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Persistence of a soil legacy following removal of a nitrogen-fixing invader

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Abstract Vast effort and resources are spent to control invasive plants. Often with the assumption that once these resources are spent and the invader is successfully removed, the impact of that species on the community is also eliminated. However, invasive species may change the environment in ways that persist, as legacy effects, after the species itself is gone. Here we evaluate the persistence of soil legacy effects following the death of *Cytisus scoparius*, an invasive nitrogen-fixer. In a field experiment, we periodically killed *C. scoparius* with herbicide, so that by the end of 2 years the invader had been absent from plots for different durations of time (22, 10, and 1 month). After the final *C. scoparius* removal treatment, we measured available soil nitrogen and phosphorus as well as the abundance of native and exotic vegetation. We planted Douglas-fir seedlings into the removal plots and tracked seedling success. One month after *C. scoparius* removal, there was a soil legacy effect in the form of a large initial pulse of inorganic N, presumably as a result of rapid decomposition of N-rich *C. scoparius* biomass. In the 10-month removal plots, this initial pulse of N had declined dramatically and was 70 % less than the invaded state. However, over the following year, there was little additional decline of N. Time since *C. scoparius* removal also affected Douglas-fir seedling growth, where seedlings planted into areas where *C. scoparius* had been removed for 22 months were smaller than seedlings planted into areas where *C. scoparius* had been removed for 1 and 10 months. This pattern may be caused by competition from a second wave of exotic invaders, whose cover increased with time following *C. scoparius* removal. Rather than providing a lasting positive fertilization effect on native vegetation, our results suggest that increased N availability instead favors the invasion of fast-growing, nitrophyllic exotic grasses and forbs, and that these species limit colonization and growth of native vegetation including the locally dominant tree Douglas-fir.

Keywords Nitrogen enrichment · Temporal invasion impacts · Soil recovery · *Cytisus scoparius* · Scotch broom · Scot's broom · Douglas-fir · Forestry · Secondary invasions · Alternative stable states

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Introduction

Vast effort and resources are spent to control invasive species. It is typically assumed that once these resources are spent and the invader is successfully removed, the impact of that species on the community is also

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eliminated. However, invasive species may change the environment in ways that persist long after the species itself is gone; this is called a "legacy effect" (Ehrenfeld and Scott 2001; D'Antonio and Meyerson 2002; Corbin and D'Antonio 2004a). Legacy effects have been shown to inhibit native species from reoccupying habitat after an invader is removed (Vitousek et al. 1987; Maron and Jefferies 2001; Corbin and D'Antonio 2004a; Maron et al. 2011). There are several possible mechanisms by which invasive plants can impart persistent soil legacy effects. Soil legacies can result if a species changes the abundance and composition of soil biota, such as increased soil pathogen loads (Eppinga et al. 2006), or reduced abundances of beneficial microbial mutualists (Stinson et al. 2006; Pringle et al. 2009; Vogelsang and Bever 2009). Legacy effects can also result through changes in the availability of soil nutrients. Soil nutrient availability and cycling can be altered if an invasive species takes up resources and renders them unavailable to other species, or if an invader increases the availability of nutrients through nitrogen fixation or increasing decomposition rates (Allison and Vitousek 2004; Rothstein et al. 2004). These changes in nutrient dynamics can also result in soil legacies if nutrient availability is not restored to conditions that favor native species following invader removal (Maron and Jefferies 2001; Ehrenfeld 2003; Corbin and D'Antonio 2012).

Some legacy effects are self-reinforcing and appear to promote an 'alternative stable state' which is difficult to successfully restore to preinvasion conditions. The discussion of whether and how often invaded ecosystems may represent a "stable state" is a major debate in invasion ecology (Suding et al. 2004; Suding and Hobbs 2009; Yelenik and D'Antonio 2013). Consensus is limited, however, by a lack of examples where the trajectory of impacts has been followed over time after invader removal as the soil environment returns to pre-invasion conditions. These gaps in our knowledge of legacies have limited our ability to successfully restore species and ecosystem functioning post-control. The legacy effects of invaders can inhibit the success of restoration by facilitating reinvasion by the same or other exotic species, which in turn, can prevent the establishment and success of native plants (Simberloff and Von Holle 1999; Richardson et al. 2000; Maron and Jefferies 2001). One approach to testing the stability of an invaded system is to compare the restorability of the system over time following invader removal. This approach cannot determine how long an

invaded system will remain stable. Nonetheless, understanding the stability of an invaded state over timescales relevant to resource managers provides information that can guide management decisions.

Nitrogen-fixing species comprise a significant proportion of invaders worldwide (Daehler 1998), and a large number of studies report N enrichment associated with various widespread or locally aggressive species such as *Morella faya* (Vitousek et al. 1987), *Prosopis glandulosa* (Archer 1995), *Acacia* spp. (Le Maitre et al. 2011) and *Robinia pseudoacacia* (Von Holle et al. 2005; Castro-Diez et al. 2009). The effects of soil N enrichment on ecosystem properties and plant communities is variable and largely depends on whether or not N is a limiting nutrient for plants (Nuñez and Dickie 2014). Nonetheless, most studies on N-fixing invaders have documented soil N enrichment with invasion, and a subset have suggested that this increased N can persist as a soil legacy and continue to have effects on ecosystems after invader removal (Vitousek et al. 1997; Corbin and D'Antonio 2004b; Vitousek et al. 2013).

A few studies have found that plants with N-fixing associations can alter N and carbon (C) pools to such an extent that it can take years to return to pre-invasion levels (Maron and Jefferies 2001; Marchante et al. 2008) while other studies have found N availability returns to pre-invasion levels quickly following invader removal (Malcolm et al. 2008; Hughes et al. 2012). However, with only a few studies to compare, it is unclear how general the legacy effects of N-fixing invaders are, how long they persist and what factors control their duration (Arkema et al. 2006; Strayer et al. 2006; Suding and Hobbs 2009). Where soil legacy effects occur, restoration may require additional efforts beyond invader removal that aim to mitigate their effects (Corbin and D'Antonio 2012).

Nitrogen enrichment may positively affect the growth of recolonizing plant species, particularly fast growing species with the ability to capitalize on increased nutrient availability such as exotic grasses and forbs (Milberg et al. 1999; Davis et al. 2000). Thus, legacies of N-fixers can be positive for some species (e.g., Maron and Jefferies 2001), but may also have negative effects on other species by changing plant community dynamics (Rook et al. 2011). For example, the secondary invasion of fast growing exotic grasses following the removal of an N-fixing invader may inhibit the establishment and growth of native species

that are less able to take advantage of increases in available N.

Here we examine the duration of a soil legacy after the removal of *Cytisus scoparius*, a widespread N-fixing invader. We removed *C. scoparius* at different times over a 22 month period and allowed areas to be free of *C. scoparius* for 0, 1, 10, and 22 months before measuring soil properties and Douglas-fir seedling growth. To evaluate how soil legacy effects influence the restoration potential of invaded areas, we measured nutrient availability at the time of tree planting, the survival and growth of Douglas-fir across time since *C. scoparius* removal treatments, and the abundance of native and exotic vegetation.

Methods

Study system

Cytisus scoparius, is a large N-fixing shrub in the Fabaceae, it is native to Europe (Hegi 1926), and has been introduced as an ornamental plant throughout the globe (North America, New Zealand, Australia, India, South Africa and Chile) where it has become an invasive pest (Mobley 1954; Gilkey 1957; Peterson and Prasad 1998; Isaacson 2000; Smith et al. 2000). In the United States, its range in the Pacific Northwest region is extensive (Hulting et al. 2008), and it invades open sites extremely rapidly (Parker and Reichard 1998; Parker 2000).

Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) is the dominant tree of lowland forests in the Pacific Northwest. Its latitudinal distribution extends from central British Columbia to central California (Hermann and Lavender 1990), and it is an economically important timber species. *C. scoparius* invades timber harvested areas forming dense stands (Parker et al. 2014), resulting in a loss of more than $100 million annually in timber revenue and control expenses in the Pacific Northwest (Hulting et al. 2008; Matsen 2011).

To determine how long the legacy effects of *C. scoparius* invasion persist after *C. scoparius* removal, we conducted a field experiment in four heavily invaded, formerly forested sites in western Washington (Mason County). The distances between field sites ranged from 1.2 to 27 aerial km. Each of these sites is managed by the Green Diamond Resource timber company and had been clearcut 9–28 years prior to the start of the experiment, then extensively invaded by *C.*

scoparius. The soils in all four sites are characterized as glacial outwash gravelly loamy sand as assigned by the WA-Natural Resource Conservation Service (USDA NRCS 2012).

In May 2011, we installed four 20 m × 20 m contiguous plots in four separate sites (16 total plots). In July 2011, July 2012, and April 2013, we removed *C. scoparius* from one randomly selected plot per site so that by the end of these removal treatments, there were 1-month removal, 10-month removal, and 22-month removal plots. In the control plots, *C. scoparius* was left alive and unmanipulated. One approach to studying legacy effects is to remove the invader and then sample the responses to invader removal at different times after initial invader removal. With this approach, time of year of sampling is confounded with time since removal. We took a different approach in order to avoid this problem: instead we varied the time of invader removal, but sampled the responses Douglas-fir survival and growth, soil nutrients, and exotic grass and forb colonization at the same time across all treatments. Soil nutrients vary significantly across seasons (Powers 1990; Laverman et al. 2000), especially in the Pacific Northwest with wet winters and dry warm summers. Our approach allowed us to minimize temporal variation in soil nutrients and to collect soil samples and plant trees at the same time. To kill *C. scoparius* in the treatment plots we hired professional contract crews associated with the Green Diamond Resources timber company to apply Garlon 4 Ultra (5 gallons/removal plot at 1.3 % concentration) herbicide treatments. The dead *C. scoparius* plants were left to decompose in place. Hereafter we refer to the plots where *C. scoparius* was killed as removal treatments, for want of a better term. Prior to each removal treatment, we used a line-intercept method to measure *C. scoparius* cover along a 30-m transect that ran diagonally across each plot, confirming that each plot started with at least 70 % cover of *C. scoparius*. In April 2013, after the final *C. scoparius* removal treatment, we planted 50 Douglas-fir seedlings, approximately 2.5 m apart, into each treatment plot (N = 50 seedlings/plot × 3 plots/site × 4 sites = 600 seedlings). Seedlings were donated from the Washington State Department of Natural Resources Webster's Forest Nursery (Tumwater, Wa) and were grown from seed collected from the Kitsap seed zone. Prior to out-planting, seedlings were grown for 1 year in a seed bed, then harvested, root pruned,

and transplanted into another nursery bed where they were grown for a second year. At the time of planting we measured initial seedling heights, which ranged from 0.11 to 0.63 m. Douglas-fir seedlings were not planted into the untreated plots because *C. scoparius* was still growing in those plots, and impacts of soil changes on Douglas-fir seedling growth would be confounded with direct competition from *C. scoparius* (Zielke et al. 1992).

Field sampling

In an effort to minimize post-planting effects such as drought and transplant shock, we followed standard forestry practices and out-planted the Douglas-fir seedlings in April. At the time of tree planting (April 27–29, 2013), we collected soil cores in order to characterize the soil legacy effects of *C. scoparius* following its removal. We collected soil samples from two of the three *C. scoparius* removal treatments (10 and 22 month removals as well as intact 'control' plots). An unfortunate logistical problem delayed the third herbicide treatment plot ('1 month removal'). Therefore the *C. scoparius* plants had not yet died at tree planting time. To address this, we collected soil cores from the final *C. scoparius* removal plot one month later (May 28–31 2013), and re-collected soils from the live intact *C. scoparius* 'control' plots to be able to account for seasonal differences between the April and May sampling points. We did not sample soil from the third herbicide treatment plot ('1 month removal') at the time of initial sampling because the herbicide application had just occurred and the plants had not yet died. One month later, after tree planting and initial soil sampling (May 28–31 2013), we collected soil cores from the final *C. scoparius* removal plot and re-collected soils from the live intact *C. scoparius* 'control' plots to account for seasonal differences between the April and May sampling points. We collected soil cores every 5-m along a 30-m transect that ran diagonally across each plot, beginning at the 5-m mark and ending at the 25-m mark to avoid sampling in the edge of plots. At each 5-m sampling interval we used a 5-cm diameter coring device, driven 20 cm into the mineral soil (N = 5 soil cores/plot × 4 plots/site × 4 sites = 80 soil cores). All soil cores were collected within 20 cm of the nearest *C. scoparius* stem (dead stems in the treated plots and live stems in the control). Large rocks and root material were removed by hand, then the samples were stored on ice, after which they were returned to a 3 °C refrigerator until shipment to Northern Arizona University for N and P analysis.

Soil samples were analyzed for available N, phosphorus (P), and pH. A 7-day laboratory aerobic incubation was conducted in order to estimate potentially mineralizable N (net $NO_3^- + NH_4^+$), an index of soil N availability (Binkley and Hart 1989). Two ~10-g subsamples of field-moist soils were weighed into specimen cups; one subsample was immediately extracted with 50 mL 2 M KCl and the other subsample was capped and incubated in a dark box at room temperature for 7 days. A third subsample was oven-dried for 48 h at 60° C in order to measure gravimetric water content in order to express net minerlization on a dry soil basis. At the end of the 7-day period the incubated subsample was extracted with 50 mL of 2 M KCl. All KCl extracts were shaken for 30 min then refrigerated for 24 h to allow samples to settle. After 24 h, extracts were filtered through Whatman #1 filters; filtrates were then frozen until analysis. Available P was assayed with a $NaHCO_3$ extraction on air-dried soils (Olsen et al. 1954; Indiati et al. 2004). Both P and N samples were analyzed on a Lachat (QuikChem Method 10-115-01-1-A, Orthophosphate in Waters for P: Method 12-107-06-2-A for NH_4^+ and 12-107-04-1-B for NO_3^-) at the Colorado Plateau Analytical Laboratory at Northern Arizona University. Soil pH was measured on all samples using a 1:1 soil slurry.

In November 2013, after one growing season, we assessed Douglas-fir seedling survivorship and measured height of all surviving seedlings. We also recorded any evidence of herbivory on all seedlings. At the same time, we used a standard point intercept method to measure the abundance (% cover) of all other individual species besides Douglas-fir and *C. scoparius* in each plot. We recorded each species encountered every 0.5 m along a 30-m transect that ran diagonally across each plot. We then classified each species observed as native or exotic and recorded its growth form (grass, forb, tree, shrub, or fern). Regeneration of *C. scoparius* was negligible in all herbicided plots and no individuals were encountered along the line intercept transects.

Statistical analyses

We compared treatments for the cover of *C. scoparius* at the time of removal with a mixed model ANOVA with time since removal included as a fixed ordinal effect and site as a random effect. Similarly, we used a mixed model ANOVA to determine the effect of time since removal on pH, availability of nitrogen and phosphorus, change in Douglas-fir seedling height, and percent cover of exotic and native plants.

To evaluate the effect of time since *C. scoparius* removal on Douglas-fir seedling survival we used a logistic regression model with time since removal and site as factors. In the field, at the time of the final growth measurements some seedlings had been damaged by herbivores, presumably deer, and often the current year's growth was absent. To determine if the degree of herbivory varied among time since removal treatments we used a logistic regression model with time since removal and site as factors.

All analyses were done in JMP v 10 (SAS Institute). For all ordinal ANOVA mixed models we used Tukey's post hoc tests to compare means among the treatment groups (time since *C. scoparius* removal).

Results

Cytisus scoparius cover was greater than 70 % in all treatments immediately prior to removal. Because the individual plants continued to grow throughout the duration of the experiment, percent cover varied across time since removal treatments (F = 7.79, $df = 3, 9$, $P = 0.007$) and treatments imposed later had higher *C. scoparius* cover at the time of removal (0-month: 121 % (SE 7.8), 1-month: 110 % (14.7), 10-month: 82 % (8.6), 22-month: 70 % (10).

We found no difference in available N between the April and May field sampling dates in the control plots where *C. scoparius* was left alive and intact. Therefore April and May data were combined to provide one pre-removal estimate of available N. Available N spiked in the 1 month *C. scoparius* removal plots (Fig. 1a); there was 35 % more available N than in intact *C. scoparius* control plots. However, in the plots where *C. scoparius* had been removed for 10 months available N was 30 % less than areas where *C. scoparius* remained intact, and where *C. scoparius* was removed
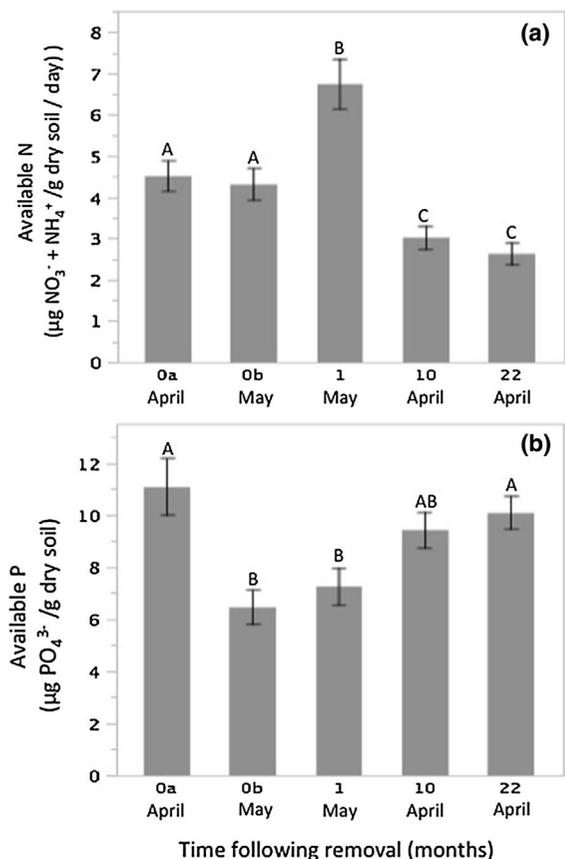

Fig. 1 **a** Available nitrogen (µg NO_3^- + NO_4^+/g dry soil/day) and **b** available phosphorus (µg PO_4^{3-}/g dry soil) availability at 0, 1, 10 and 22 months after the removal of *Cytisus scoparius*. *0a* samples were collected in April 2013 from the intact, live *C. scoparius* 'control' plots and *0b* samples were collected in the same plots in May 2013. *Letters* indicate significant differences from a Tukey's post hoc test. *Error bars* = ±1 standard error

for 22 months available N decreased another 6 % (F = 22.2, $df = 3, 80$, $P = 0.0001$).

Unlike N, available P was significantly greater in intact *C. scoparius* control plots in April compared to May (F = 26.6, $df = 1, 32$, $P = 0.0001$; Fig. 1b), limiting our ability to compare P availability across all treatments. Instead we compared P availability in soils that were collected during the same sampling point. That is, for the April sampling point we compared the 10 and 22 month *C. scoparius* removal treatments to the intact control plots sampled in April. We found no difference in P availability between the 10 and 22 month *C. scoparius* removal plots compared to the soils in the intact *C. scoparius* control plots (F = 1.8, $df = 2, 50$, $P = 0.17$). For the May

sampling point we compared the 1-month *C. scoparius* removal plots to the intact *C. scoparius* control plots sampled in May. Again, we found no difference in P availability between the 1-month removal plots compared to the plots where *C. scoparius* was left intact (F = 0.99, df = 1, 32, P = 0.33). Thus P availability varied with sampling time but not with treatment.

Similar to P availability, soil pH was 5 % higher in May compared to April in intact plots (F = 34.9, df = 1, 34, P = 0.0001), and so comparisons with intact control plots were made as above. One month following *C. scoparius* removal we found a slight (0.2) decrease in soil pH (F = 22.7, df = 1, 23, P = 0.0001) relative to live intact *C. scoparius* control plots sampled in May. We found no difference in soil pH in the 10 or 22-month post removal treatments versus *C. scoparius* intact plots sampled in April (F = 0.76, df = 2, 54, P = 0.47).

Douglas-fir seedling survival was unaffected by time since removal (χ^2 = 2.7, P = 0.26; Fig. 2). However, duration of time in the absence of *C. scoparius* affected growth of surviving seedlings (F = 7.7, df = 2, 504, P = 0.0005; Fig. 2). Seedlings planted into the 22-months post invader removal plots grew 37 % less than seedlings planted into 1-month post removal plots and 29 % less than seedlings planted in 10-month post-removal plots. There was no difference in seedling growth between seedlings planted 1 and 10 months post invader removal. The proportion of seedlings affected by herbivores (40–44 %) did not vary between time since removal treatments (χ^2 = 1.8, P = 0.41), but did vary among sites (χ^2 = 232.9, P = 0.0001). When seedlings that had experienced deer herbivory were excluded from the analysis, the effects of time following invader removal on seedling growth were in the same direction and were more extreme (F = 11.5, df = 2, 292, P = 0.0001).

The cover of exotic species, which were all grasses and forbs increased markedly with time following *C. scoparius* removal (F = 4.1, df = 3, 9, P = 0.04; Fig. 3a); whereas the cover of native vegetation, which included shrubs, trees, ferns, forbs and grasses, did not (F = 0.55, df = 3, 9, P = 0.67; Fig. 3b). None of the species were N-fixing. In the 1-month removal plots there was more than double the cover of exotic plants (40 %), compared to the control plots where *C. scoparius* was left intact (18 %). With time following *C. scoparius* removal, cover of exotics continued to increase, in the plots where *C. scoparius*
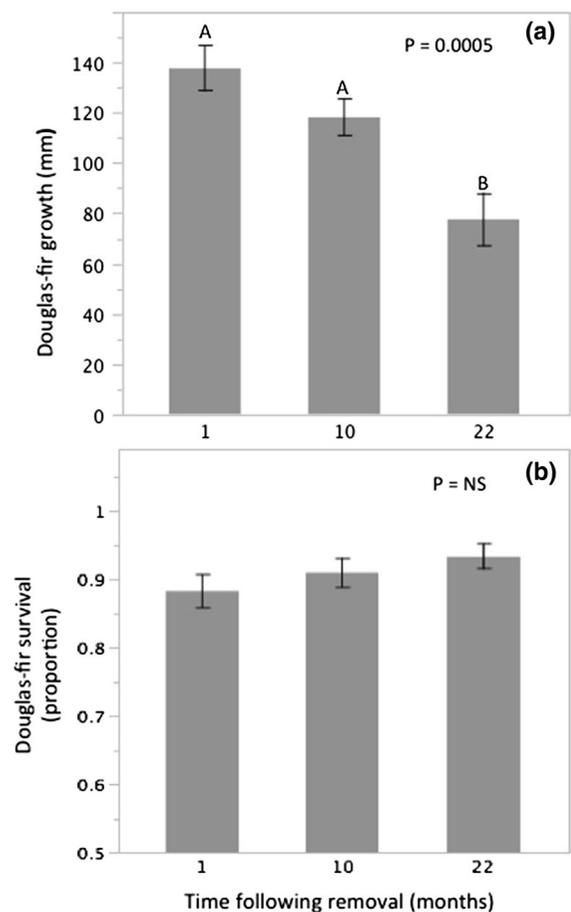

Fig. 2 a Douglas-fir growth (mm/195 days) in deforested, invaded areas that had *Cytisus scoparius* removed 1, 10 and 22 months prior to outplanting, excluding seedlings that had been browsed by deer, **b** the proportion of Douglas-fir seedlings that survived. *Letters* indicate significant differences from a Tukey's post hoc test. *Error bars* = ±1 standard error

had been removed for 22 months exotic grasses and forbs covered ~75 % of the plots.

Discussion

The legacy effect of *C. scoparius* was complex, with asynchronous soil and plant responses. Following *C. scoparius* removal, there was a large and immediate pulse of available soil N. This is consistent with other studies demonstrating enrichment of the soil N pool by N-fixing invaders in general (Liao et al. 2008; Ehrenfeld 2010; Castro Díez et al. 2014) and by *C. scoparius* in particular (Dancer et al. 1977; Wheeler
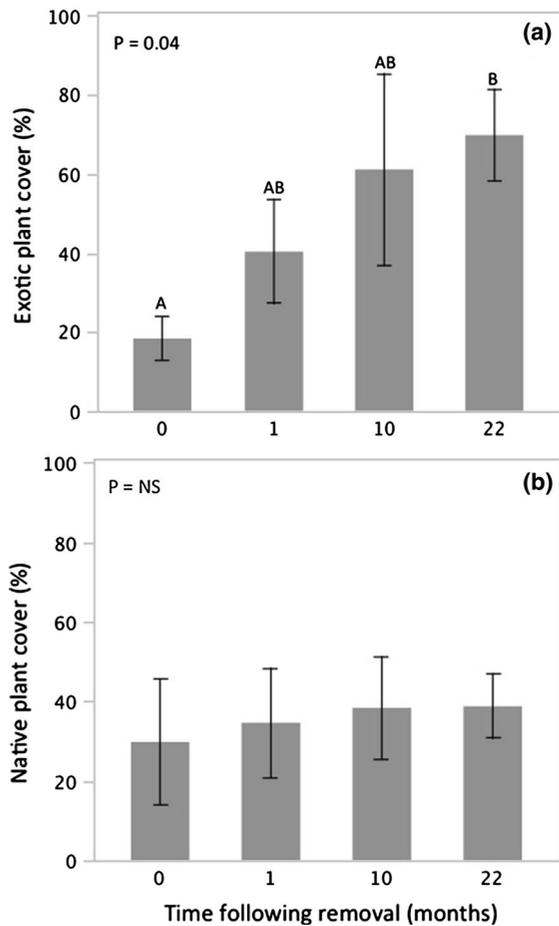
Fig. 3 The percent cover of **a** exotic and **b** native plants in areas that had *Cytisus scoparius* removed for 0, 1, 10 and 22 months. *Letters* indicate significant differences from a Tukey's post hoc test. *Error bars* = ±1 standard error

et al. 1987; Diquelou and Roze 1999; Fogarty and Facelli 1999; Haubensak and Parker 2004; Caldwell 2006). One month following the removal of *C. scoparius*, a large pulse of inorganic nitrogen was released, resulting in 35 % more available N relative to areas where *C. scoparius* remained intact and alive. However, this component of the legacy was short-lived. Where *C. scoparius* had been removed for 10 months, N availability was 30 % lower than under intact live *C. scoparius*, and in the 22-month removal plots, N availability further decreased another 6 %.

Even after this large decrease in N across treatments, the amount of available N in the oldest-removal plots was still threefold higher compared to typical values reported for Douglas-fir forest soils from the region (Sollins et al. 1980; Perakis et al. 2012).

Because each of our sites was heavily and homogeneously invaded by *C. scoparius*, it was not possible to incorporate an uninvaded treatment for comparison in this study. So, although comparisons to the literature suggest that the legacy still persisted at 22-months post-removal, caution is warranted in drawing quantitative conclusions about that long-term persistence.

Despite the widespread recognition that N-fixing invaders change nutrient dynamics and increase N availability, very few studies have tracked the persistence of N enrichment following invader removal. In a chronosequence study, Hughes et al. (2012) compared available N in soils that had been invaded by the legume *Falcataria moluccana* and eradicated for different durations of time (from 0 to 8 years). Similar to our findings, available N increased by 300 % relative to nearby uninvaded forest soils immediately following the removal of *F. moluccana*. However, by 3 years following *F. moluccana* eradication available N had returned to pre-invasion levels (Hughes et al. 2012). In contrast, Von Holle et al. (2013) detected N enrichment caused by the invasive legume *Robinia pseudoacacia* as long as 14 years after a hurricane had removed entire stands of the invader. Surprisingly, while there was less N enrichment in that system compared to ours, the legacy of *R. pseudoacacia* was more persistent than we report here for *C. scoparius*. This suggests that the impact of an N-fixer (and its legacy) may be less dependent on initial N conditions.

We did see a sudden drop in N availability between 1-month *C. scoparius* removal and 10-month removal treatments. This may have been due to NO_3^- leaching, as glacial outwash soils are relatively coarse in texture, well drained and receive considerable rainfall. It is also possible that the drop in N availability reflected rapid uptake by the fast-growing herbaceous vegetation. However, because we observed that plant cover was extremely sparse immediately following *C. scoparius* removal, we suspect NO_3^- leaching is a better explanation for the pattern. Another factor that could have contributed to the difference between the treatments is that even though it was already at 70 % cover at the start of our study, *C. scoparius* continued to grow in the un-controlled plots through time. Before they were killed, the shrubs in the '1-month' treatment grew for 9 more months than those in the '10-month' treatment, and they may have supplied additional N to the soil. We don't believe that this was a large factor because we did not see a similarly large

difference between the 10-month treatment and the 22-month treatment. We also do not expect that denitrification played a large role in the observed pattern of decline in N availability because these soils do not often experience anaerobic conditions.

Native vegetation cover was not promoted by the N fertilization effect associated with *C. scoparius* senescence. The native plants that colonize lowland Douglas-fir forest after harvest are primarily perennial shrubs and forbs, which tend to be relatively slow growing and adapted to low nutrient conditions (Kruckeberg 1995; Swanson et al. 2011). In our sites these included *Gaultheria shallon*, *Arctostaphylos uva ursi*, *Corylus cornuta*, *Cornus nuttallii*, *Symphoricarpos albus* and *Prunus emarginata*. Instead, the increased N availability that resulted from *C. scoparius* invasion appeared to have promoted the growth of exotic forbs and grasses including *Tanacetum vulgare*, *Leucanthemum vulagare*, *Hypochaeris radicata*, *Digitalis purpurea*, *Agrostis capilaris*, *Holcus lanatus*, *Arrhenatherum elates*, and *Phalaris arundinacea*. In control plots where *C. scoparius* was left untreated, we found only 20 % of the understory occupied by other exotic species. However, in the 10-month removal plots, the cover of exotic grasses and forbs more than doubled, and in the 22-month plots ranged from 60 to 70 %. Rather than providing a positive fertilization effect on native vegetation, our results suggest that increased N availability facilitated invasion of other exotic species, influencing competitive dynamics and changing the structure of the plant community from woody shrubs to grasses and annual forbs. Such soil-based facilitation of secondary invasions has also been observed in a number of other studies (Simberloff and Von Holle 1999; Ehrenfeld and Scott 2001; Von Holle et al. 2005; Liao et al. 2008; Dickie et al. 2014).

In contrast to the other native species, Douglas-fir did show an opportunistic response to the initial flush of N, as it had the highest growth rates when planted into 1-month removal plots. Douglas-fir growth also decreased along with N-availability across our treatments: both were lowest in the 22-month removal plots. This suggests Douglas-fir growth may have been tracking N availability, or it may reflect more complex ecological interactions, such as competition with exotic grasses and forbs. Harrington et al. (2013) found that early growth of Douglas-fir in this region is limited by both water and N, which suggests that competition with exotic grasses and forbs for water as

well as nutrients may be important. It is likely that both N loss and increased competition contributed to the pattern of decreased growth of Douglas-fir across our treatments.

We should note, however, that because of Douglas-fir's association with ectomycorrhizal fungi (EMF), it can access organic N which non-ectomycorrhizal plants cannot (Smith and Read 1997; Read and Perez-Moreno 2003; Hobbie and Hobbie 2006). Our measure of N availability did not address the organic N pool; rather, this index measures inorganic N that is potentially mineralizable by microbes under idealized laboratory conditions (Binkley and Hart 1989). However, inorganic N is the most easily usable form of N for all plants, including ectomycorrhizal species such as Douglas-fir (Lilleskov et al. 2002). In our previous work we found that *C. scoparius* invasion reduces the abundance of ectomycorrhizal fungi on Douglas-fir roots (Grove et al. 2012) and that addition of NO_3^- (a form of inorganic N) also reduces EMF abundance (Megan Bontrager unpublished data) on Douglas-fir seedlings. Both these pieces of evidence suggest that one effect of *C. scoparius* is a reduced ability for Douglas-fir to utilize organic N.

Because N fixation can create high demand for P, we hypothesized that P availability would be depleted in control plots (where *C. scoparius* was presumably actively fixing N) relative to removal plots where P would be made more available due to the decomposition of P-containing *C. scoparius* biomass. However, we found no pulse of P following removal. It is possible that inorganic P released via decomposition was immediately taken up by plants colonizing the plots. It is also possible that *C. scoparius* biomass was not particularly P-rich, or that mineralized P was immediately adsorbed on soil surfaces (Stewart and Tiessen 1987).

Management implications

Our work demonstrates that with time following *C. scoparius* removal, soil N-availability immediately increases in the system and then is either taken up by fast growing exotic grasses and forbs or is leached out of the soil. The initial pulse of N coincided with the invasion of other exotic grasses and forbs. From a forestry perspective, the implications of this secondary invasion will depend on the factors that are most

limiting to Douglas-fir seedling growth. If grass competition inhibits the success of planted seedlings, then applying management strategies that minimize the N inputs will be important. In our study, the herbicide-treated stands of *C. scoparius* were left to decompose in place, allowing N to be cycled back into the soil. If we had taken the aboveground portion of *C. scoparius* off-site after killing it, this pulse of N would be removed from the system thus decreasing the competitive advantage of fast growing exotic species over slow-growing native shrubs and trees. The outcome of removing the aboveground biomass will however depend on how much of the N release following *C. scoparius* treatments is from the aboveground versus the belowground tissues.

It is also worth considering timing of the herbicide application. When *C. scoparius* was sprayed in April, a large pulse of N was released into the soil during the active growing season of other plants in the lowland Douglas-fir community, particularly the exotic grasses and forbs. Knowing that a pulse of N is going to be added to the environment following *C. scoparius* removal, it may be advantageous to kill the *C. scoparius* during the fall and winter months while the exotic grasses and forbs are dormant. This approach could result in increased leaching of the N and possibly aid in the recovery of native species and the release of Douglas-fir seedlings from competition with fast growing nitrophyllic exotics.

Our results also provide some insights as to the best time to plant Douglas-fir seedlings following *C. scoparius* herbicide applications. Our findings suggest that a 'sooner the better' planting strategy following *C. scoparius* herbicide applications may be a best approach. In our study, the seedlings planted immediately following *C. scoparius* removal, grew the largest, presumably because of both the N enrichment associated with the invader and the lag time before exotic grasses and forbs became dominant. Further studies are required to disentangle the relative importance of N loss and competitive exclusion following invader removal.

References

Allison SD, Vitousek PM (2004) Rapid nutrient cycling in leaf litter from invasive plants in Hawai'i. Oecologia 141:612–619

Archer S (1995) Tree–grass dynamics in a *Prosopis*-thornscrub savanna parkland—reconstructing the past and predicting the future. Ecoscience 2:83–99

Arkema KK, Abramson SC, Dewsbury BM (2006) Marine ecosystem-based management: from characterization to implementation. Front Ecol Environ 4:525–532

Binkley D, Hart SC (1989) The components of nitrogen availability in forest soils. Adv Soil Sci 10:58–112

Caldwell B (2006) Effects of invasive Scotch broom on soil properties in a Pacific coastal prairie soil. Appl Soil Ecol 32:149–152

Castro Díez P, Godoy O, Alonso A, Gallardo A, Saldaña A (2014) What explains variation in the impacts of exotic plant invasions on the nitrogen cycle? A meta analysis. Ecol Lett 17:1–12

Castro-Diez P, Gonzalez-Munoz N, Alonso A, Gallardo A, Poorter L (2009) Effects of exotic invasive trees on nitrogen cycling: a case study in Central Spain. Biol Invasions 11:1973–1986

Corbin JD, D'Antonio CM (2004a) Competition between native perennial and exotic annual grasses: implications for an historical invasion. Ecology 85:1273–1283

Corbin JD, D'Antonio CM (2004b) Effects of exotic species on soil nitrogen cycling: implications for restoration. Weed Technol 18:1464–1467

Corbin JD, D'Antonio CM (2012) Gone but not forgotten? Invasive plants' legacies on community and ecosystem properties. Invasive Plant Sci Manag 5:117–124

D'Antonio C, Meyerson LA (2002) Exotic plant species as problems and solutions in ecological restoration: a synthesis. Restor Ecol 10:703–713

Daehler CC (1998) The taxonomic distribution of invasive angiosperm plants: ecological insights and comparison to agricultural weeds. Biol Conserv 84:167–180

Dancer WS, Handley JF, Bradshaw AD (1977) Nitrogen accumulation in kaolin mining wastes in Cornwall natural communities. Plant Soil 48:153–167

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. J Ecol 88:528–534

Dickie IA, St John MG, Yeates GW, Morse CW, Bonner KI, Orwin K, Peltzer DA (2014) Belowground legacies of *Pinus contorta* invasion and removal result in multiple mechanisms of invasional meltdown. AoB Plants 6:plu056

Diquelou S, Roze F (1999) Establishment of broom, impact of previous land use and soil dynamics in old-fields (Brittany, France). Comptes Rendus De L Academie Des Sciences Serie Iii-Sciences De La Vie-Life Sciences 322:705–715

Ehrenfeld JG (2003) Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems 6:503–523

Ehrenfeld JG (2010) Ecosystem consequences of biological invasions. In Futuyma DJ, Shafer HB, Simberloff D (eds) Annual review of ecology, evolution, and systematics. Annual reviews, Vol 41. Palo Alto

Ehrenfeld JG, Scott N (2001) Invasive species and the soil: effects on organisms and ecosystem processes. Ecol Appl 11:1259–1260

Eppinga MB, Rietkerk M, Dekker SC, De Ruiter PC, Van der Putten WH (2006) Accumulation of local pathogens: a new hypothesis to explain exotic plant invasions. Oikos 114:168–176

Fogarty G, Facelli JM (1999) Growth and competition of *Cytisus scoparius*, an invasive shrub, and Australian native shrubs. Plant Ecol 144:27–35

Gilkey HM (1957) Weeds of the Pacific Northwest. Oregon State College, Corvallis

Grove S, Haubensak KA, Parker IM (2012) Direct and indirect effects of allelopathy in the soil legacy of an exotic plant invasion. Plant Ecol 213:1869–1882

Harrington TB, Slesak RA, Schoenholtz SH (2013) Variation in logging debris cover influences competitor abundance, resource availability, and early growth of planted Douglas-fir. For Ecol Manag 296:41–52

Haubensak KA, Parker IM (2004) Soil changes accompanying invasion of the exotic shrub *Cytisus scoparius* in glacial outwash prairies of western Washington [USA]. Plant Ecol 175:71–79

Hegi G (1926) Illustrated flora of Central Europe. Carl Hanser, Munich

Hermann RK, Lavender DP (1990) *Pseudotsuga menziesii* (Mirb.) franco Douglas-fir. U.S. Department of Agricutlure, Forest Service, Washington D.C

Hobbie JE, Hobbie EA (2006) N-15 in symbiotic fungi and plants estimates nitrogen and carbon flux rates in Arctic tundra. Ecology 87:816–822

Hughes RF, Uowolo AL, Togia TP (2012) Recovery of native forest after removal of an invasive tree, *Falcataria moluccana*, in American Samoa. Biol Invasions 14:1393–1413

Hulting A, Neff K, Coombs E, Parker R, Miller G, Burrill LC (2008) Scotch broom biology and management in the Pacific Northwest. PNW 103, 7 pp

Indiati R, Diana G, Figliolia A, Perucchini I (2004) Comparison of conventional and innovative soil phosphorus tests in estimating plant-available phosphorus. Soil Fertility and Plant Nutrition. Options Mediterraneenes, Serie A, no. 50

Isaacson DL (2000) Impacts of broom (*Cytisus scoparius*) in western North America. Plant Prot Q 15:145–148

Kruckeberg AR (1995) The natural history of Puget Sound Country. University of Washington Press, Seattle

Laverman AM, Zoomer HR, van Verseveld HW, Verhoef HA (2000) Temporal and spatial variation of nitrogen transformations in a coniferous forest soil. Soil Biol Biochem 32:1661–1670

Le Maitre DC, Gaertner M, Marchante E, Ens EJ, Holmes PM, Pauchard A, O'Farrell PJ, Rogers AM, Blanchard R, Blignaut J, Richardson DM (2011) Impacts of invasive Australian acacias: implications for management and restoration. Divers Distrib 17:1015–1029

Liao CZ, Peng RH, Luo YQ, Zhou XH, Wu XW, Fang CM, Chen JK, Li B (2008) Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. New Phytol 177:706–714

Lilleskov EA, Hobbie EA, Fahey TJ (2002) Ectomycorrhizal fungal taxa differing in response to nitrogen deposition also differ in pure culture organic nitrogen use and natural abundance of nitrogen isotopes. New Phytol 154:219–231

Malcolm GM, Bush DS, Rice SK (2008) Soil nitrogen conditions approach preinvasion levels following restoration of nitrogen-fixing black locust (*Robinia pseudoacacia*) stands in a pine–oak ecosystem. Restor Ecol 16:70–78

Marchante E, Kjøller A, Struwe S, Freitas H (2008) Soil recovery after removal of the N2-fixing invasive *Acacia longifolia*: consequences for ecosystem restoration. Biol Invasions 11:813–823

Maron JL, Jefferies RL (2001) Restoring enriched grasslands: effects of mowing on species richness, productivity, and nitrogen retention. Ecol Appl 11:1088–1100

Maron JL, Connors PG, Url S, Connors G, International Association for Ecology (2011) A native nitrogen-fixing shrub facilitates weed invasion. Ecology 105:302–312

Matsen C (2011) Scotch broom, that pesky noxious weed, carries an economic cost. The Olympian, Olympia

Milberg P, Lamont BB, Perez-Fernandez MA (1999) Survival and growth of native and exotic composites in response to a nutrient gradient. Plant Ecol 145:125–132

Mobley L (1954) Scotch broom, a menace to forest, range, and agricultural land. Proceedings of the 6th Annual California Weed Conference, pp 39–42

Nuñez MA, Dickie IA (2014) Invasive belowground mutualists of woody plants. Biol Invasions 16:645–661

Olsen SR et al (1954) Estimation of available phosphorus in soils by extraction with sodium bicarbonate. US Dept Agric Circ 939:1–19

Parker IM (2000) Invasion dynamics of *Cytisus scoparius*: a matrix model approach. Ecol Appl 10:726–743

Parker IM, Reichard SH (1998) Critical issues in invasion biology for conservation science. In: Fiedler PL, Kareiva PM (eds) Conservation biology. Chapman Hall, London, pp 283–305

Parker IM, Haubensak KA, Grove S (2014) Forest regeneration under Scotch broom control: phase I final report. Submitted to The Nature Conservancy and Joint Base Lewis-McChord, 24 pp

Perakis SS, Matkins JJ, Hibbs DE (2012) N-2-fixing red alder indirectly accelerates ecosystem nitrogen cycling. Ecosystems 15:1182–1193

Peterson D, Prasad R (1998) The biology of Canadian weeds. 109. *Cytisus scoparius* (l.) Link. Can J Plant Sci 78:497–504

Powers RF (1990) Nitrogen mineralization along an altitudinal gradient—interactions of soil–temperature, moisture, and substrate quality. For Ecol Manage 30:19–29

Pringle A, Bever JD, Gardes M, Parrent JL, Rillig MC, Klironomos JN (2009) Mycorrhizal symbioses and plant invasions. Annu Rev Ecol Evol Syst 40:699–715

Read DJ, Perez-Moreno J (2003) Mycorrhizas and nutrient cycling in ecosystems - a journey towards relevance? New Phytol 157:475–492

Richardson DM, Allsopp N, D'Antonio CM, Milton SJ, Rejmánek M (2000) Plant invasions—the role of mutualisms. Biol Rev Camb Philos Soc 75:65–93

Rook EJ, Fischer DG, Seyferth RD, Kirsch JL, Leroy CJ, Hamman S (2011) Responses of prairie vegetation to fire, herbicide, and invasive species legacy. Northwest Sci 85:288–302

Rothstein DE, Vitousek PM, Simmons BL (2004) An exotic tree alters decomposition and nutrient cycling in a Hawaiian montane forest. Ecosystems 7:805–814

Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: invasional meltdown? Biol Invasions 1:21–32

Smith SE, Read DJ (1997) Mycorrhizal symbiosis, 2nd edn. Academic Press, San Diego

Smith JMB, Sheppard AW, Hosking JR (2000) An introduction to the biogeography and ecology of broom (*Cytisus scoparius*) in Australia. Plant Prot Q 15(4):140–144

Sollins P, Grier CC, McCorison FM, Cromack K, Fogel R (1980) The internal element cycles of an old-growth Douglas-fir ecosystem in western Oregon. Ecol Monogr 50:261–285

Stewart JWB, Tiessen H (1987) Dynamics of soil organic phosphorus. Biogeochemistry 4:41–60

Stinson KA, Campbell SA, Powell JR, Wolfe BE, Callaway RM, Thelen GC, Hallett SG, Prati D, Klironomos JN (2006) Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms. PLoS Biol 4:727–731

Strayer DL, Eviner VT, Jeschke JM, Pace ML (2006) Understanding the long-term effects of species invasions. Trends Ecol Evol 21:645–651

Suding KN, Hobbs RJ (2009) Threshold models in restoration and conservation: a developing framework. Trends Ecol Evol 24:271–279

Suding KN, Gross KL, Houseman GR (2004) Alternative states and positive feedbacks in restoration ecology. Trends Ecol Evol 19:46–53

Swanson ME, Franklin JF, Beschta RL, Crisafulli CM, DellaSala DA, Hutto RL, Lindenmayer DB, Swanson FJ (2011) The forgotten stage of forest succession: early-successional ecosystems on forest sites. Front Ecol Environ 9:117–125

United States Department of Agriculture, National Resources Conservation Service (USDA NRCS) (2012) Official Soil Series Descriptions. http://www.nrcs.usda.gov/Internet/technical/classification/osd/

Vitousek PM, Walker LR, Whiteaker LD, Muellerdombois D, Matson PA (1987) Biological invasion by *Myrica-faya* alters ecosystem development in Hawaii. Science 238(4828):802–804

Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH, Tilman D (1997) Human alteration of the global nitrogen cycle: sources and consequences. Ecol Appl 7:737–750

Vitousek PM, Menge DNL, Reed SC, Cleveland CC (2013) Biological nitrogen fixation: rates, patterns and ecological controls in terrestrial ecosystems. Philos Trans R Soc B Biol Sci 368:9

Vogelsang KM, Bever JD (2009) Mycorrhizal densities decline in association with nonnative plants and contribute to plant invasion. Ecology 90:399–407

Von Holle B, Joseph KA, Largay EF, Lohnes RG (2005) Facilitations between the introduced nitrogen-fixing tree, *Robinia pseudoacacia*, and nonnative plant species in the glacial outwash upland ecosystem of Cape Cod, MA. Biodivers Conserv 15:2197–2215

Von Holle B et al (2013) Ecosystem legacy of the introduced N-2-fixing tree Robinia pseudoacacia in a coastal forest. Oecologia 172(3):915–924

Wheeler CT, Helgerson OT, Perry DA, Gordon JC (1987) Nitrogen-fixation and biomass accumulation in plant-communities dominated by *Cytisus scoparius* L. in Oregon and Scotland. J Appl Ecol 24:231–237

Yelenik SG, D'Antonio CM (2013) Self-reinforcing impacts of plant invasions change over time. Nature 503:517-+

Zielke K, Boateng JO, Caldicott N, Williams H (1992) Broom and gorse in British Columbia: a forestry perspective problem analysis. British Columbia Ministry of Forests, Queen's Printer, Victoria, 19 pp