



## Why biodiversity increases after variable retention harvesting: A meta-analysis for southern Patagonian forests



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### ABSTRACT

Effects of forest harvesting on biodiversity can be varied and complex to understand. We provide a meta-analysis of 553 studies plants, insects and birds to identify the general responses to Variable Retention harvesting (VR) 1–8 years post-harvest in *Nothofagus pumilio* forests of southern Patagonia. The analysis is focused on: (i) richness and abundance, (ii) origin and habitat (native forest specialist species, native species of other habitats, alien species), and (iii) temporal trends after harvesting. Our objective was to evaluate why biodiversity increases after variable retention harvesting, by assessing the effects on (i) species richness and abundance in general, (ii) native forest specialists, native generalist species and alien species, and (iii) the recovery of biodiversity toward original conditions. Forests managed with VR supported higher overall richness and abundance of plants, insects and birds in aggregate and dispersed retention than unmanaged stands, but with similar values each other. However, origin and habitat of species affected responses to VR. Aggregates support higher native forest specialist plant and lower plants of habitats other than dispersed retention. However, both retention treatments increased alien plants, although its richness and abundance was higher in dispersed retention. Native forest specialist insects were reduced in comparison to unmanaged forest, while insects of other habitats showed a positive response to both aggregate and dispersed retention as well as did for bird species richness and abundance compared to unmanaged forests. We found evidence for recovery of original conditions for native forest specialist plants and insects, and plants of other habitats. In contrast, alien plants and native insects of other habitats increased continuously in the studies included through those representing 8 years post-harvest. Major differences among both retention patterns included significantly higher richness and abundance of alien plants and native insects of other habitats in dispersed retention. Our synthesis shows recovery toward original conditions for some taxa, but demonstrates long-term establishment of alien plants as well as insect species not associated with native *N. pumilio* forests. These have emerged as a main potential threat to conservation of forests under VR prescription, at least at the stand level. Retention forestry could play a fundamental role for conservation in productive temperate forests, but the influence of retention pattern and aggregate size are still unclear.

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### 1. Introduction

A central axiom of ecological forest management is that manipulation of forest ecosystems should work within the limits established by natural disturbance patterns prior to extensive human alteration of the landscape (Seymour and Hunter, 1999). The key assumption here is that native species evolved under these circum-

stances, and that maintaining a full range of similar conditions under management offers the best assurance against biodiversity loss (Spence, 2001). Effects of logging on forest biodiversity are complex, and range from being minimal under some selection cuts systems to maximal in extensive clear-cutting with extraction of stumps and debris (Mitchell and Beese, 2002). Intensive timber harvest, therefore, can be considered negative for conservation oriented to late-seral associated species and there are many reports of declines in forest specialist species after harvest (Rudolphi et al., 2014), although these do not necessarily result in a reduction of

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overall biodiversity (Politi et al., 2012; Fedrowitz et al., 2014; Soler et al., 2015). Logging particularly impacts forest specialist species likely because many of their original microhabitats are directly disturbed by harvesting operations (e.g., by altering understory properties) (Nelson and Halpern, 2005; Taboada et al., 2006; Lencinas et al., 2011) and by altered microclimate conditions (Chen et al., 1993, 1999). Additionally, plant communities may be affected indirectly through competition with early-successional or open-canopy species (Spyreas and Matthews, 2006) which surround managed stands on forest landscapes.

Given that most forests exploited for timber lie outside reserves, off-reserve management should include practices designed to maintain biodiversity. Thus, forests managed for multiple values can have an important role in biodiversity conservation at landscape scales (Lindenmayer and Franklin, 2002; Fischer et al., 2006). For this reason, retention forestry was adopted in productive forests about 25 years ago to promote the maintenance of original forest structural elements that promote rapid re-establishment of environmental and biological characteristics that we value highly (Franklin et al., 1997; Grove and Forster, 2010; Gustafsson et al., 2012). The variable retention (VR) approach to forest harvest combines different spatial distributions of structural retention to meet the objectives of forest managers. For example, dispersed retention (scattered trees) and aggregate retention (patches of continuous original forest) are two contrasting spatial models often applied together to gain the ecological benefits of both approaches (Franklin et al., 1997; Martínez Pastur et al., 2009; Swanson et al., 2011). By retaining patches within every harvested unit, the biological legacies associated with mature forest habitat that are important to many species are spread over the entire landscape, while dispersed retention provides diverse physical and biological properties and suitable microclimatic conditions for other species such as those adapted to early successional semi-open habitats (Swanson et al., 2011). Additionally, if the aim is to conserve flora and fauna connected to other habitats associated with productive forests (e.g., open areas, unproductive forests), the combination of aggregate and dispersed retention can be very efficient (Lencinas et al., 2005, 2009; Gustafsson et al., 2012). A significant remaining question is whether alien species or species from other non-timber habitats take advantage of recently disturbed habitats and rapidly spread into recovering forests (Pauchard and Alaback, 2006). Once successfully established, persistence of these species might represent a serious threat for native forest specialists.

There is still debate about the effects of forest management on biodiversity (e.g. Paillet et al., 2010), including those of retention approaches in production forestry (Fedrowitz et al., 2014). VR could have especially positive effects in forests which have been subject to management during several centuries. However, in bringing old-growth managed forests into harvest rotation, finding management strategies to maintain the original species composition is essential. To evaluate the extent to which VR may influence the original forest biodiversity, *Nothofagus* forests of southern Patagonia are a particularly suitable model ecosystem because they constitute a significant portion of the last unmanaged forests in the southern Hemisphere and are one of the most pristine ecoregions on the planet (Mittermeier et al., 2003).

In a recent study, Soler et al. (2015) detected an increase of overall biodiversity in *Nothofagus pumilio* forests under VR management. However, they did not assess how VR prescriptions of aggregate and dispersed retention separately affected different taxonomic groups (plants, insects, and birds), or how effects may vary with the origin and original habitat of species (native *N. pumilio* specialist, native from other habitats, and alien), or trends over time after harvest. Based on further original studies describing impacts of VR on biodiversity in *N. pumilio* forests (Deferrari

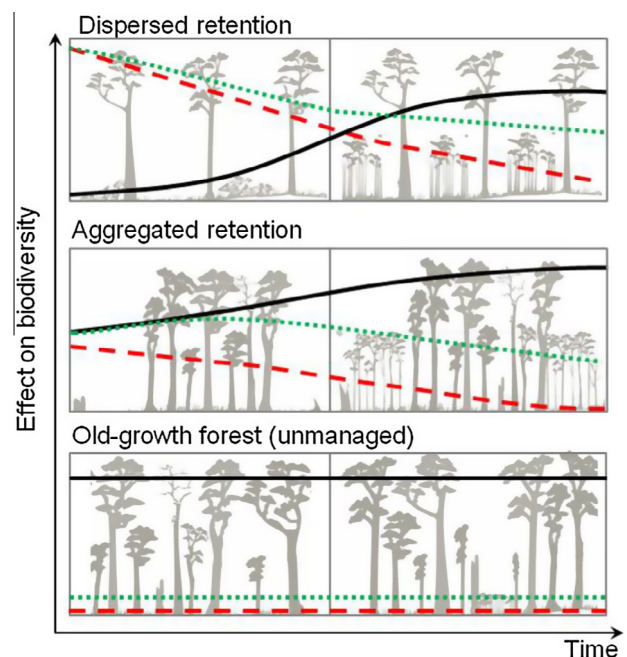
et al., 2001; Lencinas et al., 2005, 2009, 2011, 2014; Vergara and Schlatter, 2006; Gallo et al., 2013) we formulated the following hypotheses about effects of AR and DR on biodiversity (Fig. 1): (i) forest specialist species are conserved at intermediate levels in aggregates and low levels in dispersed retention immediately after harvest, and then recover under both retention treatments, but in dispersed retention do not reach the same values as in primary forests; (ii) species of non-timber habitats associated with managed forests will increase more strongly in dispersed retention than in aggregates and persist in both treatments at intermediate levels; and (iii) establishment of alien species occurs in both treatments, but this is more strongly and more persistent in dispersed retention than in aggregates (Fig. 1).

Our objective was to provide a synthesis of evidence for answering following three questions regarding the effects of VR forestry on plant, insect, and bird biodiversity of *Nothofagus* forests of southern Patagonia: (i) What are the effects of VR on species richness and abundance? (ii) Which effects can be detected for native forest species, native generalist species and alien species? and (iii) how do these effects vary over the first years after harvest?

## 2. Material and methods

### 2.1. Inclusion criteria and data extraction

We used a multi-taxon database previously compiled encompassing many published and unpublished studies from the only existing *N. pumilio* forests in which VR has been implemented as the basis for meta-analysis of biodiversity impacts of VR management.



**Fig. 1.** Hypothetical impacts of variable retention harvesting (VR) on biodiversity in *N. pumilio* forest stands (adapted from Donato et al., 2012). As VR combines aggregate and dispersed retention, the response of biological organisms would be different in each case compared to unmanaged (old-growth) forests (response curves are schematically drawn). Forest specialist species (—) are those exclusively or highly abundant in undisturbed *N. pumilio* forests, and are those considered as the most sensible to harvesting. Species of other habitat associated to *N. pumilio* forests (••••) are those native species living under varying environmental conditions in non-timber forests and open habitats. Alien species (---) are those introduced organisms in Tierra del Fuego ecosystem.

We used data from two long-term monitoring experiments in the Argentinean part of Tierra del Fuego: San Justo Ranch (54°06'S, 68°37'W) with 50 ha harvested in 2001, and Los Cerros Ranch (54°18'S, 67°49'W) with 75 ha harvested during 2004–2007 (Martínez Pastur et al., 2010; Soler et al., 2015). The retention patterning applied in this region is a unique pattern of combined aggregate forest (AR) in circular patches 30 m diameter (one per hectare), and dispersed retention (DR) consisting of 15 m<sup>2</sup> basal area in scattered trees into the harvested matrix. Then, the retention pattern was consistent in different studies included in our meta-analysis. We used only primary data sets for meta-analyses that met all of the following criteria: (1) management of the forest area was based on the concept of VR; (2) old-growth unmanaged stands were used as control sites; (3) effects of forest management on biodiversity were assessed in terms of species richness and/or abundance of organisms; and (4) raw data and sample sizes were available for aggregate retention (AR), dispersed retention (DR) and old-growth control plots (PF). We are aware that species richness and abundance of organisms are only surrogates of biodiversity, but genetic diversity and ecosystem diversity are much harder to assess and no primary data were available for our study system. For this, in this study, we used species richness and abundance as simplified measures of biodiversity.

All published and unpublished data sets were considered without bias with respect to significance of results. We considered data about three broad taxonomic groups of organisms: plants, insects and birds, and classified case studies additionally using the following criteria (Table 1, Supplementary Appendix A): (i) species richness versus species abundance, (ii) origin and habitat (c.f. Lencinas et al., 2005): native specialists of *N. pumilio* forests, i.e. species exclusively or highly abundant in undisturbed *N. pumilio* forests, considered also the most sensible to harvesting; native generalists or specialist of other habitats associated with timber forest, e.g., species mainly habiting in nearby forest stands not used for timber production such as *Nothofagus antarctica* forests, riparian forests or open areas (e.g., grasslands, peatlands); alien species (species introduced to Tierra del Fuego), and (iii) years after harvesting (YAH) grouped in three periods (1–2 YAH, 3–4 YAH, and 5–8 YAH).

We excluded data from studies that simply reported effects of natural disturbance and those that dealt with other harvesting methods, such as clear-cuts or shelterwood cuts. In total, we used data from 553 study cases; many of these were parts of larger studies. Collectively they provided data about 131 different variables related to plant, insect or bird species richness or abundance, in detail: 329 cases on plants using 71 different variables, 136 cases on insects using 34 different variables, and 88 cases on birds using 26 different variables (Table 1, summarized in Supplementary

Appendix A). All studies had been conducted in the period 2002–2013.

Use of the data for meta-analysis varied by taxon. All three taxa could be used in relation to testing hypothesis 1. Plants and insects could be used to test hypothesis 2 about origin and habitat. Plants were the only taxonomic group that could be used to test hypothesis 3 regarding alien species, because records of alien insect species were no reported. Only few alien insects species are known in Tierra del Fuego (e.g. *Vespula germanica*), and none were detected in the considered studies. Alien bird species are restricted in Tierra del Fuego to cities and their surroundings, and none were detected in any primary study.

The structure of our data analyses followed that of a previous synthesis paper (Soler et al., 2015). All primary studies contained ANOVAs for comparisons of the effects (i) AR vs. PF, (ii) DR vs. PF, and (iii) DR vs. AR, for one or more taxa. In order to standardize the results from all primary studies, *F*-statistics extracted from the ANOVA and degrees of freedom (*df*) were used to calculate Pearson correlation coefficient (*r*) for each study case (Rosenberg et al., 2000) and each of the three comparison:

$$r = \sqrt{\frac{F}{F + df}} \quad (1)$$

Then, Fisher-*z*-transformation was used as a measure of the effect size (*z*) for each study case:

$$z = \frac{1}{2} \ln \left( \frac{1+r}{1-r} \right) \quad (2)$$

where *r* is the Pearson correlation coefficient calculated above (Rosenberg et al., 2000).

## 2.2. Statistical analyses

Individual *z*-values were combined across studies for a meta-analysis using a mixed-effects model with categorical data, assuming that differences among variables within a single category or group are due to both sampling error and random variation (Leimu and Koricheva, 2006; Paillet et al., 2010; Soler et al., 2015). We used bias-corrected 95% bootstrap confidence intervals generated from 4999 iterations (Leimu and Koricheva, 2006) to define the significance of the effects of forest management treatments. Multi-annual measurements were considered as separate entries each year for studies that spanned more than one year (Jerabkova et al., 2011).

As a first step we compared the effects of the three treatments on both species richness and abundance of plants, insects and

**Table 1**

Number of study cases per organism group and variable type. S = species richness; A = abundance (including cover); YAH = years after harvesting.

Classification criteria	Categories	Number of study cases						Total
		Plants		Insects		Birds		
		S	A	S	A	S	A	
Taxonomic/functional level	Total community	17	17	4	4	4	8	54
	Taxonomic group	29	60	16	16	4	4	129
	Functional group	22	22	48	48	24	23	187
	Single species		162				21	183
Origin and habitat	Native – <i>N. pumilio</i> forest	16	136	16	16			184
	Native – other habitats	9	29	16	16			70
	Native – unspecified	30	38	36	36	32	56	228
	Alien species	13	58					71
YAH	1–2	24	71	34	34	15	27	205
	3–4	24	99	34	34	17	29	237
	5–8	20	91					111
Total		68	261	68	68	32	56	553

birds. Then we grouped the variables according to origin and habitat and separated: (i) native organisms related to *N. pumilio* forest (e.g. fern biomass, abundance of insects sensitive to clear-cuts), (ii) native organisms related to other habitats such as grasslands, peatlands or *N. antartica* forests (e.g. *Cotula scariosa* cover, richness of insects favored by harvesting), (iii) alien species (e.g. alien plant cover, alien erect herb cover), and (iv) species or groups with unspecified habitat (e.g. dicots or monocots richness and abundance, hymenoptera abundance) that were excluded from specific analyses (i.e., origin and habitat). Finally, we grouped the data according to years after harvesting: variables measured during 1 or 2 YAH were considered replicas of 1–2 YAH group, the variables measured during 3 or 4 YAH were considered replicas of 3–4 YAH group, and variables measured during 5, 6, 7 or 8 YAH were considered replicas of 5–8 YAH group (see [Supplementary Material 1](#) for the number of cases for each factor). We used the MetaWin statistical program version 2.1 (Rosenberg et al., 2000) for the meta-analyses. In the following we refer to change, increase or decrease when effects were statistically significant, i.e. the confidence intervals did not overlap  $z = 0$ .

### 3. Results

The overall effects of the two retention prescriptions were rather similar for plants and birds (Fig. 2). For both taxa, AR and DR increased species richness and abundance with respect to values of PF, and the effects for species richness were greater than for abundance. For birds effect sizes were greater than for plants. For plants, DR was associated with significantly greater increases in effect size than AR, while the data for birds did not reflect such

differences. For insects in contrast, the effects of the two retention prescriptions were comparably weak. The only statistically significant differences occurred between DR and AR, with DR showing modestly but significantly higher values of insect richness and abundance (Fig. 2).

Origin and habitat of species affected responses to variable retention. Richness and abundance of native forest specialist plants increased with AR but not with DR. Native plants of habitats other than *N. pumilio* forest, on the other hand, showed little response to AR, but in DR had higher species richness than in PF. Plants alien to Tierra del Fuego increased in both retention treatments, but DR supported both higher richness and abundance than in AR. For insects, both richness and abundance of native forest specialist species were reduced in comparison to PF, but richness and abundance of native species of other habitats increased in both prescriptions of retention. Overall, DR supported modestly lower richness and abundance of native forest specialist plants and more alien plant species than AR, but for insects the two retention treatments were more or less similar for both insect abundance and diversity (Fig. 3).

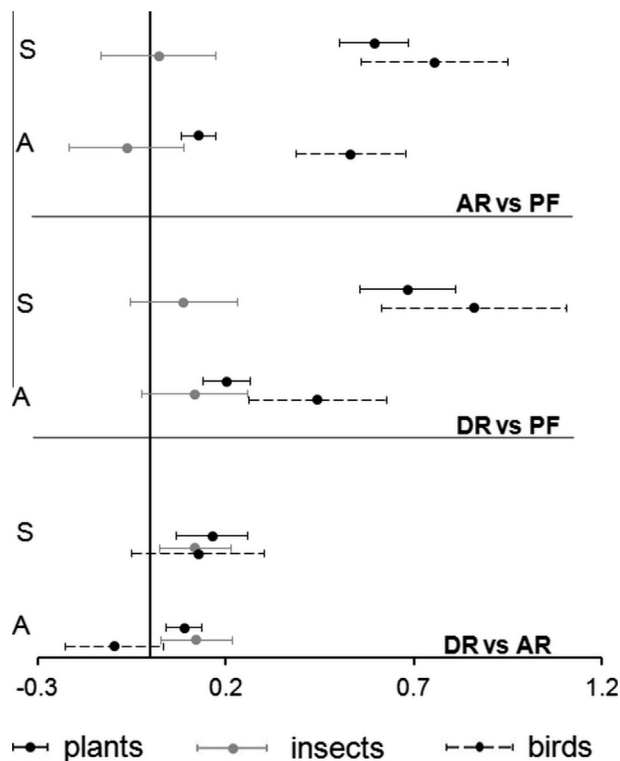
We also assessed effects of the two retention prescriptions over time after harvesting. Overall plant species richness increased from 1–2 to 5–8 YAH, while abundance remained more or less unaffected in both AR and DR compared to PF (Fig. 4). These changes were mainly determined by alien species which were consistently and it seems increasingly more common in AR and DR than in PF (Fig. 5). On the other hand, native forest specialist plants and plants of other habitats only increased during the first two years after harvest in both retention treatments, perhaps reflecting opening of the canopy, whereas values during 5–8 YAH were similar to PF (Fig. 5).

The pattern detected for insects was particularly interesting, because a slight decrease in species richness and overall abundance at 1–2 YAH, especially in AR, became clearly positive during 3–4 YAH (Fig. 4). Native forest specialist insects decreased during 1–2 YAH but recovered to original values under both treatments after 3–4 YAH. However, richness and abundance of insect species of other environments remained higher than in PF under both treatments until 3–4 YAH (Fig. 5).

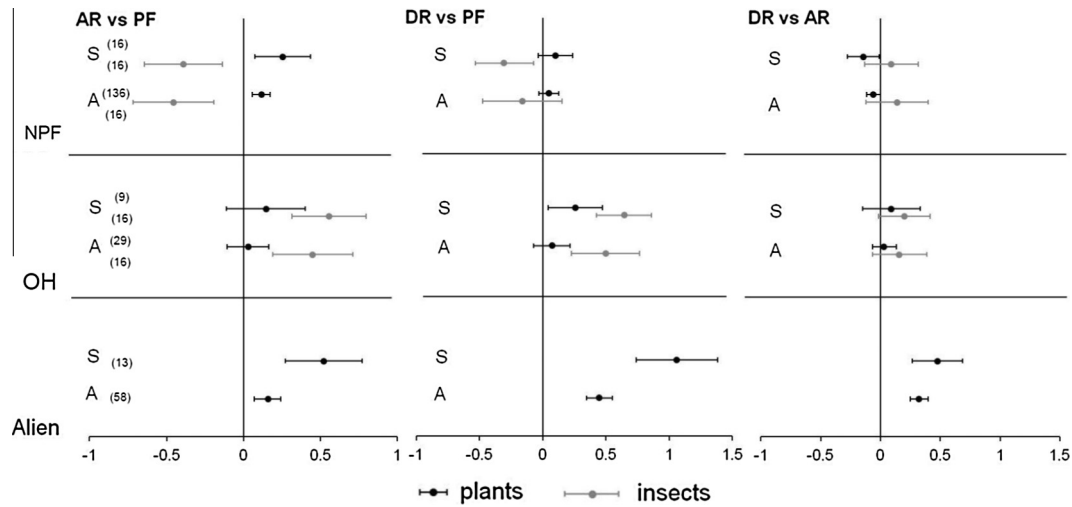
For these there were postharvest increases in species richness in both AR and DR. Effects on abundance were smaller and less consistent, and this increase was greater in abundance than in richness. During the first two years after harvesting, bird abundance was lower in DR than AR, but by 3–4 YAH it increased in DR reaching values similar to those in AR (Fig. 4).

### 4. Discussion

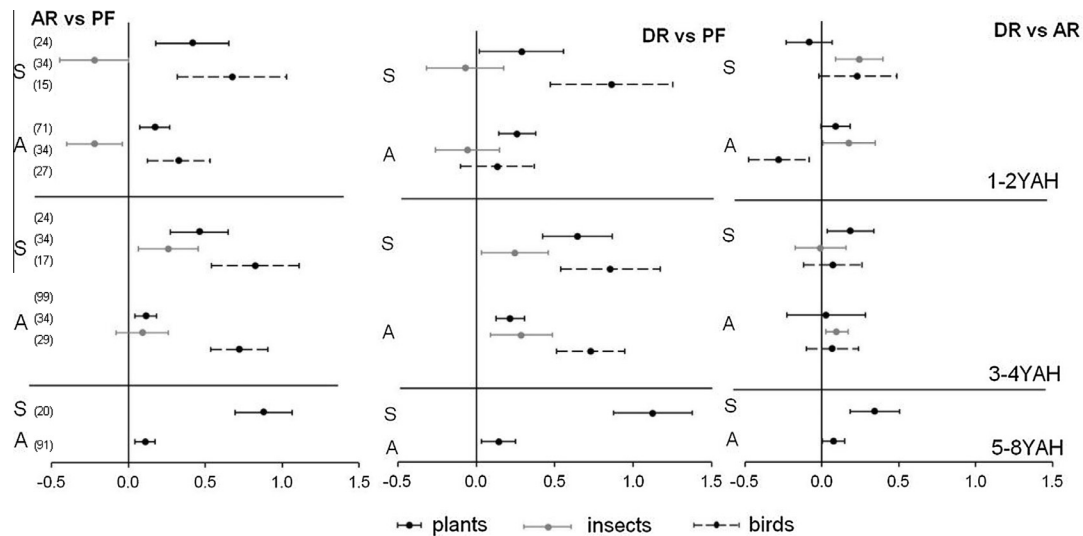
Forests under VR management support more biodiversity, as indicated by species richness and abundance of the selected taxa, than old-growth unmanaged forests both in southern Patagonia and elsewhere in the world (Paillet et al., 2010; Fedrowitz et al., 2014). However, increases in levels of biodiversity could be as undesirable as decreases ones. The goal of conservation forestry is to maintain the original biological composition within harvested forests, and thus changes in either direction could be considered adverse. In other parts of the world, forest management often tends to generate higher species richness or abundance (Paillet et al., 2010), regardless of the original levels of species diversity in these ecosystems. Although this study provides evidence for recovery of the original conditions, it also reveals potential long-term alteration in species composition after VR harvest in southern Patagonia. Our data are somewhat limited in that all forest patches were sampled from few harvest blocks using a unique retention patterning (including aggregate and dispersed retention). This spa-



**Fig. 2.** Mean effect sizes ( $\pm 95\%$  confidence intervals) for species richness (S) and abundance (A) of plants, insects and birds in *Nothofagus pumilio* managed (AR: aggregate retention, DR: dispersed retention) and unmanaged forests (PF: primary stands). The number of richness cases is 32 for birds, 68 for insects, and 68 for plants; and the number of abundance cases is 56 for birds, 68 for insects and 261 for plants. The effects of treatments are significantly different when 95% confidence intervals do not overlap 0.



**Fig. 3.** Mean effect sizes ( $\pm 95\%$  confidence intervals) for species richness (S) and abundance (A) of plants and insects considering origin and habitat of organisms (NPF = native species from *Nothofagus pumilio* old-growth forest, OH = native species of other habitats, and alien species) included in the analysis. Treatments: AR: aggregate retention; DR: dispersed retention; PF: primary forest stands (control).



**Fig. 4.** Mean effect size ( $\pm 95\%$  confidence intervals) of years after harvesting (YAH) (three different periods: 1–2, 3–4 and 5–8 YAH), for species richness (S) and abundance (A) of plants, insects and birds in *N. pumilio* managed (AR: aggregated retention, DR: dispersed retention) and unmanaged forests (PF: primary stands).

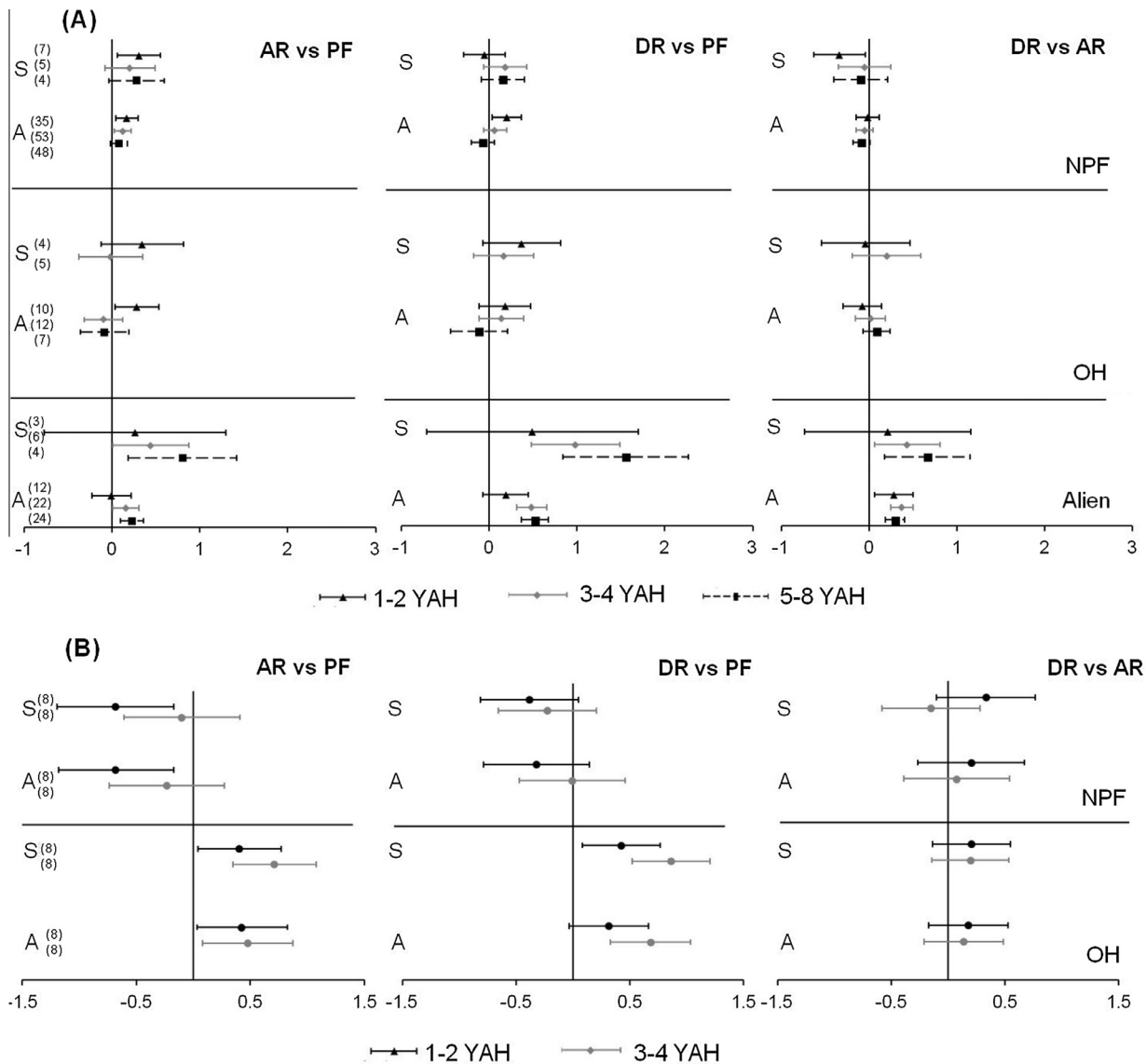
tial arrangement suggests that caution is necessary when drawing management conclusions on the impact of VR on regional biodiversity.

**4.1. Effects of VR on native forest specialist species and native species of other habitats**

We expected that native forest specialist species would decline in response to VR harvest, and that declines would be greater in DR than in AR (Fig. 1). However, our results only partly matched this hypothesis, because species richness of native forest specialist plants increased within AR and a smaller extent in DR. The effects were greater for species richness than for abundance under both AR and DR prescriptions. Native forest specialist insects followed more closely the predicted pattern, as they decreased in both treatments after harvest. Declines were similar between treatments for richness, and greater in AR than in DR for abundance. The loss of old-growth forest insect species (including both common and rare species of Coleoptera, Diptera and Lepidoptera) in harvested stands

of southern Patagonia is proportional to the amount of canopy cover remaining after treatment: from 35% of species in aggregates, 55% in dispersed retention, and 60–75% in clear-cuts (Lencinas et al., 2014). After more intense forest harvesting (i.e., clear-cuts) Buddle et al. (2006) conclude that the post-harvesting composition of the arthropod fauna in boreal forests represents a mix between open-habitat and closed-canopy species, the latter of which may be a ‘shadow’ of the pre-harvest fauna.

Response of native species of other habitats followed more closely the expected pattern (Fig. 1), i.e., plant and insect richness and abundance increased in both AR and DR. Species composition during the first YAH likely consist of habitat specialists and generalists that co-exist in the early-successional forest ecosystems (Gustafsson and Perhans, 2010; Swanson et al., 2011). In southern Patagonia, many natural species of (e.g., non-forest grasses) are tolerant to semi-open conditions, and even promoted by post-harvest environment (Martínez Pastur et al., 2002; Gallo et al., 2013; Selzer et al., 2013; Lencinas et al., 2011, 2014). Also, ruderal plants that grow on disturbed or poor-quality soils may be favored by the



**Fig. 5.** Mean effect size ( $\pm 95\%$  confidence intervals) of years after harvesting (YAH) (three different periods: 1–2, 3–4 and 5–8 YAH), on (A) plants and (B) insects included in the analysis for *N. pumilio* managed (AR: aggregated retention, DR: dispersed retention) and unmanaged forests (PF: primary stands).

presence of newly exposed soil and by litter removal generated by skidders during harvest, as has been observed on tips and mounds (Palmer et al., 2000). Insect colonization of harvested forest stands is closely related to changes in vegetation structure at the forest floor level (i.e., shrub layer, soil organic matter content, woody debris) making habitats suitable for additional curculionid and carabid species (Taboada et al., 2006).

Also greater availability of special microhabitats such as coarse woody debris can enhance insect populations (Grove and Forster, 2010). Large amounts of woody debris are derived from harvest operations in *N. pumilio* forest stands (Martínez Pastur et al., 2009). These are usually left at the edge of aggregates or scattered in areas of DR, thus adding variety to the habitats available for arthropods. Although the centers of aggregates remain relatively undisturbed, major shifts in environmental conditions occurs at edges of AR where edge-dwelling species are usually most abundant after harvest (Vergara and Armesto, 2009; Swanson et al., 2011; Rudolphi et al., 2014). Although VR approach include variable intensities of cut and spatial configurations of retained trees,

all studies considered in our analysis had the same retention pattern: AR in circular patches of 30 m radius and DR randomly scattered trees that retain 15 m<sup>2</sup> ha of basal area. This VR scheme is the only one applied in Patagonia until now. Unfortunately, there are not other retention assays or applications conducted in this region to evaluate the influence of the spatial configuration of retention (i.e., strips, irregular patches) on local species sensitiveness.

Both species richness and abundance of native bird species increase markedly in the short-term after either AR or DR. Increases were greater in species richness than in abundance, and behaved as expected for species of other habitats associated to *N. pumilio* forests. In general, retention harvests supports greater richness and abundance of open-habitat bird species than unharvested forests (Fedrowitz et al., 2014). On one hand, bird species specialized on old-growth forests (e.g., *Elaenia albiceps*) maintains its populations in VR thanks to aggregates (see Deferrari et al., 2001; Lencinas et al., 2005). On other hand, generalist species that also use old-growth forests are favored by harvest due to a major food offering (e.g. *Troglodytes aedon*).

#### 4.2. Effects of VR on alien species

Our findings match well with our hypothesis of greatest concern: it is clear that alien plants increase in harvested forest stands, and that the effect is stronger in DR than in AR. Alien plant richness was consistently more affected than alien plant abundance; many of these species are weeds (particularly the annuals) that appear during the first years after harvest but decline quickly (Swanson et al., 2011). In southern Patagonia, *Stellaria media* provides an excellent example of these dynamics (M.V. Lencinas, unpubl. data). However, other opportunistic species may persist as part of the plant community until they are overtopped by more slowly growing trees (Martínez Pastur et al., 2002; Nelson and Halpern, 2005) or, perhaps, out-competed by native species for limiting resources (Moore and Goodall, 1977) and become incorporated into forest plant communities.

Some alien plants are present in fact in unmanaged old-growth forests, although in very low abundance. These species (e.g. *Cerastium fontanum* or *Taraxacum officinale*) mainly dispersed by wind and water, were introduced to Tierra del Fuego almost 200 years ago, and have been effectively naturalized for decades. Nonetheless, increases in cover of alien species introduced either recently or long ago has been associated with changes to local soil biogeochemistry that promote self-perpetuation of invading species and a concomitant loss of native biodiversity (Cipriotti et al., 2011).

Alien birds are represented by few species in Tierra del Fuego (e.g., *Columba livia*). These mainly inhabit urban parks and rural areas near cities, but they are quite rare in natural habitats such as *Nothofagus* forests, natural grasslands, or wetlands, and such species were not recorded in the studies used for our data base.

#### 4.3. Recovery – temporal trends after harvesting

Understanding recovery of the original biological community of harvested forests is essential to evaluate the impact and desirability of the VR silvicultural method. We found an overall increasing trend of biodiversity in blocks cut to both AR and DR prescriptions relative to unharvested stands, but also note some evidence of recovery toward the original biota with relatively low diversity. While richness and abundance of native forest specialist plants remained elevated in AR during the first 8 YAH, their abundance declined in DR toward level of unharvested forest stands. Trends in richness and abundance of native plants of other habitats corroborated our hypotheses; i.e., richness and abundance both declined to the level of unharvested forest stands in both AR and DR by 3–8 YAH. For native forest specialist insects, the detected results matched our predictions because they recovered in terms of richness and abundance for both treatments after 3–4 YAH. This trend reflects reestablishment of some species removed with harvesting operations, and/or increase in populations of rare species (Lencinas et al., 2014). Work et al. (2010) conversely, did not detect initial differences between VR harvested and control compartments one year postharvest, mainly in lower retention level stands (0–20%). However, these authors did not differentiate between open-habitat and closed-canopy species, and probably it explains in part such relatively similar species composition between old and mature stands and 1-year-old harvests. In our study, the trends of richness and abundance of native insects typical of other habitats in both AR and DR indicate an increase relative to unharvested forest stands from 1–2 YAH toward 3–4 YAH. Because we have no data from 5 to 8 YAH, it remains uncertain if the extent to which insects would return to original levels and match our predictions (Fig. 1). However, other authors have reported the recovery of initial levels of insect communities after several decades post-harvesting (Buddle et al., 2006) mainly under higher levels of tree retention (Work et al., 2010). However, such recovery to

pre-disturbance conditions strongly depends on different groups within arthropod assemblages (Buddle et al., 2006).

Both richness and abundance of native bird species tended to be higher in both VR treatments in 3–4 YAH than 1–2 YAH. Bird diversity considerably increased compared to old-growth unharvested forest stands, as observed by Deferrari et al. (2001) for the whole *N. pumilio* forest management cycle under shelterwood system. Venegas (2000) and Vergara and Schlatter (2006) also found a significant increase after longer periods since harvest (e.g. 8 YAH). This pattern might be related to higher food availability (e.g., fruits, seeds and insects) in harvested forest stands and to migrant birds that newly arrive and settle in harvested stands. A follow-up study would be required to determine whether or not bird populations continue to increase after harvesting.

Species richness and abundance of alien plants, in both treatments, showed a continuous increase from 1–2 YAH to 5–8 YAH, with no sign of decline toward original levels. This increase was much greater for species richness than for abundance. This is of concern, because alien species cause severe changes to ecosystems and biodiversity in Tierra del Fuego (Cipriotti et al., 2011) and globally (Capinha et al., 2015) without indication of decline in their global spread (Tittensor et al., 2014). Eight years correspond to the initial developmental stage of a *N. pumilio* forest stand with saplings barely reaching 30–40 cm height (Martínez Pastur et al., 2014). We assume that canopy recovery can cause a decline in alien species abundance as a result of light limitation in the shaded forest interior (Pauchard and Alaback, 2006; Lindenmayer, 2009).

#### 4.4. Overall match with hypotheses and comparison across treatments and taxa

In summary, we could test our hypotheses about impact of VR forestry practices for five guilds, i.e. *N. pumilio* forest specialist plants and insects, native plants and insects of other habitats and alien plants (Fig. 1). Native forest specialist insects and native plants of other habitats (which showed an initial increase and subsequent decline to original conditions) and native forest specialist insects (which initially declined and subsequently recovered) tended to behave as predicted. In contrast, native forest specialist plants increased initially after the treatment and subsequently tended to decline to original levels, thus matching our predictions for long-term impacts, but not for the initial stages. Native insects of other habitats and alien plants increased continuously from harvest until the last surveyed year (4 and 8 YAH, respectively), and thus matched our predictions about initial but not long-term impact for insects (see Supplementary Appendix 2). Interestingly, these two guilds were the only ones that clearly matched hypothesized differences between the treatments (Supplementary Appendix 2), i.e., DR promoted significantly higher richness and abundance than did AR. Time span in this study is short and generally limited to a single study area, so conclusions should be treated with some caution; however, based on our results, aggregate retention appears to be effective in providing habitat for forest species as was reported by Venier et al. (2015), Fedrowitz et al. (2014). Positive effect on forest species richness with time since harvest is expected, at least at the stand level, as retained trees will become increasingly older compared to the production forest trees with time.

In general, data for insects generally matched our hypotheses regarding decline and subsequent increase of native forest specialist species over the short term. Overall responses for birds and plants were similar, with the main difference that the effects of the treatments led to greater increases in parameter values for birds than for plants (particularly for abundance). Potential reasons for this pattern include the high mobility of birds that enables them to rapidly exploit available resources (Vanderwel et al.,

2007), although this result might be primarily influenced by the responses of specific species, such as those dwelling in remnants of the former understory or utilizing early successional stages. Although multi-scale approaches are ultimately essential, this study generally demonstrates the contribution of retention logging as a local-scale action

## 5. Conclusion

Temperate forest stands under variable retention management in southern Patagonia supported higher diversity of plants, insects and birds (in both aggregates and dispersed retention) than unmanaged forest stands up to eight years after harvest. The long-term monitoring areas of *N. pumilio* forests harvested under VR prescriptions included here reflect a relevant operational scale for forestry management in southern Patagonia forests. Our analysis demonstrate that increases in biodiversity were mainly caused by influx of native species of other habitats than *N. pumilio* forests and alien species responding to disturbance of the original stands. Native *N. pumilio* forest specialist plants and plants of other habitats tended to recover toward the original conditions defined by levels of diversity and abundance in pristine forests in less than a decade, as did native forest specialist insects. In contrast, both richness and abundance of native insects of other habitats and alien plants continued to increase until the last surveyed year. Major differences between impacts of DR and AR include the significantly higher richness and abundance of alien plants and insects of other habitats in DR. Thus, our results highlight some advantages of variable retention methods as a tool for conservation of forest-dwelling species in a way that may be balanced with economic output. Although encouraging for maintenance of biodiversity over short time frames and at small spatial scales, increasingly widespread silvicultural applications in southern Patagonia should be coupled to a long-term biodiversity monitoring at relevant spatial scales. In particular, we recommend monitoring alien species given the increases in alien plants detected in this study. A useful possibility for further research would be systematic investigations of how changes in microhabitats and the overall habitat fragmentation caused by adoption of VR methods will influence native and alien species.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2016.02.036>.

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