



Land-use history as a guide for forest conservation and management

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Abstract: Conservation efforts to protect forested landscapes are challenged by climate projections that suggest substantial restructuring of vegetation and disturbance regimes in the future. In this regard, paleoecological records that describe ecosystem responses to past variations in climate, fire, and human activity offer critical information for assessing present landscape conditions and future landscape vulnerability. We illustrate this point drawing on 8 sites in the northwestern United States, New Zealand, Patagonia, and central and southern Europe that have undergone different levels of climate and land-use change. These sites fall along a gradient of landscape conditions that range from nearly pristine (i.e., vegetation and disturbance shaped primarily by past climate and biophysical constraints) to highly altered (i.e., landscapes that have been intensely modified by past human activity). Position on this gradient has implications for understanding the role of natural and anthropogenic disturbance in shaping ecosystem dynamics and assessments of present biodiversity, including recognizing missing or overrepresented species. Dramatic vegetation reorganization occurred at all study sites as a result of postglacial climate variations. In nearly pristine landscapes, such as those in Yellowstone National Park, climate has remained the primary driver of ecosystem change up to the present day. In Europe, natural vegetation–climate–fire linkages were broken 6000–8000 years ago with the onset of Neolithic farming, and in New Zealand, natural linkages were first lost about 700 years ago with arrival of the Maori people. In the U.S. Northwest and Patagonia, the greatest landscape alteration occurred in the last 150 years with Euro-American settlement. Paleoecology is sometimes the best and only tool for evaluating the degree of landscape alteration and the extent to which landscapes retain natural components. Information on landscape-level history thus helps assess current ecological change, clarify management objectives, and define conservation strategies that seek to protect both natural and cultural elements.

Keywords: climate change, fire history, forest management, historical ecology, humanized landscapes, land-use change, paleoecology, pollen and charcoal analysis

La Historia del Uso de Suelo como Guía para el Manejo y la Conservación de los Bosques

Resumen: Los esfuerzos de conservación para proteger los paisajes forestales tienen un reto gracias a las proyecciones climáticas que sugieren reestructuraciones sustanciales de la vegetación y regímenes de perturbaciones en el futuro. En este aspecto, los registros paleoecológicos que describen las respuestas de los ecosistemas a variaciones pasadas del clima, incendios y actividad humana ofrecen información crítica para la evaluación de las condiciones actuales y la vulnerabilidad futura de los paisajes. Ilustramos este punto a partir de ocho sitios en el noroeste de los Estados Unidos, Nueva Zelanda, la Patagonia y el centro y el

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sur de Europa que han sufrido diferentes niveles de cambio climático y del uso de suelo. Estos sitios caen dentro de un gradiente de condiciones paisajísticas que varían desde casi prístinas (es decir, la vegetación y la perturbación moldeados por principalmente por restricciones climáticas y biofísicas pasadas) hasta altamente alteradas (es decir, paisajes que han sido modificados intensamente por la actividad humana anterior). La posición dentro de este gradiente tiene implicaciones para el entendimiento del papel de la perturbación natural y antropogénica en la formación de las dinámicas del ecosistema y las valoraciones de la biodiversidad actual, incluyendo el reconocimiento de especies faltantes o mal representadas. Ocurrió una reorganización dramática de la vegetación en todos los sitios de estudio como resultado de las variaciones climáticas posglaciales. En los paisajes casi prístinos, como aquellos en el Parque Nacional Yellowstone, el clima ha permanecido como el principal conductor del cambio ambiental hasta el día de hoy. En Europa, las conexiones naturales vegetación-clima-incendios se rompieron hace 6000 - 8000 años con el inicio de la agricultura neolítica, y en Nueva Zelanda las conexiones naturales se perdieron primero hace 700 años con la llegada de los Maorí. En el noroeste de los Estados Unidos y en la Patagonia la mayor alteración del paisaje ocurrió en los últimos 150 años con el asentamiento Euro-Americano. La paleoecología es a veces la única y mejor herramienta para evaluar el grado de alteración de un paisaje y el área hasta la cual los paisajes mantienen los componentes naturales. Por lo tanto, la información sobre el paisaje a nivel histórico ayuda a evaluar el cambio ecológico actual, a clarificar los objetivos del manejo, y a definir las estrategias de conservación que buscan proteger tanto a los elementos naturales como a los culturales.

Palabras Clave: análisis de carbón y polen, cambio climático, cambio del uso de suelo, ecología histórica, historia de incendios, manejo forestal, paisajes humanizados, paleoecología

Introduction

Most sustainable forestry initiatives, whether at the international, national, or regional level, are challenged by climate projections that suggest a significant restructuring of vegetation and fire regimes in the future (e.g., Gottfried et al. 2012; Diffenbaugh & Field 2013; Elsen & Tingley 2015). To put these projections into the context of ecosystem variability, many researchers have examined global and regional biotic vulnerability to future climate change in light of what is known about past climate-vegetation-fire linkages (e.g., Willis et al. 2007; Gillson et al. 2013; Benito-Garzón et al. 2014). Broad-scale generalizations, however, often have limited application for on-the-ground decision making because they overlook a host of nonclimatic factors that shape present ecosystems at fine spatial scales, including the legacy of disturbance, biotic interactions, and, perhaps most importantly, past land use.

Present landscapes may be categorized along a gradient based on their land-use history, with natural or pristine landscapes forming largely in the absence of people at one end and landscapes subjected to long and intensive human impacts at the other (Vale 2002). Truly pristine places are nonexistent, but some of the large core-protected U.S. national parks and other nature reserves support vegetation that has experienced only short or minor human impacts (here referred to as nearly pristine landscapes). Altered or humanized landscapes at the other end of the gradient have been modified by land-use activities of different types, duration, and intensity. Most landscapes fall somewhere between the 2 end points and support both cultural and natural elements. These intermediate conditions are shaped by complex interac-

tions of changing climate and land use that operate over different temporal and spatial scales. As a result, intermediate landscapes pose a unique conservation challenge: to support natural structure and diversity on the one hand and to maintain cultural or utilitarian attributes on the other (Lindenmayer & Hunter 2010).

We considered the importance of paleoecology for evaluating current landscape status in terms of its naturalness or alteration. We built on a growing body of literature that describes the use of historical and paleoecological data to broaden understanding of long-term perspectives on the historical range of variability (e.g., Swetnam et al. 1999; Whitlock et al. 2010; Gillson 2015); climate-driven changes in species ranges and vegetation composition (e.g., Williams et al. 2004; Tinner et al. 2013; Iglesias et al. 2014); human alteration of native vegetation, biodiversity, and ecosystem services (e.g., Dearing et al. 2012; Colombaroli & Tinner 2013; Conedera et al. 2016); and potential rates of ecological change and no-analog situations (e.g., Williams & Jackson 2007; MacDonald et al. 2008; Willis et al. 2007). We drew on examples from our own research on 3 continents and 2 hemispheres with 2 objectives in mind: illustrate the extent to which present vegetation in our study regions has been shaped by past climate change and human activity and show how landscape-level paleoecological information can be incorporated into conservation strategies. Although multiple factors shape conservation strategies, we suggest knowledge of the past should be given priority consideration.

Our study sites were in 8 regions: northern and southern Switzerland; Tuscany and Sicily, Italy; interior South Island, New Zealand; northern Patagonia, Argentina; and western Washington and the Yellowstone region of the

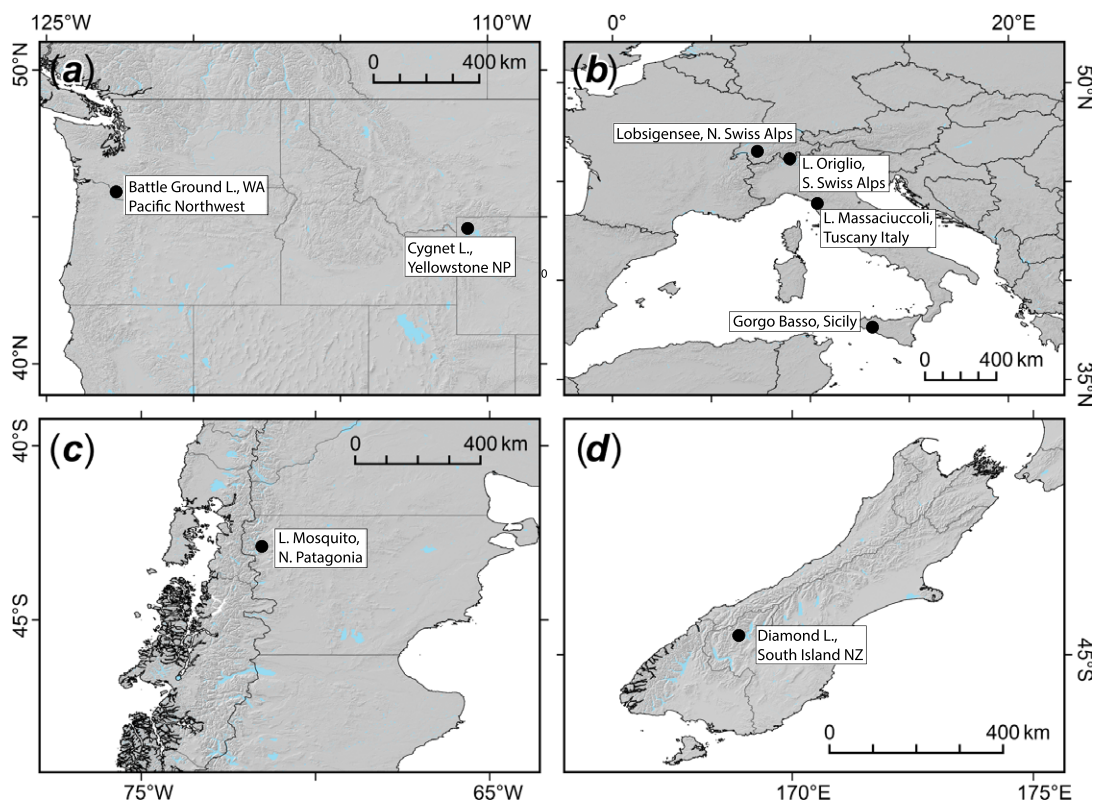


Figure 1. Study site locations in (a) northwestern United States, (b) Switzerland and Italy, (c) northern Patagonia, Argentina, and (d) South Island, New Zealand (L., lake).

northwestern United States (Fig. 1). Information on past ecological change came from pollen, plant macrofossil, and charcoal records preserved in radiocarbon-dated sediment cores from lakes and wetlands. Land-use history was inferred from archeological and historical records, ethnographic accounts, paleobotanical studies, and models that explicitly considered the impact of different types of human activity on fire, vegetation, and climate (Henne et al. 2013; Pfeiffer et al. 2013).

Past Changes in Climate and Human Activity in Landscape Development

The current vegetation in each study region is an outcome of a particular sequence of events that were caused by climate, human manipulation, and disturbance (Fig. 2). Sites in the U.S. Northwest and northern Patagonia, for example, have undergone relatively little or only recent human alteration and feature large tracts of natural vegetation. In these regions, the most intense land use occurred in the last 150 years with Euro-American settlement. New Zealand and European sites feature both natural and humanized vegetation, reflecting land use over centuries in New Zealand and millennia in Europe (Fig. 2). Among the European examples, the Italian sites have been so heavily altered that they presently support little natural vegetation. The steplike progression of land-use change in the

European sites has shifted the vegetation of the study sites to more altered conditions through time, although the pattern is not unidirectional. The extensive deforestation during the Iron Age and Roman Period in Europe was followed by a period of land abandonment and some forest recovery, and recent landscapes in Switzerland are more forested now than they were a century ago (Fig. 2).

In all these regions, the importance of climate change in shaping past vegetation is evident prior to substantial human activity (Table 1). In the northern pre-Alps, boreal species that survived the last glaciation in isolated populations (e.g., *Betula pendula*, *Juniperus communis*, and *Hippophaë rhamnoides*) rapidly expanded their range during a 5–6 °C warming at onset of the Bølling Interstadial (approximately 14,650 cal yr BP [years before AD 1950]) (Ammann et al. 2009). A subsequent south–north expansion of temperate trees, including linden (*Tilia*), elm (*Ulmus*), oak (*Quercus*), and hazel (*Corylus*), was facilitated by additional warming in the early Holocene (11,000–8200 cal yr BP) (Lang 1994; Birks & Tinner 2016). A rapid cooling of –2 °C at 8200 cal yr BP led to decline of thermophilous communities and expansion of forests dominated by European beech (*Fagus sylvatica*) and silver fir (*Abies alba*) (Tinner & Lotter 2001).

In landscapes less altered by humans, climate has remained the primary driver of vegetation dynamics up to the present day. One of the large-scale but slowly varying

Table 1. Present landscape condition and vegetation history of the study sites in response to past changes in climate and land use.

Region, site, location	Present vegetation at site	Vegetation response to past climate change over last 8000 years	Vegetation response to past land use	Current landscape condition
Yellowstone National Park, U.S.A., Cygnet Lake (44.660°N, 110.615°W; 2531 m elevation) (Whitlock 1993; Millsbaugh et al. 2004)	lodgepole pine (<i>Pinus contorta</i>) forest with sagebrush (<i>Artemisia</i> <i>tridentata</i>) steppe	8000–6000 cal yr BP (dry warm summers, high snowpack), frequent fire; 6000 cal yr BP to present (cool wet conditions), fewer fires	8000–150 cal yr BP (indigenous foragers), minimal impact; AD 1850, Euro-American settlement, logging, agriculture, fire suppression; AD 1872, Yellowstone National Park establishment; since approximately AD 1980, exurban development	nearly pristine
Northern Patagonia, Argentina, Lago Mosquito (42.489°S, 171.397°S; 553 m elevation) (Whitlock et al. 2006; Iglesias et al. 2014)	dry wood- land/shrubland (<i>Austrocedrus</i> <i>chilensis</i> , <i>Nothofagus</i> <i>antarctica</i> , <i>Maytenus</i>); nearby forest (<i>Nothofagus</i> <i>dombeyi</i> , <i>N.</i> <i>pumilio</i>), pastureland, pine plantations	8000–4000 cal yr BP (cooler than present summers), expanded <i>Nothofagus</i> forest and steppe, more fires (before 5000 cal yr BP); 4000 cal yr BP-present (wet warm conditions, increased interannual/decadal variability), expanded <i>Austrocedrus</i> , more fires	8000–4000 cal yr BP (indigenous foragers), minimal impact; approximately AD 1700 (European arrival), grazing, non-native plants; since AD 1850 (Euro-American settlement), deforestation, fires, grazing, pine plantations	natural/inhabited
Northwest U.S., Battle Ground Lake (45.804°N, 122.494°W; 154 m elevation) (Walsh et al. 2008)	mesic-dry conifer forest (<i>Pseudotsuga</i> <i>menziesii</i> , <i>Abies</i> <i>grandis</i> , <i>Tsuga</i> <i>beterophylla</i> , <i>Thuja plicata</i>); remnant prairie woodland (<i>Quercus</i> <i>garryana</i>); cultivated land; managed forests; urbanized land	8000–4000 cal yr BP (warm dry summers), expanded prairie woodland, more fires; 4000 cal yr BP-present (cool wet conditions), expansion of mesic-dry forest (<i>Pseudotsuga</i> , <i>Thuja</i> , <i>Tsuga</i>), fewer fires	8000–3000 cal yr BP (indigenous foragers), minimal impact; 3000–1500 cal yr BP (sedentary populations), more fires; AD 1820 (Euro-American settlement), deforestation, initially more fires, agriculture, managed <i>Pseudotsuga</i> forests	mosaic

Continued

Table 1. Continued.

Region, site, location	Present vegetation at site	Vegetation response to past climate change over last 8000 years	Vegetation response to past land use	Current landscape condition
South Island, New Zealand, Diamond Lake (44.648°S, 168.965°E; 593 m elevation) (McWethy et al. 2010)	open vegetation (<i>Poaceae</i> , <i>Discaria tomatou</i> , <i>Pteridium</i>); forest remnants (with <i>Lopbozonia menziesii</i> and shrubs); pastureland; pine plantations	last 1000 years (interannual climate variability), negligible impact	AD 1280–1600 (initial burning period), loss of mesic-dry <i>Lopbozonia</i> /podocarp forest, expansion of <i>Lepidospermum</i> , <i>Kunzea</i> , <i>Pteridium</i> , grassland/shrubland; AD 1600–1850 (Late Maori Period), some small-scale cultivation, small fires; since AD 1850 (European settlement), deforestation, agriculture, initially more fires, <i>Pinus</i> plantations	unevenly altered
Northern Switzerland, Lobsigensee (47.032°N, 07.265°E; 514 m elevation) (Ammann 1989; Tinner et al. 2005)	pasture and cultivated land; remnant forests of beech (<i>Fagus sylvatica</i>) with oak (<i>Quercus robur</i>) and planted spruce (<i>Picea abies</i>)	8100–5000 cal yr BP (warm moist summers), mixed forests (<i>Quercus</i> , <i>Fagus</i> , <i>Tilia</i> , <i>Ulmus</i>); 5000 cal yr BP-present (trend to cooler moist summers), no discernible impact	7200–4200 cal yr BP (Neolithic), slash and burns, deforestation, many fires, <i>Fagus</i> expansion, species reductions/extirpations (<i>Hedera</i> , <i>Ulmus</i> , <i>Tilia</i> , <i>Fraxinus</i> , <i>Acer</i>); 4200–2800 cal yr BP (Bronze Age), increased deforestation; 2800–1400 cal yr BP (Iron Age, Roman Age, Migration Period), intensive deforestation pulses, dominance of <i>Quercus</i> and <i>Fagus</i> , expansion of <i>Picea</i> , <i>Carpinus</i> and <i>Juglans</i> , most fires; AD 600–1950 (Medieval, Modern), more cultivation, managed forests, fewer fires; AD 1950–2000, industrial agriculture	unevenly altered

Continued

Table 1. Continued.

Region, site, location	Present vegetation at site	Vegetation response to past climate change over last 8000 years	Vegetation response to past land use	Current landscape condition
Southern Switzerland, Lago di Origlio (46.055°N, 08.944°E; 416 m elevation) (Tinner et al. 1999)	forests of sweet chestnut (<i>Castanea sativa</i>) and stands of mixed oak forest (<i>Quercus petraea</i> , <i>Q. robur</i> , <i>Ulmus</i> , <i>Tilia</i> , <i>Fraxinus</i> , <i>Acer</i> , <i>Fagus sylvatica</i>), pastureland	9200–5000 cal yr BP (warm moist summers), <i>Abies</i> , <i>Tilia</i> , <i>Ulmus</i> , <i>Fraxinus</i> , <i>Quercus</i> , <i>Acer</i> co-dominance; 5000 cal yr BP-present (trend to cooler summers), no discernible impact	7500–4200 cal yr BP (Neolithic), slash and burns, deforestation, high fires, species reduction/extirpations (<i>Abies</i> , <i>Hedera</i> , <i>Ulmus</i> , <i>Tilia</i> , <i>Fraxinus</i> , <i>Acer</i>) and expansions (<i>Quercus</i> , <i>Fagus</i> , <i>Alnus</i> , <i>Corylus</i> , <i>Betula</i>); 4200–2800 cal yr BP (Bronze Age), increased deforestation and open land; 2800–1400 cal yr BP (Iron Age, Roman Age, Migration Period), deforestation pulses, most fires, <i>Castanea</i> dominance, <i>Juglans</i> cultivation; AD 600–1850 (Medieval, Modern), <i>Castanea</i> cultivation, orchards, open land, fewer fires; AD 1850–1950, managed forests, intense agriculture, fewer fires; since AD 1950, afforestation, less agriculture	unevenly, intensely altered
Tuscany Italy, Lago di Massaciuccoli (43.833°N, 10.333°E; 1 m elevation) (Colombaroli et al. 2007)	meso-Mediterranean belt, mixed broadleaved-evergreen oak forest (deciduous <i>Quercus robur</i> , <i>Q. pubescens</i> , <i>Carpinus betulus</i> , <i>C. sativa</i> and evergreen <i>Q. ilex</i> , <i>Pistacia lentiscus</i> , <i>Phillyrea angustifolia</i>), cultivated fields, vineyards, orchards	8000–4000 cal yr BP (warm, dry summers), abundant <i>Abies</i> ; 4000 cal yr BP-present (trend to cooler, moister summers and warmer, drier winters, greater interannual/decadal variability), expansion of evergreen oak	8000–4500 cal yr BP (Neolithic), slash and burns, deforestation, <i>Abies</i> extirpation, more fires; 4500–2900 cal yr BP (Bronze Age), expansion of <i>Quercus ilex</i> , <i>Phillyrea</i> shrubland and grassland, fewer fires; 2900–1400 cal yr BP (Iron Age, Roman Age, Migration Period), intensive deforestation, fires; AD 600–1950 (Medieval, Modern), expansion of <i>Phillyrea</i> shrubland and cultivated land, more fires; since AD 1950, landscape abandonment, industrial agriculture, reforestation, fewer fires	intensely altered

Continued

Table 1. Continued.

Region, site, location	Present vegetation at site	Vegetation response to past climate change over last 8000 years	Vegetation response to past land use	Current landscape condition
Sicily, Gorgo Bosso (37.617°N, 12.650°E; 6 m elevation) (Tinner et al. 2009)	thermo-Mediterranean belt with relict evergreen broadleaved forest (<i>Q. ilex</i> , <i>Q. coccifera</i> , <i>Pistacea lentiscus</i>); cultivated fields, vineyards, orchards (<i>Olea europaea</i>)	8000–5000 cal yr BP (hot, dry summers, temperate, moist winters), expansion of evergreen broadleaved forests into natural maquis; 5000 cal yr BP-present (trend to cooler, moister summers and drier, warmer winters), no discernible impact	8000–4500 cal yr BP (Neolithic), short declines of evergreen oak-olive forest, <i>Ficus</i> and cereal cultivation, low fire activity; 4500–2900 cal yr BP (Bronze Age), periods of open land expansion; 2900–1400 cal yr BP (Iron Age, Roman Age, Migration Period), destruction of evergreen broadleaved forests, cultivation of <i>Juglans</i> and <i>Castanea</i> , expansion of shrubland (maquis), garrigue and grasslands, most fires; AD 600-present (Medieval/Historical), grazing, industrial agriculture, non-native plants (e.g., <i>Eucalyptus</i>), few fires initially, but increase in last 200 years	fully altered

The notation cal yr BP refers to years before AD 1950.



Figure 2. Landscape history over the last 8000 years in the study regions (BP, before AD 1950; BA, Bronze Age; IA-Rom, Iron Age-Roman period; MP-Mod, Medieval-Modern period). Changes in landscape conditions (*sensu* Vale 2002) through time are based on an interpretation of the pollen and charcoal data in Fig. 1.

climate forcings is the change in summer solar radiation (insolation) occurring over millennia. Summer insolation reached a maximum from 11,000 to 9000 years ago in the Northern Hemisphere and led to a period of warmer-than-present conditions. It steadily declined to present values and resulted in gradual cooling. The opposite trend in summer insolation characterizes Southern Hemisphere records (Fig. 3). At Cygnet Lake in Yellowstone, forests of lodgepole pine (*Pinus contorta*) were established with Holocene warming beginning 11,000 years ago, and fire activity was higher than at present between 11,000 and 6000 cal yr BP. Fire activity decreased as the climate cooled in the last 6000 years (Fig. 3a; Table 1) (Millsbaugh et al. 2004). In western Washington, high levels of prairie woodland taxa were present in western Washington during a warm period, 9000–4000 cal yr BP (Table 1; Fig. 3b), and this period was followed by an expansion of present forests of mesophytic and xerophytic conifers in the last 4000 years as the climate cooled (Walsh et al. 2008). In northern Patagonia, Chilean cedar (*Austrocedrus chilensis*) expanded after 3500 cal yr BP as a result of increased moisture and warmer summers (Fig. 3c) (Souto et al. 2015).

Climate became less important as an agent of vegetation change in Europe after the Mesolithic–Neolithic transition, approximately 8000–6000 years ago, when small foraging populations were replaced by larger more sedentary cultures that were supported by agriculture and pastoralism. In the course of this cultural change, primary forest was lost and fire activity increased (Figs. 3e–h; Table 1) (e.g., Tinner et al. 2005; Kaplan et al. 2009; Molinari et al. 2013). Changing forest composition, increased levels of burning and agriculture continued in the Bronze Age (4200–2800 cal yr BP) (Figs. 3e–h), and the most intensive period of burning and forest clearance

took place in the Iron Age (2800–2000 cal yr BP). Crop and woodland production was widespread in the Iron Age and Roman Age (2000–1450 cal yr BP) (Figs. 3e–h) and intensified in the Medieval Period (AD 500–1500). By the early Modern Period (AD 1500–1850), nearly all suitable land was under intensive crop, pasture, or forest production (Figs. 3e–h). Industrialization in the 18th–19th century led to profound deforestation in central Europe and the Alps (Figs. 3e & 3f) (Lotter 1999; Tinner et al. 2005; Conedera et al. 2016). From the end of the 19th century through the 20th century, however, declining rural populations and land abandonment reversed this trend and led to expansion and closing of many European mountain forests (Fig. 2) (Conedera et al. 2016). Similarly in the Mediterranean region, agricultural fields abandoned in the 20th century have become flammable shrubland (Figs. 3g & 3h) (garrigue, maquis) and have led to increased fire activity in recent decades (San Miguel-Ayanz et al. 2013).

In contrast to the European sites, Diamond Lake in South Island, New Zealand, has a comparatively short history of land use, and pollen and charcoal data show the vulnerability of mesic podocarp-*Lophozonia* forests to human-set fire (Wilmshurst et al. 2008; McWethy et al. 2010) (Fig. 3d; Table 1). Prior to Maori arrival, about 700 years ago, natural ignitions were exceedingly rare and the dominant forest species were poorly adapted to fire. People represented a new ignition source, resulting in a loss of approximately 50% of the native forest in a matter of decades (McWethy et al. 2013). Rapid deforestation was facilitated by the postfire expansion of highly flammable shrubs (e.g., *Lepidospermum*, *Kunzea*) (Fig. 3d; Table 1), and a positive feedback was created in which each new fire led to further forest loss (Perry et al. 2012). Additional forest clearance and burning

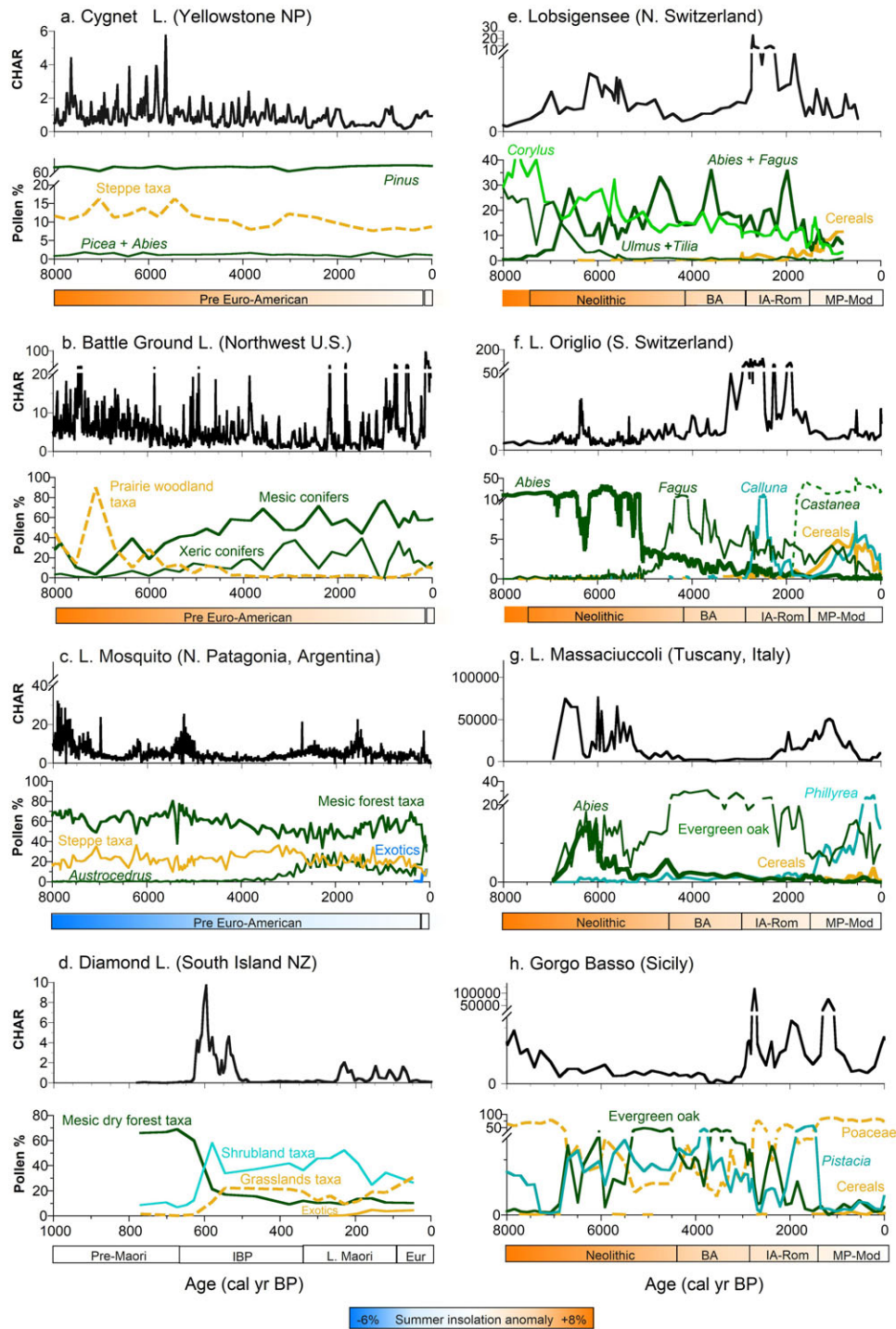


Figure 3. Data on pollen percentage and charcoal accumulation rates (CHAR [$\text{particles cm}^{-2}\cdot\text{yr}^{-1}$]) from our study sites over time: (a–d) non-European locations and (e–h) European locations. The CHAR data describe variations in fire activity, and peaks are usually interpreted as individual fire episodes (Whitlock & Larsen 2001). The bar at the base of each diagram shows the changing anomaly (relative to present) of summer insolation (the darker the shading, the more intense the radiation anomaly). Age (cal yr BP) refers to years before AD 1950. The records for (a) Cygnet Lake, (b) Battle Ground Lake, and (c) Lago Mosquito show before (prior to approximately AD 1850) and after Euro-American (after approximately AD 1850) periods. (d) Diamond Lake (South Island, New Zealand) shows no change in summer insolation because the record spans only the last 1000 years (pre-Maori, record prior to the arrival of people; IBP, initial burning period, AD 1280–1600, soon after Maori arrival; L. Maori, period prior to European settlement; Eur, the last 100 years). In (e–h), land-use abbreviations are BA, Bronze Age; IA-Rom, Iron Age-Roman period; MP-Mod, Medieval-Modern period. For additional information on the vegetation, climate, and land-use history, see Table 1.

occurred with European settlement (Fig. 3d), resulting in the present vegetation mosaic of native and non-native forest and pasturelands (Fig. 2).

The history of individual species (i.e., those of special conservation interest) supplements our general vegetation reconstructions. For example, European silver fir was once more widespread than it is today, based on paleoecological records and related model simulations (Tinner et al. 2013; Ruosch et al. 2016). Silver fir grew well under conditions that were warmer than present and relatively humid, but the species is highly sensitive to fire and browsing. As a result of increasing human activity starting in the Neolithic Period, fir forest was replaced by stands of almost pure beech, sweet chestnut (*Castanea sativa*), and deciduous or evergreen oak (*Quercus* spp.) in the lowlands and mountains (Figs. 3e–g) (Colombaroli et al. 2007; Tinner et al. 2013). Given its wide distribution prior to anthropogenic disturbance, silver fir would likely occupy a broader range in Europe than it does today, so long as browsing by domestic and wild animals and arson fires are controlled (Ruosch et al. 2016). The current disequilibrium with present climate is recognized only on the basis of paleoecological studies (Tinner et al. 2013; Ruosch et al. 2016), and ecological niche models that neglect such land-use legacies overlook a critical component of the environmental history (e.g., Maiorano et al. 2013).

In recent decades, mortality of whitebark pine (*Pinus albicaulis*), a keystone species of high-elevation forests in the U.S. Northwest, has been widespread as a result of climate change, fires, non-native pathogens, and insect outbreaks (McKinney & Tomback 2011). Ecological niche models based on present climate suggest whitebark pine will be largely extirpated from its current range with continued warming (Chang et al. 2014). Pollen and charcoal data from the Yellowstone region provide insights into white pine's vulnerability to past climate change and fire. *P. albicaulis* or *Pinus flexilis* was apparently more abundant and widely distributed in the region from 11,000 to 7000 cal yr BP when summers were warmer than at present, winters were colder and wetter, and fires were more abundant (Iglesias et al. 2015). White pine was abundant at all elevations in a period when competing species, Engelmann spruce (*Picea engelmannii*) and lodgepole pine, were poorly represented (Iglesias et al. 2015). Thus, paleoecological data provide important insights for the future: white pines have survived periods of warmer summers and higher fire activity in the past and these factors may not represent critical thresholds, at least in the near future. In contrast, recent threats from non-native white pine blister rust (*Cronartium ribicola*) and native mountain pine beetle (*Dendroctonus ponderosae*) (Logan et al. 2010; Smith et al. 2013) have no or unclear precedence and are cause for concern.

Cultivation of sweet chestnut in southern Switzerland began in Roman times as a source of fiber, intensified

in the Medieval Period as a food source, and continued through the 1950s to create a widespread monoculture in the southern Swiss lowlands that is well adapted to fire (Fig. 2f) (Conedera et al. 2004; Morales-Molino et al. 2015). Recent abandonment of chestnut cultivation has led to mixed forests of chestnut and other broad-leaved trees that are often mistaken as natural. In the last 40 years, native (e.g., *Ilex aquifolium*, *Hedera helix*, *Laurus nobilis*) and exotic evergreens (e.g., *Trachycarpus fortunei*, *Cinnamomum camphora*) are spreading in the understory of mature, former chestnut groves, and pioneer exotic species (e.g., *Ailanthus altissima*, *Pawlonia* spp.) are colonizing forest patches after windthrow and fire (Conedera et al. 2001). Forest encroachment into open areas has also resulted in loss of diverse, human-created meadows of cultural and ecological value (Colombaroli et al. 2013; Colombaroli & Tinner 2013). Without the benefit of paleoecological data, the long and intensive management history of chestnut would not be known, and the altered nature of present chestnut forests might be overlooked.

Incorporating Landscape History into Conservation Strategies

We contend that knowing ecological history, including the degree of past landscape alteration, can help clarify management objectives, conservation targets and, to some extent, the intensity of effort required to achieve conservation goals (Fig. 4) (Machado 2004). For example, paleoecological information from the most pristine landscapes provides critical insights about long-term ecological dynamics, which forms a basis for evaluating current biodiversity, disturbance regimes, and structural complexity. Pollen data from Cygnet Lake in Yellowstone suggest that lodgepole pine forests have a long history and a high tolerance for different levels of burning and climate change (Fig. 3a). This information supports hands-off management strategies as long as the frequency of fires does not exceed Holocene levels (e.g., Westerling et al. 2011).

Most of our study sites are neither completely altered nor pristine but represent an intermediate condition that falls within Vale's (2002) categories of "natural/inhabited" with large patches of nearly pristine elements and some areas of alteration, "mosaic" with both natural and humanized components, and "unevenly altered" landscapes dominated largely by a matrix of humanized elements with isolated refugia of native vegetation (Fig. 4). Paleoecological records from intermediate landscapes inform such topics as the vulnerability of the different vegetation components to a range of climate conditions (e.g., rapid warming, severe or prolonged drought in the past); the extent to which present vegetation is maintained by climate-driven or anthropogenic

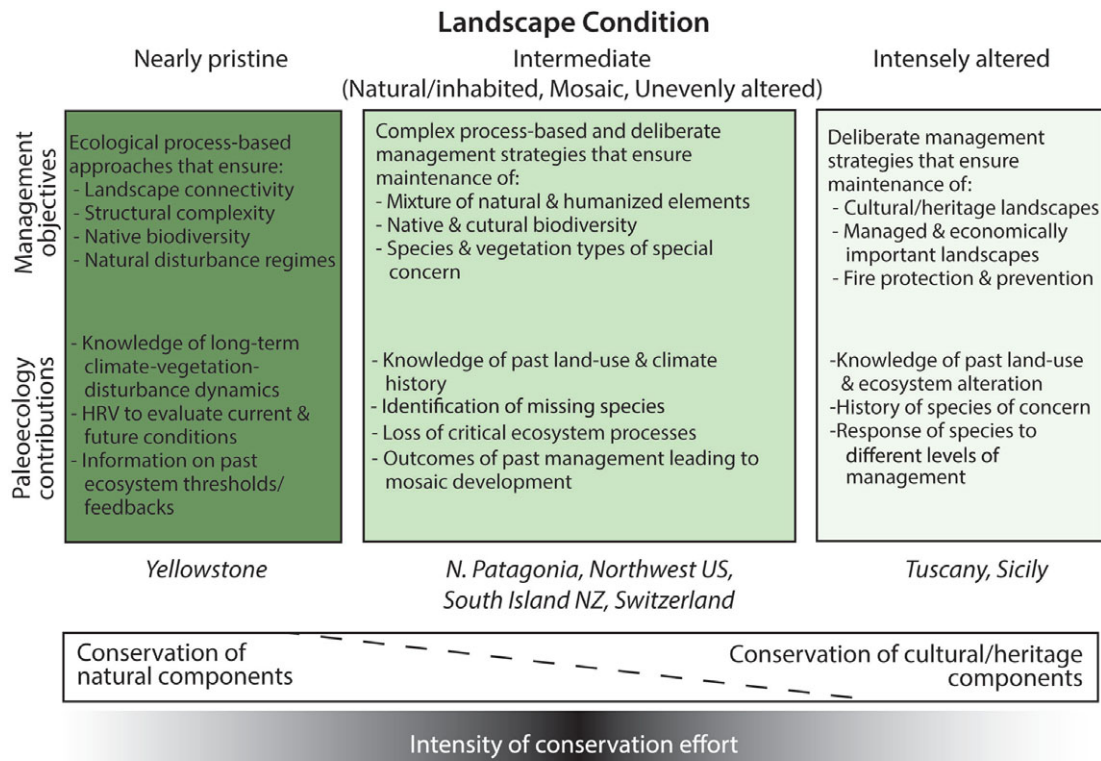


Figure 4. Use of paleoecology to inform conservation strategies, depending on the landscape condition and the legacy of past land use. In nearly pristine landscapes, management objectives to maintain ecological processes benefit from knowledge of long-term ecosystem dynamics; in intermediate landscapes, objectives to retain both cultural and natural components require information on land-use and climate history; and in highly altered landscapes, deliberate management benefits from information about past species responses to different levels of land use (HRV, historical range of variability).

fire regimes and the vulnerability of particular vegetation components and species to changes in fire activity; the identity of species that have benefited or been disadvantaged by past land-use practices, including the appearance of new taxa and elimination of others; and the role of past land-use and management in creating the current landscape pattern of natural and cultural components.

In study sites where both natural and cultural components are valued, complex management strategies are needed to protect native plant communities alongside cultural or managed vegetation. We suggest that intermediate landscapes require the most intensive conservation effort, given objectives to maintain both cultural and natural components (Fig. 4). For example, at Battle Ground Lake in the U.S. Northwest, pollen and charcoal data point to the relatively young age of the current old-growth forests, which were first established only about 4000 years ago (Fig. 3b). This insight affirms the importance of late-successional reserves to protect biodiversity and retain structural complexity as the region becomes more developed and conversion to commercial forests increases (Whitlock et al. 2015). At Diamond Lake in New Zealand (Fig. 3d), protecting remnants of native

podocarp-*Lophozonia* forest requires active fire suppression, but this objective must be balanced against the use of fire to maintain culturally important tussock grasslands created by the early Maori. In Switzerland, the high cultural value of chestnut has made it a management priority. Deciding which humanized landscape is the desired condition (i.e., chestnut groves like Roman and Medieval time or closed mixed forests of the last century) can only be informed by paleoecology (Fig. 3e & 3f), and restoration goals must be balanced against new realities including the co-occurrence of non-native forest species and recent chestnut mortality due to drought (Tinner et al. 1999; Conedera et al. 2010).

Altered landscapes, such as represented by our sites in Italy (Figs. 3g & 3h), have been manipulated for millennia to meet cultural values and utilitarian needs, including agriculture, livestock production, and silviculture. Conservation of cultural components and often small remnants of native vegetation often conflicts with present utilitarian needs (Fig. 4). The structural and biotic simplicity of managed forests in all our settings leaves them vulnerable to disturbance (e.g., monospecific beech and spruce forests at Lobsigensee; olive orchards near Lago di

Massaciuccoli and Gorgo Basso; non-native pine plantations near Diamond Lake and Lago Mosquito; commercial *Pseudotsuga* forests near Battle Ground Lake), and contrasts with the natural resilience of native forests in the past (Kulakowski et al. 2016). Altered forests can return to a more natural level of structural complexity and biodiversity in the absence of silvicultural management, but conversion can be slow and unpredictable. Moreover, back-to-nature conservation efforts may be impractical in landscapes where newly established non-native species are well adapted to disturbance and resistant to change. In the Italian sites (Figs. 3g & 3h), for example, high levels of disturbance (e.g., large severe fires, intensive grazing) and flammable shrub expansion (e.g., maquis) have reduced opportunities for native species recovery, including silver fir (Henne et al. 2015; Vanni re et al. 2016). The same issues are noted in New Zealand and northern Patagonia where establishment of flammable shrubs and pine after human-set fires has created a positive feedback that leads to more fires and native forest loss (Simberloff et al. 2010; Paritsis et al. 2015).

Future Perspectives

Ecological history is sometimes regarded as interesting background information in conservation efforts but of little practical value. This viewpoint is increasingly voiced in discussions about future climate change on the grounds that restoration to a prior state may be inadequate to address the rapid climate changes and novel conditions that lie ahead (e.g., Loarie et al. 2009; Benito-Garz n et al. 2014; Elsen & Tingley 2015). We argue that even in places where temperatures may soon exceed those of the last 11,000 years, knowledge of the past remains indispensable for the preservation of ecosystems and species of special concern (see also Hunter et al. 1988; Birks 2012). Paleoecology can help identify the levels of management required to meet desired restoration goals as part of a cost-benefit analysis. Restoring native podocarp-*Lophozonia* forests in New Zealand, for example, will require intense conservation effort with uncertain outcome, given evidence of past forest vulnerability to fire. Replanting silver fir where it once grew, in contrast, has the potential to return an important native species to Italian and southern Swiss lowland forest and help maintain biodiversity and ecosystem services under climate change (Henne et al. 2015; Ruosch et al. 2016).

Beyond serving as a guidepost for restoration, paleoecology can help in the assessment of current conditions in light of the historical range of variability (Landres et al. 1999) by providing a baseline for assessing current precedence. A temporal baseline that is too short, however, will lead to erroneous estimates about the range of conditions necessary to maintain particular species and vegetation types as well as the naturalness of present dis-

turbance regimes. It may also overlook important species that are currently missing or overrepresented as a result of active or passive management in the past (Conedera et al. 2016). Lengthening the historical baseline through paleoecology can avoid incorrectly selecting altered vegetation conditions as a back-to-nature restoration goal or adopting fire-management policies that inadvertently increase natural disturbance risk (Gillson & Marchant 2014; Whitlock et al. 2015).

Paleoecological insights from one region can also guide management actions in another (Smith et al. 2016). Responses of species to past warming (i.e., at the onset of the B lling Interstadial in Europe or during the early Holocene in the U.S. Northwest) in nearly pristine settings can suggest their response to a similar magnitude of change in more altered settings where data may not be available. Similarly, the vulnerability of introduced species to disturbances (e.g., fire, blowdown, insect outbreaks, and avalanches) can be informed by their response to past disturbances in their native range. For example, alteration of fire regimes as a result of pine expansion in New Zealand and Patagonia may best be understood by examining pine responses to past fires in North America.

Paleoecology has been an active discipline for nearly a century, and in recent decades, high-resolution records of vegetation and fire history are stimulating new research questions and applications (Seddon et al. 2014). These data sets have contributed substantially to understanding of how species and communities adapt to changes in climate and land use of varying duration and intensity. Although paleoecology is often motivated by a curiosity about environmental history, the threats of current and future changes in land use and climate have elevated its importance. Our 8 study sites show the uniqueness of the ecological history of each location and the need for landscape-level reconstructions. Inasmuch as management success relies on knowing which ecosystems are most vulnerable and why, the sequence of events leading to a landscape's current position along the pristine-to-humanized gradient is critical information for clarifying conservation objectives and evaluating outcomes.

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