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Forest Ecology and Management 215 (2005) 51–68
Forest Ecology and Management
www.elsevier.com/locate/foreco

Pine forest expansion along a forest-meadow ecotone in northeastern California, USA

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Received 10 January 2005; received in revised form 2 May 2005; accepted 4 May 2005

Abstract

Type conversions of vegetation are often triggered by changes in one or more limiting environmental factors. Such changes are particularly evident along montane forest-meadow ecotones, where historical changes in fire, grazing and climate have occurred. In this paper, we reconstruct spatial and temporal variation in climate, livestock grazing and fire for 11 meadow inclusions in the pine-dominated forest of northeastern California, USA. We then compare this environmental variation to temporal patterns of tree invasion by dating the establishment of 1420 trees, saplings and seedlings. Invasive trees included ponderosa pine (*Pinus ponderosa* Laws.), Jeffrey pine (*Pinus jeffreyi* Grev and Balf.), lodgepole pine (*Pinus contorta* var. *murrayana* Loudon (Grev and Balf.)) and western juniper (*Juniper occidentalis* Hook.). Before the arrival of Euro-Americans in 1849, fires burned with a median interval of 11 years based on 1–3 ha composite records from multiple trees, and 14 years using records from individual trees. There was substantial variation in the date of the last recorded fire within and among meadows, but fire was rare after 1905. The onset of tree establishment varied among meadows, but followed the reduction and removal of fire. Livestock grazing also varied among meadows, and the highest establishment rates occurred when grazing was moderate. Mean tree establishment was 22.9 trees/ha/decade during the late 19th century when grazing was unregulated, 62.6 trees/ha/decade when sheep were present, but regulated, and 40.7 trees/hectare/decade after sheep were replaced with cattle. Ponderosa and Jeffrey pine established during a range of temperature and precipitation conditions, but establishment was greater when summer precipitation was below normal, annual temperatures were normal and springs were cool. Although changes in disturbance and climate were associated with tree establishment, the persistence of trees at the meadow edge is best explained by continued fire exclusion. With the long-term absence of fire the local effects of different disturbance histories are being lost.

Keywords: Fire; Grazing; Climate variation; Scale; Ponderosa pine; Ecotone

1. Introduction

Ecosystem change may result from large-scale processes, related to climate, or local factors including variation in site conditions and land use (Foster, 1992; Heyerdahl et al., 2001; Hessl and Graumlich, 2002;

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doi:10.1016/j.foreco.2005.05.003

Morrison and Bolger, 2002). Management of ecosystems can be especially challenging when conditions are sensitive to multiple, interactive factors (Paine et al., 1998), particularly when only some of those factors can be altered. As an added complication for managers, both historical climate variability and anthropogenic activities can bestow long-term legacies that can mediate ecosystem dynamics for decades or centuries (Asselin et al., 2001; Foster et al., 2003; Kulakowski et al., 2003). Greater insight into these historical processes provides a context for prospective management actions and can help managers formulate more informed long-term goals (Swetnam et al., 1999; Allen et al., 2002; Hessburg and Agee, 2003).

Ecotones that separate forests and meadows are highly sensitive to variation in environmental factors, and as such, they provide useful locations to evaluate the effects of climate and land use change. Research into the causes of ecotonal change has not provided consistent results, however. At high elevations and high latitudes, tree encroachment is primarily thought to be a response to warming temperatures and reduced snow pack (Franklin et al., 1971; MacDonald et al., 1993; Taylor, 1995; Hessl and Baker, 1997), although in places, livestock grazing may have also led to subalpine tree establishment (Dunwiddie, 1977). At lower elevations, researchers have evoked a wider range of explanations for tree encroachment into meadows, in part because these elevations experienced a more complex land use history (e.g., Vale, 1977; Dublin et al., 1990; Belsky and Blumenthal, 1997; McPherson, 1997). Among the most influential factors affecting low-elevation forest-meadow ecotones is a change in the fire regime. Historically, frequent surface fires are thought to have limited the extent of woody shrubs and trees until fires were suppressed in the late 19th and early 20th centuries (Vale, 1975, 1977; Burkhardt and Tisdale, 1976; Brown and Sieg, 1999; Hadley, 1999). Others have argued that heavy livestock grazing contributed to increased tree cover by (1) reducing competition from grass and herbs and (2) by limiting fire spread by consuming fine fuel (Rummell, 1951; Madany and West, 1983; Zimmerman and Neuenschwander, 1984; Doescher et al., 1989; Savage and Swetnam, 1990; Archer, 1994; Harris et al., 2003). Yet others have documented that dynamics are dominated by climate variation that leads to pulses of tree establishment and mortality (Savage et al., 1996; Allen and Breshears, 1998). In landscapes with strong differences in slope, the importance of climate is especially notable (Mast et al., 1997; Miller and Halpern, 1998). To most of these researchers, fire suppression, livestock grazing and climate variability provided contributing, if not competing explanations for ecotonal change. In complex systems, it is not surprising that change reflects the influence of multiple factors, but when one or more factors are not likely to recur, future dynamics may differ from those of the past due to contingencies.

Historical contingencies are difficult to assess when causal factors are assumed to have been similar across the landscape. While regional trends in climate and land use are generally acknowledged, fine scale variation in disturbances from grazing and fire may have important effects on local processes. Past studies to address tree encroachment into montane meadows have focused on a relatively few sites or they have lacked a detailed knowledge of site histories. With greater attention to disturbance histories, contingent effects could become more apparent.

In this paper, we examine the effects of historical changes in fire, grazing and climate on tree establishment along the ecotone of 11 montane meadows in northeastern California, USA. We hypothesize that grazing, fire and climate each contributed to increased tree establishment. In particular, we predict that tree establishment increased with intermediate levels of grazing, in response to fire suppression and in the absence of drought. Unlike prior research, we assess the importance of grazing and fire suppression by analyzing how spatial variation in these factors across the landscape contributed to ecotonal change. We then discuss whether differences in the spatial and temporal pattern of historic disturbances have had a persistent effect on vegetation.

2. Study area

The ecotones examined are located in the southeastern Cascades Range of northern California in Lassen National Forest (Fig. 1). The landscape is composed of forested shield volcanoes, cinder cones and basalt flows that date from the Late Quaternary. These features are interspersed with a network of broad alluvial meadows that vary in elevation from