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The role of paleoecology in restoring and managing the Patagonian landscape

William P. Nanavati[1,2], C. Whitlock[3,4] and A. Holz[1]

Two studies from the Patagonian forest-steppe ecotone (36–55°S; Argentina and Chile) demonstrate how interdisciplinary research combining paleoecological, archaeological, and historical methods provide information on past landscape conditions that can help prioritize conservation efforts and assess the likelihood of restoration success.

The forest-steppe ecotone in Patagonia (36–55°S; Argentina and Chile) is a striking vegetation transition between the dense forests of the Andes and the vast steppe of eastern Argentina (Fig. 1). On the western side of the ecotone, mesic forest is maintained by high levels of moisture and infrequent, moderate-to-high-severity fires, whereas on the eastern side, steppe prevails in a region of high seasonal or annual moisture deficit and frequent, low-severity fires (Kitzberger 2012). Decades of paleoecological and ecological research document past shifts in the position of the ecotone as a result of changes in climate and fire activity occurring over millennial to interannual timescales (Whitlock et al. 2007; Kitzberger 2012; Iglesias and Whitlock 2014). Superimposed on these broad-scale climate–vegetation–fire dynamics are the landscape-to-local-scale influences of ~15,000 years of Native American land use and 200 years of Euro-American settlement, which have resulted in changes in site-specific vegetation, fuel loads, and fire regimes (Iglesias and Whitlock 2014; Holz et al. 2016; Nanavati et al. 2022).

The potential for landscape restoration depends on understanding the origins of the landscape condition, including the legacy of past climate and human activity (Gillson and Marchant 2014; Whitlock et al. 2018). Present landscape conditions lie along a gradient from *minimally altered* (or "nearly pristine") to *mosaic* to *intensively altered* (Fig. 2a); key to understanding ecosystem resilience within these landscapes is knowledge of antecedent climate variations, disturbance events, and land use.

In minimally altered landscapes, found in some national parks and other protected places, the influence of past climate change and indigenous land use on ecosystems cannot be easily disentangled. The assumption is that present ecosystem dynamics are operating within a range of variability shaped by climate–fire–human interactions that have not changed substantially through time. Paleoecological data, historical/ethnographic accounts, and ecological modeling are used to define an historical range of variability (HRV) for ecosystems in minimally altered landscapes, and this information establishes a baseline for restoration (Keane et al. 2009). Although ecosystems are expected to respond similarly to present-day disturbances as they have in the past, this assumption will be challenged given the novelty and uncertainty of future climate conditions (Williams 2021). Management objectives for minimally altered landscapes are, thus,

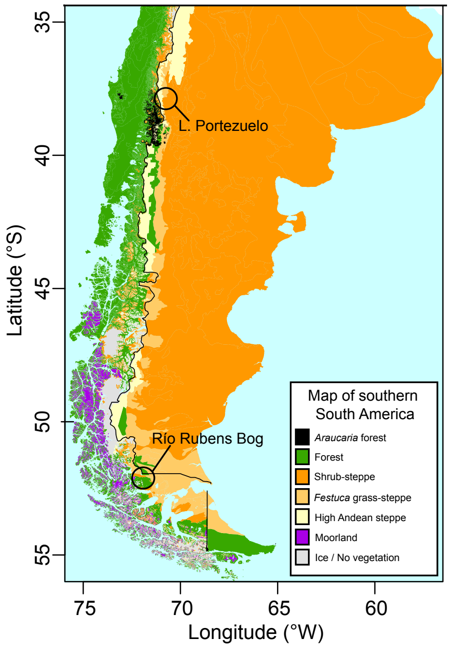

Figure 1: Map of southern South America (Chile and Argentina), showing generalized vegetation types and the ecotonal transition from wet, western forests to dry, eastern steppe. The locations of Laguna Portezuelo (Nanavati et al. 2020) and Río Rubens Bog (Huber and Markgraf 2003) are provided.

commonly to monitor and protect ecosystems from new or extreme disturbances that may signal a shift in frequency, severity, or seasonality from HRV conditions. (Fig. 2a).

At the other end of the spectrum, intensively altered landscapes have been measurably shaped by past land use through, for example, the loss of native biodiversity, changes in long-term fire regimes, and/or depletion in soil fertility. These ecosystems are often less sensitive to climatic or extreme disturbance events than those in more intact landscapes, and management objectives frequently support cultural values or commodity needs. Restoration of intensively altered landscapes to a minimally altered state requires an extensive and sustained effort and may be economically or tactically impractical considering current socioeconomic realities and future climate and development pressures. Along the Patagonian forest-steppe ecotone, among the most intensively altered landscapes are *Pinus* plantations, which have been planted for commercial use and climate change mitigation in some cases at the expense of native forest. These plantations have allowed the spread of non-native conifers far beyond their boundaries, decreasing biodiversity and increasing fire activity above the HRV (Paritsis et al. 2018; Nuñez et al. 2021).

An intermediate landscape condition is composed of a mosaic of varying degrees of minimally altered and intensively altered patches. The boundaries between these patches are often artificially defined by current land use rather than natural biophysical constraints (e.g. microclimate and soil characteristics). Ecosystems within mosaic landscapes often pose the greatest restoration challenge, since societal values assigned to individual patches may be vastly different, and minimally altered patches are easily converted to a more deteriorated state if unprotected or poorly managed (Whitlock et al. 2018).

Here, we suggest paleoecologically informed management strategies for conservation and restoration along the Patagonian forest-steppe ecotone by examining long-term ecosystem dynamics at two sites with different landscape conditions. The examples show that the restoration potential is determined by the levels of alteration prior to, and during, Euro-American settlement, as well as the likely impacts of climate change and intensified land use in the future.

Mosaic landscape: northern Patagonian *Araucaria araucana* forest

The northernmost extent of the Patagonian forest-steppe ecotone is home to the endemic and endangered *Araucaria araucana* (known as "*pehuén*" or "monkey-puzzle") tree, which presently grows along the Andes of Chile and Argentina (37–40°S) and in disjunct populations in the Cordillera de Nahuelbuta, Chile (Fig. 1). Along with its importance as a resource for food and wood, ethnographic accounts indicate that *Araucaria* plays a very significant role in Native American epistemology in northernmost Patagonia. For example, one of this region's largest groups referred to themselves as "Pehuenche", which translates to people (-*che*) of the *pehuén*. Based on written and oral histories, these people and their ancestors managed *Araucaria* forest through deliberate planting and frequent, low-severity burning to reduce competition from other species (dos Reis et al. 2014).

This hypothesis is supported by the sedimentary pollen and charcoal records from Laguna Portezuelo, which lies at the northern and eastern extent of *Araucaria*. Locally (within a radius of ~1 km), L. Portezuelo is surrounded by intensively altered pastureland, but the larger landscape (within a radius of ~10 km) consists of a mosaic of

Araucaria forest and steppe. Pollen data indicate that *Araucaria* grew near the site for the last ~6000 cal yr, but was most abundant after ~370 cal yr BP (Fig. 2b). Ethnohistorical accounts note increased Native American presence in the last four centuries in this region, which coincides with *Araucaria* expansion, charcoal evidence of increased fire activity, and pollen of native and non-native disturbance taxa (Nanavati et al. 2020). *Araurcaria* abundance declined in the 20th century with Euro-American farming and fire elimination.

These paleoecological insights suggest that efforts to protect native *Araucaria* forest at its eastern and northern limit must account not just for natural biophysical and climatological constraints, but also the likelihood that this species was maintained by Native American planting, protection, and burning practices. Projected increases in temperatures, aridity, and high-severity fires in the future (Masson-Delmotte et al. 2021) will complicate management of *Araucaria* in this region, and conservation efforts should consider planting and the promotion of frequent, low-severity fire, as was done prior to Euro-American settlement.

Intensively altered landscape: southern Patagonian Nothofagus forest

Río Rubens Bog in southernmost Patagonia can presently be described as intensively altered at the local (< 1 km radius) and landscape (within a ~10 km radius) scales. The pollen record indicates that closed *Nothofagus* forest (likely *N. pumilio*, known as "*lenga*", with some *N. antarctica*, known as "*ñire*") dominated the landscape for the last 5000 cal yr (Huber and Markgraf 2003). Charcoal data from the site suggest initially little-to-no fire, but fire activity rose to high levels between ~360 and 110 cal yr BP (Fig. 2c). Given the infrequency of lightning in southern Patagonia, these early fires were likely set by the Native American groups to facilitate hunting, communication, and travel. The onset of high fire activity also coincided with the early appearance of non-native *Rumex acetosella*-type pollen that suggests the spread of weeds three centuries before local Euro-American settlement in the late 19th century. Pollen data from Río Rubens Bog indicate little change in *Nothofagus* forest until the mid-20th century, when industrial logging became widespread and fire activity declined near the site (Huber and Markgraf 2003).

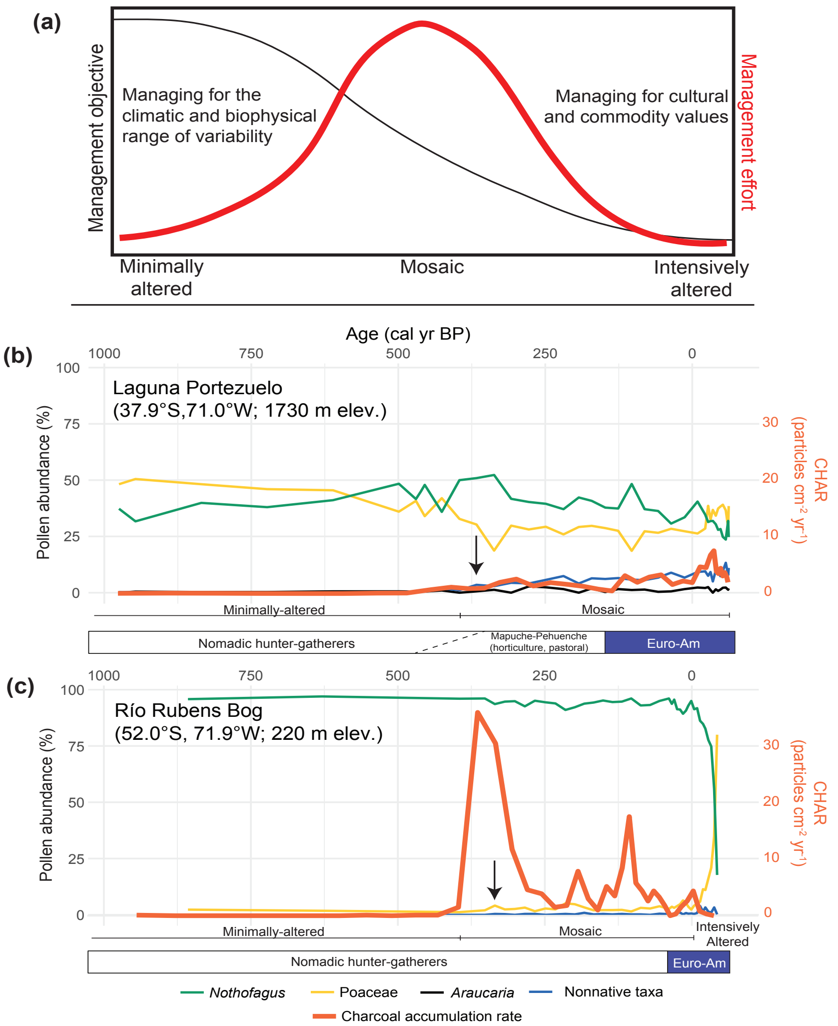

Figure 2: (A) Conceptual model for the selection of management objectives and effort based on paleoecologically informed placement of landscapes along a land use gradient (levels of alteration defined in the text; modified from Whitlock et al. 2018). **(B)** Summary plot from L. Portezuelo (Nanavati et al. 2020), showing pertinent changes in pollen, charcoal, and land-use history (diagonal, dashed line indicates gradual and dynamic transition). **(C)** Summary plot from Río Rubens Bog (Huber and Markgraf 2003), showing pertinent changes in pollen, charcoal, and land use history. Initial increases in non-native taxa are marked by arrows and landscape-scale (e.g. ~10 km radius) interpretations of alteration are provided.

In the last 100 years, Euro-American settlement and logging have greatly expanded steppe at the expense of forest cover (Fig. 2c). In intensively altered landscapes, like Río Rubens Bog, where logging and/or grazing are now widespread, conservation efforts to restore native forest are unlikely to succeed without local community support of significant land-use change. The restoration of *Nothofagus* forest in southern Patagonia will require restrictions on logging and fires, both of which will be difficult in the face of climate change and development.

Conclusions

Today's ecosystems face unprecedented rates of change as a result of anthropogenic global warming and land use (Masson-Delmotte et al. 2021). In Argentina and Chile, initiatives to restore native forests by 2035 seem increasingly unlikely to succeed given climate change projections for warmer, drier conditions, and shortages of resources and labor (Bannister et al. 2018). Paleoecological research helps contextualize the current situation within a longer ecological trajectory of change related to past climates, Native American land use, and Euro-American settlement. Whereas active restoration of intensively altered landscapes like Río Rubens may be impractical, the restoration of the *Araucaria* patches that lie within a broader forest-steppe mosaic near L. Portezuelo are more feasible with the return of indigenous practices such as controlled burns, planting, and protection. A better understanding of landscape history can, thus, inform conservation strategies and evaluate the merits of site-specific restoration efforts, as part of addressing future climate change and land use.

AFFILIATIONS

[1]Department of Geography, Portland State University, Portland, OR, USA

[2]Department of Geography, University of Oregon, Eugene, OR, USA

[3]Department of Earth Sciences, Montana State University, Bozeman, MT, USA

[4]Montana Institute on Ecosystems, Montana State University, Bozeman, MT, USA

CONTACT

William Nanavati: wnanavati@pdx.edu

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