greatly in both vegetative and non-vegetative cover categories (average cover of each species by site, zone and site type are found in Appendix S2). For example, the average total vegetation cover ranged from 0.83% (site PP2011A) to 99.58% (site SC2010C), and Scotch broom was completely absent from some zones (Puerto Pampa), while it dominated the cover of sites in other zones (Center and South Central). The exploratory PCA biplot (Appendix S3) reveals that high per cent litter and bare ground cover influence the similarity of plantation and native forest sites. Most noticeably, the sites from the South Central zone of the island stand apart, separated from the other sites due to the influence of very high Scotch broom cover. Most of the 128 species we recorded across all of the sites were noninformative in site grouping and remain clustered in the centre of the plot.

DISCUSSION

After up to ten years of recovery, the proportion of native understorey vegetation in clearcuts was still far lower than in native forest sites, while the proportion of nonnative understorey vegetation remained much higher than the level found in conifer plantations. Clearcut sites frequently had higher per cent cover in native categories than plantation sites, but they also often had more cover in nonnative categories than both native forest *and* current plantations. Invasive nonnative shrub and herbaceous species were particularly common in clearcut sites left to passively restore, whereas they were nearly absent in both undisturbed conifer plantations and native forest. Thus, by some measures clearcut sites continue to resemble current plantations more closely than they do native forests, though the species assemblage in clearcuts diverges from both references in important ways, raising serious concerns about the trajectory of natural regeneration after conifer removal.

From two to ten years after tree removal, we found modest evidence that total native vegetation cover and native herbaceous cover increased in the understorey of clearcut sites over time, though native tree and native shrub cover were not correlated to an increase in recovery time. Importantly, when native vegetation data were analysed as a proportion of total vegetation cover in clearcut sites, or when canopy cover of native forest sites was considered, results indicate that clearcuts have been colonised by a starkly different vegetation community than would be expected from natural disturbance and successional processes (Veblen & Lorenz 1987; Suarez & Kitzberger 2008).

It is important to acknowledge that our study lacked a true control in the form of clearcut native forest sites, where we would have been able to observe the process of vegetation regeneration in the absence of nonnative conifer plantation forestry impacts. Therefore, we cannot be sure that propagule pressure from nonnative invasive species would not also have led to dominance of nonnative understorey vegetation in a site where native trees had been removed. Regardless, we believe that the observations that we have recorded in clearcut sites remain relevant and applicable to future management decisions with or without such a control.

One possible explanation for our findings is that with an expected successional cycle of up to 100 years in *Nothofagus*/*Austrocedrus* forests (Veblen 1989b), the range of recovery time assessed in this study was insufficient to capture the regeneration of native vegetation that simply takes longer to establish and proliferate after a major disturbance. Two of the finer points of our results suggest strongly that this is not the case.

First, the differences that we observed between native forest and clearcut sites were not simply differences in overall cover of native vegetation or differences in abundance between various growth forms that might be expected based on variation in successional stage. Instead, conifer removal followed by passive restoration in clearcuts has so far resulted in an overall increase in total understorey vegetation cover – both native and nonnative. Thus, even

Table 3. Results of correlation analysis between 'recovery time' and understorey cover categories

Cover category	Correlation coefficient	*P*-value
Native Tree	0.20	0.43
Native Shrub	0.17	0.50
Native Herbaceous	0.34	**0.0086**
Total Nonnative	−0.065	0.87
Proportion Nonnative	0.034	0.23
Nonnative Tree	−0.21	0.43
Nonnative Shrub	**0.42**	0.094
Scotch broom	**0.40**	0.11
Nonnative Herbaceous	−0.064	0.84
Total Vegetation	−0.013	0.39
Bare Ground	−0.0095	0.37

Unshaded rows are results from linear regression analysis and show Pearson's correlation coefficients and associated *P*-values. Shaded rows are results of Spearman rank-order correlation analysis and show Spearman's rho values and associated *P*-values. Sample size $n = 17$ for all tests. Bolded values indicate significant *P*-values or strong correlation coefficients (>0.4).

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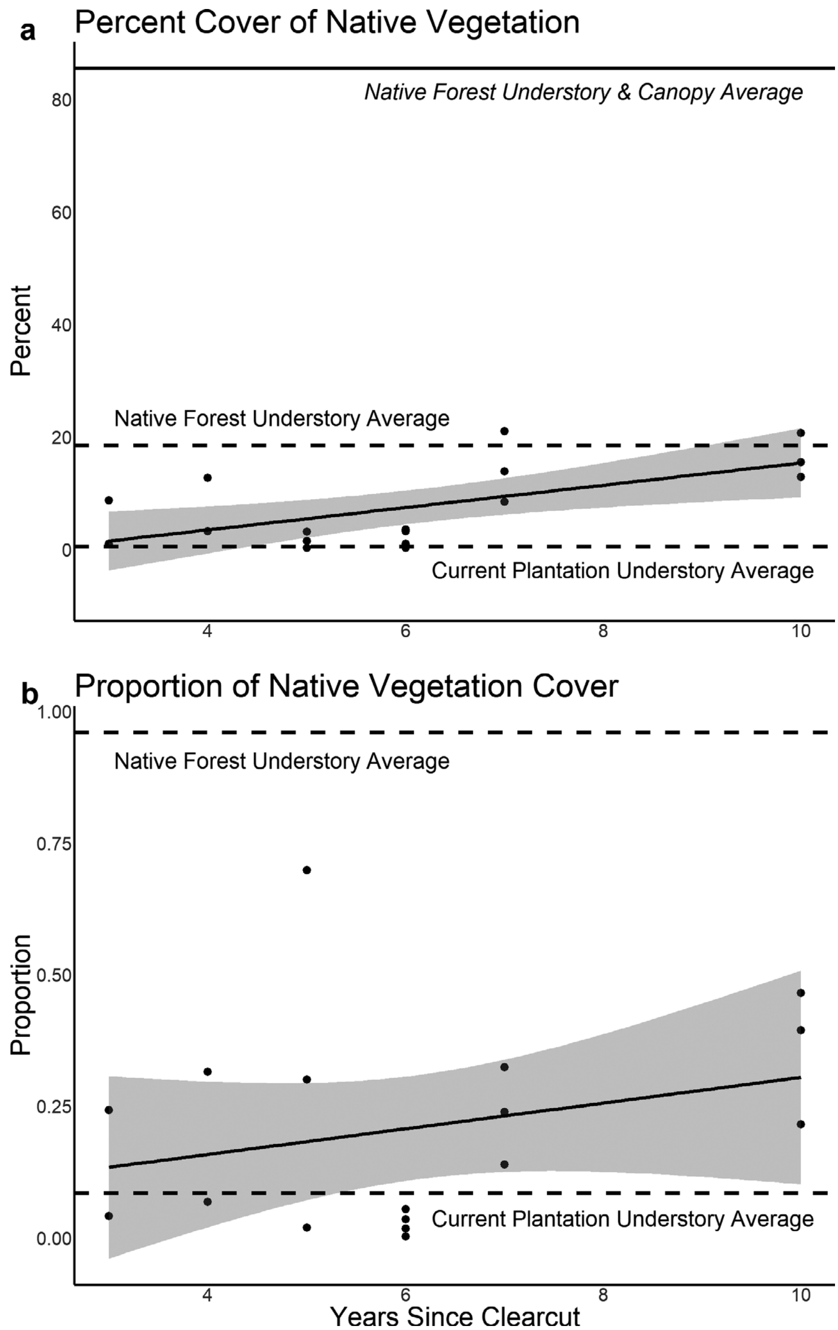

Fig. 4. Relationships between 'recovery time' and (a) per cent cover of all native understorey vegetation and (b) proportion of total understorey vegetation cover that was native. Shaded areas show the 95% confidence interval around the regression line. In each panel, the upper dashed line represents the average native understorey vegetation value recorded in native forest sites, and the lower dashed line represents the average in current plantation sites. The solid horizontal line in panel (a) is an additional reference showing the combined per cent cover of native understorey and native canopy vegetation found in native forest sites.

though we observed that per cent cover of total native vegetation increased slowly with recovery time, that trend is at odds with the observation that the proportion of vegetation cover that is native does not. Essentially, though there are some native plants, there are more nonnatives. These results provide clear evidence of secondary invasion (Pearson *et al.* 2016) by non-target species (i.e. nonnative species other than conifers), most notably Scotch broom. The high cover (up to 99.25% in site SC2010C) of invasive nonnative species adapted to high levels of disturbance (e.g. Scotch broom and thistle species)

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(Gray 2005) in clearcut sites may well be caused by competitive release of these species due to increased resource availability after tree removal (Mack & Lonsdale 2002). As a woody nitrogen-fixing species, Scotch broom also changes chemical and physical conditions, which may preferentially encourage establishment of other invasive nonnatives (Kuebbing & Nuñez 2015). In the most heavily infested sites, Scotch broom has formed a closed subcanopy after as few as four years (e.g. site SC2011A) (Fig. 5). The presence of multiple nonnative invasive species on the landscape and the ease with which they are able to spread and establish may halt and ultimately derail natural successional processes (Pearson *et al.* 2016). If that is the case, natural regeneration can no longer be expected to occur as it would have historically, regardless of the expected pace of recovery (D'Antonio & Meyerson 2002; Zavaleta 2002).

Second, the two codominant native tree species, *Nothofagus dombeyi* and *Austrocedrus chilensis*, have been reported to establish abundantly following stand-destroying fires (Veblen & Lorenz 1987). If clearcut removal of conifer plantations was able to simulate such a natural disturbance, and initiate regeneration of native forest, we would expect to see numerous seedlings or saplings of these two species, even if they only accounted for a small per cent of vegetation cover. Instead, we rarely observed *N. dombeyi* or *A. chilensis* individuals of any size, and on average, native trees accounted for only slightly more than half a per cent of understorey cover in clearcut sites. Veblen and Lorenz (1987) also describe an occasional early-successional post-fire stage of dense native shrublands interspersed with some of the common shrub and sub-tree species. This also does not appear to be the trajectory of nonnative conifer clearcuts, since the native vegetation subcategory that accounted for the lowest per cent cover in clearcut sites was native shrubs at only one half of one per cent.

Our results indicate that passive restoration has been ineffective in achieving native revegetation in nonnative conifer clearcuts. What are the possible explanations? A number of the limitations of passive restoration have been previously described in the literature and are applicable in this instance. The first set of limitations are inherent characteristics of the native ecosystem (Holl & Aide 2011). Passive restoration techniques have proven most successful in ecosystems with fast rates of natural succession, high resilience to disturbance and species with life-history traits that facilitate rapid regeneration (e.g. high propagule pressure) (Chazdon 2008; Clewell & McDonald 2009). While some of these intrinsic characteristics of the native *Nothofagus*/*Austrocedrus* forests of our study area have not been extensively studied, we do know that they have a relatively slow rate of natural regeneration following disturbance (Veblen & Lorenz 1987), and limited soil seed banks and seed dispersal capacity (Veblen *et al.* 1995, 1996; Raffaele & Gobbi 1996).

More compelling in this case are the limitations to passive restoration posed by the degree and nature of disturbance prior to initiating restoration (Holl & Aide 2011). Due to its reliance on intact natural processes, passive restoration is generally recommended only when damage to a site has been low and/or has occurred in a small area (McDonald *et al.* 2016). Especially when passive restoration is used as a follow-up to nonnative species removal, multiple authors have warned of unforeseen complications that can arise as a result of biotic and abiotic legacies that persist after the target species is gone (D'Antonio & Meyerson 2002; Zavaleta *et al.* 2001; Zavaleta 2002; Holl & Aide 2011; McDonald *et al.* 2016). These legacies often include changes to belowground ecosystem components including biological and physical soil characteristics (Bassett *et al.* 2005; Dickie *et al.* 2014a) that can be difficult to predict or detect, but often favour colonisation by target or other nonnative species and hinder native regeneration (Zavaleta *et al.* 2001; D'Antonio & Meyerson 2002). Such disturbance legacies have not been quantified in our study area, but the history of degradation in the clearcuts on Isla Victoria is long and complex, including settlement and infrastructure development by European settlers, clearing of the native forest, cattle grazing, tourism and introduction of nonnative invasive plant and animal species (Simberloff *et al.* 2003).

The final category of limitations to passive restoration that we find relevant to this study is based on

Fig. 5. From left to right, photographs of (a) a typical nonnative conifer plantation understorey, (b) a five-year-old clearcut (SC2010B) where dense Scotch broom now thrives and (c) a typical native (*Nothofagus*/*Austrocedrus*) forest understory.

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landscape context of the restoration effort, including proximity to both intact native communities and populations of invasive nonnative species, as well as the impact of continued disturbances (Zavaleta 2002; Holl & Aide 2011). Here, we can consider the more complex interactions and impacts within this system of multiple nonnative and invasive species and evolving human land use on the island, in the park and the region as a whole. Propagule pressure from populations of nonnative invasive plant species certainly affects clearcuts on Isla Victoria: PNNH has the largest number of invasive plants of any Patagonian National Park (Sanguinetti *et al.* 2014), and their spread into disturbed areas is obvious to the casual observer. The central part of the island near Puerto Anchorena where most of the clearcuts are located is also heavily visited by tourists, many of whom take walking tours from the port and are potential vectors for new introductions and spread of existing invasives (Anderson *et al.* 2015). In addition, PNNH and Isla Victoria in particular host a number of nonnative animals which often have negative interactions with native biota, whether through herbivory, physical disturbance or direct competition (Martin-Albarracin *et al.* 2015; Veblen *et al.* 1992) .

Ultimately, the combination of disadvantageous native ecosystem characteristics, extensive history of disturbance and the presence of multiple invaders and continued sources of degradation proximal to the sites may be enough to cross important thresholds and create an alternative stable state (Firn *et al.* 2010; Rohr *et al.* 2018). If clearcuts have transitioned to an alternative state with high resiliency to further change, restoration efforts will likely require much more active input, and even then native vegetation recovery may be difficult to achieve (Holl & Aide 2011; Rohr *et al.* 2018). If clearcut removal of nonnative (but not currently invasive) conifers pushes these sites into alternative stable states due to secondary invasions and continued degradation, managers must decide whether colonisation by invasive nonnatives (e.g. Scotch broom) is preferable to conditions that currently exist in plantations. There is also room to explore other, more gradual, removal techniques that could thwart or slow secondary invasions, while allowing space for active restoration of native plants.

Clewell and McDonald (2009) warn against conflating natural regeneration with ecological restoration. In the context of nonnative species removal, passive restoration may still require significant effort to reduce or eliminate the components or processes causing degradation to an ecosystem – in addition to simply removing the target species. If only one aspect of the process (removal) is embraced, while other essential principles of ecological restoration are disregarded, it is unsurprising that natural vegetation regeneration would be unable to occur as desired. 'Passive' may be a misnomer, as the use of natural successional processes in ecological restoration following nonnative species removal may require significant active input, especially in the steps before removal is initiated (Clewell & McDonald 2009).

CONCLUSIONS

Land and resource managers throughout the world commonly plan and operate on a timescale of five to ten years. In many cases, personnel, funding availability and political climate change even more frequently. Although it is possible that given more time the clearcut sites in this study area will show a trend towards regeneration of native forest, in the short to mid-term, there are red flags that current removal and restoration practices have resulted in the proliferation of nonnative invasive species in clearcut sites at the expense of native vegetation recovery.

The socioecological landscape of our study contains many challenges common throughout the southern hemisphere. Thus, it seems likely that the factors that have derailed the desired track of passive restoration in Nahuel Huapi National Park could also be indicative of restoration of nonnative conifer clearcuts elsewhere. In South America, as well as in other southern hemisphere regions where nonnative forestry species are common, conservation management is directly impacted by management resource limitation, and passive restoration is likely to remain an attractive and commonplace technique following nonnative or invasive species removal. In these situations, management prioritisation must take into consideration how the greatest good can be achieved in both social and ecological contexts (Dickie *et al.* 2014b). It may be that initiating removal will trigger a series of events leading to a less desirable condition that is costlier to fix, in which case 'no action' may be the preferable alternative. It may also be true that even a small investment in active restoration actions in the short and mid-term, such as site preparation, seeding, weeding and monitoring, may lower the long-term cost of managing such a site with the goal of ecological restoration.

SPECIES NOMENCLATURE

Catálogo de las Plantas Vasculares del Cono Sur (Zuloaga *et al.* 2008).

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SUPPORTING INFORMATION

Additional supporting information may/can be found online in the supporting information tab for this article.

Appendix S1. Methods of calculating understory cover categories.

Appendix S2 (a) Percent cover data for all clear-cut sites. (b) Percent cover data for all native forest and current plantation sites.

Appendix S3. PCA biplot.

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