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Adapting to global environmental change in Patagonia: What role for disturbance ecology?

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Abstract Research from the Patagonian-Andean region is used to explore challenges and opportunities related to the integration of research on wildfire activity into a broader earth-system science framework that views the biosphere and atmosphere as a coupled interacting system for understanding the causes and consequences of future wildfire activity. We examine how research in disturbance ecology can inform land-use and other policy decisions in the context of probable future increases in wildfire activity driven by climate forcing. Climate research has related recent warming and drying trends in much of Patagonia to an upward trend in the Southern Annular Mode which is the leading pattern of extratropical climate variability in the southern hemisphere. Although still limited in spatial extent, tree-ring fire history studies are beginning to reveal regional patterns of the top-down climate influences on temporal and spatial pattern of wildfire occurrence in Patagonia. Knowledge of relationships of fire activity to climate variability in the context of predicted future warming leads to the hypothesis that wildfire activity in Patagonia will increase substantially during the first half of the 21st century. In addition to this anticipated increase in extreme fire events due to climate forcing, we further hypothesize that current land-use trends will increase the extent and/or severity of fire events through bottom-up (i.e. land surface) influences on wildfire potential. In particular, policy discussions of how to mitigate impacts of climate warming on fire potential need to consider research results from disturbance ecology on the implications of continued planting of flammable non-native trees and the role of introduced herbivores in favouring vegetation changes that may enhance landscape flammability.

Key words: climate change, disturbance, fire ecology, herbivore, tree plantation.

INTRODUCTION

There is widespread agreement among climate scientists that the anthropogenic release of greenhouse gases has been and will continue to be the major driver of warming temperatures on earth for at least the next several decades (IPCC 2007). However, future climate changes and their ecological impacts will vary geographically and across biome types (Krawchuk *et al.* 2009). Research is needed that can guide societal adaptation to the ecological consequences of climate change and improve understanding of how ecological processes may result in feedbacks that could further accelerate future warming. For example, increased wildfire activity is recognized as a probable widespread consequence of recent and future warming with a potential positive feedback through release of CO_2 from burning vegetation (Bowman *et al.* 2009). Development of strategies to both mitigate and adapt to climate-induced increases in wildfire activity requires an interdisciplinary approach in which disturbance ecology must play a major role.

The long history of research on the controls and ecological consequences of wildfires conducted in the context of disturbance ecology and land management provides a rich theoretical and empirical foundation for meeting the challenge of integrating wildfire activity into a broad earth-system science framework that views the biosphere and atmosphere as a coupled interacting system (Bowman *et al.* 2009; Flannigan *et al.* 2009). In this review, we use the Patagonian-Andean region (western South America south of about 37°S latitude) to explore challenges and opportunities related to the integration of research on disturbance ecology into a broader earth-system science framework for understanding the causes and consequences of wildfire activity. First, we provide some background on the integration of broad-scale wildfire activity into a framework that views the biosphere and atmosphere as a coupled system and that attempts to forecast future global fire activity. Then, we use examples from the Patagonian-Andean region to explore two broad and complex questions about future wildfire activity in

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relation to global environmental changes: (i) Is the current warming trend likely to result in increased wildfire activity, and if so, how will that increase vary across major ecosystem types? (ii) Are some land-use practices unwittingly creating positive feedbacks that enhance the potential for future wildfire activity?

WILDFIRE IN AN EARTH-SYSTEM SCIENCE FRAMEWORK

Burning related to deforestation, especially in the tropics, during the late 20th century is believed to have contributed significantly to the global burden of the major greenhouse gases of CO_2 and methane (Bowman *et al.* 2009; van der Werf *et al.* 2009). Fire may also increase the potential for future warming through the release of both black carbon aerosols that have strong solar radiation absorption properties and sensible heat back to the atmosphere (Bowman *et al.* 2009). Short- and long-term effects of fire on albedo are highly variable across biomes due to strong differences in albedo of dark forests, brighter grasslands, and snow, and could have either positive or negative net impacts on warming depending on initial conditions (Flannigan *et al.* 2009). Thus, multi-scale research in disturbance ecology is needed on differential susceptibility of various vegetation types to wildfire and on post-fire transitions from one cover type to a different cover type (e.g. from closed canopy forests to shrublands or grasslands), which in turn may further enhance fire potential under a warmer climate.

At a global scale, area burned annually is estimated to have increased during the second half of the 20th century but trends are highly variable regionally (Mouillot & Field 2005). Recent increases in wildfire activity in some regions have been linked to changes in climate and land use, operating independently or in combination (Westerling *et al.* 2006; Meyn *et al.* 2007). Surges in the occurrence of large, uncontrolled fires on all vegetated continents during the last few decades of the 20th century imply that global warming is contributing to increased wildfire activity (Bowman *et al.* 2009). However, warming does not necessarily result in increased fire activity in all biomes because decreases in moisture availability can reduce amounts of biomass for burning in already low-biomass ecosystems (e.g. dry grasslands; Krawchuk *et al.* 2009). Research is needed on how past episodes of warmer and/or drier climate have affected fire activity in particular ecosystem types as historical baselines for assessing the significance of current and projected fire activity.

Forecasting future changes in wildfire activity has become a major issue in the global climate change research agenda primarily because of the potential for fire to accelerate CO_2 emissions (Running 2008). At regional and global scales the two dominant approaches to predicting future fire activity associated with climate change are statistical modelling and dynamical vegetation modelling. In statistical modelling, top-down relationships between historical fire activity and climate are used to predict future fire activity in relation to projected future climate (Krawchuk *et al.* 2009). Efforts at predicting future global fire patterns are severely limited by the short-time series and coarse spatial resolution of global fire products derived from satellite imagery. Additionally, strong associations of fire activity with human population densities and socio-economic variables (e.g. gross domestic product per capita and ratio of crop cover to other land covers) indicate that land-use practices have significant influences on wildfire activity at a global scale (Chuvieco *et al.* 2008), which in turn further increases modelling complexity. Dynamic vegetation models are bottom-up, or process-based, land biogeochemical models (Flannigan *et al.* 2009). Dynamic vegetation modelling requires a mechanistic understanding of fire determinants such as the amount and flammability of biomass to burn, fire weather, and source and probability of ignition (Arora & Boer 2005). At a landscape scale, feedbacks such as time-since-last-fire and land-use impacts on fuels have been demonstrated to be critical to future landscape heterogeneity and associated potential for fire (Flannigan *et al.* 2009). Development of fire modules for regional, and ultimately global, dynamic vegetation models requires research on post-fire recovery processes and land-use practices that affect post-fire cover type transitions, landscape flammability and sink/source carbon dynamics (Running 2008).

STUDY AREA

The area of interest in this review includes the Andean-Patagonian area extending from roughly 37 to 55°S latitude on both the western (Chile) and eastern (Argentina) sides of the Andes (Fig. 1). The vegetation of this region is characterized by temperate rainforests mostly west of the Andes as well as the cool temperate *Nothofagus* forests and woodlands mostly east of the Andes (Veblen *et al.* 1996). Throughout this latitudinal range, deciduous *Nothofagus pumilio* and *Nothofagus antarctica* dominate open woodlands transitional to the Patagonian steppe to the east, and *N. pumilio* forms dense subalpine forests at mesic high elevation sites. Evergreen conifers occur in both the rainforests dominated by evergreen broadleaf *Nothofagus* species and in the drier cool temperate forests, and include several important fire-scar recording species such as *Araucaria araucana* (north of about 40°20′S), *Austrocedrus chilensis* (north of about 44°S) and *Pilgerodendron uviferum* (39°30′ to 55°30′S) (Holz & Veblen 2009).

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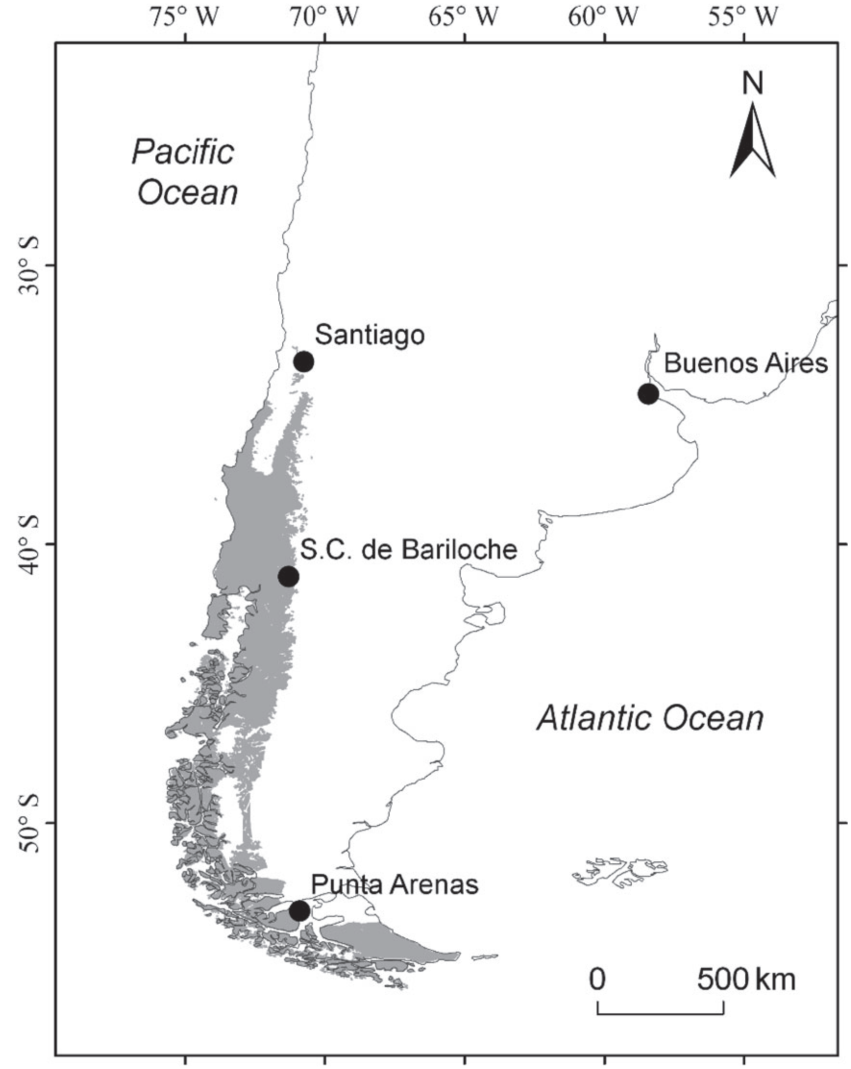

Fig. 1. Map of southern South America showing the forested area of the Andean-Patagonian area (in grey) examined in this study. Forested area is modified from Gajardo (1994) and Lara *et al.* (1999). Areas converted to non-forest land use by modern (post 1500 A.D.) humans, primarily in the central valley of Chile, are not distinguished from existing forest.

The dominant climate drivers in this region are the persistent mid-latitude westerlies, the seasonally shifting subtropical anticyclone of the south-eastern Pacific region, and the topographic influences of the coastal and Andean mountains (Garreaud & Aceituno 2007). Westerly flowing air is orographically uplifted by the mountain barriers to result in mean annual precipitations of 3000 to over 5000 mm on the windward slopes of mountains from 37°S to Tierra del Fuego (about 55°S) whereas precipitation steeply declines leeward of the Andes. Along the west coast as far south as about 42°S, Mediterranean-type precipitation seasonality is associated with the summer influence of the subtropical high-pressure cell in the south-eastern Pacific (Garreaud & Aceituno 2007). Thus, the prominent summer drought characteristic of the northern part of the region gradually declines from north to south giving way to relatively uniform high precipitation south of about 47°S. In the far south at about 52 to 55°S, the influence of the circum-Antarctic low pressure trough becomes more evident, and cool, windy conditions prevail for most of the year.

DRIVERS OF WILDFIRE VARIABILITY IN PATAGONIA

Top-down climatic influences on wildfire activity

Climate trends and linkages to major climate modes

Several analyses of available climate records have documented a strong warming trend in the

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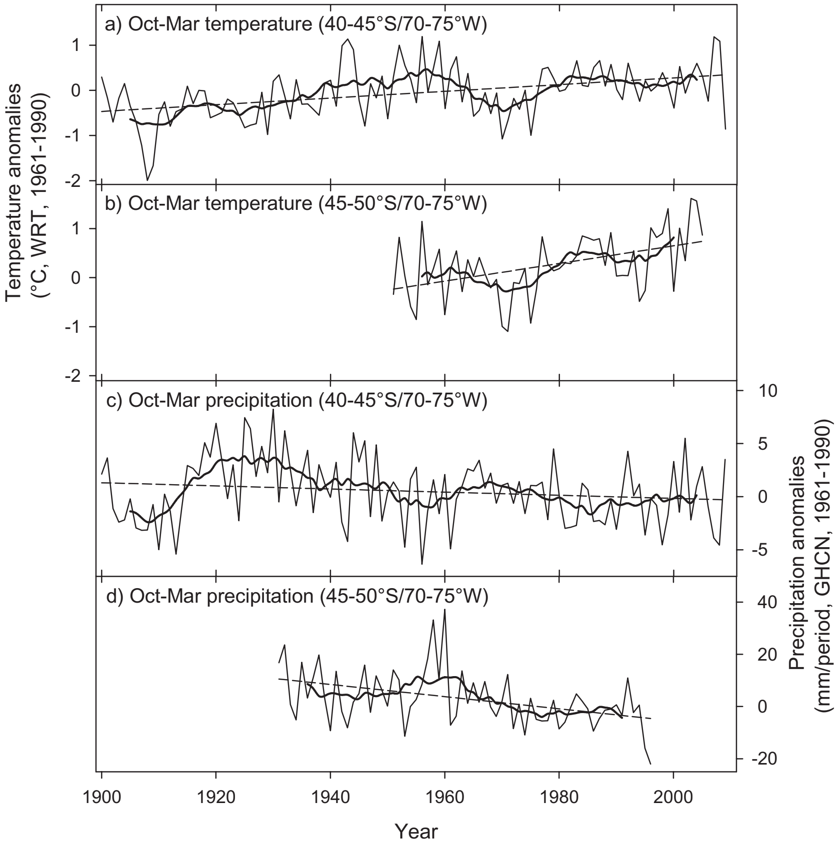

Fig. 2. Warm season (October–March) temperature variations in northern (a) and southern (b) Patagonian region expressed as mean anomalies (°C) with respect to the 1961–1990 reference period (CRUTem3v grid cells; http://www.cru.uea.ac.uk/cru/data/temperature/). Dry season (October–March) precipitation variations in northern (c) and southern (d) Patagonian region expressed as total anomalies (mm per period) with respect to the 1961–1990 reference period (GHCN, National Climate Diagnostics Center (NCDC) grid cells; http://www.ncdc.noaa.gov/oa/climate/research/ghcn/ghcngrid.html). All panels are grid cells bounded between 40–45°S and 70–75°W (a, c) and between 45–50°S and 70–75°W (b, d). Linear trends (dashed lines) and smoothed (11-year moving average; bold lines) versions of each climate series are shown to highlight the low-frequency variation in these records. The linear regression r^2 and P-values corresponding to each panel are: (a) $r^2 = 0.17$, $P < 0.001$; (b) $r^2 = 0.21$, $P < 0.001$; (c) $r^2 = 0.02$, $P = 0.11$; and (d) $r^2 = 0.18$, $P < 0.001$. GHCN, Global Historical Climate Network; WRT, World Regional Temperature.

Patagonian-Andean region during the 20th century, especially since about 1950 (Rosenblüth *et al.* 1995; Ibarzabal *et al.* 1996; Villalba *et al.* 2003). Precipitation records from western Patagonia between 41 and 47°S show a decline since about 1976, but in the far south (51 to 53°S) where there are few stations there is no clear recent trend in precipitation (Aravena & Luckman 2008). Gridded climate records interpolated from numerous (>30) widely dispersed climate stations show strong late 20th century warming trends and modest decreases in precipitation during the growing season (October–March) for both the northern (40 to 45°S) and southern (45 to 50°S) sectors of the Andean-Patagonian region (Fig. 2).

Twentieth-century warming detected in the Andean-Patagonian region is associated with a positive trend in the Southern Annual Mode (SAM), which is the most important extratropical pattern of climate variability in the southern hemisphere (Marshall 2003; Garreaud *et al.* 2009). The SAM, also known as the Antarctic Oscillation, is characterized by pressure anomalies of one sign centred in the Antarctic and anomalies of the opposite sign on a circum-global band at about 40 to 50°S (Marshall 2003). Since the inception of its measurement in 1948 SAM shows a positive trend (i.e. lower pressures in Antarctica relative to mid-latitudes) which entails an intensification and poleward shift of the southern hemisphere westerlies and mid-latitude storm tracks (Marshall 2003). Climate models attribute the about 50-year upward trend in SAM to increased greenhouse gases and/or reduced stratospheric ozone concentrations (Miller *et al.* 2006). Climate models also predict that SAM is highly likely to remain in its positive phase for the 21st century (Fyfe and Saenko 2006).

Recent climate studies have improved our understanding of regional climate variability in southern South America in relation to variability in both SAM

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and El Niño-Southern Oscillation (ENSO) and the contingent interactions of these two major climate modes. Warmer temperatures and reduced precipitation in western South America south of 40°S are associated with positive SAM at an interannual and inter-decadal time scales (Gillett *et al.* 2006; Aravena & Luckman 2008; Garreaud *et al.* 2009). ENSO variability has long been known to be a strong driver of annual variation in temperature and precipitation along the west coast of South America and into Patagonia, but there is much variability in the seasonality of associated precipitation departures along the west-to-east gradient across the Andes and southwards into higher latitudes (Daniels & Veblen 2000; Garreaud *et al.* 2009). For northern Patagonia, moisture variation related to ENSO variability is an important driver of tree growth, establishment and mortality across a wide range of tree species (Villalba & Veblen 1997, 1998; Tercero-Bucardo *et al.* 2007). There is increasing evidence that interannual and decadal variability in SAM is also reflected in a broad range of ecological processes in the Patagonian-Andean region including rodent population dynamics (Murúa *et al.* 2003), outbreaks of defoliating caterpillars (Paritsis & Veblen 2011), and streamflows (Lara *et al.* 2008; Rubio-Álvarez & McPhee 2010).

Recent and historical variability of wildfire activity related to climate variability

The documented warming and drying trends in Patagonia during the late 20th century, which appear to be strongly related to the upward trend in SAM, are likely to have profound effects on wildfire activity in the near future. Tree-ring-based research in northern Patagonia has demonstrated that interannual moisture availability related to variability in ENSO is an important driver of years of widespread fire (Kitzberger *et al.* 1997; Veblen *et al.* 1999). Tree-ring reconstructions also have shown climate teleconnections (i.e. strong statistical relationship between weather and weather-related ecological phenomena in different parts of the globe) between fire activity in northern Patagonia (38–42°S) and annual-scale anomalies in circulation patterns in the Antarctic Peninsula-South America sector of the Southern Ocean at about 50–60°S over the past about 250 years (Veblen *et al.* 1999). Variability in tree-ring reconstructed fire history in rainforests along the west coast of South America between about 43 and 48°S in Chile is also strongly linked to variability in SAM (Holz 2009).

Modern documentary records of wildfire activity in Patagonia are relatively short or geographically incomplete. For example, in Argentinean Patagonia records are available for four large national parks beginning in 1938 for most of the region from 38 to 43°S, but are lacking for a much larger surface area south 43°S. For Chile, records are geographically complete but are short in duration, beginning in the mid-1970s and are of uncertain reliability prior to 1985. Despite these limitations, relationships of interannual variability in wildfire activity to variability in SAM are informative, especially in the longer Argentine records. In northern Patagonia peaks in fire occurrence in the 1960s, late 1980s and mid-1990s coincide with peaks in SAM (Fig. 3a); annual area burned in years of above average burning is highly correlated with SAM over the 1948–2009 record ($r = 0.79$; $P < 0.001$; Spearman rank correlation). The much shorter record from Chilean Patagonia at 39°30′ to 48°40′S shows that during the sustained high values of SAM in the late 1980s, area burned was above average and peaked simultaneously with peak SAM in the late 1990s (Fig. 3b,c). Annual area burned during years of above average burning at latitudes 39°30′ to 48°40′S in Chile is positively correlated with SAM but is not statistically significant ($r = 0.33$; $P < 0.4$). In contrast, in the southernmost part of Chile (48°40′ to 55°S) years of above average area burned do not appear to depend on above average SAM, but at this high latitude positive SAM is not associated with reduced precipitation (Aravena & Luckman 2008). Conversely, in the fire records from latitudes 43° to 48°40′S where SAM is negatively correlated with annual precipitation (Aravena & Luckman 2008), peaks in area burned coincide with above average SAM.

In addition to the warming and drying trend that applies to most of the Andean-Patagonian region, there also is evidence of a substantial increase in lightning-ignited fires. For example, in northern Patagonia (Argentina) the annual mean number of lightning-ignited fires rose sharply by 250% in association with a strong shift toward warmer summer temperatures after 1976 (Veblen *et al.* 2008). The increase in lightning ignitions is associated with greater convective storm activity under the warmer conditions.

Overall, it is clear that the top-down influence of climate in Patagonia has been toward warmer and drier conditions during the latter half of the 20th century, and climate models project that these trends will continue during the 21st century (Carril *et al.* 1997; Vera *et al.* 2006). As advances in climate science continue to improve understanding of the natural and anthropogenic sources of climate variability, more realistic future climate scenarios will be feasible. Improved, long-term climate forecasting creates challenges and opportunities for fire scientists to explore effects on future fire potential that may result from changes in lightning patterns and the seasonality of temperature, and precipitation as well as trends in annual average climate conditions.

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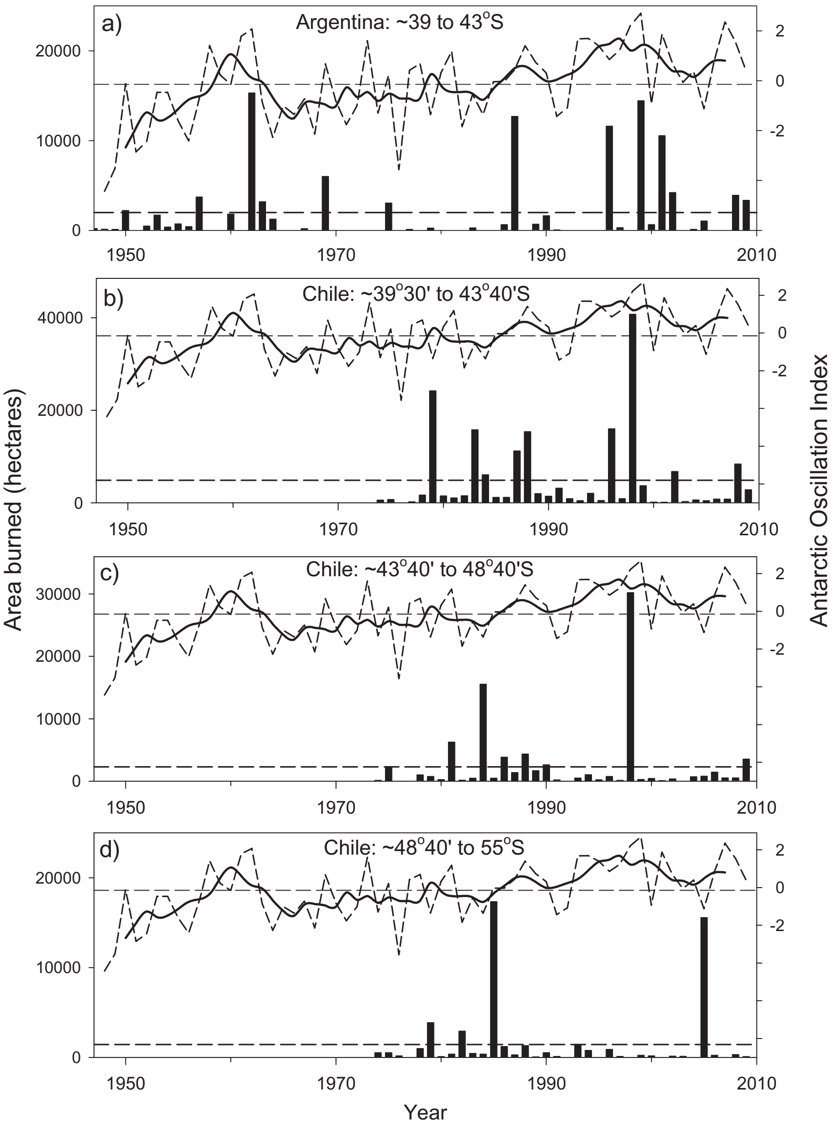

Fig. 3. The Antarctic Oscillation Index (AAOI) for Dec–Feb (dashed line) and area burned per year (bars) for (a) four adjacent Argentinean National Parks (Lanín, Nahuel Huapi, Lago Puelo and Los Alerces) and (b–d) the three southerly administrative regions of Chile. The curve (solid bold line) is the 5-year moving average of the AAOI. The upper and lower horizontal dashed lines are mean AAOI and mean area burned, respectively. The scale of the *y* axis on the left side varies among the panels. Data from: Nan and Li (2003) (updated on 03/05/2010); Administración de Parques Nacionales, Argentina; and Corporación Nacional Forestal, Chile.

Bottom-up determinants of wildfire variability

Understanding future variability of wildfire activity in Patagonia in relation to the continued top-down influence of a warming climate requires ecological research on bottom-up determinants of fire potential (Flannigan *et al.* 2009; Krawchuk *et al.* 2009). Processes and events that appear to be affecting the potential for wildfire activity during the 21st century include planting of monocultures of introduced tree species, human settlement expansion and associated changes in ignition or suppression of fire, positive feedbacks from conversion of fire-resistant forests to more fire-prone shrublands, and the cumulative effects of introduced wild and domestic herbivores on vegetation flammability.

Conversion of native vegetation to plantations of non-native trees

In both Chilean and Argentinean Patagonia the area planted to introduced tree species increased rapidly during the last few decades of the 20th century and will likely continue to increase during the 21st century. In south-central Chile (about 37 to 41°S) during the second half of the 20th century industrial forestry based on plantation of introduced conifers (mainly *Pinus radiata*) and eucalypts was heavily subsidized by the Chilean government (Armesto *et al.* 2010). Market demands for woodchip export and local pulp mills continue to drive the spread of eucalypt and exotic conifer plantations southwards. Current frontiers of plantation forestry include large scale plantings on Chiloé Island and to a lesser degree in mainland Chile at 43 to 44°S (Armesto *et al.* 2010). Construction of the austral highway south of about 41°30′S in mainland Chile during the 1980s facilitated both timber extraction from the native forest and development of exotic plantation forestry in these formerly remote areas. Watershed protection has also motivated some of the recent planting of non-native trees as it did further south at about 45°30′S, where large areas of burned *Nothofagus* forest were planted to introduced pines in the 1970s (Donoso & Lara 1996). Similarly, in northern Patagonia (about 37–41°S) in Argentina, since the early 1980s, large areas of the steppe and *Austrocedrus* woodlands, both inside and outside of National Parks, have been afforested with introduced conifers, including ponderosa pine (*Pinus ponderosa*), lodgepole pine (*Pinus contorta*) and Douglas-fir (*Pseudotsuga menziesii*). Although timber production was the initial motive for planting non-native trees, in recent years there has been interest in afforesting large areas of steppe in Patagonia to obtain carbon sequestration credits (Sedjo 1999). The future role of tree planting to sequester carbon in Patagonia is uncertain because international and national carbon policies are in flux, and concerns about impacts on other values such as biodiversity will need to be addressed. However, the efficacy of planting trees for carbon sequestration at the ecotone between woodland and steppe is questionable given the research showing that this habitat is climatically prone to wildfires (Kitzberger *et al.* 1997; Veblen *et al.* 1999). Furthermore, following the burning of plantations of exotic conifers at sites converted from dense shrublands the post-fire vegetation is dominated by exotic herbaceous species resulting in a net reduction in carbon storage (Nuñez & Raffaele 2007).

The conversion of large areas of native vegetation to plantations of non-native species constitutes a major change in fuel type over large areas of the Patagonian-Andean region, particularly because the planted species (pines and eucalypts) are fire-prone species. The proportion of plantations of non-native trees that burned in Chile from 1980 to 2005 was twice as great as the proportion of native forests and shrublands (10.4 *vs.* 5.2%; http://www.conaf.cl made available through the Global Fire Monitoring Centre http://www.fire.uni-freiburg.de/). However, without site-specific studies of fire spread in areas of plantations *versus* adjacent native vegetation it is impossible to attribute the greater proportion of burned plantations to differences in ignition sources, local variations in fire weather, or flammability of the vegetation. Empirical analyses of how fire behaviour differs among the major native vegetation types in Patagonia have only recently begun and are limited to northern Patagonia in Argentina (Mermoz *et al.* 2005). An important research agenda to which disturbance ecology can contribute is the development of fuel type classifications based on observed fire behaviour in different types of native as well as non-native vegetation. In the absence of such fuel type classification, we can only speculate on the probable consequences for fire potential of the observed conversion of native vegetation to non-native vegetation. For instance, at the xeric ecotone of woodland with steppe, where formerly there was a mosaic of patches of shrubs and extensive grasslands, introduced conifers now provide continuous and highly flammable woody fuels. The fuel-defined hazard of crown fire in these plantations is high, and our observations of recent fires (such as in 1996 near Bariloche) suggest that fire intensity and spread increase in conifer plantations in comparison with the surrounding native steppe and shrubland vegetation. In mesic forests and rainforests to the west, it is also likely that conversion of relatively fire-resistant broadleaved forests to plantations of eucalypts and introduced conifers has increased the flammability of the vegetation.

An important area of research for disturbance ecology is on the potential positive feedbacks between fire and invasive non-native trees in Patagonia. Escaped conifers are most common in the relatively xeric ecotone between forest and the Patagonian steppe, but they are becoming increasingly common in areas of mesic forest in both Argentina and Chile. The greater shade tolerance of the introduced *Pseudotsuga menziesii* compared to native *Nothofagus* species appears to give it an advantage in establishing in relatively dense native forests. Some of the introduced pines have adaptations to regenerate following fire (e.g. serotinous cones of *Pinus contorta*) or to survive fire and provide seed sources for post-fire regeneration (e.g. the thick-barked *Pinus ponderosa*), and eucalypts have epicormic buds that allow quick post-fire resprouting. Increases in pine abundance may increase the risk or spread of fires, and also create conditions that are more favourable for their own regeneration compared to some native plant species that are less adapted to withstand or regenerate after fire (e.g. *N. pumilio*). For example, post-fire pine establishment in northern Patagonia is higher at sites of former pine plantations than at adjacent sites in native vegetation (Raffaele & Enestrom 2010). Similarly, positive feedbacks from introduced invasive animals may facilitate

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invasions by non-native tree species such as *Pseudotsuga menziesii* (Relva *et al.* 2010), which in turn may be more flammable than native tree species.

Settlement expansion and associated changes in ignition or suppression of fire

Changes in fire frequency and extent related to rapid growth of urban and exurban human populations during the last half-century in Patagonia have been little studied but potentially have important implications for current and future fire regimes (Veblen *et al.* 2008). Although fire suppression is a national policy throughout Patagonia, changes from historic fire regimes due to suppression activities have only been studied in a small area of northern Patagonia (Veblen *et al.* 1999). In that area, only in one ecosystem type, xeric *Austrocedrus* woodlands, is there clear evidence that reduced fire frequency due to suppression has resulted in the potential for more severe fires due to woody fuel accumulation (Kitzberger & Veblen 1999, Veblen *et al.* 2008). Overall, however, in Patagonia it is not clear if fire suppression policy has significantly reduced modern fire occurrence, and it is more likely that expanded human settlement in the 21st century will have a net positive effect on the number of wildfire ignitions. For example, in Chilean Patagonia, most fires are either purposefully or accidentally set by humans (Corporación Nacional Forestal, Santiago, Chile, unpublished data 2010). In Patagonian rainforests, substantial increases in fire frequency coincide with known dates of Euro-Chilean settlement during the 20th century and intentional burning to facilitate timber and fuel extraction or to convert forest to cattle pasture is still a common practice in these forests (Holz 2009). In northern Patagonia, area and number of fires during the late 20th century are disproportionately high in proximity to the principal urban centre of Bariloche due to intentional burning (Mermoz *et al.* 2005; De Torres Curth *et al.* 2008). Overall, much research is needed to determine the variable importance of modern humans as sources of wildfire ignition in relation to biophysical gradients as well as socio-economic factors, and to evaluate the ecological consequences of enhanced or reduced fire potential in different ecosystem types.

Fire-induced changes in vegetation flammability

Analogous to the effects of initial burning of Amazonian rainforests that enhance subsequent susceptibility to fire (Cochrane *et al.* 1999), in the Andean-Patagonian region initial burning of fire-resistant forests promotes conditions that increase flammability of the landscape. In northern Patagonia (37–43°S) mesic *Nothofagus*-dominated forests as well as Andean rainforests dominated by the conifer *Fitzroya cupressoides* only burn under the most extreme droughts whereas tall shrublands and xeric woodlands burn more frequently and in conjunction with markedly less extreme drought (Kitzberger *et al.* 1997; Veblen *et al.* 1999). Relatively fire-resistant, dense, tall forests are dominated by obligate seeders, and when burned they are sometimes replaced by resprouting, tall (2–6 m) shrubs and small trees that dominate more fire-prone shrublands. For example, following the burning of monotypic stands of *N. pumilio*, tree regeneration often fails due to elimination of seed sources (Veblen *et al.* 1996), fire-induced edaphic changes (Kitzberger *et al.* 2005b), climatic conditions unfavourable for tree seedling survival (Tercero-Bucardo *et al.* 2007), herbivory by livestock and other introduced animals (Kitzberger *et al.* 2005a; Raffaele *et al.* 2011) or a combination of these factors. Failure of tree regeneration results in post-fire transitions to vegetation dominated by tall shrubs; this vegetation type is markedly more fire prone than tall closed forest as shown by proportions of vegetation types burned in the last half of the 20th century and by studies of fire spread in relation to vegetation type (Mermoz *et al.* 2005).

Sharp and persistent boundaries between forests and tall shrublands in northern Patagonia where there are no corresponding changes in the underlying abiotic environment have long been interpreted to be the result of a self-reinforcing relationship of shrublands with fire (Veblen & Lorenz 1988). The closed canopies of the subalpine *N. pumilio* forests create shady, mesic understories that typically do not exceed 2 m in height and consequently do not provide vertical fuel continuity with the tree canopy at heights of about 20 m. In contrast, the decurrent, multi-stemmed growth form of the shrubs creates an open upper canopy beneath which temperatures are high, relative humidity is low and fuels are vertically continuous. Abundant climbing plants (*Mutisia* spp., *Vicia nigricans*) as well as the 3–6 m tall bamboo *Chusquea culeou* provide fine fuels at all heights, further facilitating fire spread vertically from the ground surface to the top of the canopy. Efficient self-pruning of the tall tree species when growing in dense stands reduces vertical fuel continuity in tall forests. The post-fire shift in dominance from tall trees, all of which are obligate seeders, to resprouting shrubs and vines promotes an abundance of species that retain high percentages of fine dead tissue, such as the shrubs *Diostea juncea* and *Schinus patagonicus*, the bamboo *Chusquea culeou*, and the vines *Mutisia spinosa* and *Mutisia decurrens*. Retention of fine dead tissues greatly enhances a plant's flammability by reducing moisture content and therefore the heat sink role of moist living tissue (Schwilk 2003). Relative to a closed tall forest, shrubland community structure is inherently more fire prone because of its internal microclimate and fire-promoting plant architecture (Papió & Trabaud 1991; Schwilk & Ackerly 2001).

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Table 1. General mechanisms by which herbivores directly or indirectly may alter plant community properties that in turn change fuel properties and fire regime properties. Intrinsic fuel properties are the direct result of the individual plant, and extrinsic fuel properties are indirect community-level consequences

Fuel property changed	Fire regime properties changed
Intrinsic fuel properties	
Increase species with higher tissue flammability	Increase fire frequency and intensity; longer fire season
Decrease species with higher tissue flammability	Decrease fire frequency and intensity; shorter fire season
Increase species with more flammable architecture	Increase fire frequency and intensity; longer fire season
Decrease species with more flammable architecture	Decrease fire frequency and intensity; shorter fire season
Extrinsic fuel properties	
Decrease horizontal continuity and total fine fuel load	Decrease surface fire frequency and spread
Increase proportion of woody fuels	Increase fire intensity
Decrease vertical continuity (remove understory)	Reduce surface fire spread to crown
Increase vertical continuity (e.g. release understory)	Increase surface fire spread to crown
Change surface litter physical properties (size, shape, loading, arrangement and ventilation)	Change in rate of fire spread and intensity
Open formerly closed vegetation canopy; increase fuel desiccation and less sheltering from wind	Increase fire frequency, rate of spread, and extent

Greater aeration of the litter consisting of large-leaved species contributes to more intense surface fires and better fire spread compared to tightly packed litter of small leaf size (Scarff & Westoby 2006). In northern Patagonia, the leaves of the tall tree species (*Nothofagus dombeyi*, *N. pumilio* and *Austrocedrus chilensis*) are small compared to most of the dominant resprouting shrub species (*Schinus patagonicus*, *Lomatia hirsuta*, *Embothrium coccineum*, *Aristotelia chilensis*). Beneath the closed canopies of tall forests understories are characterized mainly by the bamboo *Chusquea culeou* and scarce shrubs. Consequently, there is a strong contrast between the litter dominated by large leaves beneath shrubland canopies *versus* tightly packed litter consisting of small leaf size beneath closed forests. We hypothesize that the larger leaf sizes of litter from sprouting shrubs promotes greater fire spread and/or intensity.

Once tall shrublands replace the mesic *Nothofagus* forests, the resulting higher flammability of the vegetation shortens intervals between fires so that survival probability is drastically curtailed for the juvenile trees of obligate seeders that lack any resprouting ability (Kitzberger *et al*. 2005a; Raffaele *et al*. 2011). Under short fire return intervals, continued dominance by shrubs is maintained by the resprouting capacity of the shrub species. Although this process has been studied in detail only in northern Patagonia, similar patterns have been observed throughout southern Patagonia in areas of burned *N. pumilio* forest and also in wetter *Nothofagus* forests in Chilean Patagonia.

Changes in fuel types induced by introduced herbivores

In the context of global warming, the potential of introduced plants to alter fire regimes has long been recognized (Brooks *et al*. 2004), but the possibility that introduced mammalian herbivores can increase vegetation flammability through their cumulative effects on vegetation attributes has received little research attention. Introduced mammalian herbivores may select plants of particular chemical or morphological properties, alter competitive hierarchies, and directly alter vegetation structure in ways that either promote or diminish potential wildfire activity (Table 1). In this section, we explore for northern Patagonia a working hypothesis that many of the same plant traits that allow persistence under pressure from introduced mammalian herbivores also favour species persistence following recurrent fire (Blackhall *et al*. 2008; Veblen *et al*. 2008; Raffaele *et al*. 2011). Furthermore, many of these traits increase plant flammability so that the cumulative effect of trait selection by herbivores is to increase vegetation flammability.

Key to the working hypothesis that introduced herbivores enhance vegetation flammability in Patagonia is the generalization that mammalian herbivores tend to inhibit or eliminate tree species that are dependent on seed reproduction and to shift dominance toward resprouting species (Bond & van Wilgen 1996; Pausas & Lavorel 2003). This general pattern applies to northern Patagonia where the dominant tree species of tall forests (*N. dombeyi*, *N. pumilio* and *Austrocedrus chilensis*) lack the ability to sprout in response to fire or damage by herbivores in contrast to the vigorous resprouting of shrubs and small trees, which better resist browsing by mammals (Kitzberger *et al*. 2005a; Raffaele *et al*. 2011). A common dominant of early post-fire sites is the bamboo *Chusquea culeou*, which vigorously resprouts from large rhizomes after fire, can withstand heavy herbivore pressure (Raffaele *et al*. 2011), and provides abundant fine fuels conducive to

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fire spread. The tendency for herbivores to shift post-fire vegetation trajectories away from tall forests and toward shrublands results in a gradual increase in flammability of the landscape (Mermoz *et al.* 2005). This increase in flammability reflects the gradual cumulative effects of herbivores on specific plant traits and vegetation attributes rather than the short-term impact on fuel quantities which in some ecosystems reduces fire potential.

Vigorous resprouting of shrubs following fire and under presence of herbivores may provide a further fire-enhancing feedback because of the more rapid fuel recovery in comparison with the slower growth of juveniles of obligate seeders. In northern Patagonia, most of the fuel recovery following a fire is in the form of resprouts. Monitoring of permanent plots at post-fire sites shows that in as few as 5 years following fire, even in the presence of livestock and European hares, resprouting of shrubs and bamboos attain sufficient biomass to permit re-burns (Raffaele *et al.* 2011).

Although few data are available on the selective influences of herbivory on plant chemical properties in Patagonia, we hypothesize that mammalian herbivores may increase flammability of the vegetation through selection favouring plants that are chemically defended. Chemical defences against herbivory include numerous secondary metabolites (terpenes, alkaloids and phenolics) that may be distasteful or toxic to mammals and also are highly flammable (Bond & van Wilgen 1996). The probability of a plant being eaten depends on its chemical defences as well as the quantity and quality of nutrients in the plant and its neighbours (Bergvall & Leimar 2005). Thus, herbivory potentially can change the overall chemical composition of the vegetation both by inducing production of chemical defences and by selectively removing plants that are more nutritious or less defended chemically. Further research is needed that integrates herbivore impacts on post-fire vegetation recovery with analyses of plant chemistry and morphology as well as community-level work on fuel properties and fire behaviour.

CONCLUSIONS

Earth's climate is changing rapidly primarily due to the anthropogenic release of greenhouse gases that may have profound but regionally variable impacts on wildfire activity depending on biome types and land-use components of global change. The future response of forests to global climate change and climate-related disturbances such as wildfire could result in substantial positive feedback to the carbon cycle, which in turn will affect mitigation efforts to stabilize atmospheric CO_2 concentrations (Bowman *et al.* 2009). Consequently, there is an urgent need to develop a better understanding of the role of fire in the earth system to improve modelling and forecasting of how climate change and land-use practices will influence future fire activity (Bowman *et al.* 2009; Flannigan *et al.* 2009). Integration of top-down (climate driven) and bottom-up (changes in land surface conditions) approaches to understanding spatial and temporal variability in wildfire activity are essential for advancing research on interactions of fire activity with climate and with land-use drivers of global environmental change. Many types of studies in disturbance ecology, as illustrated in this review of fire research in Patagonia, have much to contribute to this global initiative on the role of fire in earth-system science.

Important advances in climate science are resulting in improved understanding of the natural and anthropogenic sources of climate variability in the mid- and high-latitudes of the southern temperate zone (Miller *et al.* 2006). Recent research has elucidated interannual and inter-decadal scale relationships of regional precipitation and temperature anomalies in the temperate latitudes of the southern hemisphere to variability in SAM which is the leading pattern of extratropical climate variability in the southern hemisphere. These advances provide both better forecasts of future climatic conditions as well as opportunities to test hypotheses of how past variability in SAM has affected ecological processes such as wildfire activity in Patagonia. Although still limited in spatial extent, tree-ring fire history studies are beginning to reveal regional patterns of the top-down climate influences on temporal and spatial pattern of wildfire occurrence in Patagonia.

Local-scale consequences of climate-induced changes in fire regimes are strongly controlled by land-surface variables such as vegetation type and land-use practices. When aggregated over large areas these land-surface variables may have profound feedback consequences for fire-related feedbacks to the atmosphere (Flannigan *et al.* 2009). In the Patagonian-Andean region extensive areas of native forests have been converted to plantations of non-native trees believed to be inherently more fire prone than native forests and to provide continuous canopy fuels at high risk of severe burning. Research is needed on the effects of these apparently more flammable plantations on actual risk of ignition and fire spread in order to inform land-use decisions in the context of fire mitigation and carbon sequestration management policies, such as the United Nation's initiative to Reduce Emissions from Deforestation and Forest Degradation (REDD). Initial studies in a relatively small area in northern Patagonia have shown that extreme climate-driven fire events have landscape-scale feedbacks toward enhanced burning activity due to the replacement of fire-resistant forests with fire-prone shrublands. The potential for similar fire-promoting feedbacks needs to be examined through site-specific research at recently burned sites across the full range of ecosystem types in the Patagonian-Andean region. Similarly, initial studies in northern Patagonia have shown that introduced mammalian herbivores (livestock, deer and European hares) inhibit tree regeneration following burning of tall forests and thus promote conversion of fire-resistant forests to fire-prone shrublands. This pattern also needs to be examined across the full range of Patagonian-Andean ecosystems in order to improve understanding of how local land-use decisions may affect regional-scale wildfire activity and societal vulnerability to fire.

Ecosystems may be *committed* to significant changes in relation to climate forcing before the changes can actually be observed (Jones *et al*. 2009). This notion is particularly applicable to infrequent large-scale fire events for which trends are difficult to detect over short documentary records of only a few decades. The concept of committed ecosystem change supports a hypothesis that wildfire activity in Patagonia will increase substantially during the first half of the 21st century. Evidence supporting this hypothesis of committed ecosystem change includes the demonstrated historical sensitivity of Patagonian fire regimes to interannual variability in seasonal temperature and precipitation in the context of the predicted continuation of the warming and drying trends of the late 20th to early 21st centuries. Given the high likelihood of continued warming, negative precipitation anomalies similar in magnitude with those of the past and related to interannual variability in climate modes such as ENSO or SAM can be expected to produce more severe droughts than in the past few centuries when temperatures were generally cooler. It is likely that extreme fire events will be associated with these future extreme drought events. In addition to this anticipated increase in extreme fire events due to climate forcing, we hypothesize that current land-use trends will increase the extent and/or severity of these climate-induced fire events and result in land surface conditions that feed back to enhanced future fire potential. Policy discussions of how to mitigate impacts of climate warming on fire potential need to consider these hypotheses and their implications for future planting of flammable exotic trees and for management of the effects of introduced wild animals and livestock in areas of fire-prone vegetation.

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