Dendroecological analysis of defoliator outbreaks on *Nothofagus pumilio* and their relation to climate variability in the Patagonian Andes

JUAN PARITSIS and THOMAS T. VEBLEN
Biogeography Laboratory, Department of Geography, University of Colorado, Boulder, CO 80309-0260, USA

Abstract

In the temperate forests of the southern Andes, *Nothofagus pumilio*, the dominant species of the most extensive forest type, experiences severe defoliation caused by caterpillars of the *Ormiscodes* genus (Lepidoptera: Saturniidae). This study uses tree rings to reconstruct the history of *Ormiscodes* outbreaks for the 1850–2005 period and examines relationships between outbreaks and climate variability. We used local climate records to compare outbreak–climate relationships in the northern Patagonian Andes (c. 41°S) and the cooler southern Patagonian Andes (c. 49°S). We also examined relationships between outbreak events and regional climate variability driven by variability in the Southern Annular Mode (SAM) and the El Niño-Southern Oscillation. Although relationships between *Ormiscodes* outbreaks and climate proved to be complex, in northern Patagonia defoliation events are associated with drier and warmer than average growing seasons. Warming and drying trends in Patagonia during the latter part of the 20th century have been linked to a positive trend in SAM. During the post-1976 period of accelerated warming in Patagonia, widespread defoliation outbreaks have occurred in both northern and southern Patagonia but the increase in frequency of events has been greater in the south. In southern Patagonia the increases in frequency of outbreaks in the late 20th century appear to be unprecedented over the c. 150 year tree-ring record of reconstructed outbreaks. These results are consistent with the greater magnitude of recent warming in southern Patagonia, and suggest that under predicted warmer and drier climates in the 21st century, defoliator outbreaks may continue to increase in frequency. This study is the first systematic reconstruction of past insect outbreaks in South America and provides a preliminary understanding of how climate variability affects defoliator outbreaks in Patagonian *Nothofagus* forests.

Keywords: climate, defoliation, dendroecology, ENSO, insect outbreaks, *Nothofagus pumilio*, *Ormiscodes amphimone*, Patagonia, Southern Annular Mode

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Introduction

Climate warming has been suggested as a cause of increased severity and spread of forest insect outbreaks in many parts of the world (Logan *et al.*, 2003; Jepsen *et al.*, 2008). Although many studies have explored the influences of climate variability on insect outbreak activity (mostly in the northern temperate zone), the effects of climatic variation on insect outbreak dynamics remain poorly known, in part due to the lack of adequate long-term outbreak records for robust statistical analyses (Swetnam & Lynch, 1993; Rauchfuss *et al.*, 2009). Long-term records of past outbreaks are needed to determine how current outbreak trends may or may not have departed from their historical range of variability. Despite some early studies in Australia and New Zealand of outbreaks of forest insects potentially related

to climate variation (Jane & Green, 1983; Hosking & Kershaw, 1985), the lack of research on long-term patterns of forest insect outbreaks in relation to climate is particularly evident for the southern hemisphere temperate zone.

Although warming generally is expected to favor growth of herbivorous insect populations to epidemic population levels (Ayres & Lombardero, 2000), there is a wide range of actual responses of insect outbreak dynamics to climate. Some forest insects, including most *Dendroctonus* bark beetles, accelerate their life cycles under warming, favoring epidemic population growth (Hebertson & Jenkins, 2008; Raffa *et al.*, 2008). In contrast, outbreaks of other insect species such as larch bud moth (*Zeiraphera diniana*) in the Alps have declined with warming, apparently due to asynchrony between egg hatch and budburst (Büntgen *et al.*, 2009). Additionally, outbreaks of the same insect species may respond differently to warming and drying trends in different parts of the insect's geographic range (Thomson *et al.*,

Correspondence: Juan Paritsis, tel. + 303 492 4785, e-mail: paritsis@colorado.edu

1984; Swetnam & Lynch, 1993). Thus, it is difficult to predict the response of forest insect pests to the now well-established trend toward warmer temperatures in the southern hemisphere (IPCC, 2007) and in southern South America in particular (Villalba *et al.*, 2003).

Over the past three decades in southern South America, severe defoliation events caused by *Ormiscodes* (Lepidoptera: Saturniidae) species have been reported in *Nothofagus* (southern beech) forests along a large portion of the southern Andes in Patagonia (40–50°S). For instance, in 1985–1986 a large outbreak of *Ormiscodes amphimone* caterpillars, severely defoliated many tens of thousands of hectares of *Nothofagus* forests in northern Patagonia (40–41°S) (Veblen *et al.*, 1996). Severe *O. amphimone* outbreaks, also lasting for a single growing season, occurred in southern Patagonian *Nothofagus* forests in Los Glaciares National Park (50°S) in 1998–1999, and in 2002–2003 (Queiro, 2003). Although local residents and land managers regarded such outbreaks as unprecedented, the historical range of variability of *Ormiscodes* outbreaks is unknown. It is not clear whether similar severe and widespread outbreaks were common in past centuries or if the dynamics of the *Nothofagus*–*Ormiscodes* interaction have recently changed. In order to assess the temporal patterns of *Ormiscodes* defoliations on *Nothofagus pumilio* forests in Patagonia and the potential effects of climate variability on these outbreaks, we reconstructed the history of outbreak events using dendroecological methods and statistically examined their potential relationships to climate variability.

During the past decade significant advances have been made in documenting and understanding climate trends and variability in southern South America (Thompson & Solomon, 2002; Marshall, 2003; Villalba *et al.*, 2003; Aravena & Luckman, 2009; Garreaud *et al.*, 2009). Tree-ring proxy records and instrumental climate records show a clear warming in northern (0.53 °C) and southern (0.86 °C) Patagonia over the 20th century (compared with the 1640–1899 means) that accentuated in the mid-1970s (Villalba *et al.*, 2003). This warming has been accompanied by a decrease in precipitation in most of the Patagonian–Andean region (Aravena & Luckman, 2009). These trends will likely continue as predicted by several General Circulation Models that indicate a warming of c. 2–3 °C in northern Patagonia (Carril *et al.*, 1997) and predict further decreases in precipitation for the 21st century throughout Patagonia (Vera *et al.*, 2006). Additionally, the influence of broad-scale climate modes, such as El Niño-Southern Oscillation (ENSO) and the Southern Annular Mode (SAM) on the regional climate variability of Patagonia is well established (Daniels & Veblen, 2000; Garreaud *et al.*, 2009), and tree-ring proxy reconstructions of these climate modes for the past several centuries are available (e.g. Villalba *et al.*, 1997b; D'Arrigo *et al.*, 2005; Gergis & Fowler, 2009). For example, widespread trends toward warmer and drier conditions in Patagonia have been related to an upward trend in SAM since c. 1950 (Aravena & Luckman, 2009; Garreaud *et al.*, 2009). Together, these advances provide exceptional opportunities to explore the effects of climate variability at multiple scales (i.e. seasonal, interannual, and multi-decadal) on the temporal dynamics of insect outbreaks in the Patagonian Andes.

In this study we use tree-ring methods to reconstruct the outbreak history since 1850 of an insect defoliator (*O. amphimone*) of *N. pumilio* forests in two climatically contrasting regions in northern and southern Patagonia. Specifically, we address two questions: (i) Have *Ormiscodes* outbreaks changed in frequency since the inception of accelerated warming in the late 20th century? (ii) How are *Ormiscodes* outbreaks related to regional climate variation and to broad-scale climate modes (i.e. ENSO and the SAM)?

Methods

Study area

Sampling for detection of past outbreaks of *Ormiscodes* was conducted in *N. pumilio* forests on the eastern slopes of the Argentinean Andes in northern Patagonia at 40–41°S and in southern Patagonia at 49–50°S, in Nahuel Huapi and Los Glaciares National Parks, respectively (Fig. 1). The southern Andes (37–55°S) experience strong westerly winds year round that carry moist air across the Andean divide generating a steep west-to-east gradient of decreasing precipitation associated with distance from the divide. In the northern Patagonia study area the mean annual temperature in the mountain valleys is c. 12 °C and it decreases to c. 6 °C in southern Patagonia, south of 47°S (Villalba *et al.*, 2003). In northern Patagonia (c. 40°S), annual precipitation decreases from 3000 mm, at the Andean divide, to 800 mm in the foothills of the Andes <50 km eastwards (Barros *et al.*, 1983). In southern Patagonia (c. 50°S) annual precipitation declines from 7000 mm on the Pacific coast to 200 mm on the eastern side of the Andes (Aravena & Luckman, 2009). While the study area in northern Patagonia encompasses the entire gradient of precipitation, the study area in southern Patagonia only spans from 400 to 700 mm of annual precipitation.

Climate variations in the southern Andes are strongly influenced by the intensity and latitudinal position of the southeast Pacific subtropical anticyclone, which can block westerly flow of moist air masses into Patagonia causing temperature and precipitation variations. The strength of the southeast Pacific subtropical anticyclone is closely related to ENSO (Aceituno, 1988). Predominant climatic responses to El Niño (i.e. the positive phase of ENSO) at mid-latitudes (40°S) are cool and wet springs and warm and dry summers; at
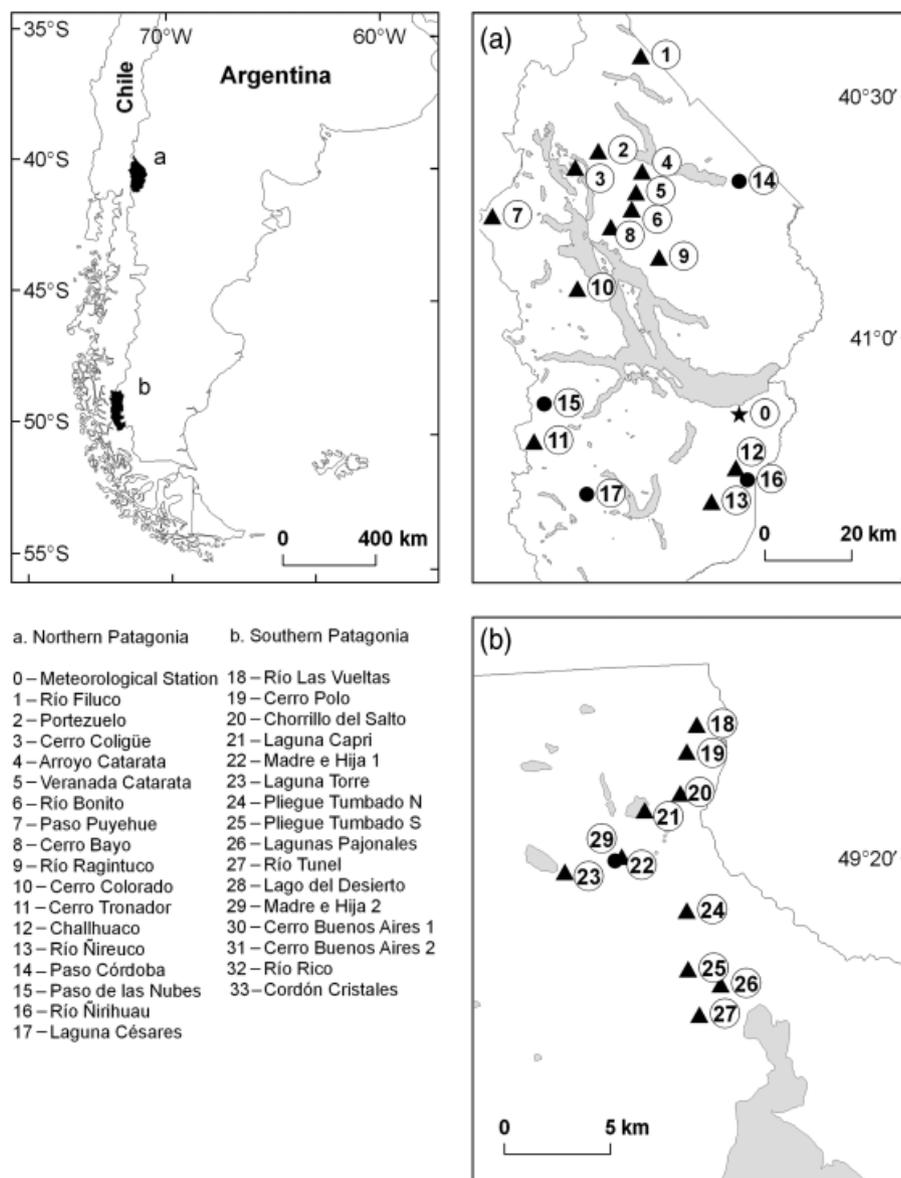
Fig. 1 Map showing the location of the study areas and the tree-ring sample sites in (a) northern Patagonia (Nahuel Huapi NP) and (b) southern Patagonia (Los Glaciares NP). Triangles represent sites used for the outbreak reconstructions and circles represent sites used for the regional climate control chronology. Sites 28, and 30–33 are outside the mapped area (b) for southern Patagonia (see Table 1 for their location).

high-latitudes (c. 50°S) El Niño generates cool and wet springs and warm but not necessarily dry summers (Daniels & Veblen, 2000; Garreaud *et al.*, 2009). Since the mid-1970s, there has been a trend toward the dominance of El Niño rather than La Niña events, with unusually long and strong episodes (Allan, 2000). This trend, in turn, has coincided with accentuated warming after 1976 in the southern hemisphere and specifically in Patagonia (Villalba *et al.*, 2003) and with declining precipitation in northern Patagonia (Aravena & Luckman, 2009). ENSO-related regional climate variation in northern Patagonia has been shown to be an important driver of tree population

dynamics (Villalba & Veblen, 1998; Daniels & Veblen, 2004) and wildfire activity (Kitzberger *et al.*, 1997; Veblen *et al.*, 1999).

Climate variability in the southern Andes is also influenced by blocking events of high pressure over the South America–Antarctic Peninsula sector of the Southern Ocean, which drive cyclonic storms northward into Patagonia. The strength and position of these blocking events are associated with the SAM (also referred as the Antarctic Oscillation) (Thompson & Solomon, 2002), which is a large-scale pattern of alternating zonal pressure anomalies with one sign centered in Antarctica (i.e. south of 65°S) and the opposite sign located in a

circumpolar band at 40–50°S (Gong & Wang, 1999). SAM modifies the atmospheric circulation pattern between high- and mid-latitudes, which in turn changes the meridional position of the westerlies. The positive phase of SAM is associated with warmer temperatures and reduced precipitation south of 40°S in South America (Gillett et al., 2006; Garreaud et al., 2009) due to reduced zonal flow at mid-latitudes resulting in less frontal activity and less orographic precipitation (Gillett et al., 2006). Since c. 1950, SAM has shown an upward trend (especially in summer to fall), which intensified in the mid-1970s, and is believed to be driven by Antarctic ozone depletion and increasing greenhouse gases (Miller et al., 2006; Fogt et al., 2009). Climate models and observations suggest that this positive trend in SAM will continue (Miller et al., 2006) as well as the warming (IPCC, 2007) and precipitation decline (Vera et al., 2006) trends documented in Patagonia. Climate variability induced by SAM has been shown to influence population trends of several species of penguins at high southern latitudes (Forcada & Trathan, 2009) and one species of rodent in northwestern Patagonia (Murúa et al., 2003), as well as fire in South Africa (Wilson et al., 2010) and southern Chile (Holz, 2009).

Studied species

The most widely distributed and economically important Nothofagus species in South America, N. pumilio, is a broad-leaved deciduous canopy tree that extends from 35°35′S in central Chile to 55°30′S in Tierra del Fuego (Veblen et al., 1996; Gea-Izquierdo et al., 2004). In southern Patagonia (i.e. south of 49°S), N. pumilio forests appear to grow under suboptimal climatic conditions related to relatively short growing seasons and strong winds year round.

O. amphimone, one of the most widespread Ormiscodes species in southern South America (Lemaire, 2002), is a native polyphagous saturniid moth known to cause severe defoliation on N. pumilio (Bauerle et al., 1997; Baldini & Alvarado, 2008; Paritsis et al., accepted). O. amphimone overwinters in the egg stage and larvae emerge during early-to-late spring and feed until mid-to-late summer depending on climate conditions and geographic location (Lemaire, 2002). Defoliation caused by O. amphimone apparently does not generate widespread mortality of mature N. pumilio trees, most likely due to the short duration of these outbreaks (i.e. one season; Carrillo & Cerda, 1987; Veblen et al., 1996). Nonetheless, Ormiscodes defoliation significantly reduces N. pumilio radial growth (Paritsis et al., 2009) and has been reported to kill saplings of Nothofagus species even under moderate larval densities (Bauerle et al., 1997). In addition, severe defoliation may promote secondary attacks by Gnathotrupes bark beetles (Baldini & Alvarado, 2008).

Although several Ormiscodes species feed on Nothofagus trees, field observations (Baldini & Alvarado, 2008; Paritsis et al., accepted), as well as the documented geographic ranges of Ormiscodes species (Lemaire, 2002) strongly suggest that O. amphimone is the species that caused all past and recent defoliations on N. pumilio (Paritsis et al., accepted). Hence, even though it is not possible to confirm that all reconstructed defoliations in this study were generated exclusively by O. amphimone, it is highly likely that this species is responsible for most, if not all, the outbreaks identified in the reconstructions.

Sampling design and field methods

We sampled 23 sites (13 in the northern and 10 in the southern Patagonian study areas) to reconstruct Ormiscodes outbreaks in N. pumilio forests (Fig. 1, Table 1). Site selection was based on the occurrence of documented O. amphimone defoliations for which there are available historical records (Veblen et al., 1996; Queiro, 2003) and/or verification in Landsat TM and ETM$^+$ images of the defoliated areas (Paritsis, 2009; Paritsis et al., 2009). Two sites were selected at locations with no documented past outbreaks to increase sample heterogeneity and verify the effectiveness of the method applied to detect past outbreaks. To incorporate stand structure variations and stand age in the sampling design, which may influence outbreak frequency, we sampled two stands with contrasting structures and ages at each site whenever such stand variation was available. Sampled stands were separated by at least 200 m and in no case were more than 500 m apart. At each stand, we recorded the latitude, longitude, elevation, slope angle, and aspect of its central point and collected two increment cores per tree at c. 1.2 m above the ground from at least 15 trees within a 40 m radius from the central point. Trees sampled included the full range of tree sizes present from a minimum of 15 cm diameter at breast height (dbh) to the largest trees in the stand. To quantify structural differences between paired stands we delimited two square plots per stand that ranged from 100 to 900 m^2 each (to include at least 10 trees per plot) and measured tree density and dbh.

Sample processing and reconstruction of outbreak history

We prepared tree-ring samples according to standard dendrochronological procedures (Stokes & Smiley, 1968). Calendar dates were assigned to rings according to the southern hemisphere tree-ring dating convention that assigns an annual ring to the calendar year in which the annual ring formation begins (Schulman, 1956). All series were initially visually crossdated using marker rings. Additionally, on all samples we measured tree-ring width to the closest 0.01 mm with a Velmex-type stage. To check for errors in the dating of the ring-width series we used time series correlation analyses using the COFECHA program (Holmes, 1983), and we excluded samples that did not crossdate with existing master chronologies (Boninsegna & Holmes, 1974; Holmes et al., 1984; Roig, 1986; Villalba & Veblen, 1997; Villalba et al., 1997a). We detrended all tree-ring series applying a double detrending procedure using a negative exponential or linear function first and a cubic-smoothing spline (with a 67% rigidity) as the second option, and we created one residual chronology per stand with the ARSTAN software (Cook & Holmes, 1986).

To reconstruct O. amphimone outbreak history on N. pumilio stands, we used the protocol designed and tested in Paritsis et al. (2009), which uses a combination of three complementary methods to detect past Ormiscodes defoliations: pointer years

Table 1 Location and characteristics of sites sampled for tree-ring chronologies

Study area and site name	Code	No. of trees	Period (AD)	Latitude (S)	Longitude (W)	Elevation (m)	Slope (°)	Aspect
Northern Patagonia								
Sites sampled for Ormiscodes outbreaks								
Río Filuco	FIL	34	1844–2005	40°24′	71°30′	1060	0–5	S
Portezuelo	POR	37	1832–2005	40°36′	71°38′	1110	0–25	E
Cerro Coligüe	CCO	18	1903–2005	40°38′	71°42′	1080	5–15	NW
Arroyo Catarata	CAT	16	1873–2004	40°38′	71°31′	1090	0–5	SE
Veranada Catarata	VER	33	1801–2005	40°41′	71°32′	1190	0–20	NE
Río Bonito	BON	37	1783–2005	40°43′	71°33′	1350	5–15	NW
Paso Puyehue	PUY	24	1850–2003	40°43′	71°56′	1150	0–5	N
Cerro Bayo	BAY	24	1868–2003	40°45′	71°36′	1470	25–35	E
Río Ragintuco	RAG	33	1828–2005	40°49′	71°28′	1230	10–20	NW
Cerro Colorado	COL	33	1744–2005	40°53′	71°42′	1450	20–40	N
Cerro Tronador	TRO	21	1815–2003	41°12′	71°50′	1050	10–20	E
Challhuaco	CHA	34	1795–2005	41°16′	71°17′	1350	5–20	NW
Río Ñireuco	NCO	33	1821–2005	41°20′	71°21′	1290	5–15	E
Sites used to generate the regional host chronology (climatic control)								
Paso Córdoba*	PCO	32	1754–1986	40°40′	71°15′	1050[†]	nd[‡]	nd
Paso de las Nubes[§]	PNU	12	1751–1991	41°07′	71°48′	1230	5–18	E
Río Ñirihuau	NIR	18	1873–2003	41°17′	71°15′	1190	25–35	SE
Laguna Césares	LCE	17	1820–2006	41°18′	71°42′	1170	0–5	SE
Southern Patagonia								
Sites sampled for Ormiscodes outbreaks								
Río Las Vueltas	VUE	21	1888–2003	49°16′	72°54′	580	15–20	SE
Cerro Polo	POL	33	1857–2005	49°17′	72°54′	460	15–35	SE
Chorrillo del Salto	CHO	32	1873–2005	49°18′	72°54′	430	0–15	NE
Laguna Capri	CAP	39	1888–2005	49°18′	72°56′	780	5–15	NW
Laguna Torre	TOR	15	1872–2003	49°20′	72°59′	660	5–15	E
Madre e Hija 1	MH1	32	1822–2005	49°20′	72°57′	600	10–20	S
Pliegue Tumbado N	PTN	34	1810–2005	49°21′	72°54′	780	0–10	NE
Pliegue Tumbado S	PTS	39	1812–2005	49°23′	72°54′	830	0–15	NE
Lagunas Pajonales	PAJ	38	1795–2005	49°23′	72°53′	810	10–20	E
Río Tunel	TUN	39	1788–2005	49°24′	72°54′	810	0–10	SE
Sites used to generate the regional host chronology (climatic control)								
Lago del Desierto[¶]	DES	28	1881–1998	49°00′	72°50′	550	nd	nd
Madre e Hija 2	MH2	18	1864–2005	49°20′	72°57′	620	10–20	S
Cerro Buenos Aires 1[‖]	BA1	31	1750–1984	50°22′	72°47′	870	nd	nd
Cerro Buenos Aires 2**	BA2	14	1823–1974	50°25′	72°45′	600	nd	nd
Río Rico	RIC	15	1789–2003	50°32′	72°43′	780	0–10	SW
Cordón Cristales	CRI	16	1766–2003	50°35′	72°52′	700	0–10	NE

The starting date listed under period corresponds to the year in which a chronology included at least five trees.

*Roig (1986).

[†]Estimated elevation based on location provided in Roig (1986).

[‡]nd, not determined.

[§]Villalba *et al*. (1997a).

[¶]Veblen *et al*. (unpublished).

[‖]Holmes *et al*. (1984).

**Boninsegna *et al*. (1974).

(Weber & Schweingruber, 1995), departure from a regional host chronology control (Swetnam *et al*., 1985), and a morphological tree-ring signature (Hogg *et al*., 2002). Past outbreak events were identified with either a high or moderate confidence level by testing for three conditions for a potential outbreak year. Condition (1): the tentative outbreak year must be associated with a narrow ring (>50% reduction compared with the six neighboring tree rings) based on the pointer year method. Condition (2): at least 10% of the trees (minimum sample of 20 trees) in a tentative outbreak year must have the morphological signature associated with known outbreaks. Condition (3): the observed tree-ring index must be at least

2 SDs less than the index of the regional-host chronology. If only condition 1 is met, it is more probable that the suppressed tree ring was caused by climatic conditions rather than defoliation. If condition 1 and either condition 2 or 3 are met, then, it is more likely that the suppressed ring was due to a defoliation event rather than climate unfavorable to tree growth; consequently, an outbreak can be inferred with moderate confidence. Finally, if all three conditions are met, an outbreak defoliation event in that year is inferred with a high degree of confidence. The current study includes only outbreak years of moderate confidence (two out of three conditions) and high confidence (all three conditions). The protocol was previously tested against direct observations of outbreaks in five stands in the northern Patagonian study area (Paritsis et al., 2009), and in the current study with an additional eight and 10 stands in northern and southern Patagonia, respectively. In addition to the outbreaks documented by tree-ring attributes, we included in the reconstruction a recent outbreak (austral summer 2004–2005) directly observed in southern Patagonia but not sampled for tree-ring attributes.

Reconstructions of outbreaks were initially performed on a stand basis and plotted from the year when at least five trees were included in the stand chronology. For analyses of climatic relationships of outbreak occurrence, we aggregated stand chronologies into regional composite time series of outbreak events for the northern and southern Patagonian study areas. To avoid spurious interpretations of past outbreak frequency due to low sample size, we began our analyses of the composite time series in 1850 for each study area (i.e. when at least 50% of the sites and c. 25% of the trees were included in the composite; Fig. 2). Given that the reduced ring width generated by the defoliation is formed in the growing season after the outbreak event, we reassigned the outbreak year to the growing season in which the defoliation occurred (e.g. a defoliation occurring during January–March 1986, was assigned to the 1985 calendar year, which represents the 1985–1986 growing season).

Climate datasets

We used instrumental climate data (i.e. monthly temperature and precipitation) from representative climate stations in each of the two study areas to examine the associations between Ormiscodes outbreaks and climate variability. For the study area in northern Patagonia mean monthly temperature and total monthly precipitation records were obtained from the Bariloche meteorological station (41°09′S, 71°16′W; elevation 825 m) located at c. 60 km on average from the sampled sites. For southern Patagonia, we used temperature and precipitation records from the Balmaceda meteorological station (45°55′S, 71°41′W; elevation 223 m) located at c. 380 km on average from the sampled sites. These stations were selected based on three criteria: closest linear distance to the study areas, similar relative position from the Andean divide as the study areas, and sufficiently long records to perform climatic analyses. For Bariloche, the record spans from 1914 to 2005 and from 1905 to 2005 for temperature and precipitation, respec-

tively; and for Balmaceda it spans from 1963 to 2005 and 1950 to 2005 for temperature and precipitation, respectively.

To explore relationships of outbreaks to ENSO and SAM, we used tree-ring reconstructed sea surface temperature anomalies (SST, December–February) for ENSO (Cook reconstruction, Niño3 region; D'Arrigo et al., 2005), and tree-ring reconstructed mean sea level pressures (MSLP) anomalies (November–February) for the South American sector of Antarctica for SAM (Villalba et al., 1997b). Given that these reconstructions end in 1978 (Cook Niño3) and 1984 (MSLP), we extended them to 2005 using instrumental records. We used Niño 3.4 December–February SST instrumental records for the 1950–2005 period (http://www.cpc.noaa.gov/data/indices/sstoi.indices) to extend the Cook Niño3 reconstruction. We used Marshall's (2003) SAM index (December–February), which is the monthly mean difference between MSLP anomaly at six stations near 40°S and six stations near 65°S, for the 1957–2005 period to extend MSLP. MSLP annual values were multiplied by -1 to allow these to correspond to Marshall SAM index values. To extend the reconstructions we adjusted their SDs and means (calculated for the overlap period between these and the detrended instrumental record) and we replaced the reconstructed series with the detrended instrumental values for the 1950–2005 and 1957–2005 periods for Cook Niño3 and SAM, respectively (Schoennagel et al., 2007). Finally, we normalized the extended reconstructions for the 1850–2005 time period. Hereinafter we will refer to the reconstructed Cook Niño3 extended with Niño 3.4 as 'Niño3' and to the reconstructed MSLP extended with the SAM Marshall index (Marshall, 2003) as 'SAM.'

Climate–outbreak analyses

We examined the association of outbreak occurrence and climate warming in Patagonia by calculating the mean number of outbreak events per decade per region and compared these means with a t-test for the 1850–1975 vs. the 1976–2005 periods in northern and southern Patagonia. The selection of these time periods is based on the well documented acceleration of warming that started around 1976 in the southern Andes (Villalba et al., 2003).

To quantitatively examine interannual associations between outbreak occurrence and climate variables we used Superposed Epoch Analysis (SEA) (Grissino-Mayer, 1995). SEA compares the mean values of climate conditions during outbreak years and the mean values of climate conditions during the entire period of analysis. Mean values of climate conditions were calculated for each year in a window of 5 years (3 years preceding the outbreak year, the outbreak year itself, and 1 year following the outbreak). Statistical significance was determined by a bootstrap method in which years are selected randomly and expected mean values of climate conditions are calculated for the entire period of analysis (Grissino-Mayer, 1995). Because of the small number of outbreak events during the period covered by the instrumental climate record, we also assessed climate conditions during all nonoutbreak years using SEA. If mean climate conditions during the nonoutbreak
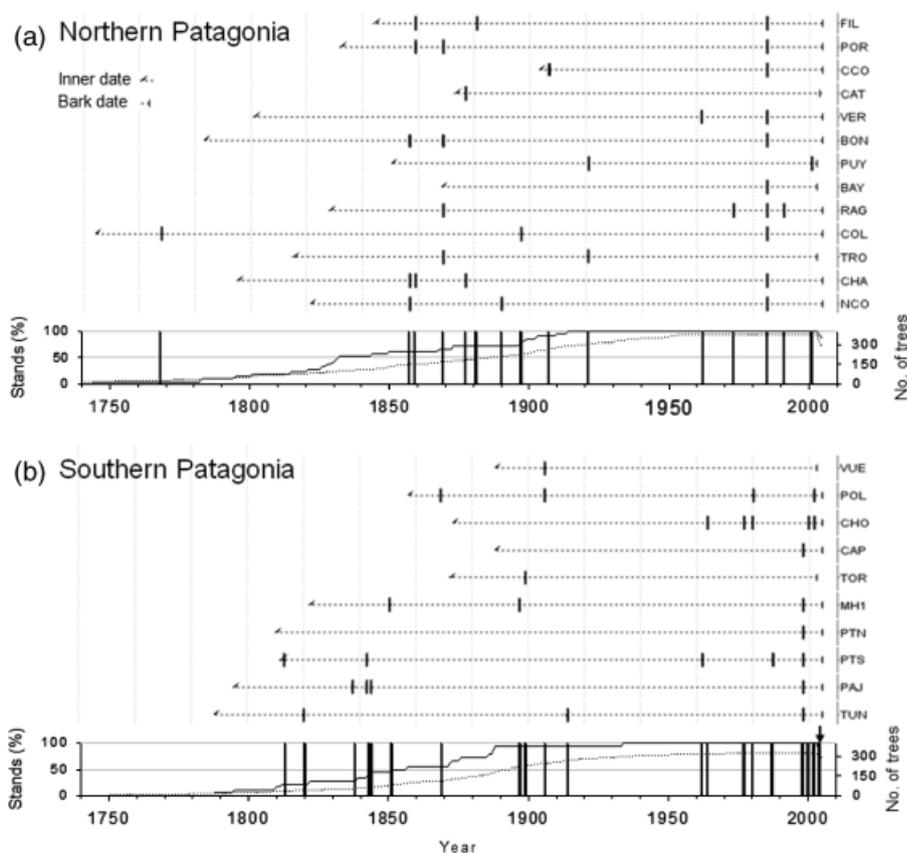
Fig. 2 Tree-ring reconstructions of *Ormiscodes* outbreak events in (a) northern and (b) southern Patagonia. Dotted lines represent chronology length and vertical bars are outbreak years. Composite chronologies (lower portion of each sub figure) indicate total outbreaks per region and sample depth (solid and dotted lines represent percentage of stands and number of trees, respectively). See Table 1 for site codes. Outbreak events are defined as years in which either three (pointer year, morphological signature, and regional host) or two criteria (pointer year and morphological signature or regional host) indicate an outbreak event. The 2004 outbreak, directly observed for southern Patagonia, did not affect any of the sampled stands but is included in the composite (indicated with an arrow).

years are the opposite of those during outbreak years, then the latter results based on small sample sizes are more likely to have a causal explanation. We performed SEA for climate data by single months, 2- and 3-month seasons, and annual time periods but we only present results if they are statistically significant and consistent across different data arrangements. Additionally, we conducted SEA analyses with a moisture index calculated as precipitation departures minus temperature departures (both in SDs) following Villalba & Veblen (1998). We performed SEA between outbreaks and the climate indexes for the entire study period, as well as for the recent period of increasingly positive SAM (1951–2005) vs. the previous 101 years when SAM fluctuated between positive and negative departures at a multidecadal scale (Miller *et al.*, 2006; Fogt *et al.*, 2009).

Variability in timing of initiation, duration, and strength of ENSO events is known to affect teleconnections to climate, and outliers can obscure statistical associations of ecological phenomena with ENSO variability in Patagonia (Villalba, 1994; Veblen *et al.*, 1999). Therefore, we qualitatively examined the associations between ENSO phases and regional outbreak

years (i.e. years when outbreaks were recorded in at least two sites within the same study area) based on a multiproxy reconstruction of intensities of individual ENSO events (Gergis & Fowler, 2009). Because a portion of any calendar year can be El Niño (La Niña) and then shift to the opposite phase during the same calendar, some years in Gergis and Fowler's (2009) reconstruction are indicated as both ENSO phases simultaneously.

Given that climate responses to Niño3 and SAM are not uniform over all of Patagonia (Daniels & Veblen, 2000; Gillett *et al.*, 2006; Garreaud *et al.*, 2009), we performed correlation functions between local climate data (monthly and seasonal means) from the Bariloche and Balmaceda climate stations and these climate indices for the time period common to both stations (1963–2003). Correlation functions with their respective calculated bootstrapped confidence intervals allowed us to estimate the strength of the relationship between local climate data from meteorological stations and index variability. The software DENDROCLIM2002 was used to perform the correlation functions and to calculate the bootstrapped confidence intervals (Biondi & Waikul, 2004).

Results

Tree-ring reconstructions of Ormiscodes outbreaks

Based on the tree-ring reconstructions, there were 14 *O. amphimone* outbreaks (71% high and 29% moderate confidence levels) in the northern Patagonia study area, and 15 outbreaks (67% high and 33% moderate confidence levels) in the southern Patagonia study area over the 1850–2005 time period (Fig. 2). In the northern Patagonia study area outbreak events occurred mostly during the 1857–1897 (50% of the events) and the 1962–2001 (36%) periods; in the southern Patagonia study area most of the outbreaks (60%) occurred during the 1962–2004 period (Fig. 2). In both study areas, the post-1961 period of frequent outbreaks was preceded by a 40-year period (1922–1961) time period lacking outbreaks (Fig. 2). Outbreak occurrence per decade for the 1850–1975 period was significantly lower than for the 1976–2005 period in southern ($P = 0.01$) but not in northern Patagonia ($P = 0.4$; Table 2).

Despite the low occurrence of multiple outbreaks at the same site, many outbreaks are regionally synchronous with at least one other site at an annual scale (Fig. 2). On average, c. 1.5 outbreaks occurred in a given site per century per study area and c. 10 outbreaks occurred per century per study area (i.e. regional scale). Outbreak frequency is not consistently or significantly related to stand structure variables (i.e. dbh and tree density) in either study area (results not shown).

Associations of outbreaks with variability in instrumental climate records

SEA reveals that outbreaks in northern Patagonia are associated with warmer and drier than average springs during the year of the outbreak based on the c. 100-year Bariloche climate record (Fig. 3a, c, and e). Consistent with this pattern is the association of nonoutbreak years with cooler and moister than average springs (Fig. 3b, d, and f). There are no significant or consistent associa-

Table 2 Mean ($\pm$ SD) outbreak events per decade for the 1850–1975 and 1976–2005 periods in the northern and southern study areas

Time period	Outbreaks/decade
Northern Patagonia	
1850–1975	0.8 ± 0.7
1976–2005	1.0 ± 0.0
Southern Patagonia	
1850–1975	0.6 ± 0.8
1976–2005	$2.3 \pm 1.5^*$

*Significant difference between periods (*t*-test; $P < 0.05$).

tions of outbreaks with other 2–3-month seasons or single months (results not shown).

Given the distance of the study area from the Balmaceda climate station, it is not surprising that statistical relationships of outbreaks in southern Patagonia with the instrumental record are weak and/or unclear as proximate causes for outbreak occurrence. SEA indicate that over the past c. 50 years, springs are cooler than average 2 years before the outbreak (Fig. 3g). Springs the year before outbreaks are slightly drier than average but springs in the outbreak year show average precipitation (Fig. 3i). These temperature and precipitation patterns resulted in above average spring moisture 2 years before the outbreak and during the year of the outbreak (Fig. 3k). The SEA results with the dataset of nonoutbreak years show the opposite patterns, implying the weak outbreak–climate patterns found with the outbreak dataset reflect causal relationships (Fig. 3h, j, and l). As with northern Patagonia, there are no significant or consistent associations of outbreaks with other seasons or months using the instrumental record that can be interpreted as proximate causes of outbreak occurrence.

Associations of outbreaks with variability of ENSO and SAM

In northern Patagonia, there are no significant departures with SEA for the Niño3 index over the 5-year window before, during and after outbreak years (Fig. 4a). However, of the seven regional outbreak events in northern Patagonia, all four 19th century outbreaks either coincide with or lag El Niño by 1 year (Table 3). In contrast, during the 20th century, the three regional outbreaks in northern Patagonia lag La Niña events by 1–3 years (Table 3). SST (Niño3) positively correlate with spring moisture availability in northern Patagonia (Fig. 5a–c). Thus, La Niña events (cool SST) indicate dry and relatively warm springs preceding the three 20th century regional outbreaks which is consistent with the association of outbreaks with warm and dry springs in the Bariloche climate record (Fig. 3a–f). On the other hand, the association of the four regional outbreak years from 1857 to 1877 in northern Patagonia with El Niño is not consistent with the moister springs expected during El Niño events. However, the lack of local instrumental records during this period and the known decadal variations in the relationships of ENSO to climate and ecological processes in Patagonia (Daniels & Veblen, 2000, 2004) make interpretations uncertain.

In southern Patagonia, SST (Niño3 index) over the 1850–2005 period are significantly above average 1 year before outbreak events indicating El Niño conditions (Fig. 4c). This pattern is consistent with the qualitative
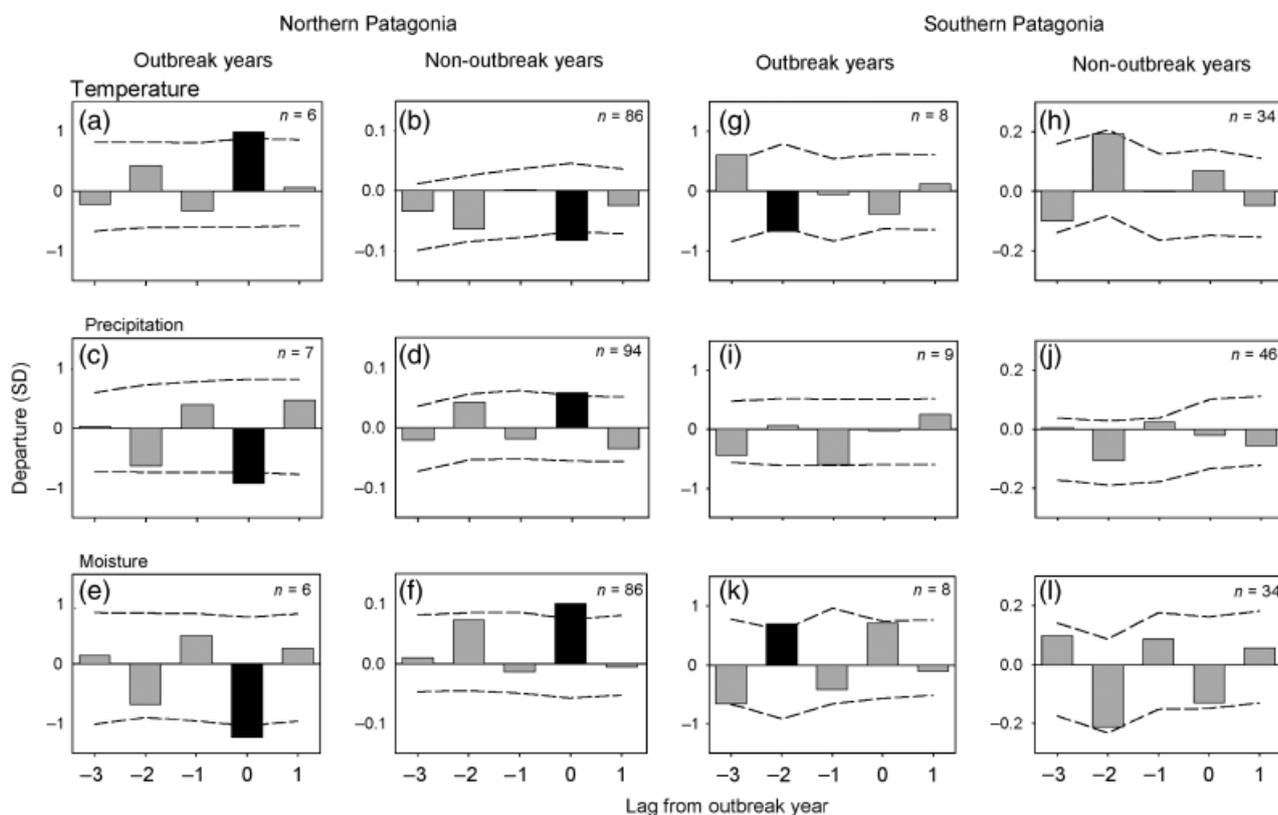
Fig. 3 Mean departures for spring (September–November) temperature, precipitation, and moisture index for years before, during, and after outbreak events for the northern (Bariloche meteorological station; 1915–2005 for temperature and moisture index, and 1905–2005 for precipitation) and southern Patagonia study areas (Balmaceda meteorological station; 1963–2005 for temperature and moisture index, and 1950–2005 for precipitation). Outbreak years are years in which either three (pointer year, morphological signature, and regional host) or two criteria (pointer year and morphological signature or regional host) indicate an outbreak event. Nonoutbreak years correspond to the entire period of analysis minus the outbreak years. The number of outbreak event years is given by n. Black bars indicate significant departures from the mean (95% confidence interval, represented by dashed lines).

association between outbreaks and El Niño events, in which all five regional outbreaks in southern Patagonia either coincide with El Niño or followed it by 1 year (Table 3). The correlations of the Niño3 index with the Balmaceda climate record (Fig. 5g–i) indicate that El Niño events during the second half of the 20th century are associated with wet springs and dry and relatively warm summers. The lack of climate data for the Balmaceda record before 1950 and the temporal instability of ENSO teleconnections to climate at multidecadal time scales (Daniels & Veblen, 2000) create uncertainty in any climatic interpretation of the association of outbreaks with El Niño events. However, the outbreak–ENSO associations shown for northern and southern Patagonia (Fig. 4a and c) were the same when the 1850–1950 and the 1951–2005 periods were analyzed separately (results not shown).

In both northern and southern Patagonia, outbreaks are not significantly associated with the SAM index at interannual scales when SEA is conducted over the entire 1850–2005 period (Fig. 4b, and d). However, when SEA is conducted for the 1850–1950 and the 1951–2005 periods separately for northern Patagonia, there is a reversal in the sign of SAM for the outbreak year (Fig. 6a, and b). Over the 1850–1950 period SAM is negative in outbreak years but over the 1951–2005 period SAM becomes positive (but not significantly so). This is consistent with the association of positive SAM with warm–dry springs and summers during the second half of the 20th century (Fig. 5d–f). Analogously, in southern Patagonia outbreaks are strongly associated with negative SAM before 1950 (1 and 2 years before outbreak events; Fig. 6c), but over the 1951–2005 period SAM does not show any consistent association with outbreak events (Fig. 6d). The lack of pre-20th century climate data for northern and southern Patagonia limits the interpretation of climate conditions associated with outbreak and SAM associations during the earlier time period.
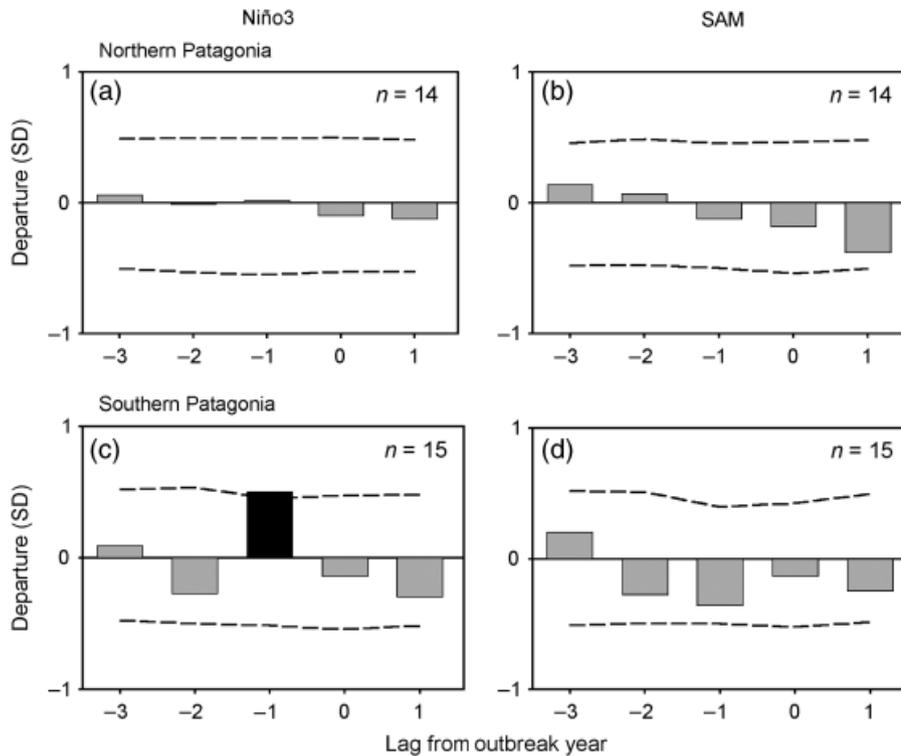
Fig. 4 Mean departures for Niño3 (December–February sea surface temperature, calendar year assigned to December calendar year) and for Southern Annular Mode (SAM; SAM index from Marshall, 2003 extended with reconstructed mean sea level pressure) for years before, during, and after outbreak years in northern and southern Patagonia (1850–2005 period). Positive departures (warm phase) indicate El Niño conditions while negative departures (cool phase) indicate La Niña conditions. The number of outbreak event years is given by *n*. Outbreak years are years in which either three (pointer year, morphological signature, and regional host) or two criteria (pointer year and morphological signature or regional host) indicate an outbreak event. Black bars indicate statistically significant departures from the mean (95% confidence intervals are represented by dashed lines).

Discussion

Tree-ring reconstructions of Ormiscodes outbreaks

To our knowledge this is the first regional tree-ring reconstruction of insect outbreaks in South America, and consequently, it represents a crucial first step toward the understanding of long-term dynamics of insect outbreaks in the temperate forests of the southern hemisphere. We found that *Ormiscodes* outbreaks in the northern and southern study areas in Patagonia are relatively rare over most of the study period (i.e. 1850–2005) but their frequency increased markedly in the late 20th century (Fig. 2). The conservative nature of the tree-ring methods used to reconstruct outbreak events identified only moderate and high severity outbreaks, and it is not known if there are long-term trends in less severe outbreaks.

This study confirms previous observations (i.e. Carrillo & Cerda, 1987; Veblen *et al.*, 1996) regarding the 1 year duration of *Ormiscodes* outbreaks in Patagonia. Conversely, the observed acyclic occurrence of

outbreaks at individual sites or groups of nearby sites (Fig. 3) contrasts with a suggested 4-year cycle for *Ormiscodes cinnamomea* (a close relative of *O. amphimone*) in the Concepción region (36°S; 73°W) in Chile (Artigas, 1972). However, Artigas (1972) did not present any quantitative evidence of a 4-year cycle of *O. cinnamomea* outbreaks. Based on the temporal patterns of outbreaks qualitatively described in the current study, there is no evidence of any regular periodicity in *Ormiscodes* outbreaks.

Ormiscodes outbreaks and climate variability

Although the associations found between *O. amphimone* outbreaks and climate are complex and variable, they provide a preliminary understanding of climatic influences on defoliation events. In northern Patagonia, the relatively long instrumental climate record shows that outbreak events are associated with drier and warmer than average springs during the 20th century (Fig. 3a–f). Conversely, and supportive of that conclusion, nonout-

Table 3 Regional outbreak events (i.e. events that occurred in at least two sites) and associated El Niño and La Niña years from Gergis & Fowler (2009) from 1850 to 2005

Regional outbreak year	El Niño	Intensity	La Niña	Intensity
Northern Patagonia				
1857	1856, 1857	M	–	–
1859	1858	M	–	–
1869	1868	VS	1867, 1868	S
1877	1877	VS	1875	S
1921	1918, 1919	VS, S	1918	S
1985	1983	E	1984	M
2001	–	–	2000	S
Southern Patagonia				
1906	1905	E	–	–
1980	1980	M	–	–
1998	1997	E*	1998	E
2002	2002	E	2000	S
2004	2004	?	–	–

Intensities of El Niño/La Niña events are given as: M, moderate; S, strong; VS, very strong; E, extreme (weak events are not shown). Some years are listed as both El Niño and La Niña because of phase flipping during the same calendar year.
*Although according to Gergis & Fowler (2009) 1997 El Niño has a weak intensity, it is considered an intense El Niño year by Cook Niño3 reconstruction (D'Arrigo *et al.*, 2005) and instrumental data (http://www.cdc.noaa.gov/enso/).

break years are significantly above average in spring moisture availability. This finding is consistent with the association of outbreaks with La Niña events during the 20th century (Table 3). Likewise, it is consistent with the positive (but nonsignificant) departures of SAM during outbreak years in the 1951–2005 period (Fig. 6b) and the association of positive SAM with drier and warmer springs (Fig. 5d–f).

In southern Patagonia, analyses based on the relatively short Balmaceda meteorological station, located c. 380 km north of the study area, did not yield any conclusive associations of outbreak events with seasonal precipitation or temperature departures. Data from other stations closer to the study area were of shorter duration and were of poor quality due to missing data. Analyses based on these other stations also did not show clear or consistent associations of outbreak events with seasonal climate anomalies. A key limitation of the outbreak–climate analyses is the low number of outbreak events overlapping with the relatively short climate record from southern Patagonia. Consequently, associations between outbreaks and the instrumental climate record are inconclusive for southern Patagonia.

Despite the limitations imposed by the lack of a long instrumental climate record near the outbreak events in southern Patagonia, associations of outbreak events with ENSO and SAM indicate the importance of climatic variability in triggering outbreaks. Over the 1850–2005 period, outbreaks are significantly associated with above average SST (El Niño events) during the prior year (Fig. 4c). Likewise, during the 1850–1950 period outbreaks are strongly associated with negative departures in SAM (Fig. 6c) but the absence of a long, local climate record makes the climatic interpretation of this pattern uncertain. Nevertheless, the warming trend recorded after the mid-1970s in the southern hemisphere is much more pronounced in southern than in northern Patagonia (Villalba *et al.*, 2003). Consistent with this pattern, the frequency of outbreaks during the 1976–2005 period increased fourfold compared with the previous 126 years in southern Patagonia, whereas the increase in outbreak frequency in northern Patagonia was less dramatic (Table 2; Fig. 2). Hence, despite the lack of significant departures of seasonal climate variables during outbreak years for southern Patagonia (Fig. 3), the increase in outbreak frequency in southern Patagonia coincides with the post-1976 accelerated warming. Synchronous defoliation over large areas (e.g. defoliated patches during the 1985–1986 outbreak were distributed over a north–south distance >130 km) strongly suggests that regional climate variability rather than density-dependent factors (e.g. dispersal, local stand conditions) is the main driver of outbreak occurrence (Zhang & Alfaro, 2003).

Implications of the outbreaks–climate relationships for *N. pumilio* forests

In both study areas there were several years of warmer and drier than average springs during the periods of instrumental climate records that were not associated with outbreaks. Thus, although particular climate conditions appear to be an important precondition for *Ormiscodes* outbreaks, other unknown and perhaps density-dependent factors (Peltonen *et al.*, 2002; Zhang & Alfaro, 2003) are likely contributing to the observed population dynamics. Direct long-term monitoring of variations in *O. amphimone* demography as well as manipulative experiments are needed in order to identify density-dependent factors and their interactions with climate variability. However, based on the preliminary findings presented here, current and predicted warming and precipitation decline in Patagonia (Carril *et al.*, 1997; Villalba *et al.*, 2003; Vera *et al.*, 2006; IPCC, 2007; Aravena & Luckman, 2009) as well as the continued positive trend in SAM (Miller *et al.*, 2006) are likely to favor increased outbreak frequency (and potentially severity and extent) during the 21st century.

This prediction raises important but complex questions about how increased defoliator activity will affect
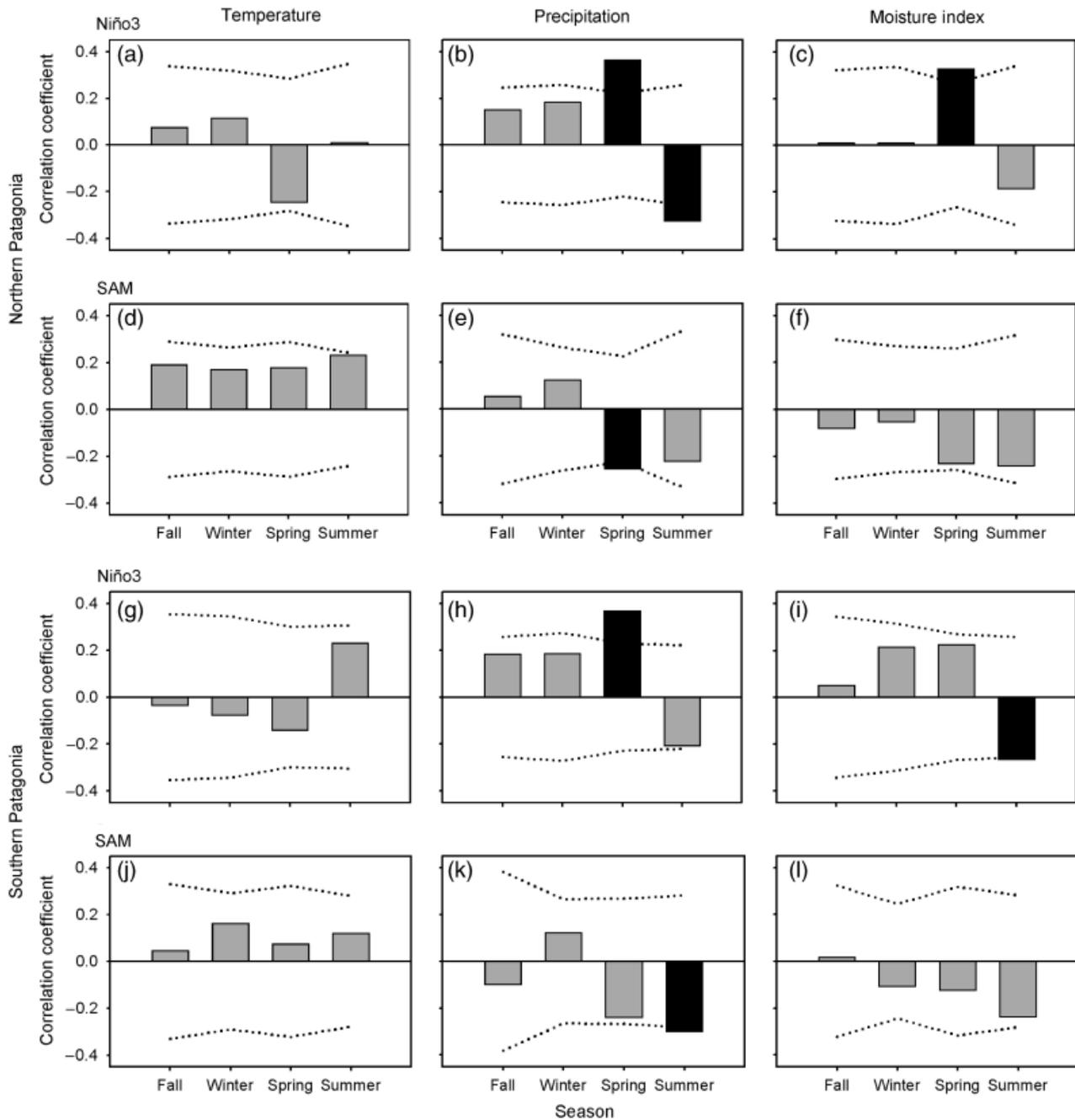
Fig. 5 Correlation function analysis of seasonal temperature, precipitation, and moisture index with December–February. Niño3 and Southern Annular Mode (SAM) by region (1963–2003 period). Bootstrapped 95% confidence intervals (dotted lines) are used to estimate the statistical significance of the correlations (black bars indicate significant correlations). The meteorological stations used are Bariloche (northern Patagonia) and Balmaceda (southern Patagonia). Seasons are defined as Fall, March–May; Winter, June–August; Spring, September–November; Summer, December–February. Positive (warm) Niño3 indicates El Niño conditions and negative (cool) Niño3 indicates La Niña conditions.

the demography and ecosystem processes of *N. pumilio* forests. Historically, defoliation events have been limited to a single growing season, have been relatively rare events in these forests, and have not been asso-

ciated with any obvious tree mortality. However, if the outbreak frequency observed in southern Patagonia over the last c. 30 years (and especially over the last 10 years) continues, *N. pumilio* forests may start show-
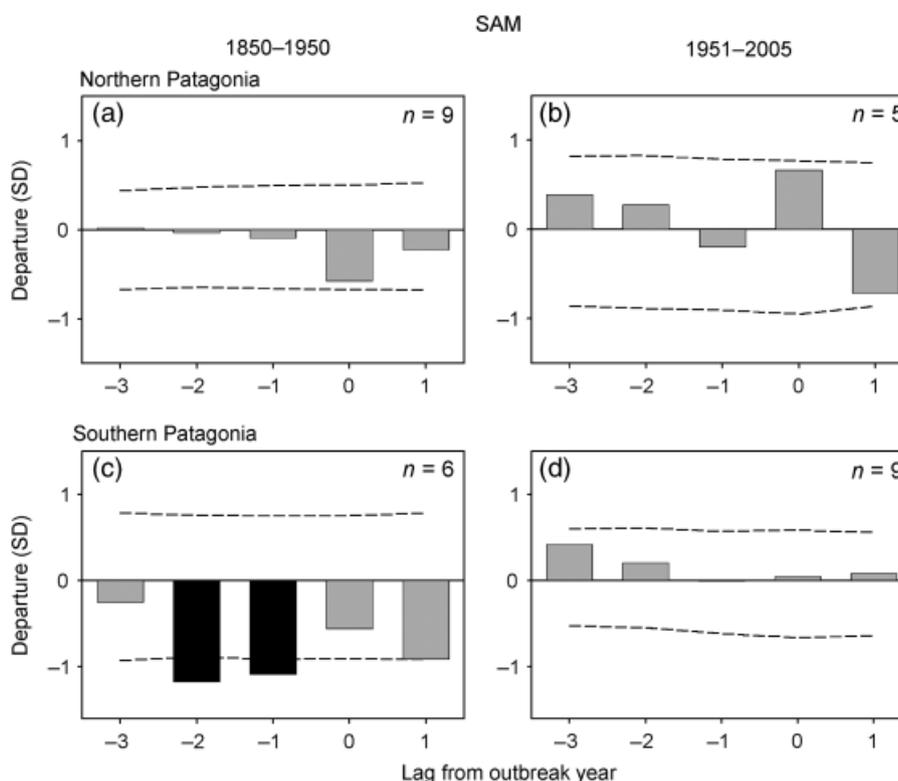
Fig. 6 Mean departures for Southern Annular Mode (SAM) for years before, during, and after outbreak years for the 1850–1950 and the 1951–2005 time periods in the northern Patagonia (a, b) and southern Patagonia study areas (c, d). The number of outbreak event years is given by n. Outbreak years are years in which either three (pointer year, morphological signature, and regional host) or two criteria (pointer year and morphological signature or regional host) indicate an outbreak event. Black bars indicate statistical significant departures from the mean (95% confidence interval).

ing mortality caused directly by defoliation or greater susceptibility to other stressors such as drought and secondary insect attacks (Manion, 1981). Recent drought episodes in northern Patagonia are already causing significant mortality of *Nothofagus dombeyi*, a closely related species that grows at lower elevation (Suarez *et al.*, 2004). Higher mortality rates of *N. dombeyi* are associated with previous attacks by insect borers, which render the trees more susceptible to hydric stress (Suarez *et al.*, 2004). Defoliation events may make *N. pumilio* more susceptible to subsequent attack by other insects such as has occurred in closely related *Nothofagus* spp. in New Zealand where drought and defoliation by scale insects weaken trees and make them susceptible to other lethal agents such as pinhole beetles (Hosking & Kershaw, 1985; Hosking & Hutcheson, 1988). In order to understand similar plausible synergistic effects of defoliations and climate change on *N. pumilio* forests, it is crucial to combine assessments of the historical regime of variability of these outbreaks with long-term monitoring of severely defoliated and nondefoliated (or lightly defoliated) stands. Likewise, indirect climate influences on the *Ormiscodes–Nothofagus* system via effects on food quality and predator

populations of the defoliators will require manipulative and long-term studies (Barbosa & Schultz, 1987; Ayres & Lombardero, 2000).

Overall, the results of the current study imply that climate warming has promoted *O. amphimone* outbreaks in southern Patagonia. Although there is evidence supporting the view that climate warming and drought is favoring outbreaks of some guilds of forest insects, such as bark beetles (*Dendroctonus* spp.) in the northern hemisphere (Logan *et al.*, 2003; Berg *et al.*, 2006), support for this idea for insect defoliators has been variable and inconclusive (Huberty & Denno, 2004; Rouault *et al.*, 2006; Büntgen *et al.*, 2009). Therefore, our study adds to this general knowledge by providing information on historical activity of defoliator outbreaks and preliminary data on their relationship to climate variability from an understudied region that is experiencing considerable warming and an apparent increase in insect defoliation.

Acknowledgements

References

Aceituno P (1988) On the functioning of the Southern Oscillation in the South American sector. *Monthly Weather Review*, **116**, 505–524.

Allan R (2000) ENSO and climatic variability in the past 150 years. In: *El Niño and the Southern Oscillation: Multiscale Variability and Global and Regional Impacts* (eds Diaz H, Markgraf V), pp. 3–35. Cambridge University Press, Cambridge, UK.

Aravena JC, Luckman BH (2009) Spatio-temporal rainfall patterns in Southern South America. *International Journal of Climatology*, **29**, 2106–2120.

Artigas J (1972) Ritmos poblacionales de Lepidópteros de interés agrícola. *Boletín de la Sociedad Biológica de Concepción (Chile)*, **45**, 5–94.

Ayres MP, Lombardero MJ (2000) Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *The Science of the Total Environment*, **262**, 263–286.

Baldini A, Alvarado A (2008) *Manual de plagas y enfermedades del bosque nativo en Chile. Asistencia para la recuperación y revitalización de los bosques templados de Chile, con énfasis en los Nothofagus caducifolios*. FAO/CONAF, Santiago de Chile.

Barbosa P, Schultz JC (eds) (1987) *Insect Outbreaks: Ecological and Evolutionary Perspectives*. Academic Press, London.

Barros V, Cordón V, Moyano C, Méndez R, Forquera J, Pizzio O (1983) *Cartas de precipitación de la zona oeste de las provincias de Río Negro y Neuquén*. Report to the Facultad de Ciencias Agrarias, Universidad Nacional del Comahue, Cinco Saltos, Neuquén.

Bauerle P, Rutherford P, Lanfranco D (1997) Defoliadores de roble (*Nothofagus obliqua*), rauli (*N. alpina*), coigue (*N. dombeyi*) y lenga (*N. pumilio*). *Bosque*, **18**, 97–107.

Berg EE, Henry JD, Fastie CL, De Volder AD, Matsuoka SM (2006) Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: relationship to summer temperatures and regional differences in disturbance regimes. *Forest Ecology and Management*, **227**, 219–232.

Biondi F, Waikul K (2004) DENDROCLIM2002: a C++ program for statistical calibration of climate signals in tree-ring chronologies. *Computers & Geosciences*, **30**, 303–311.

Boninsegna J, Holmes R (1974) *Nothofagus pumilio Tree-Ring Chronology, Cerro Buenos Aires, Santa Cruz. IGBP PAGES/World Data Center for Paleoclimatology*. NOAA/NCDC Paleoclimatology Program, Boulder.

Büntgen U, Frank D, Liebhold A et al. (2009) Three centuries of insect outbreaks across the European Alps. *New Phytologist*, **182**, 929–941.

Carril AF, Menendez CG, Nuñez MN (1997) Climate change scenarios over the South American region: an intercomparison of coupled general atmosphere–ocean circulation models. *International Journal of Climatolo*, **17**, 1613–1633.

Carrillo R, Cerda L (1987) Zoofitofagos en *Nothofagus* chilenos. *Bosque*, **8**, 99–103.

Cook ER, Holmes RL (1986) Users manual for program ARSTAN. In: *Tree-Ring Chronologies of Western North America: California, Eastern Oregon and Northern Great Basin* (eds Holmes RL, Adams RK, Fritts HC), pp. 50–65. Laboratory of Tree-Ring Research, the University of Arizona, Tucson.

Daniels LD, Veblen TT (2000) ENSO effects on temperature and precipitation of the Patagonian–Andean region: implications for biogeography. *Physical Geography*, **21**, 223–243.

Daniels LD, Veblen TT (2004) Spatiotemporal influences of climate on altitudinal treeline in northern Patagonia. *Ecology*, **85**, 1284–1296.

D'Arrigo R, Cook ER, Wilson RJ, Allan R, Mann ME (2005) On the variability of ENSO over the past six centuries. *Geophysical Research Letters*, **32**, L03711, doi: 10.1029/2004GL022055.

Fogt RL, Perlwitz J, Monaghan AJ, Bromwich DH, Jones JM, Marshall GJ (2009) Historical SAM variability. Part II: twentieth-century variability and trends from reconstructions, observations, and the IPCC AR4 models. *Journal of Climate*, **22**, 5346–5365.

Forcada J, Trathan PN (2009) Penguin responses to climate change in the Southern Ocean. *Global Change Biology*, **15**, 1618–1630.

Garreaud RD, Vuille M, Compagnucci R, Marengo J (2009) Present-day South American climate. *Palaeogeography Palaeoclimatology Palaeoecology*, **281**, 180–195.

Gea-Izquierdo G, Pastur GM, Cellini JM, Lencinas MV (2004) Forty years of silvicultural management in southern *Nothofagus pumilio* primary forests. *Forest Ecology and Management*, **201**, 335–347.

Gergis JL, Fowler AM (2009) A history of ENSO events since AD 1525: implications for future climate change. *Climatic Change*, **92**, 343–387.

Gillett NP, Kell TD, Jones PD (2006) Regional climate impacts of the Southern Annular Mode. *Geophysical Research Letters*, **33**, L23704, doi: 10.1029/2006GL027721.

Gong DY, Wang SW (1999) Definition of Antarctic Oscillation Index. *Geophysical Research Letters*, **26**, 459–462.

Grissino-Mayer HD (1995) *Tree-ring reconstructions of climate and fire history at El Malpaís National Monument, New Mexico*. PhD Dissertation, University of Arizona, Tucson, 405 pp.

Hebertson EG, Jenkins MJ (2008) Climate factors associated with historic spruce beetle (Coleoptera: Curculionidae) outbreaks in Utah and Colorado. *Environmental Entomology*, **37**, 281–292.

Hogg EH, Hart M, Lieffers VJ (2002) White tree rings formed in trembling aspen saplings following experimental defoliation. *Canadian Journal of Forest Research*, **32**, 1929–1934.

Holmes RL (1983) Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin*, **43**, 69–75.

Holmes RL, Ambrose JE, Boninsegna JA (1984) *Nothofagus pumilio Tree-Ring Chronology, Cerro Buenos Aires, Santa Cruz. IGBP PAGES/World Data Center for Paleoclimatology*. NOAA/NCDC Paleoclimatology Program, Boulder.

Holz A (2009) *Climatic and Human Influences on Fire Regimes and Forest Dynamics in Temperate Rainforests in Southern Chile*, Unpublished PhD University of Colorado, Boulder.

Hosking GP, Hutcheson JA (1988) Mountain beech (*Nothofagus solandri* var *cliffortioides*) decline in the Kaweka range, north island, New Zealand. *New Zealand Journal of Botany*, **26**, 393–400.

Hosking GP, Kershaw DJ (1985) Red beech death in the Maruia valley, South Island, New Zealand. *New Zealand Journal of Botany*, **23**, 201–211.

Huberty AF, Denno RF (2004) Plant water stress and its consequences for herbivorous insects: a new synthesis. *Ecology*, **85**, 1383–1398.

IPCC (2007) Climate change 2007: synthesis report. In: *IPCC Fourth Assessment Report* (eds Pachauri RK, Reisinger A), pp. 26–73. Cambridge University Press, Cambridge, UK.

Jane GT, Green TGA (1983) Episodic forest mortality in the Kaimai Ranges, North Island, New Zealand. *New Zealand Journal of Botany*, **21**, 21–31.

Jepsen JU, Hagen SB, Ims RA, Yoccoz NG (2008) Climate change and outbreaks of the geometrids *Operophtera brumata* and *Epirrita autumnata* in subarctic birch forest: evidence of a recent outbreak range expansion. *Journal of Animal Ecology*, **77**, 257–264.

Kitzberger T, Veblen TT, Villalba R (1997) Climatic influences on fire regimes along a rain forest to xeric woodland gradient in northern Patagonia, Argentina. *Journal of Biogeography*, **24**, 35–47.

Lemaire C (2002) *The Saturniidae of America. Les Saturniidae Americains*. Druckhaus Frankenbach, Lindenberg.

Logan JA, Regniere J, Powell JA (2003) Assessing the impacts of global warming on forest pest dynamics. *Frontiers in Ecology and the Environment*, **1**, 130–137.

Manion PD (1981) *Tree Disease Concept*. Prentice-Hall, Englewood Cliffs, NJ.

Marshall GJ (2003) Trends in the southern annular mode from observations and reanalyses. *Journal of Climate*, **16**, 4134–4143.

Miller RL, Schmidt GA, Shindell DT (2006) Forced annular variations in the 20th century intergovernmental panel on climate change fourth assessment report models. *Journal of Geophysical Research-Atmospheres*, **111**, D18101, doi: 10.1029/2005JD006323.

Murúa R, Gonzalez LA, Lima M (2003) Population dynamics of rice rats (a Hantavirus reservoir) in southern Chile: feedback structure and non-linear effects of climatic oscillations. *Oikos*, **102**, 137–145.

Paritsis J (2009) *Insect Defoliator Outbreaks and Environmental Heterogeneity in Nothofagus Forests in the Patagonian Andes*, Unpublished PhD University of Colorado, Boulder.

Paritsis J, Elgueta M, Quintero C, Veblen TT New host-plant records for the defoliator *Ormiscodes amphimone* (Fabricius) (Lepidoptera: Saturniidae). *Neotropical Entomology*, (in press).

Paritsis J, Veblen TT, Kitzberger T (2009) Assessing dendroecological methods to reconstruct defoliator outbreaks on *Nothofagus pumilio* in northwestern Patagonia, Argentina. *Canadian Journal of Forest Research*, **39**, 1617–1629.

Peltonen M, Liebhold AM, Bjornstad ON, Williams DW (2002) Spatial synchrony in forest insect outbreaks: roles of regional stochasticity and dispersal. *Ecology*, **83**, 3120–3129.

Queiro SM (2003) Untitled report no. 39/03. Administración de Parques Nacionales, Parque Nacional Los Glaciares, Chaltén, Argentina.

Raffa KF, Aukema BH, Bentz BJ, Carroll AL, Hicke JA, Turner MG, Romme WH (2008) Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *Bioscience*, **58**, 501–517.

Rauchfuss J, Ziegler SS, Speer JH, Siegert NW (2009) Dendroecological analysis of spruce budworm outbreaks and their relation to climate near the prairie-forest border in northwestern Minnesota. *Physical Geography*, **30**, 185–204.

Roig FA (1986) *Nothofagus pumilio Tree-Ring Chronology, Paso Córdoba, Neuquén. IGBP PAGES/World Data Center for Paleoclimatology.* NOAA/NCDC Paleoclimatology Program, Boulder.

Rouault G, Candau JN, Lieutier F, Nageleisen LM, Martin JC, Warzee N (2006) Effects of drought and heat on forest insect populations in relation to the 2003 drought in Western Europe. *Annals of Forest Science*, **63**, 613–624.

Schoennagel T, Veblen TT, Kulakowski D, Holz A (2007) Multidecadal climate variability and climate interactions affect subalpine fire occurrence, Western Colorado (USA). *Ecology*, **88**, 2891–2902.

Schulman E (1956) *Dendroclimatic Change in Semiarid America*. University of Arizona Press, Tucson.

Stokes MA, Smiley TL (1968) *An Introduction to Tree-Ring Dating*. University of Chicago Press, Chicago.

Suarez ML, Ghermandi L, Kitzberger T (2004) Factors predisposing episodic drought-induced tree mortality in *Nothofagus* – site, climatic sensitivity and growth trends. *Journal of Ecology*, **92**, 954–966.

Swetnam TW, Lynch AM (1993) Multicentury, regional-scale patterns of western spruce budworm outbreaks. *Ecological Monographs*, **63**, 399–424.

Swetnam TW, Thompson MA, Sutherland EK (1985) *Spruce Budworms Handbook: Using Dendrochronology to Measure Radial Growth of Defoliated Trees. Agriculture Handbook No. 639*. Cooperative State Research Service, Forest Service, USDA, Washington, DC.

Thompson DWJ, Solomon S (2002) Interpretation of recent Southern Hemisphere climate change. *Science*, **296**, 895–899.

Thomson AJ, Shepherd RF, Harris JWE, Silversides RH (1984) Relating weather to outbreaks of western spruce budworm, *Choristoneura occidentalis* (Lepidoptera: Tortricidae) in British Columbia. *Canadian Entomologist*, **116**, 375–381.

Veblen TT, Donoso C, Kitzberger T, Rebertus AJ (1996) Ecology of southern Chilean and Argentinean *Nothofagus* forests. In: *The Ecology and Biogeography of Nothofagus Forests* (eds Veblen TT, Hill RS, Read J), pp. 293–353. Yale University Press, New Haven.

Veblen TT, Kitzberger T, Villalba R, Donnegan J (1999) Fire history in northern Patagonia: the role of humans and climatic variation. *Ecological Monographs*, **69**, 47–67.

Vera C, Silvestri G, Liebmann B, Gonzalez P (2006) Climate change scenarios for seasonal precipitation in South America from IPCC-AR4 models. *Geophysical Research Letters*, **33**, L13707, doi: 10.1029/2006GL025759.

Villalba R (1994) Tree-ring and glacial evidence for the Medieval Warm Epoch and the little ice age in southern South America. *Climatic Change*, **26**, 183–197.

Villalba R, Boninsegna JA, Veblen TT, Schmelter A, Rubulis S (1997a) Recent trends in tree-ring records from high elevation sites in the Andes of northern Patagonia. *Climate Change*, **36**, 425–454.

Villalba R, Cook ER, D'Arrigo RD, Jacoby GC, Jones PD, Salinger MJ, Palmer J (1997b) Sea-level pressure variability around Antarctica since A.D. 1750 inferred from subantarctic tree-ring records. *Climate Dynamics*, **13**, 375–390.

Villalba R, Lara A, Boninsegna JA *et al.* (2003) Large-scale temperature changes across the southern Andes: 20th-century variations in the context of the past 400 years. *Climatic Change*, **59**, 177–232.

Villalba R, Veblen TT (1997) Spatial and temporal variation in *Austrocedrus* growth along the forest-steppe ecotone in northern Patagonia. *Canadian Journal of Forest Research*, **27**, 580–597.

Villalba R, Veblen TT (1998) Influences of large-scale climatic variability on episodic tree mortality in Northern Patagonia. *Ecology*, **79**, 2624–2640.

Weber UM, Schweingruber FH (1995) A dendroecological reconstruction of western spruce budworm outbreaks (*Choristoneura occidentalis*) in the front range, Colorado, from 1720 to 1986. *Trees-Structure and Function*, **9**, 204–213.

Wilson AM, Latimer AM, Silander JA, Gelfand AE, de Klerk H (2010) A hierarchical Bayesian model of wildfire in a Mediterranean biodiversity hotspot: implications of weather variability and global circulation. *Ecological Modelling*, **221**, 106–112.

Zhang QB, Alfaro RI (2003) Spatial synchrony of the two-year cycle budworm outbreaks in central British Columbia, Canada. *Oikos*, **102**, 146–154.