Plant Ecol (2012) 213:555–568
DOI 10.1007/s11258-012-0021-9

Spatio-temporal patterns of tree establishment are indicative of biotic interactions during early invasion of a montane meadow

Janine M. Rice · Charles B. Halpern ·
Joseph A. Antos · Julia A. Jones

Received: 27 June 2011 / Accepted: 5 January 2012 / Published online: 29 January 2012

Abstract Tree invasions of grasslands are occurring globally, with profound consequences for ecosystem structure and function. We explore the spatio-temporal dynamics of tree invasion of a montane meadow in the Cascade Mountains of Oregon, where meadow loss is a conservation concern. We examine the early stages of invasion, where extrinsic and intrinsic processes can be clearly delineated. In a 0.21-ha plot, we mapped and aged 929 trees $\geq$0.3-m tall, yielding a detailed record of the spatio-temporal dynamics of invasion. For the primary species, *Abies grandis* and *Pinus contorta*, we correlated age structures (unimodal in both species) with climate (precipitation, temperature, and snowpack) and cone production, but found weak or non-significant relationships. Evidence of biotic interactions within and between species was obtained by examining the spatial associations of trees to a distance of 5 m and how these changed over time. We used multiple methods including uni- and bivariate forms of the Ripley's K and pair-correlation function (pcf) (corrected for inhomogeneity), the J-function, an evolving nearest-neighbor metric, and a test for directional bias in establishment. *Pinus* and *Abies* contributed in contrasting ways to the pace and spatial structure of invasion. Shade-intolerant *Pinus* tended to establish in the open, initiating clusters. In contrast, shade-tolerant *Abies* established in association with *Pinus* or in conspecific clusters. Preferential establishment of *Abies* to the north of older *Pinus* suggests that facilitation occurs by shading. The factors responsible for initial establishment remain unresolved, but positive interactions are pivotal in accelerating invasions, once initiated. Similar processes are likely to occur in other grasslands undergoing rapid conversion to woodland or forest. In combination, analyses of spatial and temporal patterns of establishment provide insight into the processes that structure invasions.

Keywords Biotic interactions · Tree invasion · Spatial point-pattern analysis · Facilitation · Tree–tree interactions

Introduction

Woody plant invasions of grasslands are occurring globally with major consequences for biodiversity and

J. M. Rice · J. A. Jones
Department of Geosciences, Oregon State University,
Corvallis, OR 97331, USA

J. M. Rice (✉)
Cooperative Institute for Research in Environmental
Sciences, University of Colorado, 240 W. Prospect St.,
Fort Collins, CO 80526, USA
e-mail: j9rice@hotmail.com

C. B. Halpern
School of Environmental and Forest Sciences, University
of Washington, Box 352100, Seattle, WA 98195, USA

J. A. Antos
Department of Biology, University of Victoria,
P.O. Box 3020, Victoria, BC V8W 3N5, Canada

ecosystem functioning (Scholes and Archer 1997; Jackson et al. 2002; Browning et al. 2008). Conversion to woodland or forest in systems long dominated by herbaceous plants implies a shift in the processes that once limited tree establishment—typically, extrinsic factors, such as fire, grazing, or climate (Vale 1981; Scholes and Archer 1997; Coop and Givnish 2008). However, limited attention has been paid to intrinsic factors—biotic interactions or positive feedbacks—that can maintain or accelerate tree invasions. For example, trees can modify their environments in ways that enhance further recruitment (Scholes and Archer 1997; Pugnaire et al. 2004; Haugo and Halpern 2010). Evidence of these biotic interactions can be inferred from spatial associations and how these develop over time relative to other temporally varying influences (disturbance, climate, or seed availability).

Spatial patterns of association are commonly used as evidence of negative or positive interactions (Kenkel 1988; Duarte et al. 2006; Gray and He 2009). Inferring process from pattern requires caution, however. Negative associations may reflect not only competitive interactions, but differing responses to environmental heterogeneity. Conversely, positive associations can reflect facilitation, but also dispersal limitation or similar responses to environmental heterogeneity. Contrasting patterns of association within versus between species can be indicative of biotic versus environmental controls on establishment. Timing of spatial aggregation can also provide evidence of biotic interactions. Facilitation is unlikely to explain establishment in even-aged cohorts, but more likely when individuals differ in age.

Incorporating time in the analysis of spatial pattern poses challenges. Accurate estimates of tree age are needed, but can be compromised by damage or disease. In addition, mortality erodes evidence of past establishment and of tree–tree interactions. Second-order point-pattern analyses, especially the widely used Ripley's K, have limited capacity to accurately detect the scale and statistical significance of pattern, but can be used to seek bivariate relationships (Goreaud and Pelissier 2003; Wiegand and Moloney 2004; Loosmore and Ford 2006; Lynch and Moorcroft 2008). Other methods, such as the J-function (van Lieshout and Baddeley 1996) or modifications of nearest-neighbor analysis permit finer resolution of patterns in space and time, but are constrained in other ways. Ultimately, multiple approaches are needed to fully assess the dimensions of species, time, and space in the dynamics of tree invasions.

Here, we explore how abiotic and biotic factors shape invasions of a montane meadow by *Pinus contorta* and *Abies grandis*. We focus on recent invasions (mid- to late 1900s), a period for which trees can be precisely aged, mortality is limited, climate records are complete, and cone-production data exist. Our objectives are threefold: (1) to quantify the importance of climate, seed availability, and biotic interactions for tree establishment, (2) to employ spatial point-pattern analyses at increasingly finer temporal resolution to examine changes in the nature and strength of interactions within and between tree species, and (3) to illustrate how multiple sources of evidence, including age structures, climate and cone-production data, life histories, and spatial associations offer insight into the dynamics of tree invasions.

Methods

Study area and species

The study was conducted at Bunchgrass Ridge in the central Cascade Range, Oregon, USA (44°17′N, 121°57′W). The site is on a gently sloping plateau with a southwest exposure at ~1350-m elevation on the western margin of the High Cascades province. Soils are Vitric Melanocryands—generally deep fine to very-fine-sandy loams derived from andesitic basalt and tephra deposits (D. Lammers, personal communication). Climate is characterized by cool wet winters and warm dry summers. For 1905–2004, mean monthly temperature averaged 3.2°C (Jan) and 17.7°C (Jul) at Cascadia (293 m) and 1.1°C (Jan) and 18.5°C (Jul) at McKenzie Bridge (451 m), the nearest climate stations 10–20 km to the southwest (http://cdiac.ornl.gov/epubs/ndp/ushcn/ushcn.html). Annual precipitation averaged 1,567 mm (Cascadia) and 1,631 mm (McKenzie Bridge). At Bunchgrass Ridge, most precipitation falls as snow; snowpack can exceed 2 m in late winter and persist into June.

Fire is the primary agent of disturbance but is infrequent (>100 years). There is no direct evidence of fire for the past two centuries at Bunchgrass Ridge (Halpern et al. 2010). However, Native Americans or European settlers may have set low-intensity fires to maintain openings (Boyd 1999). Fire suppression in this region has occurred since the early 1900s (Takaoka and Swanson 2008). Although there are no records of sheep grazing for the study area, grazing was widespread in the Cascades from the late 1800s to early 1900s (Elliot 1946; Johnson 1985). Grazing allotment closure correlates with the onset of invasion in other meadows of this region (Miller and Halpern 1998).

The study area is a mosaic of meadows and forests of varying age resulting from two centuries of tree encroachment (Halpern et al. 2010). Meadows are diverse communities of graminoids and forbs (Haugo and Halpern 2007). *Pinus contorta* and *Abies grandis* are the principal invading tree species, but differ in reproductive and ecophysiological traits (Minore 1979; Foiles et al. 1990; Lotan and Critchfield 1990). *Pinus* is shade intolerant and shorter lived (>100 years), but tolerates a broad range of environments. It has rapid early growth, can reproduce at a young age (5–10 years), and produces abundant cone crops every 1–3 years. Germination and early survival are inhibited by shade and competition, but seedlings are more frost- and drought-tolerant than those of *Abies* (Minore 1979; Lotan and Critchfield 1990). *Abies* is longer lived (>300 years), shade tolerant, reproduces later (~20 years), and produces cone crops every 2–3 years. Its seeds are smaller and disperse further than those of *Pinus* (Foiles et al. 1990; Lotan and Critchfield 1990). Seedling survival is inhibited by summer heat and drought, but favored by moderate shade (Minore 1979; Foiles et al. 1990).

Plot selection, tree mapping, and aging

Aerial photographs and field reconnaissance were used to identify a >0.5-ha area of open meadow and recent encroachment. Surrounding areas included larger meadows and older forests stemming from previous invasions (Halpern et al. 2010). In 2004, we established a 50 × 100-m grid and targeted a smaller area (30 × 70 m; 0.21 ha) for detailed analysis. Within this, all live trees ($n = 929$) and snags ($n = 44$) $\geq$0.3-m tall were mapped (nearest 0.1 m). Live trees were aged from increment cores ($n = 42$) or basal cross-sections ($n = 887$). Samples were prepared using standard methods and annual rings were counted under 10–40× magnification. Ring-pattern templates were used to estimate ages for cores lacking pith ($n = 31$). As needed, ages were adjusted for sample height from age–height regressions. However, >95% of trees were aged from basal sections, providing highly accurate estimates of establishment dates. Population age structures were developed for *Pinus* ($n = 231$) and *Abies* ($n = 644$).

Correlations of tree establishment with climatic variables and cone production

We tested whether timing of establishment correlated with variation in climate. For each species, we correlated (Pearson's r) annual rates of establishment with monthly or seasonal air temperature, precipitation, and snowpack (snow water equivalent or SWE, Jan–Apr) for 1964–1996, the period of non-zero establishment in both species. Seasonal means were computed for fall (Sept–Nov), winter (Dec–Feb), spring (Mar–May), and summer (Jun–Aug). Temperature and precipitation data were from meteorological stations at Cascadia and McKenzie Bridge (see above) and SWE data, from SNOTEL sites at Hogg Pass (1,460 m) and McKenzie Pass (1,463 m) (ftp://ftp-fc.sc.egov.usda.gov/OR/snow/snowcourse/or_data/). SWE before 1982 was estimated from snow depth using assumptions about snow density. Significance was judged at $\alpha = 0.01$.

We tested whether rates of *Abies* establishment correlated with regional trends in cone production in the previous year (no similar data for *Pinus*) using cone-count records from four Cascade Range locations: Lost Prairie (1963–1986), Peterson Prairie (1963–2003), Bessie Rock (1967–2003), and Big Meadow Creek (1963–1978) (http://lterweb.forestry.oregonstate.edu/mdaccess/metadownload.aspx?dbcode=TV019). These consist of annual visual counts of cones on marked trees ($n = 20$–32 trees/location). Correlations were based on the average count for all locations censused in a particular year ($n > 60$ trees), but were limited to the period of non-zero tree establishment (1964–1996). Synchrony of cone production within locations was high ($r > 0.85$, $P < 0.02$, for > 85% of pairs of trees), but more variable among locations (r: 0.48–0.92, $P < 0.003$). Given the cyclical nature of cone production, we also tested for annual deviations in establishment from longer-term trends. We first used a χ^2 test to determine whether positive deviations from the local mean (7-year running average) occurred more frequently than expected after mast years (years with mean cones/tree >20 at all locations; Foiles et al. 1990). We then correlated the mean cone count with the magnitude of departure of establishment in the following year from the local mean (7-year running average).

Spatial patterns of tree establishment and changes over time

To describe changes in overall density and spatial distributions of *Pinus* and *Abies*, we used establishment dates and *x*/*y* locations of trees to produce stem maps of cumulative establishment at 20-year intervals (1945–2004). These revealed large-scale heterogeneity in tree distributions—elongate (10–20 m) clusters oriented SW–NE, likely related to unmeasured edaphic features—but of limited relevance to our objectives. We address this heterogeneity by applying statistical methods that accommodate inhomogeneity (Perry et al. 2006), and by limiting interpretations to the small spatial scales (<5 m) at which biotic interactions can occur among these small trees.

We conducted second-order point-pattern analyses of tree-location data to test for associations within and between *Pinus* and *Abies*. These examine the frequencies of all pairwise distances in a dataset. We used five second-order functions: uni- and bivariate forms of Ripley's *K* corrected for inhomogeneity (KI and cross-KI); uni- and bivariate pair-correlation functions corrected for inhomogeneity (pcfI and cross-pcfI), and the J-function. Second-order analysis involves consideration of multiple issues: (1) inhomogeneity in the data, (2) whether the function is cumulative or not, (3) edge correction, (4) determination of statistical significance, and (5) whether data involve pairwise distances among points, empty space, or both. Inhomogeneity, or large-scale clustering (revealed by our tree maps), can bias detection of clustering at finer scales (Wiegand and Moloney 2004, Schiffers et al. 2008). KI is a univariate second-order function that computes a generalization of Ripley's *K* function for inhomogeneous point patterns (Baddeley et al. 2000b). KI adjusts the expected frequency of points separated by a given distance according to the non-stationary observed frequencies of these pairs. Because Ripley's *K* (and hence KI and cross-KI) is a cumulative distribution function (Ripley 1977; Diggle 1983), patterns at a finer scales can influence patterns apparent at larger scales. The pair-correlation function (pcf) (Perry et al. 2006) avoids this problem by examining frequencies of pairs of points in successive rings.

To test for conspecific clustering in *Abies* and *Pinus*, we used univariate KI and pcfI. For each species, we tested all stems and stems of two age classes, "mature" and "juvenile." Mature trees were $\geq$30 years ($n = 135$ *Abies*, $n = 42$ *Pinus*), and juveniles were <30 years ($n = 509$ *Abies*, $n = 189$ *Pinus*) in 2004. Mature trees represented a protracted period of low-density establishment (1916–1965) and juveniles, more recent, high-density establishment beginning in ~1967 for *Abies* and ~1980 for *Pinus* (Fig. 1). To examine relationships between species or age classes of trees (six pair-wise comparisons), we used bivariate second-order analysis (cross-KI and cross-pcfI). For each method, we used an isotropic edge correction developed by Ripley (Yamada and Rogerson 2003). Each function was computed at 0.1-m interval up to 5 m.

In second-order point-pattern analysis, clustering or dispersion is inferred if the observed function departs from a simulation envelope representing a random distribution. The latter is created from minima and maxima of functions estimated from random distributions generated with the same number of points as the dataset. However, an envelope of, e.g., 100 simulated distributions is not equivalent to a significance level of 0.01 because the minima and maxima that define the envelope may derive from <100 simulations (Loosmore and Ford 2006). We interpret clustering and dispersion based on envelopes of 500 simulations, but do not assign a specific statistical significance.

In second-order analysis, pairwise distances are usually among points but also may involve empty space or both. The J-function (van Lieshout and Baddeley 1996; Thonnes and van Lieshout 1999) is the ratio of G(r), the cumulative distribution function of distances between nearest-neighbor points (g-function), and F(r), the cumulative distribution function of distances between randomly selected points and their nearest neighbors (f-function). J-function values <1 indicate clustering; values >1 indicate dispersion. The function does not require an edge correction (Baddeley et al. 2000a). We tested how clustering changed over time within each species computing the function at 0.1-m interval (up to 5 m) at 5- to 10-year interval from 1965 to 2000. All point-pattern analyses were conducted in R using the spatstat package (for KI, pcfI, cross-pcfI, and J-function;

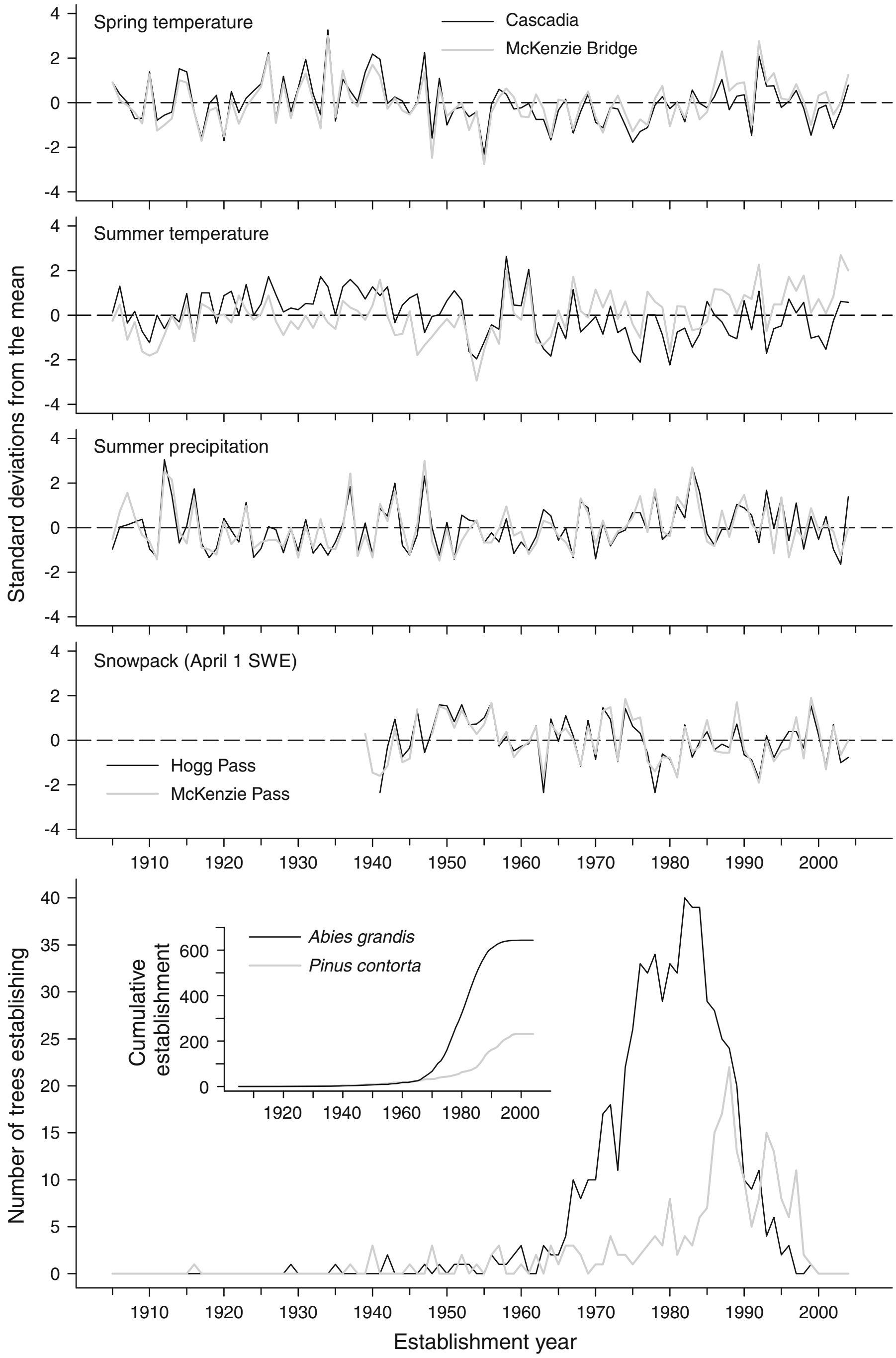

Fig. 1 Temporal variation in climate between 1905 and 2004 (expressed as standard deviations from the mean) and the population age structure and cumulative establishment of *Pinus* ($n = 231$) and *Abies* ($n = 644$) $\geq$ 0.3-m tall in the 0.21-ha plot. See "Methods", "Study area and species" sections for details on climate stations and variables

http://www.spatstat.org/) or ecespa package (cross-KI; http://cran.r-project.org/web/packages/s/ecespa/).

We used an evolving nearest-neighbor algorithm (developed in Visual Basic) to describe changes in average distance between each newly established tree and its nearest preceding neighbor. Distances were computed for each species for each of 13 intervals (1935–1997). Interval widths varied from 20 years when establishment was low, to 2–3 years when establishment was high. We excluded 34 trees with nearest neighbors outside the plot.

Finally, we assessed whether directional bias in recruitment could have contributed to infilling within the large SW- to NE-trending clusters evident in the tree maps. We quantified the angular distributions of trees establishing adjacent to potential "benefactors" (Callaway 2007), limiting the radius of influence to 2 m (a distance suggested by previous analyses). We used benefactors that established at ≥4 m from neighbors to avoid overlap in zones of influence. For each of 17 benefactors (4 *Abies*, 13 *Pinus*), we computed cumulative establishment in four quadrants defined by the orientation of the elongate clusters—SW, NW, NE, and SE. We then determined whether establishment was biased (1) parallel with the clusters (SW + NE vs. NW + SE), or (2) to the north (NW + NE vs. SW + SE), consistent with a shading effect (Haase 2001). We limited these to qualitative comparisons because of large variation in recruitment density.

Results

Timing and density of invasion

Trees first established in 1916 (*Pinus*) and 1929 (*Abies*) although recruitment remained low for many decades (Fig. 1). Establishment of *Abies* increased markedly in the late 1960s, peaked in 1983, and then declined abruptly. Establishment of *Pinus* increased more slowly and peaked later (1988), then declined. In 2004, densities of live *Pinus* and *Abies* ≥0.3-m tall were 1,100 and 3,067 ha^{-1}, respectively. Dead stems comprised <7% of the total (81 *Pinus* ha^{-1} and 181 *Abies* ha^{-1}).

Correlations of tree establishment with climatic variables and cone production

Tree establishment rates showed weak, mostly non-significant relationships with climate (Fig. 2). Although weak, patterns were consistent with species' life histories. For *Pinus*, correlations with monthly

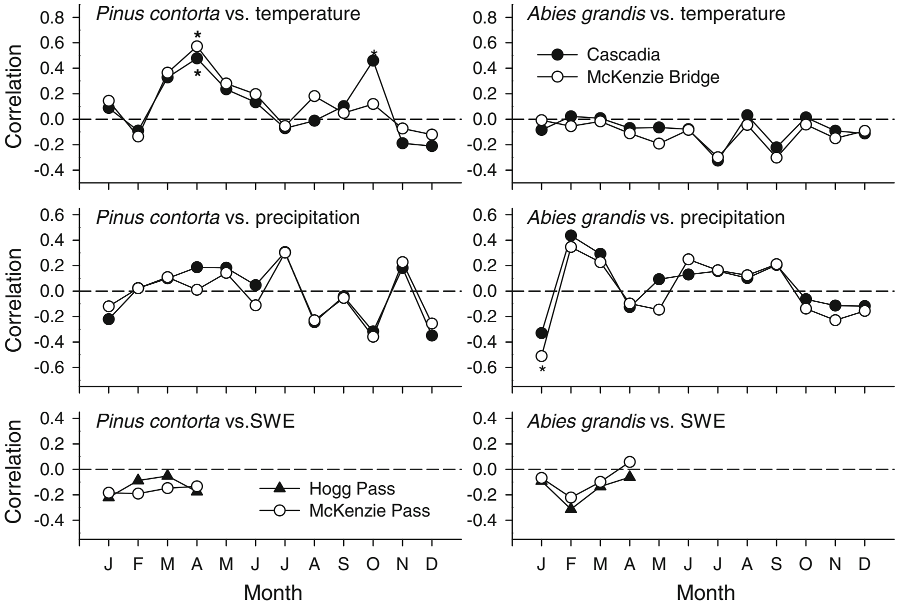

Fig. 2 Correlations between establishment of *Pinus* (*left column*) or *Abies* (*right column*) with mean monthly air temperature (*top row*), mean monthly precipitation (*middle row*), and snowpack (expressed as snow water equivalent, SWE, for the period Jan–Apr) (*bottom row*). For each analysis, tree establishment was correlated (Pearson's *r*) with data from two weather stations (see Fig. 1). Significant correlations ($P < 0.01$) are marked with *asterisks*

temperatures were positive for Mar–Jun and Oct, but significant only in Apr ($r > 0.48$, $P < 0.005$, both stations) and Oct ($r = 0.46$, $P = 0.007$; Cascadia). Correlations with mean spring temperature were also significant ($r > 0.48$, $P < 0.005$, both stations). In contrast, for *Abies* correlations with monthly temperature were negative for Apr–Nov (except Aug), but not significant. For *Pinus*, correlations with monthly precipitation were positive for Mar–May, but highly variable during summer and fall; however, none were significant. In contrast, for *Abies*, correlations with precipitation were positive for Jun–Sept and Feb, but negative for Jan; only Jan was significant ($r = -0.51$, $P = 0.002$, McKenzie Bridge). For both species, correlations between establishment and snowpack were weak and non-significant.

Abies cone production was highly cyclical (biennial or triennial). However, we were unable to detect a relationship between cone production and subsequent establishment. Cone production was not correlated with establishment or deviations in establishment from longer-term trends associated with mast years or with the magnitude of cone production.

Spatio-temporal patterns of tree establishment

Stem maps illustrate an initially sparse distribution of trees (primarily *Pinus*) through 1965 (Fig. 3). Within two decades, however, *Abies* formed dense aggregations, often associated with earlier recruitment. Consistent with population age structures, there was a noticeable increase in *Pinus* after 1985 (primarily in open areas), but minimal change in *Abies*. By 2004, elongate clusters (10–20 m) oriented SW–NE occupied parts of the plot, but other areas contained few or no trees.

Abies was strongly clustered—juvenile stems to >4.0 m for KI (Fig. 4), but to <2.0 for pcfI (Fig. 5). Clustering at longer distances in KI likely relates to the cumulative nature of the function. Mature *Abies* showed weaker clustering and to shorter distances (KI and pcfI), but sample sizes were much smaller. In

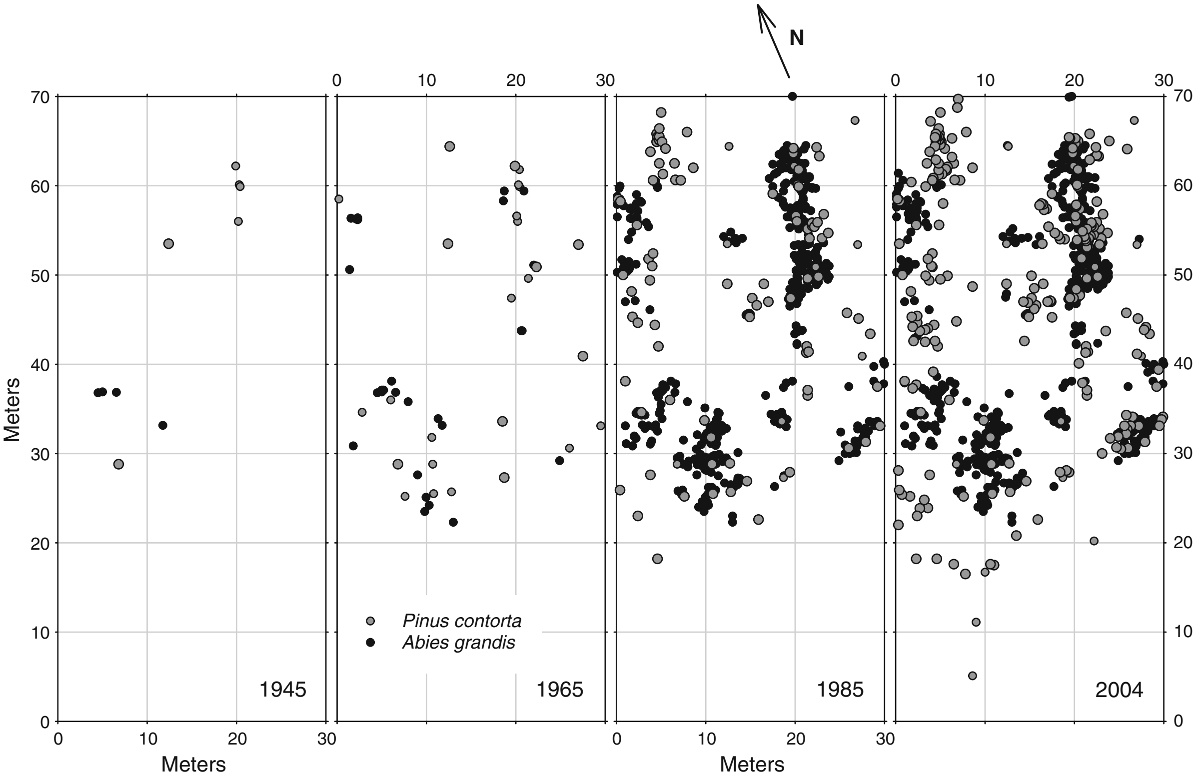

Fig. 3 Spatial maps of *Pinus* (*gray circles*) and *Abies* (*filled circles*) at four points in the invasion process, including dates before (1945, 1965), during (1985), and after (2004) the period of high-density establishment

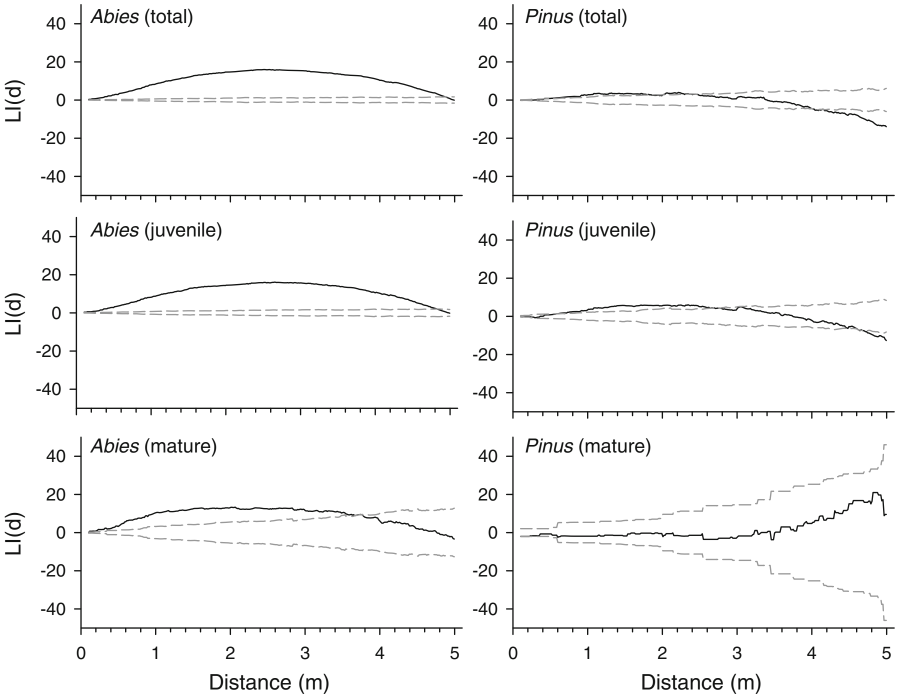

Fig. 4 The strength of conspecific clustering, LI(d), measured by KI, a Ripley's *K* function corrected for inhomogeneity in the data, for total, juvenile, and mature stems of *Abies* (*left column*) and *Pinus* (*right column*). LI(d) equals 0 for a random distribution of points, >0 indicates clustering, and <0 indicates dispersion. *Dashed lines* indicate the simulation envelope based on Monte Carlo sampling of 500 random distributions of the points. Sample sizes are: *Pinus* (total) = 231, *Pinus* (juvenile) = 189, *Pinus* (mature) = 42, *Abies* (total) = 644, *Abies* (juvenile) = 509, and *Abies* (mature) = 135

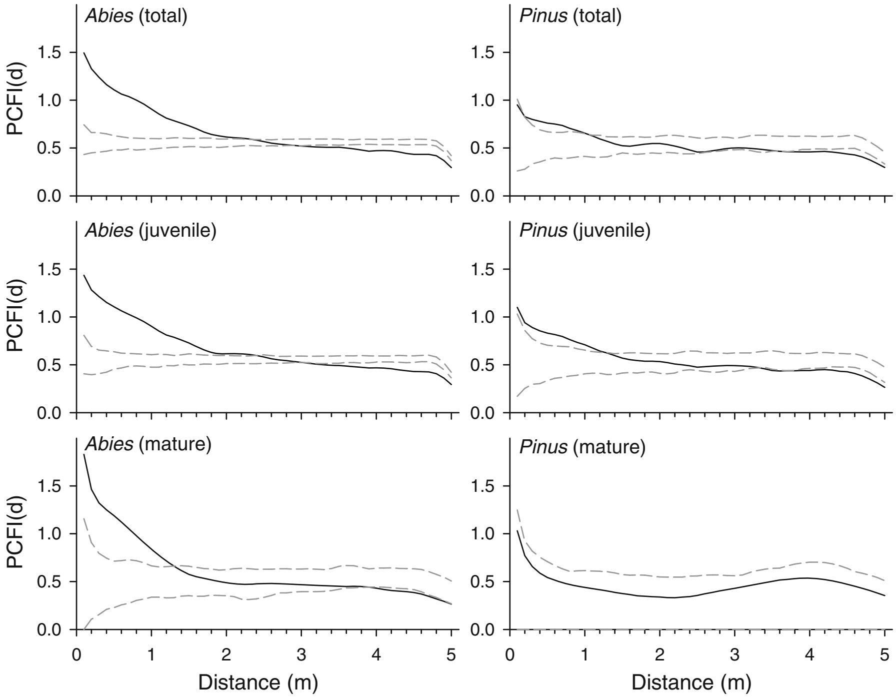

Fig. 5 The strength of conspecific clustering, PCFI(d), measured by the pair-correlation function corrected for inhomogeneity in the data, for all (total), juvenile, and mature stems of *Abies* (*left column*) and *Pinus* (*right column*). *Dashed lines* indicate the simulation envelope based on Monte Carlo sampling of 500 random distributions of the points. See Fig. 4 for other details

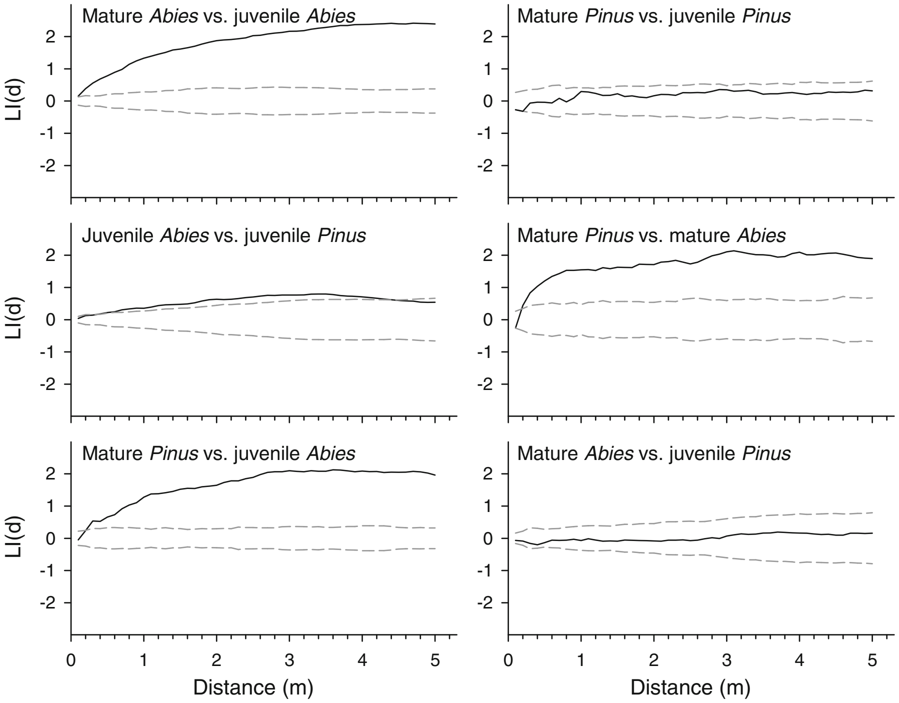

Fig. 6 The strength of bivariate clustering, LI(d), measured by cross-KI, a bivariate form of Ripley's *K* corrected for inhomogeneity in the data, for combinations of juvenile (<30 years) and mature (≥30 years) stems of *Abies* and *Pinus* in 2004. See Fig. 4 for other details

contrast to *Abies*, clustering in juvenile *Pinus* was weak and limited to short distances (~1 m in pcfI) and mature *Pinus* was not clustered (Figs. 4, 5). Among bivariate comparisons, cross-KI indicated strong clustering of juvenile *Abies* relative to mature *Abies* and *Pinus*, but minimal clustering relative to juvenile *Pinus* (cross-KI, Fig. 6). Similar clustering was not evident from cross-pcfI. Instead juvenile *Abies* was randomly distributed relative to mature *Abies* and to juvenile *Pinus* at short distances (<1 m), and dispersed at larger distances (Fig. 7). Associations with mature *Pinus* were random, but with large confidence envelopes reflecting the small number of mature stems. Mature *Abies* and mature *Pinus* were strongly clustered according to cross-KI (Fig. 6), but not so for cross-pcfI (Fig. 7), which had a large confidence envelope. For most comparisons, juvenile *Pinus* was randomly distributed relative to mature stems (*Pinus* or *Abies*; Figs. 6, 7). However, for cross-pcfI, it was dispersed relative to mature *Abies* at distances >1 m (Fig. 7).

The J-function revealed strong clustering of conspecifics over the full range of distances (Fig. 8). The strength of association increased with time in both species, but more rapidly for *Abies*, which reached a given intensity of clustering earlier and at much lower density than *Pinus*. By 1965, clustering of *Abies* (cumulative density of 119 stems ha^{-1}) was as strongly expressed as that of *Pinus* in 2000 (cumulative density of 1,100 stems ha^{-1}). Clustering of *Abies* increased rapidly between 1965 and 1975 at nearly all distances. During peak establishment (1975–1985, Fig. 1), however, increases were more gradual and limited to shorter distances (<0.8 m). Thereafter, intensity of clustering remained unchanged as rates of establishment declined. In contrast, for *Pinus*, intensity of clustering increased more gradually and less steeply at smaller distances. Unlike *Abies*, increases in intensity of clustering of *Pinus* were greatest during peak establishment (1985–1995; Fig. 1).

The evolving nearest-neighbor analysis indicated that *Pinus* consistently established at greater distances (1.7–3.5×) from nearest neighbors than did *Abies* (Fig. 9). However, for both species, distances declined with time and increasing density. Early in the invasion

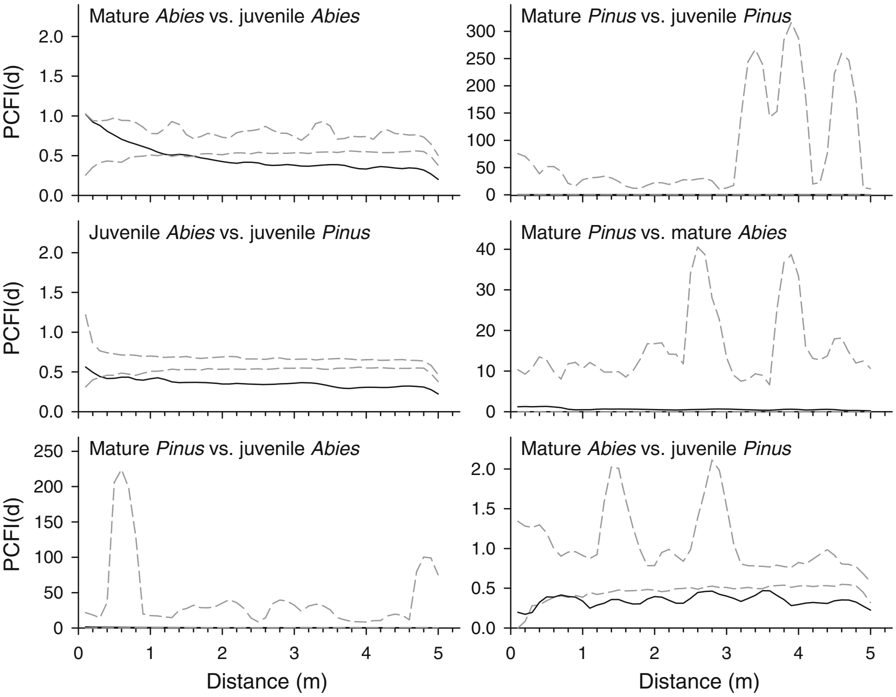

Fig. 7 The strength of bivariate clustering, cross-PCFI(d), measured by the pair-correlation function corrected for inhomogeneity in the data, for combinations of juvenile (<30 years) and mature (≥30 years) stems of *Abies* and *Pinus* in 2004. See Figs. 4 and 5 for other details

process (1935–1955) *Pinus* established on average >4.5 m from the nearest stem, but *Abies* only ~ 2.5 m. Four decades later, distances averaged ~ 1 and 0.5 m, respectively. By 2004, 89% of *Abies* were within 1 m of a neighbor (vs. 54% of *Pinus*).

Nearly 30% of trees recruited within 2 m of benefactors (i.e., trees that had previously established ≥4 m from neighbors). Most recruitment was *Abies* (85%). Among benefactors, recruitment was highly variable in density (1–67 seedlings) and direction. For only half of the benefactors (9 of 17), greater recruitment occurred in parallel with the elongate tree clusters (SW + NE quadrants). However, recruitment was highly biased to the north: 13 of 17 benefactors had greater recruitment in northern (NW + NE) than in southern (SW + SE) quadrants.

Discussion

Recent encroachment of conifers into mountain meadows of western North America has been ascribed to changes in climate or disturbance (Vale 1981; Miller and Halpern 1998; Takaoka and Swanson 2008). Here we combine evidence from multiple sources—climate and seed production records, spatio-temporal reconstructions, and knowledge of species' traits—to demonstrate that although extrinsic factors may have triggered recent invasion in this meadow, biotic interactions have been integral to maintaining and enhancing the process.

Temporal trends in establishment: roles of climate, disturbance, and cone production

Temporal variation in climate played a minor role in invasions. Establishment of *Pinus* and *Abies* was unrelated to snowpack and weakly correlated with precipitation and temperature, although the directions of correlation were consistent with species' environmental tolerances. *Pinus*, which is tolerant of warmer, drier conditions, tended to establish in years with warmer early- and late-summer temperatures (Widenmaier and Strong 2010). *Abies*, which is less tolerant of drought, tended to establish in years with wetter springs (Miller and Halpern 1998). For both species, however, recruitment was uncommon before 1940, when drought conditions may have been too extreme

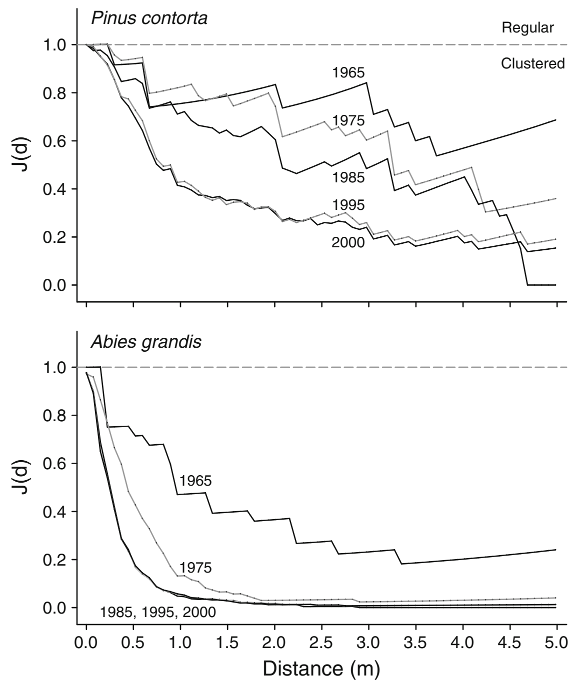

Fig. 8 Changes in the strength of clustering, J(d), the J-function, within 5 m of conspecific individuals for *Pinus* (*top panel*) and *Abies* (*bottom panel*) at five points in time between 1965 and 2000. J(d), equals 1 for randomly distributed points; values below 1 indicate clustering. Sample sizes for trees >5 m from plot edges for 1965, 1975, 1985, 1995, and 2000 are, respectively: *Pinus* = 18, 30, 84, 122, and 152; *Abies* = 18, 104, 375, 472, and 504

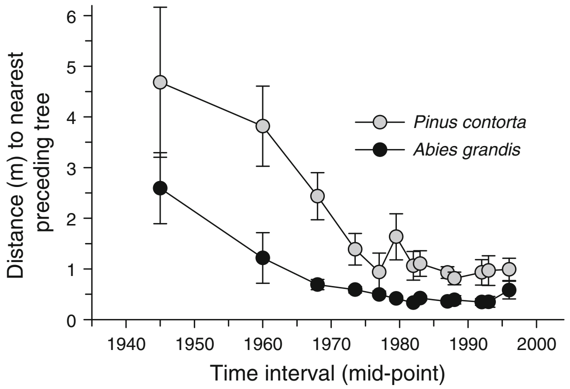

Fig. 9 Results of the evolving nearest-neighbor analysis, illustrating the mean distance (±1 SE) between establishing *Pinus* and *Abies* and the nearest preceding tree for 13 time intervals between 1935 and 1997. Time intervals, represented by their mid-points, vary in width: 1935–1955, 1955–1965, 1966–1970, 1971–1975, and thereafter 2- to 3-year interval through 1997. Thirty-four trees whose nearest preceding neighbors were beyond the plot boundary were excluded

for either species to establish. Conversely, for decades with rapid invasion, climatic conditions were neither consistent, nor exceptionally conducive to establishment. These results provide strong evidence that climate has been less influential in patterns of tree establishment than in other forest-grassland systems (League and Veblen 2006).

Onset of invasion in the mid 1930s could reflect a change in disturbance regime. Initial invasions of other meadows in this region coincide with closure of grazing allotments and with regional suppression of fire (Vale 1981; Miller and Halpern 1998; Takaoka and Swanson 2008). However, historical data and other evidence of a change in disturbance regime are lacking for Bunchgrass Ridge. Whether cessation of grazing or the absence of fire triggered establishment, neither factor can explain patterns in subsequent decades.

We were unable to detect relationships between timing or magnitude of seed production and establishment in *Abies*. However, aspects of the timing of establishment in both tree species suggest that invasions may have been constrained at least initially, by seed limitations. For both species, onset of establishment in the study plot coincided with maturation (seed production) of trees that had established in adjacent meadows 20–40 years earlier (Halpern et al. 2010). The more rapid establishment of *Abies* may reflect greater densities in these source areas and lighter, more readily dispersed seed (Foiles et al. 1990; Lotan and Critchfield 1990). The lag for *Pinus* may reflect lower densities and poorer dispersal of heavier seeds: abundant establishment may not have been possible until initial colonists in the plot achieved reproductive maturity. Similar contributions of distant and local seed sources to the pace and intensity of invasion have been described for *Pinus* in other grasslands (Langdon et al. 2010) and for plant invasions in general (Pyšek and Hulme 2005).

Inferring biotic interactions from spatio-temporal patterns of association

Analyses of spatial patterns of establishment provide strong evidence that biotic interactions, namely facilitation, have influenced the pace and intensity of tree invasion in this system. Univariate Ripley's K and the pair-correlation function (corrected for inhomogeneity), showed more intense fine-scale

(1–2 m) clustering for *Abies* than for *Pinus*. Similarly, bivariate *K* indicated strong clustering of juvenile *Abies* (but not *Pinus*) within 2 m of mature stems of both species. This local clustering was not detected with the pair-correlation function, which is more sensitive to the small sample sizes of mature stems. Bivariate KI and pcfI also produced contrasting patterns of association between juvenile stems of *Abies* and *Pinus*—random to very weak clustering in cross-KI versus dispersed (except at short distances) in cross-pcfI. A dispersed pattern is consistent with timing of establishment and differences in shade tolerance, of *Pinus* and *Abies*. The vast majority of juvenile, shade-intolerant *Pinus* recruited after *Abies*, thus established away from preceding trees. Had *Pinus* arrived first, fine-scale clustering would have been more likely, as it was between juvenile *Abies* and mature *Pinus*.

The J-function and evolving nearest-neighbor analyses also indicated distinct differences in invasion patterns in *Abies* and *Pinus*. When their densities were low and comparable, *Abies* showed more intense clustering, with shorter distances (<1 m) to nearest neighbors than in *Pinus* (>2 m). As *Abies* attained peak rates of establishment, differences became accentuated, underscoring the propensity of *Abies* to establish close to neighbors, facilitated by larger trees (Pugnaire et al. 2004; Baumeister and Callaway 2006; Kunstler et al. 2006). Preferential recruitment to the north of benefactors suggests that facilitation occurs through shading, as in other nurse-plant systems (Haase 2001; Phillips and Barnes 2003). However, this directional bias did not explain the orientation of infilling within larger clusters, which likely reflect underlying heterogeneity in soils.

Characteristics of the age structures and spatial associations of trees were also suggestive of processes that eventually reduced rates of establishment. For *Abies*, the steep decline in establishment after 1985 may reflect a shift from positive to increasingly negative interactions. Similar shifts in the facilitative and competitive roles of nurse plants have been observed in other systems (Miriti 2006; Reisman-Berman 2007). The J-function and evolving nearest-neighbor analyses showed rapid increases in clustering of *Abies* before 1985, but little change thereafter. *Pinus* exhibited a similar dynamic, but a decade later and at lower density and intensity of clustering. Mean distances to nearest neighbors were twice those of *Abies* and the most recent recruitment was limited to open portions of the plot—patterns consistent with *Pinus*' intolerance of shade. Contrasts in the spatio-temporal dynamics of *Abies* and *Pinus* support the hypothesis that tree invasions of grasslands can be more rapid or intense when they include species with differing regenerative traits or functional roles (Duarte et al. 2006; Halpern et al. 2010).

Conclusions

Woody plant invasions of grasslands are occurring globally. Retrospective studies in western North America have focused on climate and disturbance as causal, but less so on biotic interactions that can maintain or enhance invasions. We considered multiple, temporally varying influences and fine-resolution age and spatial data to assess the contributions of extrinsic and intrinsic factors to recent invasions of a western Cascade grassland by *Pinus contorta* and *Abies grandis*. Spatio-temporal patterns of establishment provide strong evidence that biotic interactions are integral to the invasion process. Although extrinsic factors can trigger establishment, positive interactions and density-dependent feedbacks can regulate the pace and intensity of invasion, enhancing recruitment even when climatic conditions are not optimal for establishment. We illustrate how methods of spatial point-pattern analysis applied at progressively finer temporal resolution can be used to assess changes in the nature and strength of interactions over time. Ecological theory and knowledge of species' traits can be combined with spatio-temporal analyses to elucidate the importance of biotic interactions in structuring early invasions of grasslands before mortality erases evidence of these processes.

Acknowledgments For field assistance we thank Byron Ball, Lorin Bumbarger, Ryan Haugo, Nicole Lang, Jennifer Leach, Kyle Smith, Florian Steer, Tina Võlkl, and Katrin Wendt. Cheryl Friesen and staff from the McKenzie River Ranger District provided logistical support. We thank two anonymous reviewers for comments. Funding was provided by the Joint Fire Science Program (1422RAH03-0021). JMR was supported by an NSF IGERT Ecosystem Informatics Fellowship (NSF DGE-0333257).

References

Baddeley AJ, Kerscher M, Schladitz K, Scott BT (2000a) Estimating the J function without edge correction. Stat Neerl 54:315–328

Baddeley AJ, Møller J, Waagepetersen R (2000b) Non- and semi-parametric estimation of interaction in inhomogeneous point patterns. Stat Neerl 54:329–350

Baumeister D, Callaway RM (2006) Facilitation by *Pinus flexilis* during succession: a hierarchy of mechanisms benefits other plant species. Ecology 87:1816–1830

Boyd R (1999) Indians, fire, and the land in the Pacific Northwest. Oregon State University Press, Corvallis, OR

Browning DM et al (2008) Woody plants in grasslands: post-encroachment stand dynamics. Ecol Appl 18:928–944

Callaway R (2007) Positive interactions and interdependence in plant communities. Springer, Dordrecht

Coop JD, Givnish TJ (2008) Constraints on tree seedling establishment in montane grasslands of the Valles Caldera, New Mexico. Ecology 89:1101–1111

Diggle PJ (1983) Statistical analysis of spatial point patterns. Academic Press, London

Duarte LS, Machado RE, Hartz SM, Pillar VD (2006) What saplings can tell us about forest expansion over natural grasslands. J Veg Sci 17:799–808

Elliot RA (1946) Grazing policy statement, 5-year period 1946–1950. Willamette National Forest supplement to the forest grazing plan. Supervisor's Office, Willamette National Forest, USDA Forest Service, Springfield, OR

Foiles MW, Graham RT, Olson, DF Jr (1990) *Abies grandis* (Dougl. ex. D. Don) Lindl. Grand Fir. In: Burns RM, Honkala BH (eds) Silvics of North America. Vol. 1. Conifers. Agriculture Handbook 654, USDA Forest Service, pp 80–96

Goreaud F, Pelissier R (2003) Avoiding misinterpretation of biotic interactions with the intertype K_{12}-function: population independence vs. random labeling hypotheses. J Veg Sci 14:681–692

Gray L, He F (2009) Spatial point-pattern analysis for detecting density-dependent competition in a boreal chronosequence of Alberta. For Ecol Manage 259:98–106

Haase P (2001) Can isotropy vs. anisotropy in the spatial association of plant species reveal physical vs. biotic facilitation? J Veg Sci 12:127–136

Halpern CB et al (2010) Tree invasion of a montane meadow complex: temporal trends, spatial patterns, and biotic interactions. J Veg Sci 21:717–732

Haugo RD, Halpern CB (2007) Vegetation responses to conifer encroachment in a western Cascade meadow: a chronosequence approach. Can J Bot 85:285–298

Haugo RD, Halpern CB (2010) Tree age and tree species shape positive and negative interactions in a montane meadow. Botany 88:488–499

Jackson RB et al (2002) Ecosystem carbon loss with woody plant invasion of grasslands. Nature 418:623–626

Johnson RR (1985) Historical records inventory for the Willamette National Forest: forest grazing permits. Forest Service Warehouse, Willamette National Forest, USDA Forest Service, Eugene, OR

Kenkel NC (1988) Pattern of self-thinning in jack pine: testing the random mortality hypothesis. Ecology 69: 1017–1024

Kunstler G, Thomas C, Bouchaud M, Lepart J (2006) Indirect facilitation and competition in tree species colonization of sub-Mediterranean grasslands. J Veg Sci 17:379–388

Langdon B, Pauchard A, Aguayo M (2010) *Pinus contorta* invasion in the Chilean Patagonia: local patterns in a global context. Biol Invasions 12:3961–3971

League K, Veblen T (2006) Climatic variability and episodic *Pinus ponderosa* establishment along the forest-grassland ecotones of Colorado. For Ecol Manage 228:98–107

Loosmore NB, Ford ED (2006) Statistical inference using the G or K point pattern spatial statistics. Ecology 87: 1925–1931

Lotan JE, Critchfield WB (1990) *Pinus contorta* Dougl. ex. Loud. Lodgepole pine. In: Burns RM, Honkala BH (tech coords) Silvics of North America. 1. Conifers. Agriculture Handbook 654, USDA Forest Service, pp 604–629

Lynch H, Moorcroft PR (2008) A spatiotemporal Ripley's *K*-function to analyze interactions between spruce budworm and fire in British Columbia, Canada. Can J For Res 38:3112–3119

Miller EA, Halpern CB (1998) Effects of environment and grazing disturbance on tree establishment in meadows of the central Cascade Range, Oregon, USA. J Veg Sci 9:265–282

Minore D (1979) Comparative autecological characteristics of Northwestern tree species, a literature review. USDA Forest Service General Technical Report PNW-GTR 87

Miriti MN (2006) Ontogenetic shift from facilitation to competition in a desert shrub. J Ecol 94:973–979

Perry GLW, Miller BP, Enright NJ (2006) A comparison of methods for the statistical analysis of spatial point patterns in plant ecology. Plant Ecol 187:59–82

Phillips PL, Barnes PW (2003) Spatial asymmetry in tree-shrub clusters in a subtropical savanna. Am Midl Nat 149:59–70

Pugnaire FI, Armas C, Valladares F (2004) Soil as a mediator in plant–plant interactions in a semi-arid community. J Veg Sci 15:85–92

Pyšek P, Hulme PE (2005) Spatio-temporal dynamics of plant invasions: linking pattern to process. Ecoscience 12:302–315

Reisman-Berman O (2007) Age-related change in canopy traits shift conspecific facilitation to interference in a semi-arid shrubland. Ecography 30:459–470

Ripley BD (1977) Modelling spatial patterns. J R Stat Soc B 39:172–212

Schiffers K, Schurr FM, Tielbörger K, Urbach C, Moloney K, Jeltsch F (2008) Dealing with virtual aggregation— a new index for analyzing heterogeneous point patterns. Ecography 31:545–555

Scholes RJ, Archer SR (1997) Tree–grass interactions in savannas. Annu Rev Ecol Syst 28:517–544

Takaoka S, Swanson FJ (2008) Change in extent of meadow and shrub fields in the central western Cascade Range, Oregon. Prof Geogr 60:1–14

Thonnes E, van Lieshout M-C (1999) A comparative study on the power of van Lieshout and Baddeley's J-function. Biometr J 41:721–734

Vale TR (1981) Tree invasion of montane meadows in Oregon. Am Midl Nat 105:61–69

van Lieshout MNM, Baddeley AJ (1996) A nonparametric measure of spatial interaction in point patterns. Stat Neerl 3:344–361

Widenmaier KJ, Strong WL (2010) Tree and forest encroachment into fescue grasslands on the Cypress Hills plateau, southeast Alberta, Canada. For Ecol Manage 259: 1870–1879

Wiegand T, Moloney KA (2004) Rings, circles, and null-models for point pattern analysis in ecology. Oikos 104:209–229

Yamada I, Rogerson P (2003) An empirical comparison of edge effect correction methods applied to K-function analysis. Geogr Anal 35:97–109