Removal of invasive Scotch broom increases its negative effects on soil and plant communities

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Abstract

Scotch broom is an aggressive invasive species of major concern in coast Douglas-fir forests of the Pacific Northwest USA. Control efforts are common, but potential for ecosystem recovery following Scotch broom removal is unclear. We assessed the potential for ecosystem recovery following broom removal at two sites that contrasted strongly in soil quality (i.e., texture and nutrient pool size) in western Washington and Oregon. Comparisons were made among replicated plots where Scotch broom was never present (uninvaded), retained, or removed. Microclimate (photosynthetically active radiation (PAR), soil temperature and moisture), soil properties, and vegetation were monitored during 2013 to 2017. Scotch broom removal increased PAR and soil temperature at both sites but had limited effects on soil moisture. Concentrations of Ca, Mg, K, and P were significantly lower with Scotch broom removal compared to the uninvaded and retained treatments, with the effect being most pronounced at the low-quality site. NMS ordinations indicated that the treatments differed in vegetation composition, with limited evidence for recovery in the removal treatment. Nonnative and native species varied inversely in their abundance responses, where nonnative species abundance was greatest in the removal treatment, intermediate in the retained treatment, and lowest in the uninvaded treatment, indicating occurrence of a secondary invasion following removal. As with the soil response, effects were more pronounced at the low-quality site. Our findings indicate that Scotch broom removal exacerbates negative effects on soil and plant communities, with little evidence of ecosystem recovery over our study period. These findings highlight the importance of controlling Scotch broom invasions immediately after the species establishes, especially at low-quality sites that are more susceptible to Scotch broom invasion and negative legacy effects.

Introduction

Scotch broom (*Cytisus scoparius* (L.) Link) is an N-fixing invasive species of major ecological concern capable of dominating sites (Bossard and Rejmanek 1994; Richardson et al. 2002) and altering ecosystem function (Parker et al. 1997). Scotch broom is an aggressive invader in early-successional coast Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) forests of the Pacific Northwest (PNW), USA which can impact soil properties (Slesak et al. 2016, Grove et al. 2015, Caldwell 2006), alter vegetation communities (Carter et al. 2018, Shaben and Meyers 2010), and reduce site productivity (Harrington et al. 2018).   Because of this, it is common for managers to aggressively control Scotch broom when present, especially during the early phase of stand establishment. Although these efforts can be successful at reducing Scotch broom abundance, the potential for and patterns of ecosystem recovery following removal of this invasive are unknown. In this context, we define ecosystem recovery as a return to pre-invasion conditions inferred through either direct observation or via comparison to areas never invaded (cf. Prior et al. 2018).

Scotch broom can fix moderate quantities of nitrogen (N) (20-100 kg ha^{-1} year; Carter et al. 2019a, Watt et al. 2003a), and studies have shown that it can increase soil N availability over time (Caldwell 2006). Soil N enrichment associated with plant invasions has been shown to facilitate the establishment and

success of other nonnative invaders (Walker and Vitousek 1991, Weidenhamer and Callaway 2010). Given this, it is possible that increased N pools could hamper recovery of site productivity and native plant community composition even after Scotch broom removal (i.e., soil legacies, Corbin and Antonio 2012). Legacy effects on other soil nutrients are also possible. For example, some studies have shown lower soil P in the presence of broom (Caldwell 2006, Shaben and Meyers 2010) which can vary depending on site or soil quality (Slesak et al. 2016). Similarly, Carter et al. (2018) found higher soil water N, magnesium (Mg), and calcium (Ca) and lower potassium (K) at plots where broom was experimentally planted relative to unplanted, broom-free control plots. Changes in soil nutrient availability may alter plant community composition, but the direction and magnitude of change is unclear. Further, although many studies have documented altered soil properties in the presence of Scotch broom, almost none have assessed the possible recovery of these properties following its removal.

Scotch broom also has potential to alter plant function via pathways other than altered nutrient dynamics, or indirectly in response to altered nutrient dynamics. Previous work has shown the Scotch broom is associated with reduced ectomycorrhizal fungi (EMF) colonization of Douglas-fir roots, possibly due to direct suppression via allelopathic compounds, or indirect suppression via reduced nutrient availability (Grove et al. 2017; Grove et al. 2012). In a recent bioassay study (Slesak et al. 2020), we documented reduced growth of Douglas-fir grown on broom invaded soil, but increased growth of yarrow (*Achillea millefolium* L.) and Roemer's fescue (*Festuca idahoensis* Elmer ssp. *Roemeri*) demonstrating the potential for Scotch broom to alter plant resource acquisition (both positive and negative) following its removal.

Because plant invasions often result in decreased native biodiversity (Powell et al. 2011), removal of the invasive plant may result in recovery of native biodiversity. However, positive outcomes do not always occur (Prior et al. 2018, Kettenring and Adams 2011) and control efforts can often lead to secondary invasions following removal of the dominant invasive (Kuebbing and Nunez 2015, Reid et al. 2009). These secondary invasions are most commonly associated with changes in resource availability combined with changes in microclimate that allow initially minor invasive species to become more dominant. For example, Maron and Jefferies (1999) showed how mortality and loss of the N-fixing yellow bush lupine (*Lupinus arboreus* Sims) increased N and light availability, leading to invasion by nonnative grasses that dominated the plant community. Similarly, shade and litter accumulation under large Scotch broom affect soil temperature and light conditions, often modifying germination responses of other species (Waterhouse 1986; Wearne and Morgan 2004). Change in these conditions following Scotch broom removal, coupled with altered soil properties, may hinder native plant community recovery or increase the likelihood of secondary invasive by other invasive species.

Although ecosystem recovery can be variable following invasive species control, it is likely to depend on site (soil) quality (i.e., texture and nutrient pool sizes). For example, Dassonwille et al. (2008) found that invasive plant feedbacks to soil depended on soil quality, being generally positive (increased nutrient pools) at sites with low soil nutrient status but negative at sites with initially high nutrient status. This

difference in the magnitude and direction of change is likely to lead to different recovery trajectories. Soil quality is also likely to influence plant community recovery, but there is little empirical information as to how such effects may be manifested. Understanding the effects of site quality on recovery is important for the development of restoration strategies across a range of site conditions.

Here, we report on changes in soil chemical properties, microclimate, and plant community structure over a four-year period following Scotch broom removal at two Douglas-fir sites that contrasted in site quality. In a prior assessment at these sites comparing areas with broom present to areas where it was absent (Slesak et al. 2016), we found that Scotch broom presence was associated with higher total C and N, lower nutrient cations (particularly K), and lower intermediately-available P, but the magnitude of effect varied and was generally more pronounced at the higher quality site. In this study, our primary objective was to assess the potential for soil and plant community recovery over a period of four years following removal of Scotch broom. We expected that Scotch broom removal would be associated with a recovery of soil chemical properties and plant communities to conditions in which broom had never been present, but that recovery trajectories would vary depending on initial site (soil) quality.

Methods

Site Descriptions

The study was conducted at two Douglas-fir sites affiliated with the North American Long-Term Soil Productivity (LTSP) study located near Matlock, Washington (WA) and Molalla, Oregon (OR) USA (Harrington and Schoenholtz 2010) (Table 1). Soil characteristics and stand productivity varied strongly between sites (Harrington et al. 2020), with the WA site having lower site quality and the OR site generally having high site quality as evidenced by large differences in limiting resources including available water and total soil N (Table 1). Soils at the WA site are classified as sandy-skeletal, mixed, mesic, Dystric Xerorthents formed in glacial outwash with slopes ranging from 0 to 3% (Soil Survey Staff, USDA-NRCS). Soils at the OR site are classified as fine-loamy, isotic, mesic Andic Dystrudepts formed in basic agglomerate residuum with slopes ranging from 2 to 40% (Soil Survey Staff, USDA-NRCS). The regional climate is Mediterranean, characterized by cool, wet winters and warm, dry summers with periods of prolonged drought. Potential natural vegetation includes the western hemlock (*Tsuga heterophylla* (Raf.) Sarg.)/salal (*Gaultheria shallon* Pursh) plant association at the WA site (Henderson et al., 1989) and the western hemlock/Oregon-grape (*Mahonia nervosa* (Pursh) Nutt.)/swordfern (*Polystichum munitum* (Kaulf.) Presl) and western hemlock/Oregon grape-salal plant associations at the OR site (Halverson et al., 1986).

Experimental Design

Each of the sites was clearcut harvested in spring 2003. Following cutting, Scotch broom began to proliferate across each of the sites. In the fall of 2013, 3-m radius circular plots were replicated 10 times for each of the following Scotch broom treatments: i) Scotch broom present since harvest and then removed in 2013 (removed; see details below), ii) Scotch broom present since harvest (retained) or iii)

Scotch broom absent since harvest (uninvaded) . We were able to locate areas where Scotch broom was present or uninvaded with high confidence due to our past work at these sites (Harrington et al. 2010). Because we could not randomly assign the presence or absence of Scotch broom to a given replication, we identified double the number of candidate replications for each treatment and then randomly selected half for inclusion in this study. This approach allowed for unbiased estimation of soil conditions within each of the Scotch broom conditions. For removal treatments, Scotch broom was cut near ground surface, aboveground biomass removed from the plots, and stumps were sprayed with a 20% solution of Garlon®4 (triclopyr ester) herbicide in an oil carrier to ensure complete mortality. Thereafter, any Scotch broom germinants in the plots were removed by hand throughout the duration of the study. Scotch broom basal area (at 15-cm height), stem density, average height, and crown cover were measured in both the retained and removed treatment plots prior to treatment application (Table 1).

Microclimate measurements

Soil moisture was monitored in each of the Scotch broom removal and retained treatment plots with soil moisture sensors (model EC-5, Meter Corporation, Pullman WA) attached to dataloggers (model EM-5, Meter Corporation, Pullman WA). Sensors were installed 50 cm from the center of the plot at a depth of 30 cm. Soil moisture readings were logged every four hours throughout the duration of the study. Soil temperature was also measured in each of the Scotch broom removal and retained treatment plots with ibutton dataloggers (model DS1921G, Maxim Integrated Technologies, Inc., Sunnyvale CA) that were installed 50 cm from plot center (opposite from the soil moisture sensor) and at a depth of 5 cm. The ibuttons were programmed to log temperature at 2-hour intervals throughout the duration of the study. Light availability was assessed with a PAR sensor (Accupar LP-80 ceptometer, Meter Corporation, Pullman WA) at each of the plots once during each year from 2015-2017. Readings were taken around the summer solstice between 11:00 and 14:00 Pacific Daylight Time at six locations in each plot on a 1-meter grid centered on plot center. Readings were taken at 0.5 m height and expressed relative to an above canopy reading taken immediately prior to below canopy readings.

Soil collection, processing, and analytical procedures

Soil samples were collected in the fall of 2013, 2015, and 2017 at both sites using bucket augers. At each treatment replication, three samples were collected at 0-15 and 15-30 cm depth increments, composited in a bucket by depth increment, thoroughly mixed, and a subsample was placed in a Ziploc bag for transport. Soil samples were returned to the laboratory, air-dried, and sieved to pass a 2-mm mesh. Total soil C and N were measured on a 1-g subsample that was ground with a mortar and pestle to pass a 0.25-mm mesh, followed by dry combustion using a LECO Dumas combustion technique on a Fisons NA1500 NCS Elemental Analyzer (ThermoQuest Italia, Milan, Italy). The Mehlich method was used to extract Ca, Mg, and K, and extract concentrations were measured with inductively coupled plasma spectroscopy (Varian Vista MPX, Varian, Palo Alto, CA, USA). Available soil P was estimated using the Bray extraction followed by calorimetric estimation of P on a spectrophotometer (Spectronic 20 Genesys, Model 4001, Thermo Electron Corporation).

Vegetation measurements

Vegetation measurements were conducted once in each 3-m radius plot in June-July from 2014-2017. For each measurement, visual estimates of percent cover were made for each species in the entire plot to the nearest 5% (to the nearest 1% for covers <5%). In this method, a single species cover is constrained to 100%, but the sum of cover for a given plot can exceed 100% due to overlap. We also made an independent measure of total understory and overstory canopy cover that ranged from 0-100%. The same individual performed all vegetation measurements to maintain consistency in visual estimates over time.

Analysis

Each site was analyzed independently to assess treatment effects on response variables. Treatment effects on soil chemistry (total C and N, extractable Ca, Mg, K, and P), microclimate (soil moisture, temperature, PAR), and the amount and abundance (cover) of native and nonnative species in each plot were assessed with mixed effects repeated measures analysis of variance (ANOVA). Plot within treatment was modeled as a random effect and treatment, time, and their interaction were modeled as fixed effects. For all models, we used a first order autoregressive covariance matrix to account for serial correlation among successive measurements. For soil moisture and temperature, data was first averaged by day and then by month; models were run independently for each year to conform with the chosen covariance matrix (i.e., avoid high correlation for a given month across years). Soil chemistry responses were analyzed separately for each depth increment to simplify interpretation of model output. We used the USDA Plants Database (The Plants Database 2020) for our taxonomic treatment and to code each plant species according to their life form and whether they were native or nonnative. For each plot, we calculated total cover for native and nonnative species groups (including Scotch broom) and used ANOVA to compare treatment effects between the two groups. We also analyzed differences in cover by life form among treatments. All mixed effects analysis was conducted in SAS 9.4 using an alpha of 0.05. When F statistics indicated significant treatment effects, we used Tukey's adjustment (for soil chemistry and plant responses) or slicing (for microclimate variables) to determine differences between treatments.

Nonmetric multidimensional scaling (NMS) ordination was used to graphically assess gradients in plant community composition across treatments and explore relationships with soil chemical properties. Rare species found on <5% of plots were deleted prior to analysis. The community matrix consisted of measurements from 2014-2017 for each site. Ordinations were run in PC-ORD (Version 7.08, McCune and Mefford 2018) on autopilot mode using Sørenson (Bray−Curtis) distance measures with 500 iterations. Community composition was displayed graphically by taking the mean of plot values in each treatment and year and plotting them. Relationships between ordination axis and soil chemical properties were made using biplot overlays using an r^2 cutoff of 0.2 (McCune et al. 2002). For these analyses, we explored relationships between pretreatment soil properties and vegetation composition in each of the measurement years and determined relationships across years using soil data collected from the

associated year (i.e., 2014 (using pretreatment), 2015, and 2017). Using the same data matrices as above, treatment effects on plant communities were assessed with permutational multivariate analysis of variance (PERMANOVA) conducted in PC- ORD. When significant treatment effects were observed, post hoc comparisons among treatments and years were conducted using a Bonferroni adjustment.

Results

Microclimate response

There was significant interaction between treatment and year for PAR at the low-quality site (Table S1). PAR in the Scotch broom removed and uninvaded treatments was 1.5 to 3.3 times greater than in the retained treatment in each year, except for 2017 when the uninvaded treatment was not different from the retained treatment (Figure 1). At the high-quality site, there was a main effect of treatment and no interaction between treatment and year on PAR (Table S1). At that site, PAR in the removed treatment was 3.2 and 4.6 times greater than that in the retained and uninvaded treatments, respectively.

Soil temperature results largely mirrored those for PAR. At both sites and in each year of the study, there was significant interaction between treatment and measurement month on soil temperature ($p < 0.025$, Table S2).   At the low-quality site, the Scotch broom retained treatment had significantly lower soil temperature than the other treatments during growing season months (May-Sept, Figure 2). Mean monthly differences averaged between 2-3 °C depending on month and year. At the high-quality site, the Scotch broom removed treatment had significantly greater soil temperature than the other treatments during growing season months. Mean monthly differences at that site ranged from 0.5-1.5 °C.

Treatment effects on soil water were small and limited to the first year after treatment application (Figure 3, Table S3). At the low-quality site, there was a main effect of treatment (p=0.021) on soil water content, but multiple comparisons failed to identify differences among treatments. At the high-quality site, there was no effect of treatment on soil water content in the first year (p=0.087) or any year thereafter (Table S3). At both sites, mean soil water content was higher in the removed treatment than in the retained treatment in the first year, but these differences were not significant.

Soil responses

Main effects of treatment on soil chemical properties were found at both sites but were more common at the low-quality site (Table S4). At the high-quality site at 0-15 cm depth, C concentration was higher when broom was retained compared to when it was uninvaded, but there was no difference between broom removal and uninvaded treatments. There were no other treatment effects on C or N at either depth increment or site. At the low-quality site, treatment effects on extractable P, Mg, K, and Ca were consistent and manifested as lower concentrations in the broom removal treatment relative to the broom retained and uninvaded treatments (Table 2). This pattern was consistent across depth increments (except for P at 15-30 cm) and lower concentrations in the removal treatment ranged from ~25% (relative to the uninvaded treatment) for P to ~40% for K. For K at 0-15 cm depth, there was a significant interaction

between treatment and year which was caused by no difference at time 0 among treatments, followed by the same pattern that occurred for main effects in later years (i.e., broom removed< broom retained and uninvaded treatments). Similar trends were observed at the high-quality site, but the main effect of treatment was only significant for Ca at 15-30 cm depth increment (Table 3).

Vegetation Response

There were main effects of treatment on the number and cover of nonnative and native plant species at both sites (P<0.001, Table S5) and only one interaction between treatment and year (see below). In general, nonnative and native species varied inversely in their abundance responses to treatment, and the responses were consistent at both sites. At both sites, nonnative species richness and cover was lowest in the uninvaded treatment, intermediate in the broom retained treatment, and highest in the broom removal treatment (Table 4). In the case of nonnative species cover at the low quality site, there was significant interaction between treatment and year where the broom removal treatment started out similar to the uninvaded treatment, but then nonnative cover steadily increased until it exceeded the broom retained treatment by the end of the study (Figure 4).   There was no effect of treatment on native species richness at the high-quality site (p=0.456), but native species richness at the low-quality site and native cover at both sites all responded in the same manner. In those cases, native species richness and cover was significantly greater in the uninvaded treatments, intermediate in broom retained treatments, and lowest in broom removal treatments (Table 4).

        The gradients in vegetation community composition at each site were best explained by a three-dimensional NMS ordination solution. There was clear separation among treatments in community composition at both sites, but differences among years within a treatment were limited to the low-quality site (Figure 5).   At the low-quality site, the ordination had a final stress of 13.43 and instability <0.001. Axis 1 (accounting for 23.1% of variance) was associated with plots dominated by native forbs, ferns, and shrubs (*Linnaea borealis* L., *Gaultheria shallon* Pursh, *Pteridium aquilinum* (L.) Kuhn, *Hieracium albiflorum* Hook.) in the negative portion to those dominated by the non-native species Scotch broom and velvet grass (*Holcus lanatus* L.) in the positive portion. Axis 2 (17.1% of variance) was associated with plots containing native forbs (*Crepis capillaris* (L.) Wallr.) and graminoids (*Luzula comosa* E. Mey.) in the negative portion to those dominated by native shrubs and trees in the positive portion (*Amelanchier alnifolia* (Nutt.) Nutt. ex M. Roem., *Frangula purshiana* (DC.) Cooper, *Pseudotsuga menziesii* (Mirb.) Franco var. menziesii, *Symphoricarpos albus* (L.) S.F. Blake). At the high-quality site, the ordination had a final stress of 14.89 and instability <0.001. At that site, Axis 1 (33.3% of variance) trends from plots dominated by native trees in negative portions (*Frangula purshiana* (DC.) Cooper, *Pseudotsuga menziesii* (Mirb.) Franco var. menziesii) to non-native grasses and forbs in positive portions (*Holcus lanatus* L., *Leucanthemum vulgare* Lam., *Hypericum perforatum* L.). Axis 2 (17.2% of variance) trends from plots dominated by Scotch broom in negative portions to those dominated by native vegetation in positive portions (*Pteridium aquilinum* (L.) Kuhn, *Viola sempervirens* Greene, *Prunus emarginata* (Douglas ex Hook.) D. Dietr.).

PERMANOVA results indicated that compositional differences among Scotch broom treatments were significant at each site (p<0.001 at both sites, Table S6). There was a main effect of year at the low-quality site, but no interaction between treatment and year at either site. Pairwise comparisons indicated all treatments were significantly different (p<0.001) in their community composition at each of the sites (Figure 5). At both sites, composition in the removal treatment tended to move along Axis 1 toward the uninvaded treatment over time, possibly indicating limited recovery in that treatment. Correlations between the axis and soil chemical properties did not exceed an r^2 of 0.2 in any year (data not shown).

Discussion

Removal of invasive species is often thought to lead to recovery, with plant communities and soil properties returning to pre-invasion conditions over time (Prior et al. 2018). Here, we monitored the response of soil and vegetation for four years after the removal of Scotch broom to assess the potential for ecosystem recovery. Our results indicate that broom removal can decrease soil C compared to where it is retained and decrease nutrient cations relative to where it was retained or uninvaded. However, Scotch broom removal resulted in a distinctly different community composition compared to where it was retained, but the community composition was also distinctly different from where broom was uninvaded. Further, Scotch broom removal increased the richness and cover of nonnative species and decreased the richness and cover of native species. Taken together, our findings indicate that Scotch broom removal exacerbates negative effects on soil and plant communities, with little evidence of ecosystem recovery over our study period. Effects were consistent between sites but generally more pronounced at the low-quality site, highlighting the role of site quality on responses following Scotch broom removal.

Microclimate responses

The significant effect of Scotch broom removal on PAR and soil temperature was a direct result of reduced canopy cover that occurred in that treatment. Scotch broom tends to form dense thickets which shade the soil surface and lower soil temperatures (Waterhouse 1988). Here, canopy removal resulted in relatively large increases in PAR and soil temperature, especially at the low-quality site where PAR was increased by a factor of three or more. At the high-quality site, effects of Scotch broom removal on PAR and soil temperature were more muted because the Douglas-fir overstory was more uniform. Effect of overstory other than Scotch broom is apparent in that there was no difference in PAR or soil temperature between the retained and uninvaded treatments at that site (Figs. 1 and 2). Still, the observed increases in PAR following Scotch broom removal at both sites would be likely to facilitate the release or establishment of vegetation in the absence of Scotch broom.

The lack of any treatment effect on soil water content was surprising, as broom has been shown to be effective at acquiring soil water (Carter et al. 2019b) and we expected that its removal would result in a concurrent increase in soil water availability associated with a reduction in transpiration losses. The lack of treatment effect indicates that any increase in soil water availability was quickly utilized by colonizing vegetation or offset by increased surface evaporation following canopy removal. It is difficult to quantify

the relative contribution of these processes, but Carter et al. (2018) showed that background vegetation in the presence of Scotch broom can have a pronounced effect on soil water content in this region. The lack of any treatment effect could also be because of the depth at which soil water content was measured, as Scotch broom may acquire water from deeper portions of the soil profile.

Soil responses

Given that Scotch broom is a N-fixing plant capable of fixing moderate quantities of N (Carter et al. 2019a, Watt et al. 2003a), there is potential for Scotch broom to increase soil N pools over time (Fogarty and Facelli 1999, Grove et al. 2015) with concurrent increases in soil C. The significantly higher soil C concentration at the high-quality site where Scotch broom was retained supports this general reasoning and agrees with previous work conducted at these sites evaluating effects of Scotch broom absence or presence on soil chemical properties (Slesak et al. 2016). In contrast, there was no significant effect of Scotch broom on soil C and N at the low-quality site, which is consistent with past work in these areas (Slesak et al. 2016), likely because Scotch broom effectively retains fixed N in its biomass at sites with low soil quality (i.,e, soils with low initial N, Carter et al. 2019a). To the extent that Scotch broom may influence soil C and N at these sites, trends in response from this study suggest that C and N pools are recovering following Scotch broom removal (Tables 2 and 3).

The lower amounts of extractable nutrient cations and P associated with Scotch broom removal indicate that negative soil feedbacks are being amplified in that treatment. Increased N availability associated with symbiotic N fixation is known to increase nutrient cation mobility and loss (Van Miegrot and Cole 1984, Montagnini et al. 1991), and Carter et al. (2018) observed higher concentrations of soil water Ca and Mg where Scotch broom was experimentally planted, which would be susceptible to leaching. It seems plausible that leaching contributed to a loss of nutrient cations when broom was present, but it is not clear why continued or accelerated loss would occur after broom removal. Most of the removal effects occurred at the low-quality site which is inherently more susceptible to leaching losses because of its coarse texture and low cation exchange capacity (Slesak et al. 2009). Alternatively, it is possible that colonizing vegetation increased net nutrient uptake, resulting in a reduction in soil pools. Uptake may have been particularly high because we physically removed Scotch broom from the plot, and any nutrients bound within its biomass would have been lost, leading to increased demand for the soil nutrient pool. On the other hand, the lack of any significant correlations in the NMS ordinations with soil variables does not provide evidence in support of increased uptake. The underlying mechanism leading to greater nutrient loss following Scotch broom removal has important implications in evaluating recovery and deserves further study.

Plant community responses

Treatment clearly influenced plant community structure, resulting in distinctly different communities among the three treatments (Fig. 5). Given this, it is apparent that vegetation communities have not recovered in the four years since Scotch broom was removed. A lack of recovery following removal is not uncommon, especially when the invasive plant has caused soil legacies (Corbin and Antonio 2012) which

can lead to modified plant competitive relationships (Weidenhamer and Callaway 2010). We note that our study period was only four years in length, and recovery could possibly occur at longer durations.

The lack of plant community recovery we observed occurred because Scotch broom removal facilitated the establishment of nonnative species and a reduction in native species. Secondary invasions, where removal of an invasive species leads to an increase in other invasive species, have been reported in a number of studies (Kuebbing and Nunez 2011, Prior et al. 2018), and it appears that Scotch broom removal can also facilitate secondary invasion. Carter et al. (2018) previously showed that Scotch broom can promote the establishment of nonnative species via its influence on the microenvironment. The increase in richness and cover of nonnative species we observed following Scotch broom removal is likely a result of higher initial abundances of nonnative species when Scotch broom was present (Table 4) combined with an increase in light availability following its removal. Changes in nutrient availability (e.g., N) following broom removal may have also contributed to the response (Grove et al. 2015), but the lack of relationship between soil variables and the NMS ordinations makes this unlikely.

There were clear differences between sites in the response of native and nonnative species following Scotch broom removal. Shaben and Myers (2010) attributed differential response of nonnative species response to Scotch broom at two sites to differences in the abundance of nonnative species initially present at each site. Changes in resource availability following broom invasion or removal cannot favor other invasive species if they are not present on the site (Maron and Jefferies, 1999). The relatively larger response at the low-quality site is likely associated with a larger abundance of nonnative species present (Table 4), the larger response in PAR following Scotch broom removal at that site (Fig. 1), and constrained soil resource supply (water and nutrients) associated with the coarse soil texture (Table 1). The likelihood of Scotch broom invasion and re-invasion has been greatest at the low quality-site (Harrington and Schoenholtz 2010, Harrington et al. 2020), likely because of brooms generalist ecology and physiological adaptations which make it particularly competitive on poor-quality sites with coarse textured soils (Carter et al. 2019b, Watt et al. 2003b). Thus, low quality sites are both more susceptible to broom invasion and long-term, negative legacy effects.

Conclusion

Scotch broom is an invasive species of major concern and managers often actively try to control broom to restore and maintain ecosystem functions. Our results indicate that Scotch broom can negatively affect soil properties and plant communities, which can be exacerbated following Scotch broom removal. Effects on soil nutrient cations and the abundance of native vs. nonnative species are likely to hamper ecosystem recovery, and it is unclear when these negative legacies will begin to diminish. Given our results, management actions are likely to be more effective if they focus on preempting establishment of Scotch broom or aggressively controlling any populations immediately after establishment. Low-quality sites are both more susceptible to invasion and negative legacies, suggesting that similar site types be targeted for control efforts.

Declarations

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Tables

Table 1. Site characteristics, pre-treatment soil properties to a depth of 60 cm, and Scotch broom characteristics for study sites in Washington and Oregon.

Characteristic or property	WA site (low quality)	OR site (high quality)
Location (latitude, longitude)	47.206 °N, 123.442 °W	45.196 °N, 122.285 °W
Elevation (m)	118	449
Mean annual temperature (°C)	10.7	11.2
Mean annual precipitation (mm)[1]	2412	1688
Soil texture (% sand/silt/clay)[2]	65 / 14 / 21	37 / 34 / 29
Bulk density (Mg m^{-3})	1.45 (0.05)[3]	0.98 (0.02)
Soil coarse fragments by mass (%)	67.6 (1.3)	37.7 (2.2)
Soil water holding capacity (mm)[4]	55	142
Total soil C (0-60 cm; Mg ha^{-1})[5]	92.4 (5.8)	169.5 (12.0)
Total soil N (0-60 cm; Mg ha^{-1})	3.3 (0.15)	7.2 (0.41)
Scotch broom density (stems m^{-2})	0.22 (0..13)	0.21 (0.13)
Scotch broom basal area (cm^2 m^{-2})	1.37 (0.86)	2.22 (1.07)
Scotch broom mean height (cm)	176 (23)	272 (38)
Scotch broom crown cover (%)	76.5 (17.2)	61.3 (17.5)

[1]Precipitation was estimated for the period, 1950-2005 (PRISM Climate Group, 2012).

[2]Determined with the hydrometer method.

[3]Standard error in parentheses

[4]Estimated from pressure plate analyses for the 0-60 cm depth.

[5]Determined with dry combustion

Table 2. Back transformed mean soil chemical characteristics by treatment and depth increment at the low-quality site. Values within a depth and column containing different letters are significantly different. 95% confidence limits are shown in parentheses

Treatment	C (%)	N (%)	P (mg kg^{-1})	Mg (mg kg^{-1})	K (mg kg^{-1})	Ca (mg kg^{-1})
0-15 cm						
Retained	9.5 (8.1,11.1)	0.28 (0.25,0.32)	37 (32,43) **ab**	50 (38,64) **a**	51 (45,58) **a** [1]	410 (315,530) **a**
Removed	8.5 (7.2,9.9)	0.27 (0.23,0.30)	33 (29,39) **a**	29 (22,37) **b**	36 (31,40) **b**	225 (175,290) **b**
uninvaded	8.7 (7.5,10.2)	0.25 (0.22,0.28)	45 (39,52) **b**	46 (35,59) **a**	59 (52, 67) **a**	305 (235,295) **ab**
15-30 cm						
Retained	5.5 (4.8,6.3)	0.18 (0.16,0.30)	25 (20,30)	20 (15,26) **a**	31 (27, 35) **a**	185 (145, 240) **a**
Removed	4.9 (4.3,5.7)	0.16 (0.15,0.18)	21 (17,25)	12 (9,16) **b**	21 (19,24) **b**	105 (80, 135) **b**
uninvaded	4.85 (4.2,5.6)	0.16 (0.14,0.18)	29 (26,33)	15 (11,19) **ab**	30 (27,35) **a**	110 (85,140) **b**

1 – significant interaction with time at 0-15 cm depth. Similar pattern as main treatment effect where NB>BP>BR. No diff at time 0 causes the interaction

Table 3. Back transformed mean soil chemical characteristics by treatment and depth increment at the high quality site. Values within a depth and column containing different letters are significantly different. 95% confidence limits are shown in parentheses

Treatment	C (%)	N (%)	P (mg kg^{-1})	Mg (mg kg^{-1})	K (mg kg^{-1})	Ca (mg kg^{-1})
0-15 cm						
Retained	11.4 (9.5,13.7) **a**	0.37 (0.32,0.42)	5 (4,6)	178 (127,250)	302 (231,295)	1070 (880,1310)
Removed	10.5 (8.7, 12.7) **ab**	0.36 (0.31,0.41)	5 (4,6)	149 (106,209)	290 (221,379)	1000 (820,1210)
uninvaded	8.2 (6.8,9.9) **b**	0.30 (0.26, 0.34)	5 (4,7)	254 (181,356)	403 (308,526)	1310 (1080,1600)
15-30 cm						
Retained	7.9 (6.4,9.8)	0.26 (0.23,0.30)	3 (2,4)	115 (72,182)	213 (158,189)	690 (510,930) **ab**
Removed	7.3 (5.9, 9.1)	0.27 (0.24,0.32)	3 (2,4)	94 (59,149)	214 (158,289)	630 (460,850) **a**
uninvaded	5.8 (4.7,7.2)	0.23 (0.25,0.31)	3 (2,4)	205 (129,325)	280 (207, 378)	1060 (780,1440) **b**

Table 4. Mean native and nonnative plant species richness and cover by broom removal treatment

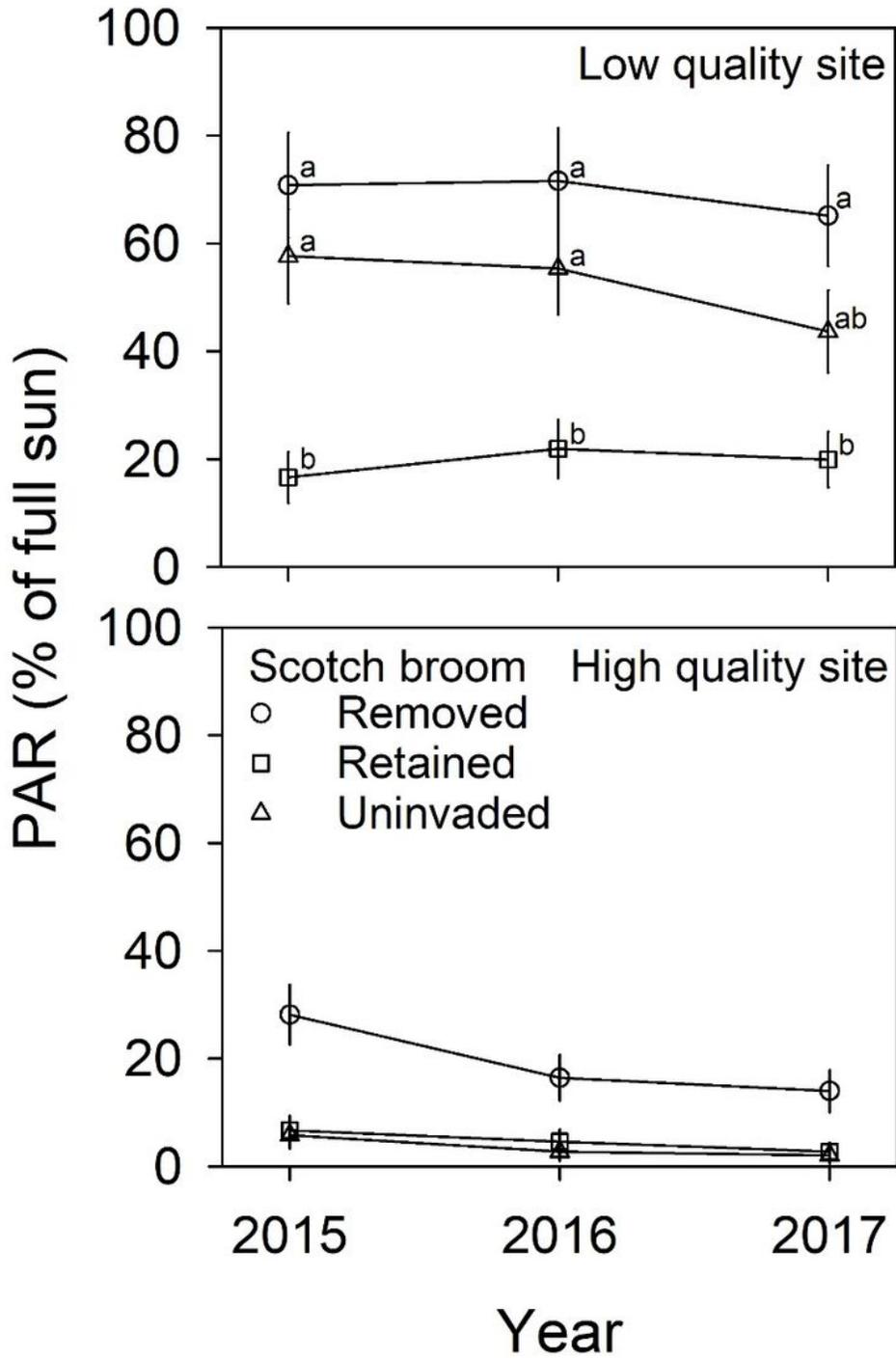| Site	Treatment	Nonnative species richness	Native species richness	Nonnative cover (%)	Native cover (%)
Low Quality	uninvaded	3.4 (0.3) a	11.4 (0.4) a	19.0 (4.7) [1]	129.7 (8.1) a
	Retained	4.7 (0.3) b	8.4 (0.4) b	68.6 (4.7)	113.2 (8.1) b
	Removed	6.3 (0.3) c	5.5 (0.4) c	58.0 (4.7)	69.1 (8.1) c
High Quality	uninvaded	1.2 (0.4) a	9.3 (0.4) a	3.2 (3.2) a	267.8 (8.4) a
	Retained	2.2 (0.4) b	9.4 (0.4) a	51.8 (3.2) b	224.2 (8.4) b
	Removed	3.8 (0.4) c	8.7 (0.4) a	16.8 (3.2) c	196.5 (8.4) c

Figures

Figure 1

Average growing season photosynthetically active radiation (PAR) in the understory of Scotch broom removal treatments during 2015-2017. For a given year at the low-quality site, treatment means followed by different letters were significantly different at P < 0.05.
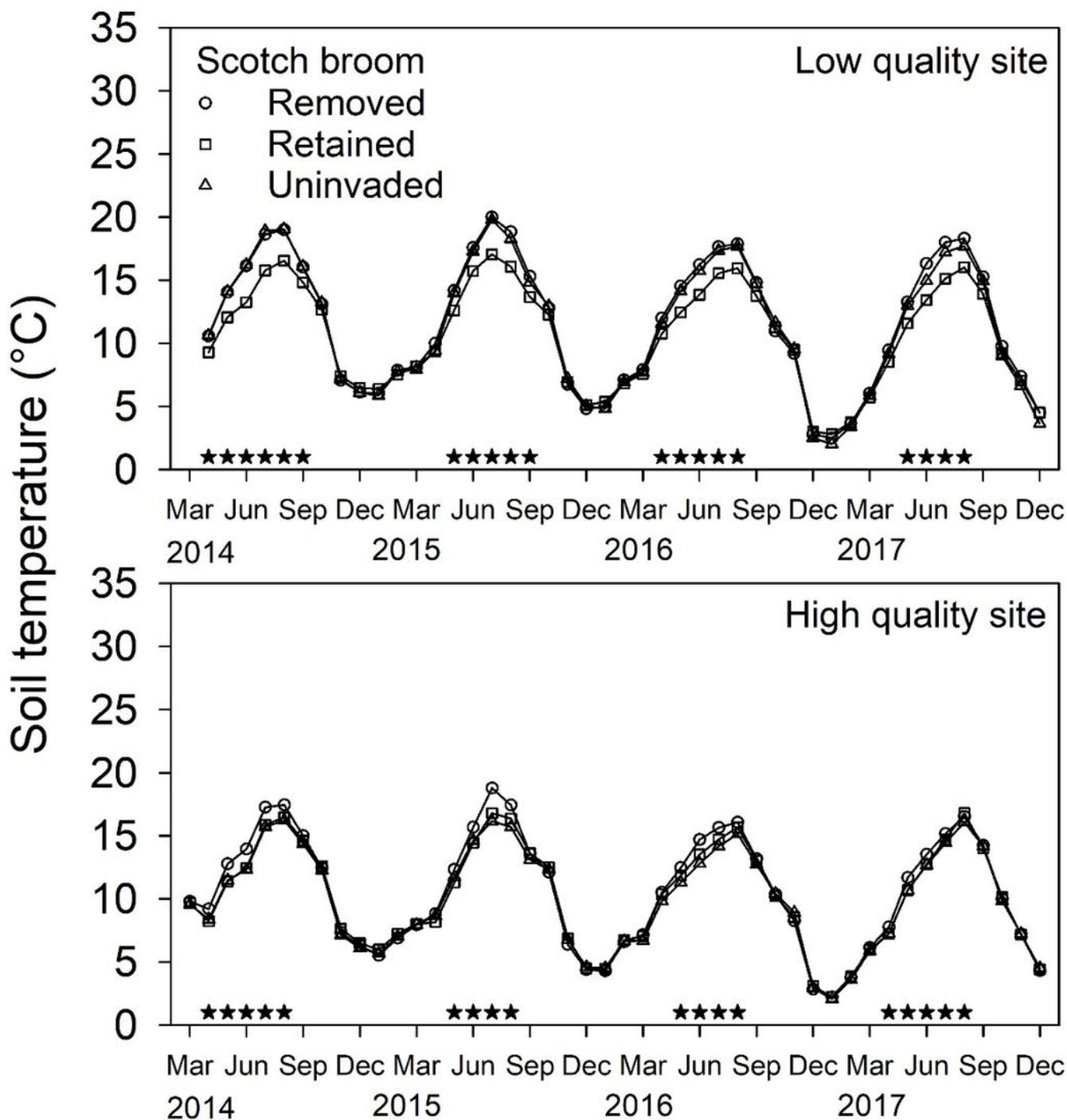

Figure 2

Average monthly soil temperature at 5 cm depth in the Scotch broom removal treatments during 2014-2017. Asterisks indicate time periods when temperatures differed significantly among treatments at P <
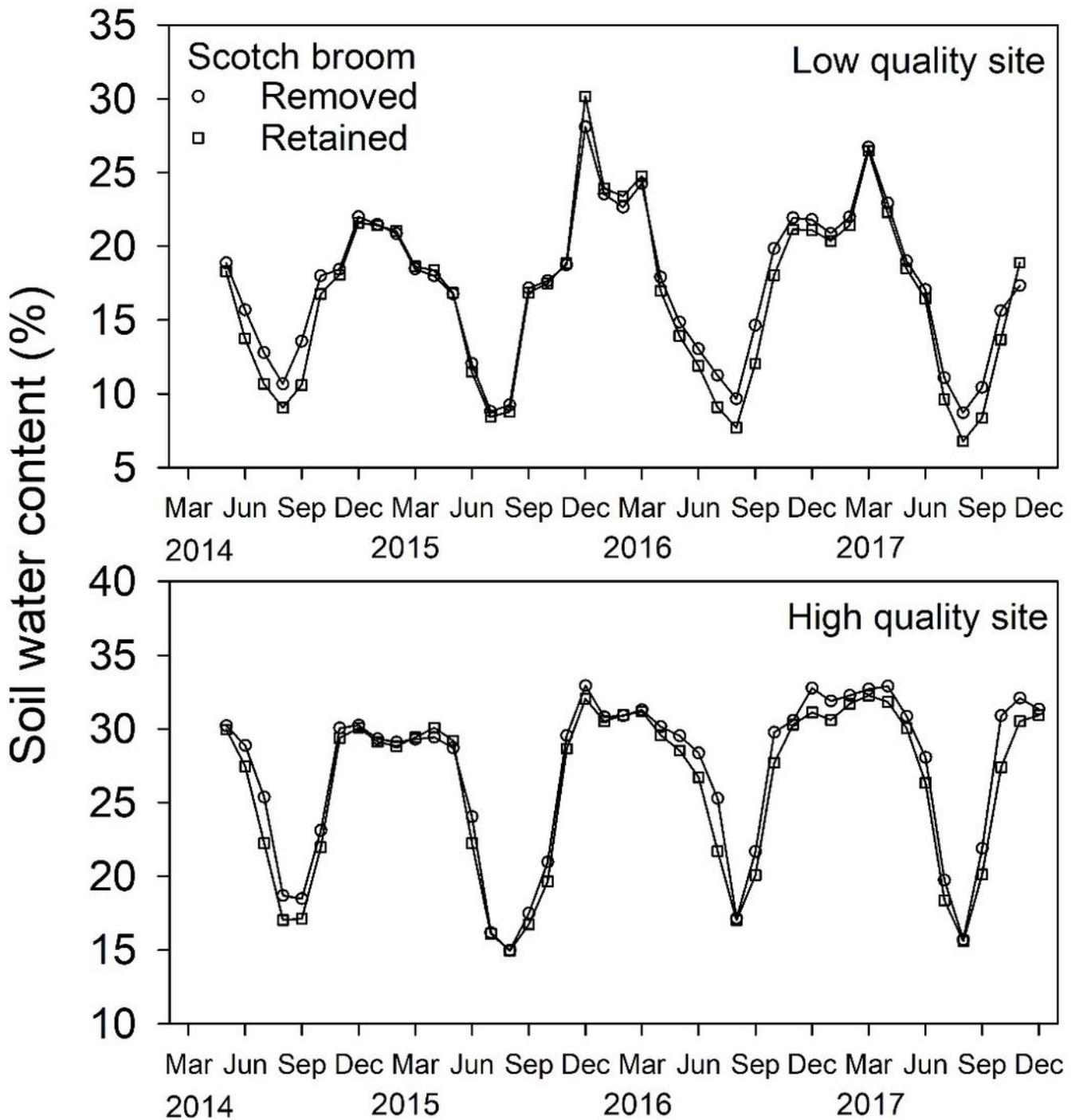
0.05.

Figure 3

Average monthly soil moisture content at 30 cm depth in Scotch broom removal and retention treatments during 2014-2017. Differences were not significantly different between treatments at any time period. Note that soil moisture content was not measured in the uninvaded treatment.
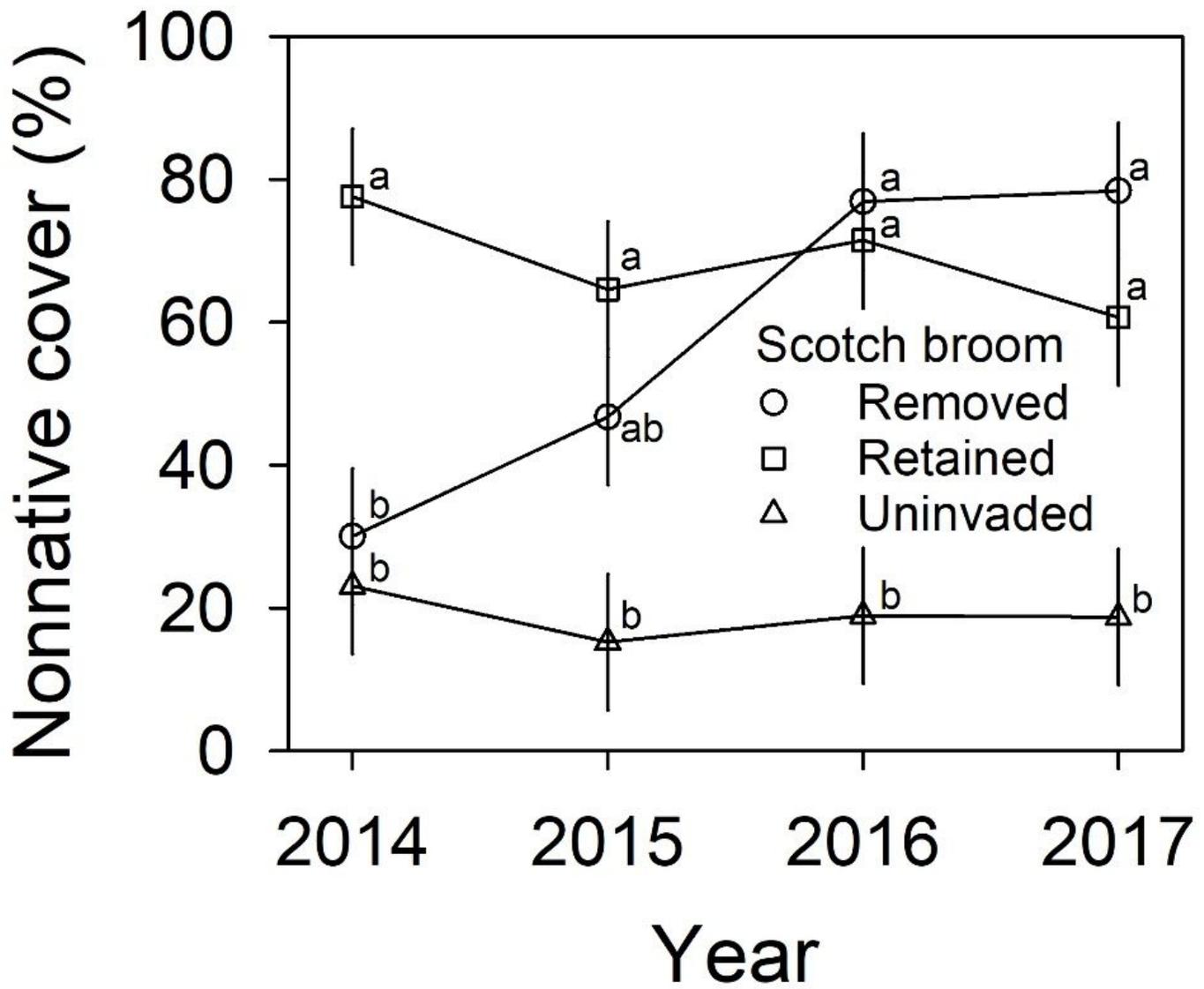
Figure 4

Average nonnative species cover in the Scotch broom removal treatments at the low-quality site during 2014-2017. For a given year, treatment means followed by different letters were significantly different at P < 0.05.
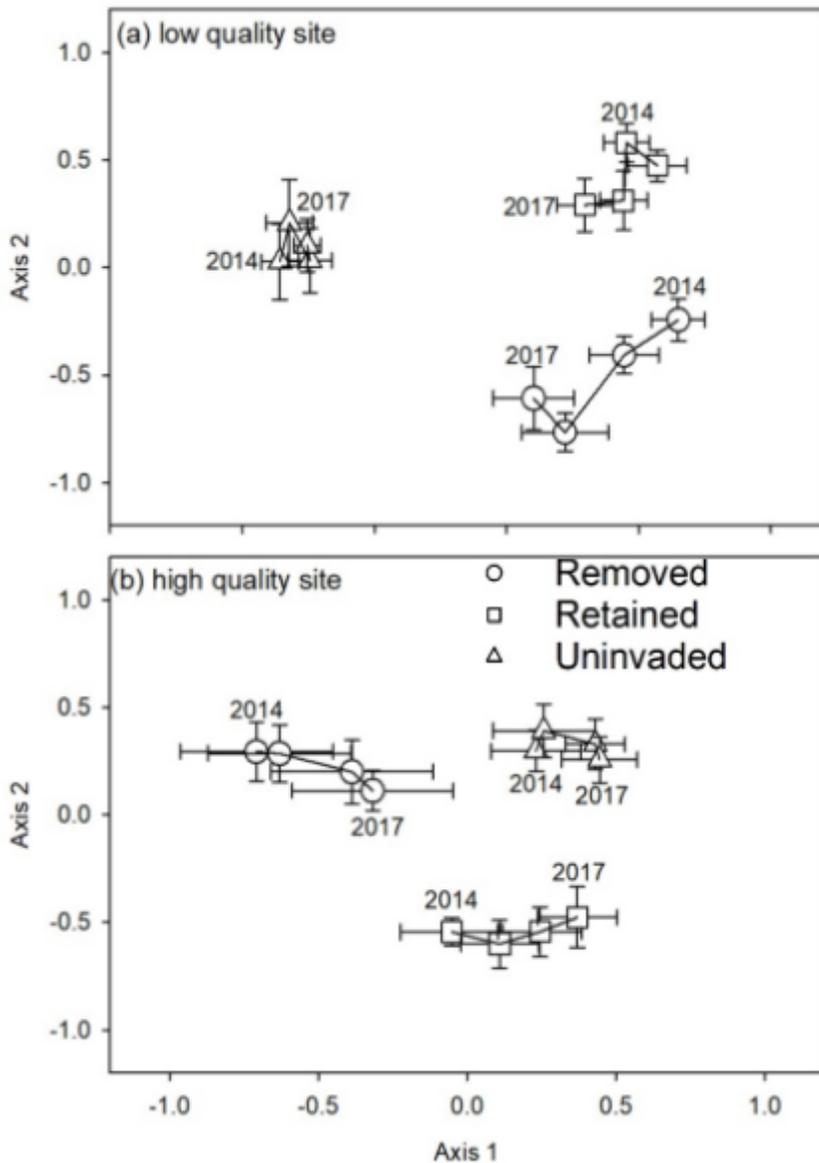
Figure 5

Non-metric multidimensional scaling ordination of plant community composition (mean axis scores of 10 replicates ± standard error) over time at the (a) low and (b) high quality sites in western Oregon and Washington. Years indicate beginning and end of study period.

Supplementary Files

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- SupplementaltablesFstatprobsbroomremovalstudy.docx