

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 significant 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

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future landscape vulnerability. We illustrate this point drawing on eight sites in the northwest U.S., New Zealand, Patagonia, and central and southern Europe that have experienced different levels of climate and land-use change. These sites fall along a gradient of landscape conditions that range from near-pristine (i.e., where vegetation and disturbance have been significantly shaped 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. All the study sites reveal dramatic vegetation reorganization in the past as a result of postglacial climate variations. In nearly-pristine landscapes, like Yellowstone, 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 ~700 years ago with arrival of the Māori people. In the northwestern U.S. and Patagonia, greatest landscape alteration has occurred in the last 150 years with Euro-American settlement. Paleoecology is sometimes the best and only tool for evaluating the degree of this 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.

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

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 (Krawchuk et al. 2009; Gottfried et al. 2012; Duffenbaugh & Field 2013; Elsen & Tingley 2015). To put these projections into the context of ecosystem variability, many studies have examined global and regional biotic vulnerability to future climate change in light of what we know about past climate-vegetation-fire linkages (e.g., Williams & Jackson 2007; 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 non-climatic factors that shape and influence 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 those that have experienced long and intensive human impacts at the other end (Vale 2002). Truly pristine places are mostly non-existent, 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 “near-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. In reality, most landscapes fall somewhere between the two endpoints, supporting both cultural and natural elements. These “intermediate” conditions are shaped by complex interactions 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 both natural structure and diversity on the one hand, while maintaining cultural or utilitarian attributes on the other (Lindenmayer & Hunter 2010).

In this essay, we discuss the importance of paleoecology for evaluating current

landscape status in terms of its naturalness or alteration. We build on a growing body of literature that describes the use of historical and paleoecological data to broaden understanding of: (1) long-term perspectives on the historical range of variability (e.g., Swetnam et al. 1999; Whitlock et al. 2010; Gillson 2015); (2) climate-driven changes in species ranges and vegetation composition (e.g., Williams et al. 2004; Tinner et al. 2013; Iglesias et al. 2014); (3) human alteration of native vegetation, biodiversity and ecosystem services (e.g., Dearing et al. 2012; Colombaroli & Tinner 2013; Conedera et al. 2016); and (4) potential rates of ecological change and no-analog situations (e.g., MacDonald et al. 2008 Williams & Jackson 2007; Willis et al. 2010). We draw on examples from our own research in three continents and two hemispheres with two objectives in mind: illustrate the extent to which the 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. While multiple factors shape conservation strategies, we suggest that knowledge of the past should be given priority consideration.

Our study sites lie within eight 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 northwest U.S. (Fig. 1). Information on past ecological change comes from pollen, plant macrofossil, and charcoal records preserved in radiocarbon-dated sediment cores from lakes and wetlands. Land-use history is inferred from archeological and historical records, ethnographic accounts, paleobotanical studies and models that explicitly consider 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 northwest U.S. and northern Patagonia, for example, have experienced 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 trajectory of land use change is not always unidirectional. For example, land abandonment at the end of the Roman Age in our European sites was associated with forest recovery and a brief return to more natural vegetation (Fig. 2).

In all these regions, the importance of climate change in shaping past vegetation is evident prior to significant human activity (e.g., Whitlock 1993; Tinner et al. 2005, 2009; Colombaroli et al. 2007; Iglesias et al. 2014; Walsh et al. 2015). 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 (~14,650 cal yr BP; “cal yr BP” refers to years before 1950 AD) (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. 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-present between 11,000-6000 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), 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 than before (Fig. 3c; Souto et al. 2015).

Climate became less important as an agent of vegetation change in Europe after the Mesolithic-Neolithic transition, ca. 8000-6000 years ago, when small foraging populations were replaced by larger more sedentary cultures supported by agriculture and pastoralism. In the course of this cultural change, primary forest was lost and fire activity increased (Fig. 3e-h; Table 1) (Tinner et al. 2005; Kaplan et al. 2009; Molinari et al. 2013; Navarro et al. 2015). Changing forest composition, increased levels of burning and agriculture continued in the Bronze Age (~4200-2800 cal yr BP; Fig. 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 Period (~2000-1450 cal yr BP) (Fig. 3e-h) and intensified in the Medieval Period (~500-1500 AD). By the early Modern Period (~1500-1850 AD), nearly all suitable land was under intensive crop, pasture or forest production (Fig. 3e-h). Industrialization in the 18th to 19th century led to profound deforestation in central Europe and the Alps (Fig. 3e,f; 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 converted to flammable shrubland (Fig. 3g,h; garrigue, maquis), leading to increased fire activity in recent decades (San Miguel-Ayanz et al. 2013).

In contrast to the European sites, Diamond L. 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 Māori arrival, ca. 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 ~50% of the native forest in a matter of decades (McWethy et al. 2013). Rapid deforestation was facilitated by the post-fire 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 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 (*Abies alba*) 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, deciduous or evergreen oak in the lowlands and mountains (Fig. 3e,f,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 the finding challenge the validity of ecological niche models that neglect such land-use legacies (Maiorana et al. 2013).

Whitebark pine (*Pinus albicaulis*), a keystone species of high-elevation forests in the northwest U.S., has experienced widespread mortality in recent decades as a result of climate change, fires, non-native pathogens and insect outbreaks (McKinney and Tomback 2011). Ecological niche models based on present climate suggest that 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 about white pine's vulnerability to past climate change and fire. *P. albicaulis* and/or *P. flexilis* was apparently more abundant and widely distributed in the region from 11,000 to 7000 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 and lodgepole pine, were poorly represented (Iglesias et al. 2015). Thus, paleoecological data provides 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*) infestations (Smith et al. 2013; Logan et al. 2010) have no or unclear precedence and are cause for concern.

Cultivation of sweet chestnut (*Castanea sativa*) 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 L. 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, so 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 near-pristine elements with 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: (1) the vulnerability of the different vegetation components to a range of climate conditions (e.g., rapid warming, severe or prolonged drought in the past); (2) the extent to which present vegetation is maintained by climate-driven or anthropogenic fire regimes, and the vulnerability of particular vegetation components and species to changes in fire activity; (3) the identity of species that have benefitted or been disadvantaged by past land-use practices, including the appearance of new taxa and elimination of others; and (4) 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 (Fig. 4). For example, at Battle Ground L. in the northwest U.S., 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 converted to commercial forests (Whitlock et al. 2015). At Diamond L. 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 Māori. 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), recognizing that any restoration goal 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 (Fig. 3g,h), 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 L. Massaciuccoli and Gorgo Basso; non-native pine plantations near Diamond L. and L. Mosquito; commercial *Pseudotsuga* forests near Battle Ground L), in contrast to 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 (Fig. 3g,h), 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; Vannièrè 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 (Paritsis et al. 2015; Simberloff et al. 2010).

Future Perspectives

Ecological history is sometimes regarded as interesting background information in conservation efforts but of little practical value. This viewpoint is becoming 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; Elsen & Tingley 2015; Benito-Garcón et al. 2014). 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, on the other hand, has the potential to return an important native species to Italian and southern Swiss lowland forest, helping to maintain biodiversity and ecosystem services under global warming (Henne et al. 2015; Ruosch et al. 2016).

Beyond serving as a guidepost for restoration, paleoecology can help assess current conditions in light of the historical range of variability (HRV) (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 disturbance 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 (a “new to you” approach; Smith et al. 2016). Responses of species to past warming (i.e., at the onset of the Bølling Interstadial in Europe or during the early Holocene in the northwest U.S.) in near-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, avalanches and landslides) may 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.

In conclusion, paleoecology has been a lively 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 datasets have contributed significantly to our 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 eight 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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Table 1. Information about study sites, their present setting and vegetation history

Region: Site, location, and citation	Present vegetation at site (low to high elevation)	Vegetation response to past climate change	Vegetation response to past land use	Current Landscape condition
Yellowstone National Park, U.S.:	Lodgepole pine (<i>Pinus contorta</i>) forest, with sagebrush (<i>Artemisia tridentata</i>) steppe	8-6 kyr (dry warm summers, high snowpack): more fires	8-0.15 kyr (indigenous foragers): minimal impact	Near-pristine
Cygnets L.		6 kyr-present (cool wet conditions): less fires	~1850 AD (Euro-American settlement): logging, agriculture, fire suppression	
44.660N, 110.615W				

2531 m elev (Whitlock 1993; Millspaugh et al. 2004)			1872 AD: Yellowstone National Park; Since ~1980 AD: ex-urban development	
Northern Patagonia, Argentina: L. Mosquito	Dry woodland/shrubland (<i>Austrocedrus chilensis</i> , <i>Nothofagus antarctica</i> , <i>Maytenus</i>); nearby forest (<i>Nothofagus dombeyi</i> , <i>N. pumilio</i>), pastureland, pine plantations	8-4 kyr (cooler than present summers): expanded <i>Nothofagus</i> forest and steppe, more fires (before 5 kyr) 4 kyr-present (wet warm conditions, increased interannual/decadal variability): expanded <i>Austrocedrus</i> , more fires	8-0.4 kyr (indigenous foragers): minimal impact ~1700 AD (European arrival): grazing, non-native plants Since 1850 AD (Euro-American settlement): deforestation, fires, grazing, pine plantations	Natural/ inhabited
42.489S, 71.397S 553 m elev (Whitlock et al. 2006; Iglesias et al. 2014)				
Northwest U.S.: Battle Ground L.	Mesic-dry conifer forest (<i>Pseudotsuga menziesii</i> , <i>Abies grandis</i> , <i>Tsuga heterophylla</i> , <i>Thuja plicata</i>); remnant prairie woodland (<i>Quercus garryana</i>); cultivated land; managed forests; urbanized land	8-4 kyr (warm dry summers): expanded prairie woodland, more fires 4 kyr-present (cool wet conditions): expansion of mesic-dry forest (<i>Pseudotsuga</i> , <i>Thuja</i> , <i>Tsuga</i>), less fires	8-3 kyr (indigenous foragers): minimal impact 3-0.15 kyr (sedentary populations): more fires ~1820 AD (Euro-American settlement): deforestation, initially more fires, agriculture, managed <i>Pseudotsuga</i> forests	Mosaic
45.804N, 122.494W 154 m elev (Walsh et al. 2008)				
South Island, New Zealand:	Open vegetation (<i>Poaceae</i> , <i>Discaria toumatou</i> , <i>Pteridium</i>);	1 kyr-present: high Last 1000 years (interannual climate	1280 AD-1600 AD (Initial Burning Period): loss of mesic-dry	Unevenly altered

<p>Diamond L.</p> <p>44.648S, 168.963 E, 393 m elev</p> <p>(McWethy et al. 2010)</p>	<p>forest remnants (with <i>Lophozonia menziesii</i> and shrubs); pastureland; pine plantations</p>	<p>variability): negligible impact</p> <p>1400-1850 AD (LIA cooling): negligible impact</p>	<p><i>Lophozonia</i>/podocarp forest, expansion of <i>Lepidospermum</i>, <i>Kunzea</i>, <i>Pteridium</i>, grassland/shrubland</p> <p>1600-1850 AD (Late Māori Period): some small-scale cultivation, small fires</p> <p>Since 1850 AD (European settlement): deforestation, agriculture, initially more fires, <i>Pinus</i> plantations</p>	
<p>Northern Switzerland: Lobsigensee</p> <p>47.032N, 07.265E 514 m elev</p> <p>(Ammann 1989; Tinner et al. 2005)</p>	<p>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>)</p>	<p>8.1-5 kyr (warm moist summers): mixed forests with (<i>Quercus</i>, <i>Fagus</i>, <i>Tilia</i>, <i>Ulmus</i>)</p> <p>5 kyr-present (trend to cooler moist summers): no discernible impact</p>	<p>7.2 -4.3 kyr (Neolithic): slash and burns; deforestation, high fire, <i>Fagus</i> expansion, species reductions/extirpations (<i>Hedera</i>, <i>Ulmus</i>, <i>Tilia</i>, <i>Fraxinus</i>, <i>Acer</i>)</p> <p>4.2-2.8 kyr (Bronze Age): increased deforestation</p> <p>2.8-1.4 kyr (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>, highest fires</p> <p>600-1950 AD (Medieval, Modern): more cultivation, managed forests, less fires</p> <p>1950-2000 AD: industrial agriculture</p>	<p>Unevenly altered</p>

<p>Southern Switzerland:</p> <p>L. Origlio</p> <p>46.055N, 08.944E</p> <p>416 m elev</p> <p>(Tinner et al. 1999)</p>	<p>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</p>	<p>9.2-5 kyr (warm moist summers): <i>Abies</i>, <i>Tilia</i>, <i>Ulmus</i>, <i>Fraxinus</i>, <i>Quercus</i>, <i>Acer</i> co-dominance</p> <p>5 kyr-present (trend to cooler summers): no discernible impact</p>	<p>7.5 -4.3 kyr (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>) & expansions (<i>Quercus</i>, <i>Fagus</i>, <i>Alnus</i>, <i>Corylus</i>, <i>Betula</i>)</p> <p>4.2-2.8 kyr (Bronze Age): increased deforestation & open land</p> <p>2.8-1.4 kyr (Iron Age, Roman Age, Migration Period): deforestation pulses, highest fires, <i>Castanea</i> dominance, <i>Juglans</i> cultivation</p> <p>600-1850 AD (Medieval, Modern): <i>Castanea</i> cultivation, orchards, open land, less fires</p> <p>1850-1950 AD: managed forests, intense agriculture, less fires</p> <p>Since 1950 AD: afforestation, less agriculture</p>	<p>Unevenly-intensely altered</p>
<p>Tuscany Italy:</p> <p>L. Massaciuccoli</p> <p>43.833N, 10.333E</p> <p>1 m elev</p> <p>(Colombaroli</p>	<p>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> & evergreen <i>Q. ilex</i>, <i>Pistacia lentiscus</i>, <i>Phillyrea angustifolia</i>); cultivated fields, vineyards, orchards</p>	<p>8-4 kyr (warm, dry summers): abundant <i>Abies</i></p> <p>4 kyr-present (trend to cooler, moister summers and warmer, drier winters, greater interannual/decadal variability): expansion of</p>	<p>8-4.5 kyr (Neolithic): slash & burns, deforestation, <i>Abies</i> extirpation, more fires</p> <p>4.5-2.9 kyr (Bronze Age): expansion of <i>Quercus ilex</i>, <i>Phyllirea</i> shrubland & grassland, less fires</p> <p>2.9-1.4 kyr (Iron Age, Roman Age, Migration Period): intensive</p>	<p>Intensely altered</p>

et al. 2007)

evergreen oak

deforestation, fires

600-1950 AD (Medieval, Modern): expansion of *Phyllirea* shrubland & cultivated land, more fires

Since 1950 AD: landscape abandonment, industrial agriculture, reforestation, less fires

<p>Sicily:</p> <p>Gorgo Bosso</p> <p>37.617N, 12.650E</p> <p>6 m elev</p> <p>(Tinner et al. 2009)</p>	<p>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>)</p>	<p>8-5 kyr (hot, dry summers, temperate, moist winters): expansion of evergreen broadleaved forests into natural maquis</p> <p>5 kyr - present: (trend to cooler, moister summers and drier, warmer winters): no discernible impact</p>	<p>8-4.5 kyr (Neolithic): short declines of evergreen oak-olive forest, <i>Ficus</i> & cereal cultivation, low fire activity</p> <p>4.5-2.9 kyr (Bronze Age): periods of open land expansion</p> <p>2.9-1.4 kyr (Iron Age, Roman Age, Migration Period): destruction of evergreen broadleaved forests, cultivation of <i>Juglans</i> & <i>Castanea</i>, expansion of shrubland (maquis), garrigue & grasslands, highest fires</p> <p>600 AD-present (Medieval/Historical): grazing, industrial agriculture, non-native plants (e.g. <i>Eucalyptus</i>), few fires initially, but increase in last 200 years</p>	<p>Fully altered</p>
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Figure Captions

Figure 1. Maps showing the location of the study sites in a) northwestern U.S., b) Switzerland and Italy, c) northern Patagonia in Argentina, and d) South Island, New Zealand.

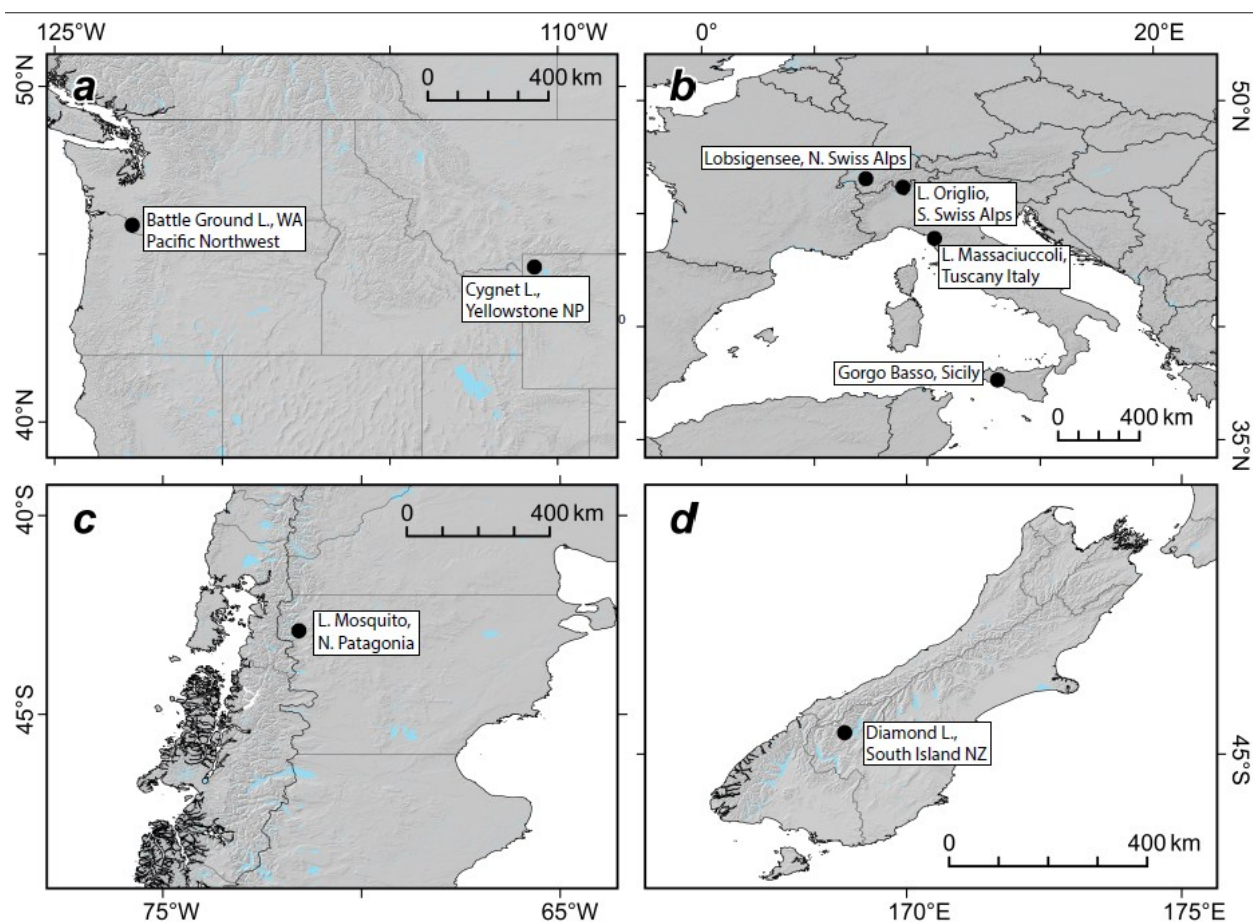


Figure 2. Degree of landscape alteration during the last 8000 years in the study regions. The y-axis ranks landscape conditions from pristine to altered (*sensu* Vale, 2002) based on an interpretation of the pollen and charcoal data in Figure 1. The graph shows the steplike progression of land-use change, which over time has shifted the vegetation of the study sites to more altered conditions. Note that the extensive deforestation during the Iron Age/Roman Age 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.

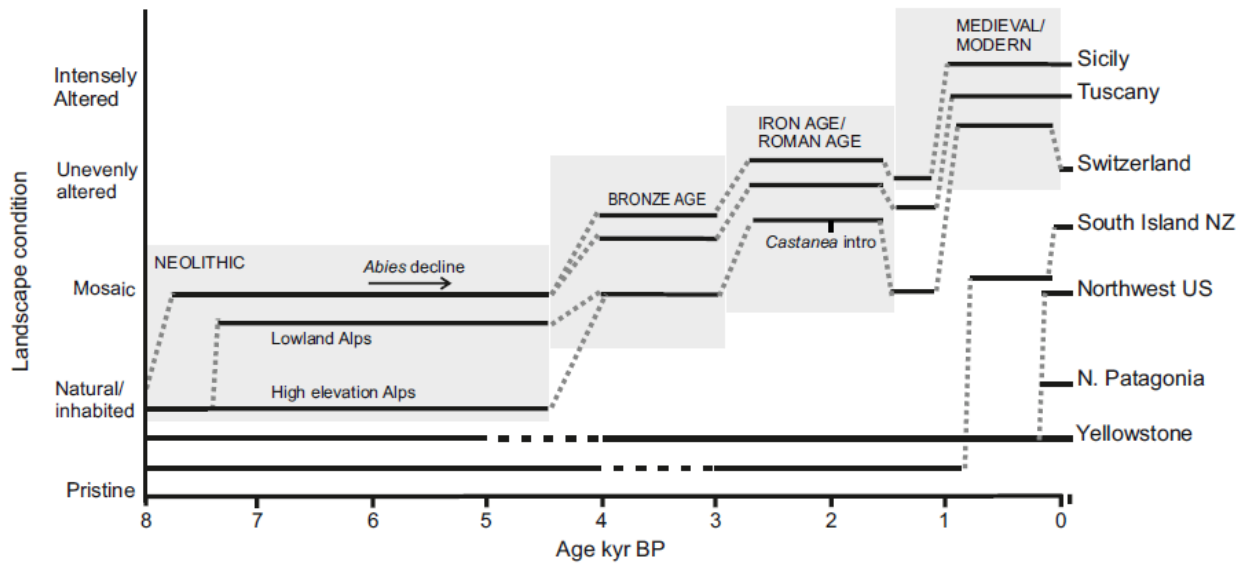


Figure 3. Pollen percentage data and charcoal accumulation rates (CHAR) from our study sites.

The left column features non-European examples and the right column shows European records. CHAR data ($\text{particles cm}^{-2} \text{yr}^{-1}$) describe variations in fire activity and peaks of high CHAR are usually interpreted as individual fire episodes (Whitlock & Larsen 2001). The colored bar at the base of each diagram shows the changing anomaly (relative to present) of incoming summer radiation (i.e., summer insolation), one of the large-scale, but slowly varying climate forcings over the last 8000 years. Summer insolation reached a maximum between 11,000-9000 years ago in the Northern Hemisphere, leading to a period of warmer-than-present conditions; it steadily declined to present values, resulting in gradual cooling. The opposite trend in summer insolation characterizes the Southern Hemisphere records. The records for Cygnet L., Battle Ground L., and L. Mosquito (Fig. 3a-c) show Pre-Euro-American (prior to ~1850AD) and Post-Euro-American (after ~1850 AD) periods. Diamond L. (South Island NZ) (Fig. 3d) shows no change in summer insolation as the record shown only spans the last 1000 years. Pre Māori refers to the record prior to the arrival of people, IBP is the Initial Burning Period (1300-1600 AD) soon after Māori arrival, and Late Māori is the period prior to European

settlement (Eur) in the last 100 years. Land-use periods in Fig. 3e-h are abbreviated as follows: BA=Bronze Age, IA-Rom=Iron Age-Roman period, MP-Mod=Medieval-Modern period. For additional information, see Table 1.

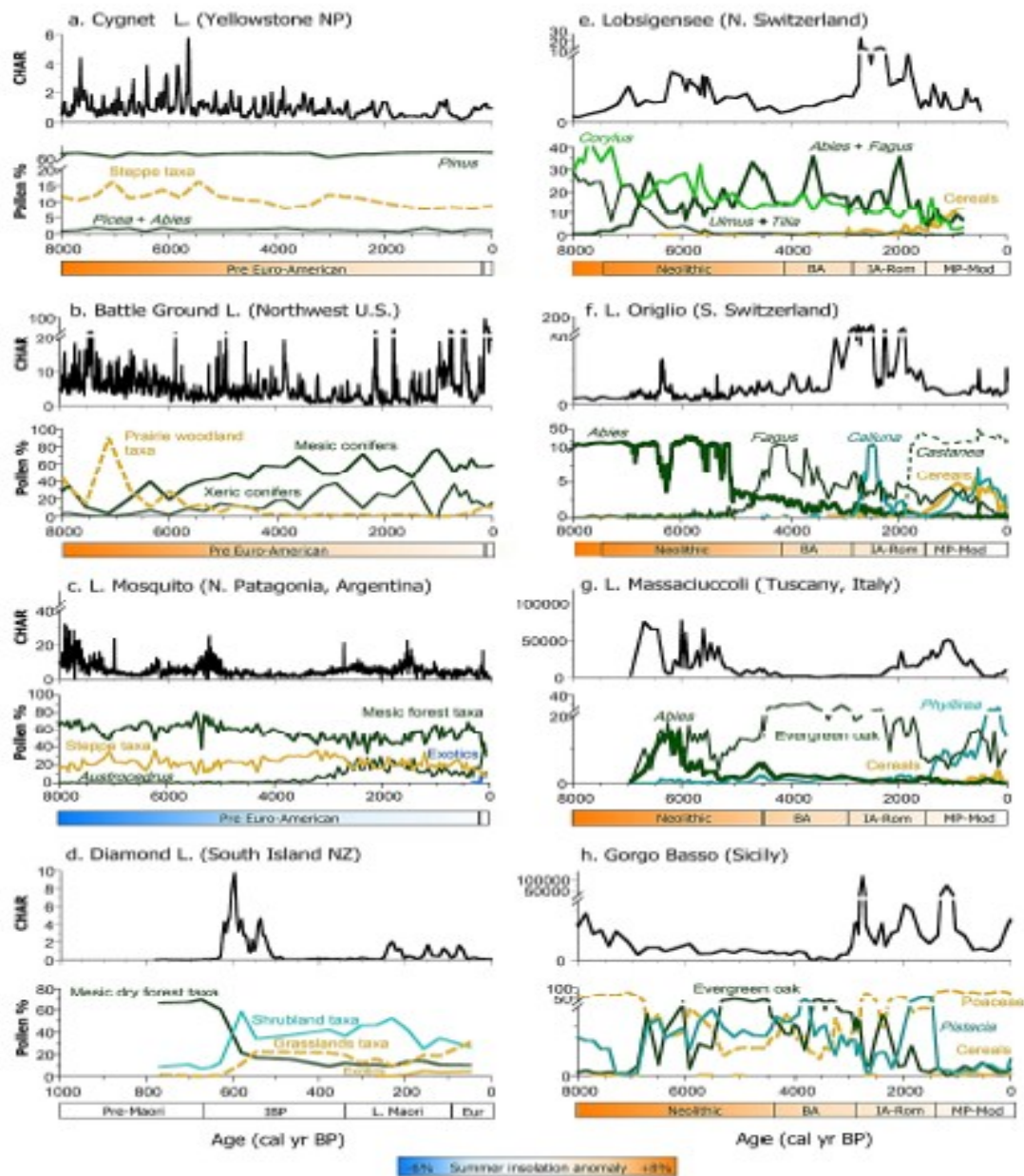


Figure 4. Environmental and conifer history in the Greater Yellowstone region over the last 15,000 years, based on 14 pollen records and 6 charcoal records (see Iglesias et al. 2015). Shown are long-term climate trends (see Fig. 3 for explanation of insolation anomalies), generalized trends in pollen abundance of Engelmann spruce, fire activity, white pines, and lodgepole pine (after Iglesias et al. 2015). Because charcoal data were not analyzed the same at every site, fire activity is presented as charcoal anomalies with respect to the Holocene mean, scaled by the standard deviation of each record. The data suggest that white pines were abundant during the early-Holocene (11,000-7000 cal yr B), when summers were warmer than present, fire activity was higher, and competing spruce and lodgepole pine trees were at a relatively low level.

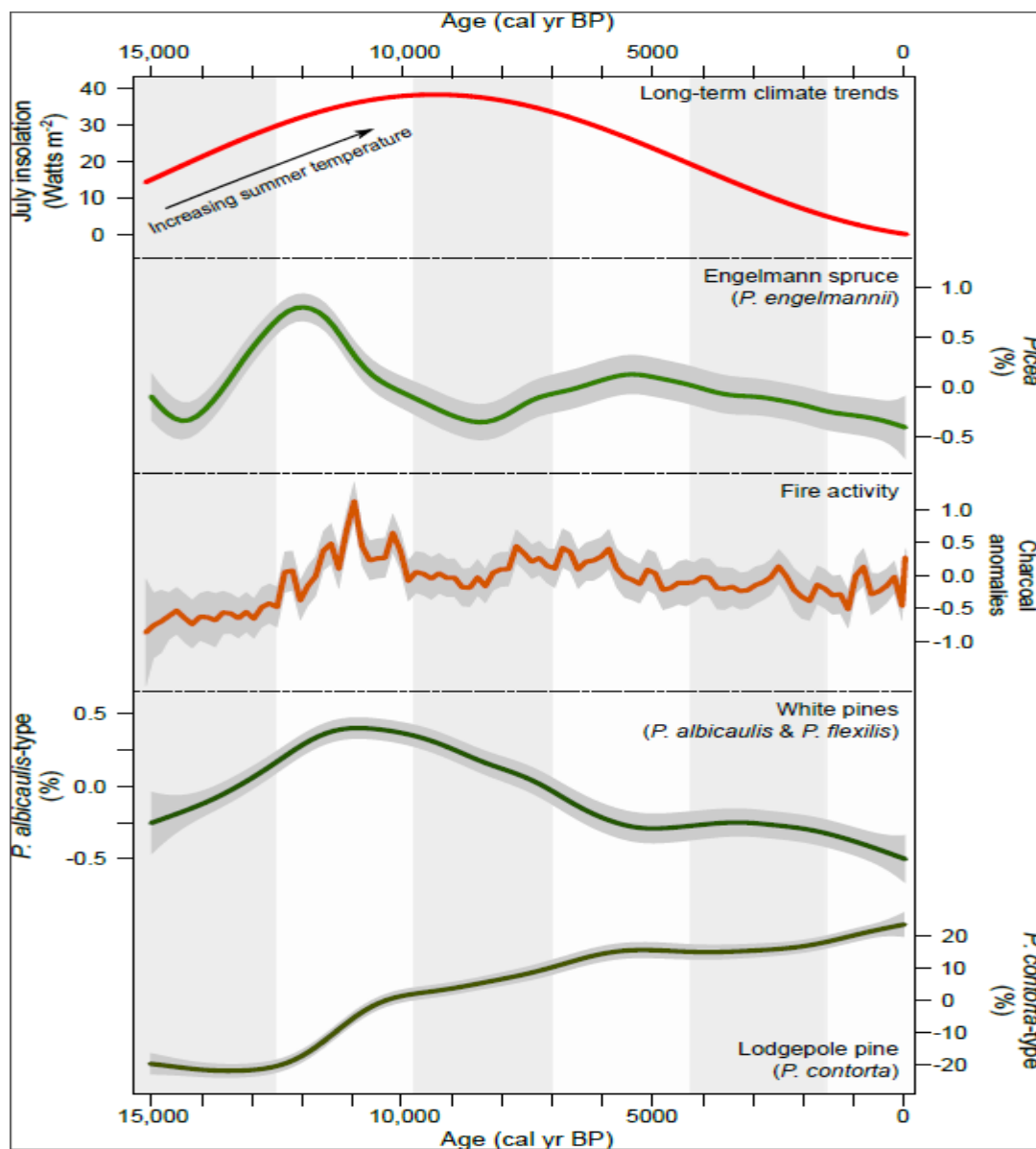


Figure 5. The application of paleoecology in informing conservation strategies, depending on the the landscape condition and the legacy of past land use. In near-pristine landscapes, management objectives to maintain ecological processes benefit from knowledge of long-term ecosystem dynamics; in intermediate landscapes, objectives to retain both cultural and natural components require information on past 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. We suggest that intermediate landscapes require the most intensive conservation effort, given the objectives to maintain both cultural and natural components. HRV=Historical range of variability.

