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Articles

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Abstract

Impacts of invasive species on rare species are relevant to conservation. We studied the response of Leedy's roseroot *Rhodiola integrifolia* subsp. *leedyi*, a subspecies listed as threatened under the Endangered Species Act, to removal of the invasive species Japanese knotweed *Fallopia japonica*. Japanese knotweed has invaded the largest known population of Leedy's roseroot, affecting about 10% of all Leedy's roseroot in the world. Japanese knotweed shaded Leedy's roseroot, but the two did not share belowground resources because of their position on cliffs. To study this interaction and, ultimately, to restore Leedy's roseroot habitat to an open, high-light condition, we removed Japanese knotweed in a three-treatment block design. We measured Leedy's roseroot abundance, growth, and reproduction in treatment blocks and in uninvaded areas before and after treatment. Compared with uninvaded areas, Japanese knotweed invasion negatively affected Leedy's roseroot abundance, growth, and reproduction. Light interception by Japanese knotweed degraded the habitat for Leedy's roseroot. Herbicide removal of Japanese knotweed resulted in increased light and temperature compared with untreated invaded plots but did not affect Leedy's roseroot abundance, growth, or reproduction over the 2 y of our study. These results show that invasive species removal is conducive to restoring Leedy's roseroot habitat, but recovery in the subspecies may lag behind restoration of the habitat, suggesting that additional action or time may be required to restore preinvasion performance of Leedy's roseroot. Results of this study may inform restoration efforts for other systems and contribute to the literature on interspecific interactions.

Keywords: competition; *Fallopia japonica*; habitat management; invasive species; rare species; restoration; *Rhodiola integrifolia*

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Introduction

Along with land use, climate change, and alteration of biogeochemical cycles, human contribution to the spread of invasive species represents a substantial alteration of the global environment (Vitousek et al. 1997). In recent decades, biologists have uncovered many examples of the negative environmental and economic impacts of invaders, prompting significant investments to be made in invasive species management (Pyŝek and Richardson 2010). Some important negative impacts of invasive species relate to the threats they pose to global biodiversity; invasive species can indirectly affect other species by acting as ecosystem engineers that modify large-scale processes like nutrient or hydrology regimes, or may directly outcompete native species (Vilà et al. 2011).

Competition between invaders and co-occurring species is a major conservation concern, but interspecific interactions may also be neutral or facilitative. The possibility of neutral interactions among species is often overlooked (Hubbell 2001) and serves as a null model for considering invasive species interactions. Neutral interactions may be observed when patterns of species co-occurrence are more controlled by demographic processes like dispersal and recruitment than by competition, as has been described for tropical tree species (Hubbell 2005). Facilitation is also important for persistence of many species, especially plant species (McIntire and Fajardo 2014). In stressful environments, facilitation might be more common than competition (Bertness and Callaway 1994). Individuals inhabiting stressful conditions may be concentrated near nurse plants (individuals that create microhabitats suitable for recruitment of heterospecific seedlings). For example, desert shrubs create shaded, moist microsites that facilitate the establishment of other species (Turner et al. 1966).

Evaluations of competitive vs. facilitative interactions are informed by the characteristics of the individual species under consideration. Although the interspecific impacts of many invasive species remain poorly understood (Barney et al. 2013), invasive species are often highly competitive. In contrast to invasive species, rare species occupy the opposite end of an ecological success spectrum (sensu Colautti et al. 2017). Many rare plant species occupy specific, marginal niches (Rabinowitz 1981) and are thought to be stress tolerators with poor competitive ability (Grime 2001). A systematic review of interactions among invasive and rare species showed that 80% of studies reported competition (Roberts et al. 2015). Over time, competition from invasive species can lead to rare species extinctions, especially if populations are small or vulnerable to multiple threats. An assessment of the causes of recent species extinctions showed that invasive species were the second leading cause of extinction, after overexploitation, and contributed to 58% of all extinctions (Bellard et al. 2016). Though potentially widespread, interactions among rare and invasive species have been studied for only about 6% of species listed as endangered, threatened, or candidate under the U.S. Endangered Species Act (ESA 1973, as amended; Roberts et al. 2015). Among those studies, many have failed to measure mechanisms of interspecific impacts or causes of population declines in species of concern (Roberts et al. 2015).

Figure 1. Male individual of Leedy's roseroot *Rhodiola integrifolia* subsp. *leedyi* at Glenora Cliffs, New York, in late spring of 2014.

We focused on the cliff-dwelling Leedy's roseroot *Rhodiola integrifolia* subsp. *leedyi* (Figure 1), a subspecies federally listed as threatened (ESA 1973; USFWS 1994) and considered critically imperiled globally (NatureServe 2017). The world's largest Leedy's roseroot population occurs at Glenora Cliffs, New York (Figure 2). At this location, Japanese knotweed *Fallopia japonica* formed a monoculture in the talus (loose gravel) below the cliff that shaded Leedy's roseroot growing on the lower portion of the cliff (Figure 3). Japanese knotweed invasion was a novel influence on this system because no other member of the talus community had a similar growth form to Japanese knotweed (Mattingly 2016), which is characterized by thick stands producing dense shade. Understanding the nature of the interaction between Japanese knotweed and Leedy's roseroot was considered crucial to the conservation of this rare subspecies. The Federal Recovery Plan for Leedy's roseroot (a type of document that identifies potential threats and mitigation strategies for an Endangered Species Act-listed taxon) suggested that potential negative impacts of Japanese knotweed shade on Leedy's roseroot at Glenora Cliffs could represent a significant threat to the subspecies (USFWS 1998, 2015). An estimated 15% of Leedy's roseroot at Glenora Cliffs interacted with Japanese knotweed (Mattingly 2016), approximately 10% of all known Leedy's roseroot. Because Glenora Cliffs is the largest, most genetically diverse Leedy's roseroot population (Ejupovic 2015), its reduction or extirpation would be detrimental to the subspecies.

The objectives of this study were: 1) to quantify the interaction between Japanese knotweed and Leedy's roseroot, and 2) to determine whether large-scale removal of Japanese knotweed would restore Leedy's roseroot habitat and improve the condition of this

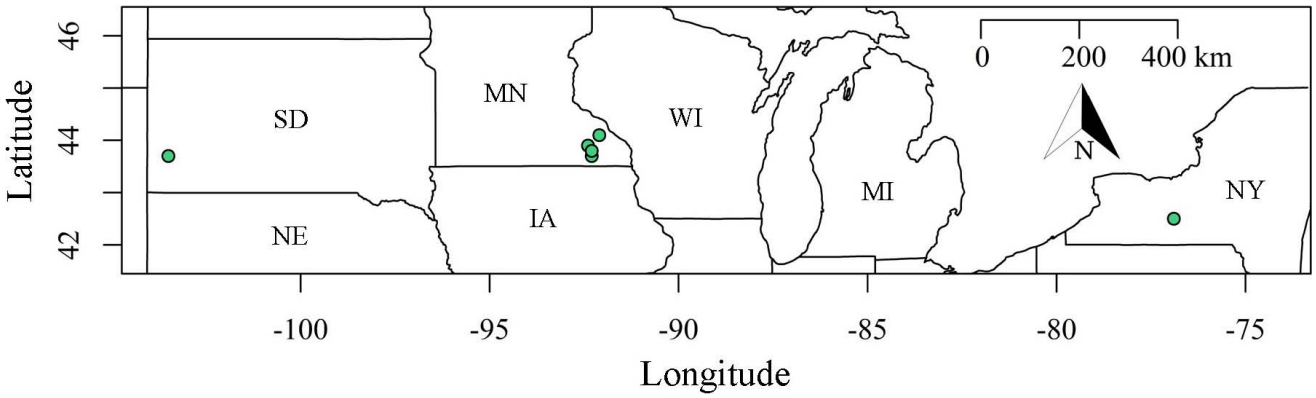

Figure 2. Geographic distribution of populations of Leedy's roseroot *Rhodiola integrifolia* subsp. *leedyi*. Populations form three disjuncts across New York (Glenora Cliffs, 4,515 individuals in 2015 [Mattingly 2016]), Minnesota (Whitewater WMA, 1,019 individuals in 1997; Simpson Cliffs, 639 individuals in 1997; Deer Creek, 322 individuals in 1997; and Bear Creek, 173 individuals in 1994 [Olfelt et al. 1998]), and South Dakota (Harney Peak, 100 individuals in 2015 [K. Z. Mattingly, personal observation]).

subspecies. We expected to find: 1) competitive interactions between Japanese knotweed and Leedy's roseroot, and 2) increased Leedy's roseroot abundance, growth, and reproduction after removal of Japanese knotweed. Several characteristics of Leedy's roseroot suggested that it might respond positively to removal of Japanese knotweed shade. Olfelt and Freyman (2014) proposed that Leedy's roseroot occurred adjacent to glacial margins during the Pleistocene. Such periglacial relicts may be characterized by open, high-light habitats and low-competition conditions (Horsák et al. 2015). Supporting this suggestion, Mattingly and Leopold (2018) found Leedy's roseroot concentrated at some of the highest light microsites present at Glenora Cliffs. Consistent with the hypothesis of a competitive interaction, we expected to see fewer Leedy's roseroot individuals in areas of Japanese knotweed invasion and an increase of Leedy's roseroot abundance (total counts) after removal of Japanese knotweed, with changes in Leedy's roseroot abundance due to mortality and recruitment events. We also expected that changes would be apparent in functional traits prone to environmental influence (Lavorel et al. 2007), including flowering, stem length, and number of leaves. Individuals experiencing adverse effects due to competition may exhibit changes in biomass allocation (e.g., Hedi Wenk and Falster 2015). We predicted that Leedy's roseroot competition with Japanese knotweed would be expressed through increased allocation of biomass toward growth and maintenance (stems, leaves) and decreased allocation toward reproductive structures (flowers). We were particularly interested in impacts on flowering because decreased reproduction in populations with already low effective population sizes could exacerbate extinction risk (Olfelt et al. 1998; Ejupovic 2015). Our overall goal was to inform conservation of Leedy's roseroot by quantifying the impact of Japanese knotweed on this subspecies.

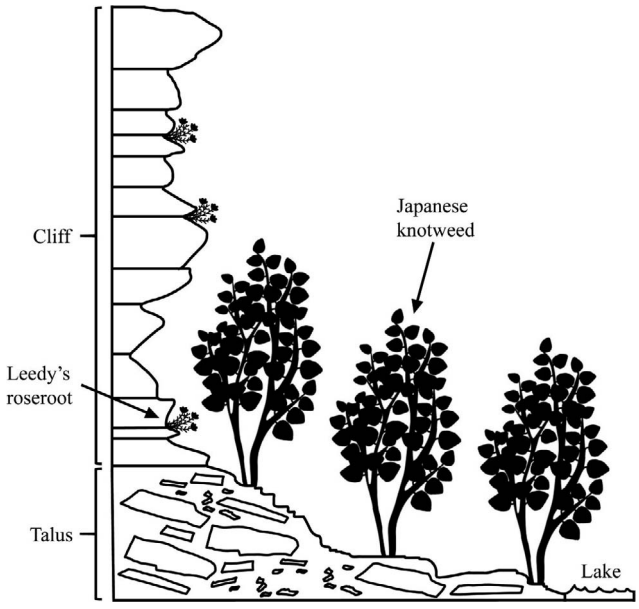

Figure 3. Depiction of the cliff and talus habitat at Glenora Cliffs, New York. Leedy's roseroot *Rhodiola integrifolia* subsp. *leedyi* grew on the cliff face, whereas Japanese knotweed *Fallopia japonica* grew in the talus. Prior to 2013, Japanese knotweed shaded co-occurring Leedy's roseroot at the cliff/talus interface. In fall 2013, we removed some Japanese knotweed in a pre–post block design for our study of the effects of Japanese knotweed on Leedy's roseroot.

Study Site

The Glenora Cliffs Leedy's roseroot population is located at Glenora, Yates County, New York (Figure 2), along Seneca Lake in the Finger Lakes region (USFWS 1998). In 2015, the final year of this study, Glenora Cliffs had 4,515 individuals (Mattingly 2016), two-thirds of all known Leedy's roseroot. The east-facing cliff habitat stretches 2.25 km and is composed of horizontally bedded calcareous shale and siltstone (USFWS 1998). For the period of the study (2013–2015), the region had a mean annual temperature of 9.0°C, a mean winter temperature of −3.4°C, and a mean summer temperature

of 20.4°C. The mean annual precipitation was 75.5 cm, with heaviest precipitation in the summer (Data S1, *Supplemental Material*). The plant community at Glenora Cliffs is within the Laurentian Mixed Forest Province ecoregion (Bailey 1994) and New York State's calcareous cliff community type (Edinger et al. 2014). Leedy's roseroot grows in cliff crevices, where gravel and sparse soil collect. In the northern 1.25 km of Glenora Cliffs, Japanese knotweed forms dense stands in the talus between the cliff base and the lake. The date of first invasion is unknown, but Japanese knotweed has been present in Upstate New York since at least the 1920s (Weldy et al. 2018).

Methods

Experimental design

To quantify the interaction between Japanese knotweed and Leedy's roseroot and determine the effects of restoration, we compared Leedy's roseroot abundance, growth, and reproduction in areas of Glenora Cliffs never invaded by Japanese knotweed with Leedy's roseroot in invaded areas both before and after removal of Japanese knotweed. We suspected that light competition was the primary interaction between these species because they inhabit different rooting spaces and differ considerably in size (maximum stem length about 40 cm for Leedy's roseroot and 2 m for Japanese knotweed, Figure 3). Therefore, we quantified competition for light by measuring temperature and photosynthetically active radiation (PAR).

We established 20 treatment blocks within the area of Japanese knotweed invasion at Glenora Cliffs. Habitat conditions within a block were relatively homogenous in terms of cliff seepage, angle, orientation, and amount of talus. In this way, a random effect for block could statistically account for environmental variability across the site. Blocks were positioned from south (block 1) to north (block 20), covering 0.75 km (50% of the area of Japanese knotweed/Leedy's roseroot interaction and 33% of the entire length of the Glenora Cliffs population). Spacing between blocks was variable because block establishment required presence of both Leedy's roseroot and Japanese knotweed, and landowner access. All consecutive blocks were separated by at least a 1-m buffer, but some large buffers (50–100 m) were required.

Blocks included a Leedy's roseroot dimension extending vertically up the cliff and a Japanese knotweed dimension extending across the talus (Figure 4). Within a block, each plot was 3 m wide, extended 2 m vertically ("Leedy's roseroot dimension"), and had a side of variable length (range 2.8–7.1 m, mean 4.8 m) extending from the cliff base to the lake shore ("Japanese knotweed dimension"). Although undesirable, variable plot lengths were necessary to capture all Japanese knotweed shading the plots. We considered Japanese knotweed abundance as density (stand basal area [SBA], cm^2/m^2) to correct for these variable plot lengths. Final correlations between plot length and all response variables were low (< 0.3), suggesting that there was little confounding effect of plot length in this study. We did not convert Leedy's roseroot metrics to densities because sampling in this dimension was within a fixed area (3 m width $\times$ 2 m height). Within each block, we established three experimental plots: control, cut, and herbicide (Figure 4). We ordered placement of plots within each block, with control in the southernmost plot, herbicide in the northernmost plot, and cut in the middle of each block. We ordered plots rather than randomizing within blocks to control herbicide dosage and minimize potential herbicide impacts on control plots (herbicide translocation can occur through the underground rhizomes of Japanese knotweed; Bashtanova et al. 2009). Plots were also separated from each other by 1-m buffers to minimize edge effects.

We applied Japanese knotweed removal treatments to treatment blocks in fall 2013 and fall 2014 to assess impacts of Japanese knotweed on Leedy's roseroot. In fall 2013, herbicide plots received a cut-stem application of a solution containing 54% glyphosate (Rodeo), a herbicide safe to use in aquatic areas and effective for Japanese knotweed control. In fall 2014, a cut stem method was not appropriate because remaining Japanese knotweed stems in herbicide plots were heavily stunted from the previous year of herbicide application. Fall 2014 treatment consisted of foliar spray from a backpack sprayer containing glyphosate (Rodeo, 54% glyphosate) diluted to a 3% concentration, imazapyr (Arsenal, 28% imazapyr) at a 0.139% concentration, and Kingpin spray adjuvant at a 1% concentration. Amount and pressure of foliar spray varied depending on density of Japanese knotweed stems. We applied the spray carefully to prevent impacts on Leedy's roseroot. For herbicide application, we chose days with low wind. In 2013, treatments were applied on September 25, when average wind speed was 1.3 m/s, and on October 3, when average wind speed was 1.1 m/s (Data S2, *Supplemental Material*). Application in 2014 took place on September 26, when wind speed averaged 1.5 m/s (Data S2, *Supplemental Material*).

We removed Japanese knotweed stems with pruning shears from cut plots in fall 2013 and 2014. In 2013, We applied cut treatments concurrently with herbicide on September 25 and October 3, and in 2014, we applied all cut treatments on a separate day, September 28, 2014. Because Japanese knotweed readily resprouts after cutting, the utility of the cut treatment was not to serve as a Japanese knotweed removal treatment. Unlike herbicide plots, which had greatly reduced Japanese knotweed after 1 y of treatment and had virtually no Japanese knotweed by the second year posttreatment, the cut treatment did not reduce Japanese knotweed biomass or shade (Mattingly 2016). Rather than serving to remove Japanese knotweed, the cut treatment served as a comparison with the control plots that would allow us to detect potential impacts of herbicide drift. Although we applied herbicide carefully to avoid drift,

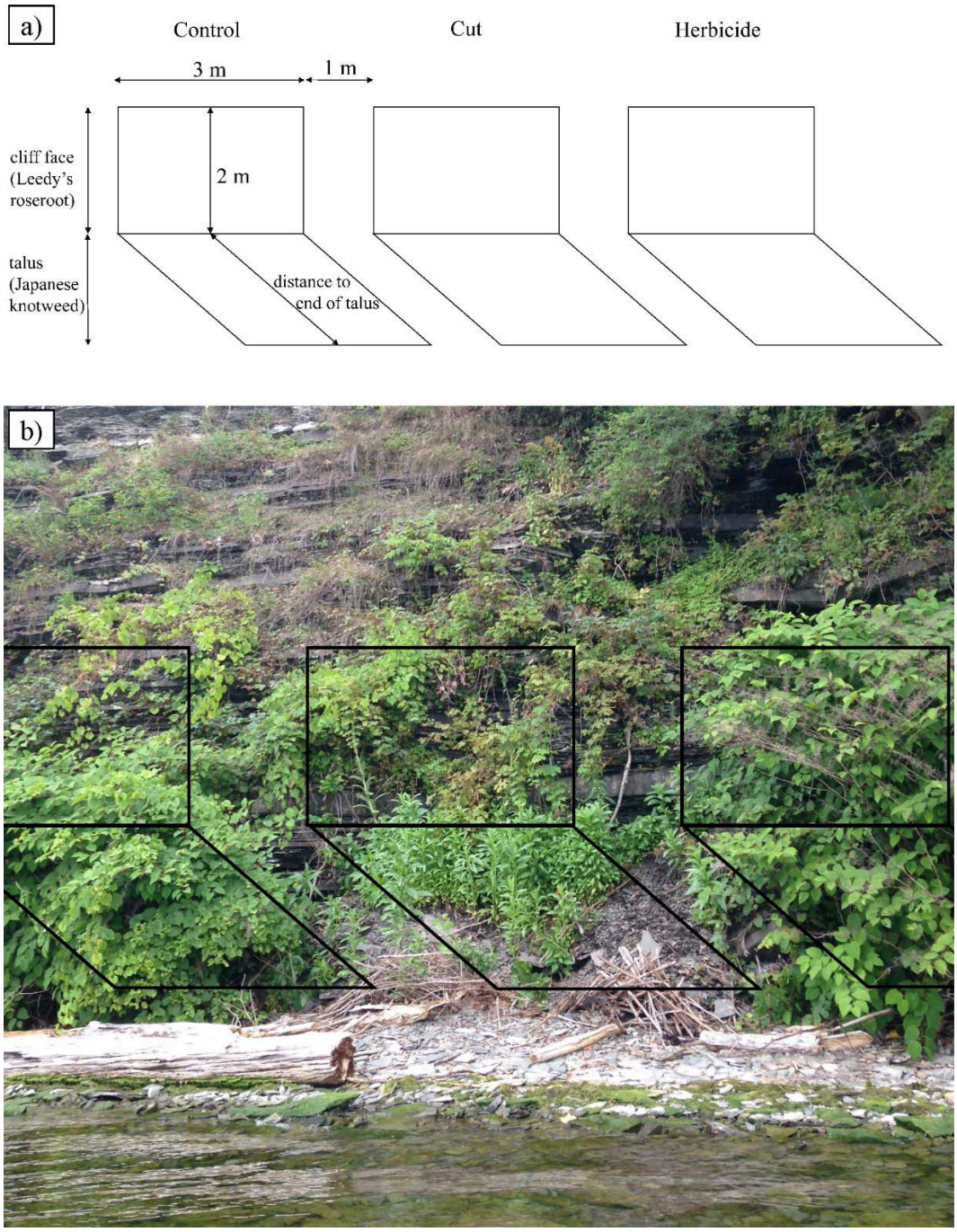

Figure 4. (**a**) Layout of a treatment block used in a pre–post block design study (2013–2015) of the effects of Japanese knotweed *Fallopia japonica* on Leedy's roseroot *Rhodiola integrifolia* subsp. *leedyi* at Glenora Cliffs, New York. Each treatment block included three ordered plots called control, cut, and herbicide plots. These names refer to the type of treatment applied to invasive Japanese knotweed that was shading Leedy's roseroot. Each plot captured Leedy's roseroot growing on the cliff, Japanese knotweed growing in the talus, and abiotic conditions on both the talus and cliff. (**b**) A photograph of the site taken July 2015, after two years of treatment application. The photograph includes parts of two adjacent treatment blocks. From left to right: (left) cut plot of first block, (center) herbicide plot of first block, (right) control plot of adjacent block.

if present, drift would be more likely to affect cut plots than control plots because of the ordering of our treatments within blocks. Cut plots always bordered herbicide plots within each block (Figure 4), whereas only some control plots bordered a herbicide plot in an adjacent block. If no herbicide drift effects were present, we would expect similar Leedy's roseroot abundance and traits in cut and control plots. If posttreatment cut plots had lower Leedy's roseroot abundance than control plots, or showed differences in traits such as reduced

Table 1. Summary of all variables analyzed for a pre–post block design study of the effects of Japanese knotweed *Fallopia japonica* on Leedy's roseroot *Rhodiola integrifolia* subsp. *leedyi* at Glenora Cliffs, New York. Variables included: (**a**) Leedy's roseroot response variables, (**b**) one Japanese knotweed variable, (**c**) abiotic variables measured in both the talus and cliff, including photosynthetically active radiation (PAR, μmol m^{-2} s^{-1}) and temperature (°C), and (**d**) experimental design factors used as explanatory variables or random effects. For all variables, we indicated the data type and whether natural log transformations were applied. For measured variables (**a**, **b**, **c**), we indicated the years for which we obtained measurements and in which treatment plots measurements were taken. For abiotic variables (**c**), different variables were measured in different years and plots on the basis of availability of measurement devices and small refinements in methodology.

	Data type	Transformation	Years	Treatment plots
(**a**) Leedy's roseroot responses				
Total stems	Count	Yes	Pre, Post, Post2	U, Hrb, Cut, Control
Proportion of flowering stems	Proportion	Yes	Pre, Post, Post2	U, Hrb, Cut, Control
Mean stem length (cm)	Continuous	No	Pre, Post, Post2	U, Hrb, Cut, Control
Mean leaves per stem	Continuous	No	Pre, Post, Post2	U, Hrb, Cut, Control
(**b**) Japanese knotweed variable				
Presence/absence	Binomial	No	Pre, Post, Post2	Hrb, Cut, Control
(**c**) Abiotic variables				
Talus PAR (μmol m^{-2} s^{-1})	Continuous	Yes	Pre, Post2	Hrb, Cut, Control
Cliff PAR (μmol m^{-2} s^{-1})	Continuous	Yes	Pre, Post2	Hrb, Cut, Control
Talus maximum iButton temperature (°C)	Continuous	Yes	Pre	U, Hrb, Cut, Control
Cliff maximum iButton temperature (°C)	Continuous	Yes	Pre	U, Hrb, Cut, Control
Talus rock temperature (°C)	Continuous	Yes	Post2	Hrb, Cut, Control
Cliff rock temperature (°C)	Continuous	Yes	Post2	Hrb, Cut, Control
(**d**) Experimental design variables				
Treatment	Ordered factor	No		
Time	Ordered factor	No		
Block	Unordered factor	No		
Plot	Unordered factor	No		

Pre = pretreatment, 2013; Post = 1 y posttreatment, 2014; Post2 = 2 y posttreatment, 2015; U = uninvaded; Hrb = herbicide.

flowering, negative effects of herbicide drift could be present.

We selected plots containing Leedy's roseroot but no Japanese knotweed (hereafter, "uninvaded") randomly from global positioning system points at which Leedy's roseroot was known to occur without Japanese knotweed. Uninvaded plots contained a Leedy's roseroot dimension (3 m width × 2 m height) but no Japanese knotweed dimension (however, to obtain talus temperature data we placed an iButton in the talus of 11 uninvaded plots). We randomly selected and measured different uninvaded plots in 2013 ($n = 30$), 2014 ($n = 15$), and 2015 ($n = 15$). Because we randomly selected uninvaded plots and they did not occur within blocks, for analysis we coded the variable "block" as a unique number for all 45 uninvaded plots measured over the 3 y of the study. We intended for the uninvaded plots to provide a restoration target to compare with herbicide plots. A successful restoration would mean that abiotic conditions and Leedy's roseroot responses in herbicide plots converged toward those in uninvaded plots. However, we established, by definition, uninvaded plots outside of the Japanese knotweed treatment blocks. This physical separation may have caused uninvaded plots and treatment blocks to differ in site conditions other than Japanese knotweed presence. If this was the case, our uninvaded plots may not have been feasible standards for determining restoration success. To provide further criteria for assessment, in the Discussion, we synthesize the results of this study with a separate study (Mattingly and Leopold 2018) that assessed habitat conditions associated with Leedy's roseroot. Establishing a restoration target is often difficult, but even an imperfect target is better than the alternative of no target.

We measured vegetation in mid- to late summer (July or August), at which point Leedy's roseroot and Japanese knotweed had reached maximum size for the year. We sampled Japanese knotweed and Leedy's roseroot pretreatment (2013; "Pre"), 1 y posttreatment (2014; "Post"), and 2 y posttreatment (2015; "Post2"). We expected that 2 y of posttreatment assessment would be sufficient to detect potential changes in Leedy's roseroot response traits. We expected changes in abundance due to recruitment; we were able to readily germinate Leedy's roseroot seeds in the greenhouse (K.Z.M., personal observation), and we observed Leedy's roseroot seedlings in the field in 2014 (Mattingly 2016). For plots within treatment blocks (control, cut, and herbicide plots), we estimated Japanese knotweed percent cover (to the nearest 10%), calculated SBA (cm^2/m^2) as stem area per plot area, and defined Japanese knotweed presence as SBA > 2 cm^2/m^2 and absence as SBA ≤ 2 cm^2/m^2. For both uninvaded plots and treatment blocks, we recorded the total number of Leedy's roseroot individuals and stems ("total stems"), counted the number of inflorescences from which we calculated the "proportion of flowering stems" out of total stems, measured the length of each stem (cm) from rhizome to stem apex to calculate "mean stem length" of all stems

in a plot, and counted the number of leaves on each stem to obtain "mean leaves per stem" across all stems in a plot. Table 1a lists Leedy's roseroot responses for which we present analyses. We also analyzed total Leedy's roseroot individuals and flowers, which we omit here for brevity because these variables were highly correlated with total Leedy's roseroot stems and proportion of flowering stems, respectively.

Abiotic sampling

Table 1c lists abiotic variables analyzed, the years in which they were measured, and whether they were measured in both uninvaded plots and treatment blocks or in only treatment blocks. We measured different variables in different years on the basis of availability of measurement devices and small refinements in methodology. Light and temperature in both the talus and cliff were important elements of Leedy's roseroot habitat because although Leedy's roseroot grows almost exclusively on the cliff, reradiation of solar energy from the talus could affect Leedy's roseroot growing at the base of the cliff.

We measured temperature pretreatment using Thermochron iButtons waterproofed with silicone. In 10 of 20 treatment blocks, we placed iButtons in both the talus and in a crevice of the cliff face. In uninvaded plots, we placed iButtons on the cliff face of 12 plots and the talus of 11 plots. We collected temperature readings to the nearest 0.1°C every hour for the period of August 30–September 27, 2013. For each iButton, we extracted minimum and maximum temperatures for the entire period. Because minimum and maximum temperatures were highly correlated, we present analyses for only maximum temperatures.

Two years posttreatment, we measured temperatures using an Extech dual-laser infrared thermometer. We took rock temperatures to the nearest 0.1°C at the talus and cliff in treatment blocks. We recorded rock temperatures on two separate days (1100 to 1600 hours on July 31 and August 7, 2015). We used the mean of these two observations for analysis.

We measured PAR (μmol m^{-2} s^{-1}), which is the photon flux density measured at wavelengths available to plants for photosynthesis, 400 to 700 nm (Biggs 2015). We measured PAR using a LI-COR LI-250A light meter with an LI-190R quantum sensor. In Pre and Post2, we took PAR recordings at the talus and cliff of each treatment plot. We collected pretreatment PAR recordings immediately before application of treatments, with measurements for 10 blocks taken on September 25 and the remaining 10 blocks measured on October 3, 2013; we collected 8 PAR recordings for a single plot and used the mean for analysis. For each Post2 PAR recording, we took single PAR readings for all plots on 2 d (July 31 and August 7, 2015) and used the mean for analysis. Although we collected PAR measurements during fall for Pre and late summer for Post2, these measurements accurately represent the amount of light exclusion created by the Japanese knotweed canopy, which was fully intact at the time of measurement. We account for variation between Pre and Post2 statistically in the main effect of time, independent of treatment. Error in PAR readings can occur when measurements are taken under inconsistent sunlight conditions. We attempted to address this potential error by taking the mean of multiple measurements, as suggested by LI-COR documentation (Biggs 2015). We also aimed to collect consistent measurements by recording PAR at consistent times midday (1100 to 1600 hours) and on low cloud-cover days, but some scattered clouds were present on one of the Post2 dates (August 7, 2015, Data S3, *Supplemental Material*). We found low correlation between time of PAR recording and PAR value ($r = -0.240$ for July 31, $r = -0.367$ for August 7; Table S1, *Supplemental Material*), suggesting that cloud-cover variation or changing light intensity over the course of a day did not introduce substantial error into our analyses. We account for this variation statistically by taking the mean of multiple measurements, and by including the random effect for block in all models (PAR measurements within a block were taken within 10 min of each other).

Analysis

We used R version 3.3.3 (R Development Core Team 2017) for statistical analyses. We required significance of $\alpha = 0.05$ to reject null hypotheses. Table 1 contains a summary of variables analyzed, and see Table S2 (*Supplemental Material*) for the full data set analyzed. We natural-log-transformed some variables for analysis (Table 1) because transformation improved the distribution of residuals compared with nontransformed linear, Poisson-distributed, and gamma-distributed models.

For analysis of Leedy's roseroot responses, we omitted from analysis observations in which a treatment plot contained no Leedy's roseroot. Treating these observations as zeroes would have been inappropriate because all uninvaded plots had nonzero values for Leedy's roseroot by design. We omitted missing values rather than using an imputation procedure because Clewer and Scarisbrick (2001) advise against imputation of data having $>$ 10% missing values. Of 60 treatment plots, 12 lacked Leedy's roseroot for the entire duration of the study, and an additional 12 lacked Leedy's roseroot in some years (i.e., year-to-year fluctuation). Omitting observations created unequal sample sizes across years and reduced our sample sizes; however, we do not expect missing data to confound treatments because missing values were distributed relatively evenly across treatments (plots missing for entire study: 2/20 control, 5/20 cut, 5/20 herbicide; plots missing for some years of study: 4/20 control, 5/20 cut, 3/20 herbicide). After omission of missing values, we retained 188 observations of Leedy's roseroot responses. Table S3 (*Supplemental Material*) shows the breakdown of these observations across treatments and years.

We report the results of linear mixed models (LMMs, nlme::lme, Pinheiro et al. 2017). All LMMs included at least a random intercept for block. Our experimental design does not adhere to the assumption that treatments be randomly assigned within blocks; instead, we ordered treatments within blocks. Ordered treatments would only pose a problem if a latent periodic trend was present along each block. We have no evidence supporting periodicity in structure, making this statistical method the most appropriate for our data. We had repeated measures across multiple years for most variables (Table 1), so we included in these models a random intercept for plot nested within block, and a first-order temporal autocorrelation structure modeled within levels of plot and block. Temperatures were not treated as repeated measures because they were measured differently in Pre and Post2 (Table 1c); LMMs with temperature analyzed as the response variable contained only a random intercept for block. We checked model assumptions by examining residual plots, which suggested no serious violations. Despite inconsistent spacing between blocks, we treated each block as independent for analysis because treatments within a block were, in general, closer to each other than to other blocks and therefore comprised a statistical unit. Including a random intercept for block improved model fits and estimated random intercepts were normally distributed (nlme::ranef, Pinheiro et al. 2017).

To explore how Japanese knotweed affects Leedy's roseroot through manipulation of abiotic conditions, we used confirmatory path analysis (piecewiseSEM, Lefcheck 2016). This method assembles a series of LMMs defining relationships among several variables into a single structural equation model (SEM). Measurement of different variables in different years (Table 1) limited SEM definition and sample size. Inclusion of Post2 data in SEMs was essential to capture the most variation in Japanese knotweed and abiotic conditions; however, by Post2 our treatments had produced a bimodal distribution of Japanese knotweed SBA and percent cover such that these analyses were reduced to Japanese knotweed presence/absence. Autocorrelation among abiotic conditions restricted the combinations of variables that could be included in SEMs. Specifically, including multiple temperature or PAR variables (Table 1c) in the same model produced spurious relationships among other variables. For example, including both cliff and talus rock temperatures resulted in a significantly positive relationship between Japanese knotweed presence and cliff PAR, a pattern that did not appear in models containing subsets of these variables. On the basis of these considerations and knowledge of the biology of the system, we defined two SEM configurations (Figure S1, *Supplemental Material*) to analyze each Leedy's roseroot response (Table 1a). We assessed SEM fit with Shipley's test of d-separation (Shipley 2009), where $P > 0.05$ for the chi-square test of the Fisher's C statistic suggested that a SEM adequately estimated the data and no paths were missing from the analysis. We reported standardized β coefficients to assess direction and strength of relationships among variables.

To examine changes due to treatments, we used repeated-measures LMMs with planned contrasts based on treatment. We modeled Leedy's roseroot responses (Table 1a) and abiotic conditions (Table 1c) as functions of the interaction between treatment and time. We calculated F-tests for these models using type III (marginal) sums of squares (nlme::anova.lme, Pinheiro et al. 2017). To test the hypothesis of competition between Japanese knotweed and Leedy's roseroot, we developed a set of planned contrasts. For contrast 1, we tested whether abiotic conditions or Leedy's roseroot responses in plots not associated with Japanese knotweed invasion differed from those of plots potentially experiencing legacy effects due to having been affected by Japanese knotweed invasion in the past. This contrast ("uninvaded–invaded") compared the restoration target (uninvaded) with all plots within the treatment blocks (control, cut, herbicide). Contrast 2 ("herbicide–control & cut") tested whether plots from which we successfully eradicated Japanese knotweed differed from plots where Japanese knotweed persisted. Implicit in contrast 2 is the assumption that control and cut plots are indistinguishable from one another. These two treatments did not differ in Japanese knotweed cover at any time in the experiment (Mattingly 2016). However, to test whether cutting of Japanese knotweed did produce a latent effect on abiotic conditions or Leedy's roseroot responses, or whether cut plots (always adjacent to herbicide plots) experienced herbicide drift, we performed contrast 3 ("control–cut").

Results

Impacts of Japanese knotweed on abiotic conditions and Leedy's roseroot

Both structural equation model configurations yielded complete solutions with no missing paths (Fisher's $C = 2.6$, $P = 0.273$, $df = 2$, $n = 86$, Figure 5a; Fisher's $C = 3.87$, $P = 0.144$, $df = 2$, $n = 41$, Figure 5b). The SEM showed that Japanese knotweed presence reduced talus PAR ($\beta = -0.69$, Figure 5a) but had no significant impact on cliff PAR (Figure 5a and 5b) or cliff rock temperature (Figure 5b). Abiotic conditions were highly correlated with each other: SEMs showed significant positive relationships between talus PAR and cliff PAR ($\beta = 0.25$, Figure 5a) and between cliff PAR and cliff rock temperature ($\beta = 0.58$, Figure 5b). Lengthened Leedy's roseroot stems were produced by decreased talus PAR ($\beta = -0.29$, Figure 5a) and cliff rock temperature ($\beta = -0.51$, Figure 5b), but SEMs showed no other significant impacts of abiotic conditions on Leedy's roseroot.

Treatment effects on abiotic conditions

Trends in light and temperature corresponded to experimental plots. Pretreatment, uninvaded plots had

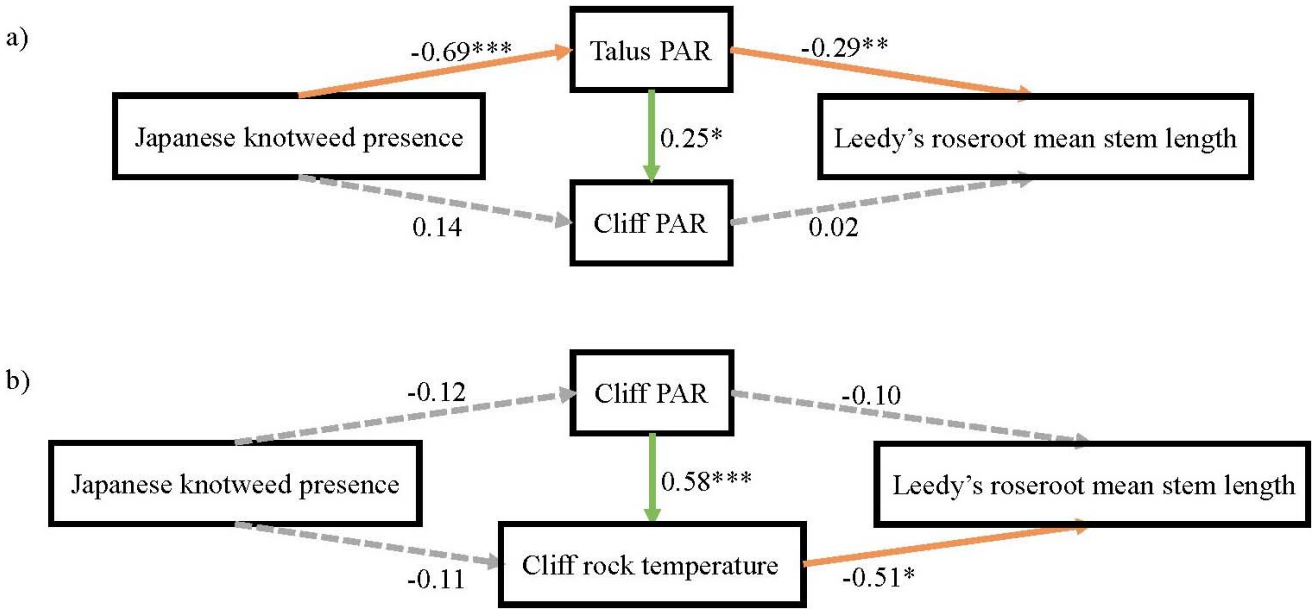

Figure 5. Structural equation models describing impacts of Japanese knotweed *Fallopia japonica* on abiotic conditions and Leedy's roseroot *Rhodiola integrifolia* subsp. *leedyi*, from a pre–post block design study (2013–2015) of the effects of Japanese knotweed on Leedy's roseroot at Glenora Cliffs, New York. (**a**) Structural equation model describing the impact of Japanese knotweed on photosynthetically active radiation (PAR, μmol m^{-2} s^{-1}) in plots on the cliff and talus, and subsequent effects on Leedy's roseroot, with repeated measures taken pretreatment (2013, Pre) and 2 y posttreatment (2015, Post2). (**b**) Structural equation model describing the impact of Japanese knotweed on cliff rock temperature and cliff PAR measurements, and subsequent effects on Leedy's roseroot, for measurements taken only 2 y posttreatment (2015, Post2). Arrows specify relationships defined by the model. Gray dashed arrows indicate nonsignificant relationships; green and orange arrows indicate significant ($P < 0.05$) positive and negative relationships, respectively. Standardized β coefficients are reported next to each arrow. Asterisks denote level of significance: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

higher talus maximum iButton temperatures than invaded plots (Figure 6; $F_{3,17} = 10.535$, $P < 0.001$, uninvaded–invaded: $t_{20} = 5.237$, $P < 0.001$). Two years posttreatment, herbicide plots had higher rock temperature in talus and cliff than control & cut (talus: $F_{2,38} = 45.315$, $P < 0.001$, herbicide–control & cut: $t_{38} = 9.517$, $P < 0.001$; cliff: $F_{2,38} = 3.911$, $P = 0.028$, herbicide–control & cut: $t_{38} = 2.541$, $P = 0.015$). For talus PAR (Figure 7), we found differences on the basis of the interaction of treatment by time ($F_{2,57} = 22.474$, $P < 0.001$). Two years posttreatment, herbicide plots had increased talus PAR relative to control & cut (herbicide–control & cut, for Pre–Post2: $t_{57} = 6.691$, $P < 0.001$).

Treatment effects on Leedy's roseroot

We found significant differences in Leedy's roseroot abundance and response traits on the basis of treatment and time, but the overall interaction of treatment by time was not significant in any model (Table 2a). Treatment predicted Leedy's roseroot total stems and flowering, whereas time predicted proportion of flowering stems, mean stem length, and mean leaves per stem, and was marginally significant for total stems (Table 2a). Planned contrasts on the basis of treatment revealed significant differences in uninvaded and invaded plots (contrast 1, Table 2b), but not due to experimental manipulations (contrasts 2 and 3, Table 2b). Uninvaded plots had higher total stems and proportions of flowering stems than invaded plots. There were marginally significant differences in mean stem length between control and cut plots, with longer stems in cut than control plots.

Discussion

Impacts of Japanese knotweed on abiotic conditions and Leedy's roseroot

In line with the hypothesis of aboveground resource competition, our LMM analyses indicated that removal of Japanese knotweed allowed more light to reach the talus and produced higher temperature in both talus and cliff. Shade may also affect soil moisture, which was not measured in this study; the Japanese knotweed canopy could either decrease precipitation received by Leedy's roseroot or reduce evaporation and increase humidity. However, Mattingly and Leopold (2018) found that Leedy's roseroot is concentrated at areas of seepage from the cliff face—a water source that Japanese knotweed presumably cannot affect. In general, both our LMM and SEM analyses showed strong impacts of Japanese knotweed on talus abiotic conditions, whereas on the cliff, some relationships were nonsignificant. Although Leedy's roseroot's core habitat is concentrated on the cliff, the amount of solar energy reradiating from

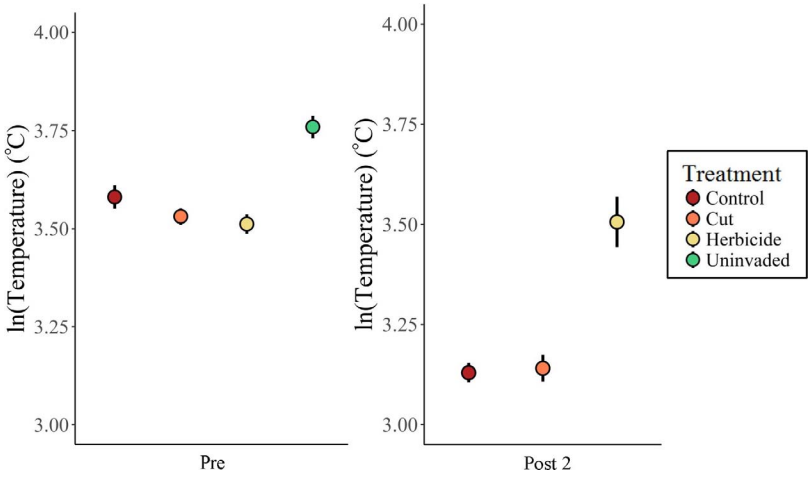

Figure 6. Temperatures across treatments and time in talus plots used for a pre–post block design study (2013–2015) of the effects of Japanese knotweed *Fallopia japonica* on Leedy's roseroot *Rhodiola integrifolia* subsp. *leedyi* at Glenora Cliffs, New York. Each treatment block was within the area of Japanese knotweed invasion, and included three ordered plots called control, cut, and herbicide plots. These names refer to the type of treatment applied to invasive Japanese knotweed that was shading Leedy's roseroot. Uninvaded plots containing Leedy's roseroot were located outside of the invaded area. Temperature measurements were collected using different methodology pretreatment (2013, Pre) and 2 y posttreatment (2015, Post2). For Pre, we reported the maximum temperature (°C) recorded over the period of August 30–September 27, 2013 using Thermochron iButtons. For Post2, we reported rock temperatures (°C) measured using an Extech dual-laser infrared thermometer (in Post2, uninvaded plot temperatures were not sampled). We applied natural log transformations to both temperature variables. Points are means and bars are standard error.

open talus is still relevant to the microclimate experienced by Leedy's roseroot near the cliff/talus interface; using SEMs we found that talus PAR affected Leedy's roseroot mean stem length. In an observational study outside the area of invasion at Glenora Cliffs, Mattingly and Leopold (2018) likewise found lengthened Leedy's roseroot stems in response to decreased light and temperature. Lengthened stems, though not necessarily detrimental to Leedy's roseroot, provide evidence of individuals responding to changed environmental conditions in the presence of Japanese knotweed.

As we originally posited, Japanese knotweed's effects on Leedy's roseroot could be facilitative, competitive, or neutral. Our LMM contrast results support competitive effects: plots with a history of Japanese knotweed invasion had fewer total Leedy's roseroot stems and fewer flowering stems than uninvaded plots. Some evidence also suggests that our finding from SEMs of etiolated Leedy's roseroot stems in lower light and temperature could indicate stress. Olfelt and Freyman (2014) proposed that Leedy's roseroot may have occurred along glacial margins during the Pleistocene. Glacial margins would represent open, high-light, low-competition environments (Horsák et al. 2015), suggesting that Leedy's roseroot would be intolerant of low light. Likewise, Mattingly and Leopold (2018) found that Leedy's roseroot occurrence was concentrated at hotter and higher light areas of the cliff. The effects of Japanese knotweed on temperature and light appear to create suboptimal Leedy's roseroot habitat. The lower portion of the cliff would otherwise be optimal habitat for Leedy's roseroot; outside of the Japanese knotweed invasion at Glenora Cliffs, Leedy's roseroot was more likely to be found at lower heights on the cliff, probably because the lower part of this cliff also had higher seepage (Mattingly and Leopold 2018).

Although adult Leedy's roseroot individuals can tolerate some of the higher temperatures and light present on the

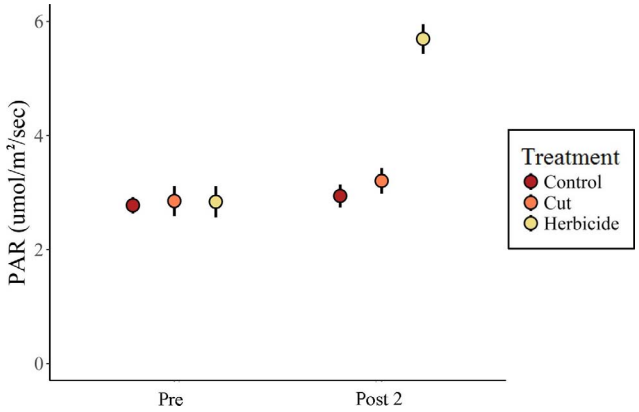

Figure 7. Photosynthetically active radiation (PAR, μmol m^{-2} s^{-1}) across treatments and time in talus plots used for a pre–post block design study (2013–2015) of the effects of Japanese knotweed *Fallopia japonica* on Leedy's roseroot *Rhodiola integrifolia* subsp. *leedyi* at Glenora Cliffs, New York. Pre measurements were taken in 2013 and Post2 measurements were taken in 2015. Each treatment block was within the area of Japanese knotweed invasion, and included three ordered plots called control, cut, and herbicide plots. These names refer to the type of treatment applied to invasive Japanese knotweed that was shading Leedy's roseroot. We applied natural log transformations to the PAR observations. Points are means and bars are standard error.

Table 2. Summary of statistics for linear mixed models from a pre–post block design study of the effects of Japanese knotweed *Fallopia japonica* on Leedy's roseroot *Rhodiola integrifolia* subsp. *leedyi* at Glenora Cliffs, New York. Each treatment block was situated within the invaded area of the Leedy's roseroot population, and included three ordered plots called control, cut, and herbicide plots. These names refer to the type of treatment applied to invasive Japanese knotweed shading Leedy's roseroot. Uninvaded plots containing Leedy's roseroot were located outside of the invaded area. Models describe Leedy's roseroot functional trait responses to treatments (control, cut, herbicide, or uninvaded plots) and over time: (**a**) analysis of variance (ANOVA) statistics, (**b**) planned contrasts based on specific hypotheses about treatment effects. Bold denotes terms with significant *P*-values. Subscripts of *F*-values are numerator degrees of freedom, denominator degrees of freedom. Positive *t*-values indicate that the first group listed in the contrast pair has higher values for the response variable; negative *t*-values show that the second group has higher values.

	Total stems	Proportion flowering stems	Mean stem length (cm)	Mean leaves per stem
(**a**) ANOVA				
Treatment	$\mathbf{F_{3,25} = 3.960, P = 0.019}$	$\mathbf{F_{3,25} = 3.297, P = 0.037}$	$F_{3,25} = 1.185, P = 0.336$	$F_{3,25} = 0.631, P = 0.602$
Time	$F_{2,72} = 3.107, P = 0.051$	$\mathbf{F_{2,72} = 5.274, P = 0.007}$	$\mathbf{F_{2,72} = 20.330, P < 0.001}$	$\mathbf{F_{2,72} = 3.926, P = 0.024}$
Treatment × time	$F_{6,72} = 0.970, P = 0.452$	$F_{6,72} = 0.551, P = 0.768$	$F_{6,72} = 1.040, P = 0.407$	$F_{6,72} = 1.953, P = 0.084$
(**b**) Treatment contrasts				
(1) Uninvaded – invaded	$\mathbf{t_{78} = 3.207, P = 0.002}$	$\mathbf{t_{78} = 3.098, P = 0.003}$	$t_{78} = 0.086, P = 0.932$	$t_{78} = 0.686, P = 0.494$
(2) Herbicide – control & cut	$t_{26} = 0.060, P = 0.953$	$t_{26} = -0.254, P = 0.802$	$t_{26} = 0.321, P = 0.751$	$t_{26} = -1.003, P = 0.325$
(3) Control – cut	$t_{26} = 1.396, P = 0.174$	$t_{26} = -0.373, P = 0.712$	$t_{26} = -1.838, P = 0.078$	$t_{26} = -0.659, P = 0.516$

cliff face (Mattingly and Leopold 2018), Leedy's roseroot seedlings are almost certainly less drought tolerant than adults because of their lack of a developed storage rhizome and may benefit from light, temperature, or moisture conditions associated with Japanese knotweed shade. We were not able to measure abiotic or biotic gradients associated specifically with seedlings, though seedlings are included in our total counts, and represent most of the year-to-year variation in totals for this long-lived species. Our finding of decreased stem totals in areas with history of invasion suggests that shade may not be conducive to seedling establishment.

Treatment effects on abiotic conditions and Leedy's roseroot

Plots in which Japanese knotweed was removed with herbicide experienced environmental changes consistent with restoration to the uninvaded habitat condition: creation of an open talus with increased light and temperature relative to adjacent areas where the Japanese knotweed stand remained intact. This finding suggests that removal of Japanese knotweed may be a productive strategy for restoring Leedy's roseroot habitat at Glenora Cliffs. Removal can be efficiently accomplished through cut-stem herbicide treatment, followed by targeted spraying of regrowth. Additionally, our results indicate that this removal strategy does not produce nontarget herbicide effects on Leedy's roseroot; cut plots (always adjacent to herbicide plots, so subject to drift if present) did not differ from control plots in Leedy's roseroot abundance or traits. One Leedy's roseroot response, mean stem length, showed a marginally significant difference between cut and control plots, but the trend was the opposite of what would be expected in the presence of herbicide stress. Herbicide often produces stunted stems, but cut plots had longer mean stem lengths than control plots.

Though habitat restoration was successful in areas where Japanese knotweed was treated with herbicide, Leedy's roseroot abundance and response traits were not restored to the uninvaded target condition. Rather, all areas with a history of invasion had lower Leedy's roseroot abundance and flowering than uninvaded areas. However, our study included only 2 y of posttreatment observations, which may not be long enough to see effects on Leedy's roseroot. We had expected that 2 y would be sufficient to detect both changes in traits of adults and recruitment of seedlings. However, as long-lived stress tolerators with storage-organ rhizomes (Clausen 1975), Leedy's roseroot adults are apparently robust to short-term environmental change. Likewise, seedling recruitment in stressful, heterogeneous habitats may be exceedingly rare and difficult to predict (Matthes-Sears and Larson 1999), or may occur in response to a distinct regeneration niche at the microscale (Grubb 1977; Graae et al. 2011). Despite lack of Leedy's roseroot response to Japanese knotweed removal, we did find decreased totals and flowering associated with invasion. This finding suggests that Japanese knotweed is outcompeting Leedy's roseroot and should be removed at Glenora Cliffs.

Japanese knotweed shade in combination with other threats, such as lakeshore development, upland land use, and increased extreme weather events due to climate change, could amplify negative impacts on Leedy's roseroot at Glenora Cliffs. Even periodic impacts on Leedy's roseroot flowering could affect fitness. Over time, impacts could deplete genetic diversity, decrease population size, and increase extinction risk.

Conclusions

We see potential for using cliff-dwelling species as model systems for disentangling above- and belowground interactions among species in the field. In studies of plant species interactions, ecologists face the significant challenge of separating the influences of aboveground and belowground interactions (van der Putten et

al. 2009). In cliff systems, aboveground and belowground interactions among plants may be decoupled if individuals occupy different rooting spaces, as with Japanese knotweed and Leedy's roseroot in our study. Future studies could compare functional traits and fitness of cliff species planted in the same cliff crevice (representing above- and belowground interactions), neighboring crevices (aboveground interaction only), shared crevice with tie-backs (belowground interaction only), and isolated crevices (no interaction).

We explored aboveground interactions between the rare subspecies Leedy's roseroot and invasive Japanese knotweed, which was experimentally removed in a three-treatment block design. Consistent with a competitive interaction, Japanese knotweed shade was associated with decreased Leedy's roseroot abundance and flowering. Two years of Japanese knotweed removal restored the habitat by allowing more light to reach the talus and increasing temperature of the talus and cliff. However, removal of Japanese knotweed did not significantly restore the Leedy's roseroot population. Over time, interventions that restore habitat to the open, high-light target condition may allow for increased Leedy's roseroot numbers at previously invaded areas.

Land stewards invest considerable time and resources in invasive species management, hoping that removal of competitors will positively affect populations and communities of conservation concern. Our study measured the impacts of such an intervention. Our findings underscore the fact that recovery may lag behind restoration efforts or, as other studies have found, may require intervention beyond mere invasive species removal (e.g., Dornbush and Hahn 2013). Deep understanding of the natural history and life history of species of concern will help us to predict which taxa may require more in-depth interventions. For Leedy's roseroot, although adults are long lived and currently seem secure, persistent reduced flowering in formerly invaded areas could translate into limited regeneration of seedlings, suggesting that this population may require continued monitoring, mitigation of other threats, and perhaps replanting.

Supplemental Material

Please note: The *Journal of Fish and Wildlife Management* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Data S1. National Oceanic and Atmospheric Administration. U.S. daily precipitation and temperature data for Penn Yan Airport, New York (2013–2015 data).

Found at DOI: https://doi.org/10.3996/022018-JFWM-010.S1 (42 KB XLSX).

Data S2. National Oceanic and Atmospheric Administration. U.S. daily wind speed data for Penn Yan Airport, New York (2013–-2015 data).

Found at DOI: https://doi.org/10.3996/022018-JFWM-010.S2 (30 KB XLSX).

Data S3. National Oceanic and Atmospheric Administration. Surface data hourly global for Penn Yan Airport, New York (2015 data).

Found at DOI: https://doi.org/10.3996/022018-JFWM-010.S3 (13 KB XLSX).

Table S1. For a pre–post block design study of the effects of Japanese knotweed *Fallopia japonica* on Leedy's roseroot *Rhodiola integrifolia* subsp. *leedyi* at Glenora Cliffs, New York, a supplementary data set consisting of all photosynthetically active radiation ("PAR_μmol") measurements taken in treatment plots 2 y posttreatment (Post2, 2015), and time ("Time") and date ("Date") of recording. "Time_decimal" is time converted from hours and minutes to decimal format using the Excel INT() function.

Found at DOI: https://doi.org/10.3996/022018-JFWM-010.S4 (21 KB XLSX).

Table S2. For a pre–post block design study of the effects of Japanese knotweed *Fallopia japonica* on Leedy's roseroot *Rhodiola integrifolia* subsp. *leedyi* at Glenora Cliffs, New York, the data set used to perform analyses. Column headers are as follows: plot = unique identifier for a plot, block = identifier for block, jkw_plot_length = distance to end of talus (m), trt_name = treatment type, year = year of observation, prepost = time relative to treatment application, leedys_plant_count_transformed = log-transformed total number of individuals, leedys_stem_count_transformed = log-transformed total stems, leedys_flower_proportion_transformed = log-transformed proportion of flowering stems, leedys_stem_length = mean stem length (cm), leedys_leaf_count = mean leaves per stem, leedys_flower_count_transformed = log-transformed total number of flowers, jkw_stand_basal_area_transformed = log-transformed Japanese knotweed stand basal area (cm^2/m^2), jkw_stems_per_m2_transformed = log-transformed Japanese knotweed total stems per m^2, jkw_percent_cov_transformed = log-transformed Japanese knotweed cover (%), jkw_pres_absence = Japanese knotweed presence/absence, PAR_talus_transformed = log-transformed talus photosynthetically active radiation ($\mu mol\ m^{-2}\ s^{-1}$), PAR_cliff_transformed = log-transformed cliff photosynthetically active radiation ($\mu mol\ m^{-2}\ s^{-1}$), rock_temp_talus_transformed = log-transformed talus rock temperature (°C), rock_temp_cliff_transformed = log-transformed cliff rock temperature (°C), iB_temp_talus_hi_transformed = log-transformed talus max iButton temperature (°C), iB_temp_talus_lo_transformed = log-transformed talus min iButton temperature (°C), iB_temp_cliff_hi_transformed = log-transformed cliff max iButton temperature (°C), iB_temp_cliff_lo_transformed = log-transformed cliff min iButton temperature (°C).

Found at DOI: https://doi.org/10.3996/022018-JFWM-010.S5 (47 KB XLSX).

Table S3. For a pre–post block design study of the effects of Japanese knotweed *Fallopia japonica* on Leedy's roseroot *Rhodiola integrifolia* subsp. *leedyi* at Glenora Cliffs, New York, breakdown of the 188 Leedy's

roseroot response observations retained for analysis after removal of missing values.

Found at DOI: https://doi.org/10.3996/022018-JFWM-010.S6 (17 KB DOCX).

Figure S1. For a pre–post block design study of the effects of Japanese knotweed *Fallopia japonica* on Leedy's roseroot *Rhodiola integrifolia* subsp. *leedyi* at Glenora Cliffs, New York: (**a**) repeated-measures structural equation model configuration including both photosynthetically active radiation (PAR, μmol m^{-2} s^{-1}) variables with repeated measures across the years of the study: pretreatment (Pre) and 2 y posttreatment (Post2). (**b**) Structural equation model configuration including cliff temperature and PAR measurements taken in Post2.

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