CONTRIBUTED PAPER

Ten years of pulling: Ecosystem recovery after long-term weed management in Garry oak savanna

Nancy Shackelford[1,2] | Sean M. Murray[1] | Joseph R. Bennett[3] | Patrick L. Lilley[4] | Brian M. Starzomski[1,5] | Rachel J. Standish[6]

[1]School of Environmental Studies, University of Victoria, Victoria, British Columbia, Canada

[2]Ecology and Evolutionary Biology, University of Colorado Boulder, Boulder, Colorado

[3]Department of Biology, Carleton University, Ottawa, Ontario, Canada

[4]Kerr Wood Leidel, Burnaby, British Columbia, Canada

[5]Hakai Institute, Heriot Bay, British Columbia, Canada

[6]School of Veterinary and Life Sciences, Murdoch University, Murdoch, Western Australia, Australia

Correspondence
Nancy Shackelford, Nancy Shackelford Institute of Arctic and Alpine Research University of Colorado, Boulder Campus Box 450 Boulder, Colorado 80309-0450.
Email: nancy.shackelford@gmail.com

Abstract

Ecosystem restoration is the practice of assisting recovery in degraded ecological communities. The aims of restoration are typically broad, involving the reinstatement of composition, structure, function, and resilience to disturbances. One common restoration tactic in degraded urban systems is to control invasive species, relying on passive restoration for further ecosystem-level recovery. Here, we test whether this is an effective restoration strategy in Garry oak savanna, a highly threatened and ecologically important community in the North American Pacific Northwest. In urban savanna patches surrounding Victoria, British Columbia, community members have been actively removing aggressive invasive exotic species for over a decade. Based on vegetation surveys from 2007, we tested ecosystem changes in structure, composition, and resilience (i.e., functional redundancy and response diversity) across 10 years of varied management levels. We expected higher levels of invasive species management would correspond with improvements to these ecosystem metrics. However, management explained little of the patterns found over the 10-year-period. Woody encroachment was a complicated process of native and exotic invasion, while resilience and compositional changes were most closely tied with landscape connectivity. Thus, though invasive species management may prevent further degradation, active restoration strategies after removal are likely required for recovery of the ecosystem.

KEYWORDS
functional redundancy, resilience, response diversity, woody encroachment

1 | INTRODUCTION

Restoration ecology often has aspirational goals. The internationally accepted foundation documents from the Society of Ecological Restoration list whole-ecosystem attributes as the aims of successful restoration, including species composition, ecosystem structure and function, and ecosystem resilience (McDonald, Gann, Jonson, & Dixon, 2016; SER, 2004). These are complex targets, even under ideal circumstances (Miller & Hobbs, 2007). Most restoration occurs in less than ideal circumstances, however, because it occurs in highly degraded ecosystems and grapples with challenges like altered environmental conditions, altered regional species pools, and cross-boundary disturbances that are beyond practitioner control (Higgs, 2003; Perring et al., 2015). Compounding these external constraints is the reality of limited management resources. All restoration practitioners have finite access to financial, logistical, and biological resources needed to achieve ecosystem-level restoration practices (Holl & Aide, 2011; Miller et al., 2017). Thus, restoration actions often

2 of 11 | **WILEY**_ **Conservation Science and Practice** _A journal of the Society for Conservation Biology_ Open Access

SHACKELFORD ET AL.

target the most impactful threat to the ecosystem undergoing management, allowing natural recovery, that is, passive restoration, to ensure the return of complex ecological targets and to maximize use of limited resources.

In many semi-natural, degraded areas, the primary threat to restoration and recovery is invasion by exotic species (Gaertner, Holmes, & Richardson, 2012). Invasive species can change fundamental processes, community structure, and local species composition (Mack et al. 2000; Simberloff et al. 2013), potentially leading to dramatic state changes and loss of native ecological communities (Gaertner et al., 2012; Suding & Hobbs, 2009). Restoration actions therefore often focus on invasive species removal and a subsequent passive recovery of ecosystem structure and composition. For example, *Phragmites* invasion in North American wetlands can lead to dense monoculture stands that drive down native diversity and decrease habitat provision services (Bolton & Brooks, 2010). Beneath these dense stands, however, diverse native seedbanks are often still intact, and restoration actions focus primarily on *Phragmites* removal with no further interventions needed for ecosystem recovery (Hazelton, Downard, Kettenring, McCormick, & Whigham, 2018). More broadly, effective control of invasive species has also been shown to support the retention and successful expansion of native species (e.g., de Lange & van Wilgen, 2010; Meyer & Fourdrigniez, 2011).

Passive ecological restoration, when it occurs after a single effort of weed removal, is ideal. In many instances, however, the removal of an exotic invasive species is followed by the emergence of an alternative invader (Buckley, Bolker, & Rees, 2007) or other unforeseen negative results (Gaertner et al., 2012). Additionally, intense one-time removal may be inadequate to control invasion, and continuous removal may be required, sometimes without a foreseeable eradication timeline (e.g., Cordell, Ostertag, Michaud, & Warman, 2016). Thus, the restoration goal of halting and removing invasive species can require long-term management actions. Given the resources required for long-term invasive species control, as well as the potentially neutral or perverse outcomes that may result, managers need to understand whether control followed by passive restoration is adequate to achieve restoration goals. Thus, monitoring the ecosystem outcomes of invasive species removal, such as ecological structure, species composition, and resilience to disturbances, is essential to effective restoration and the efficient allocation of limited restoration resources.

In the Pacific Northwest of North America, Garry oak savannas are important both culturally and for biodiversity conservation (Pellatt & Gedalof, 2014). They are highly threatened, with only a small percentage of their original distribution remaining (Bjorkman & Vellend, 2010). The historical extent was largely converted for agriculture and development, with the remaining areas now threatened primarily by exotic species invasion and continued land use change. Small patches of savanna can be found in urban areas, but they are highly degraded and in need of restoration to maintain their structure, function, and conservation values. The restoration actions in these urban parks focus on annual invasive species removal but monitoring of restoration outcomes is rare given the community-driven nature of the work. In this study, we aimed to quantify the ecosystem-level outcomes of invasive species removal by assessing site-level changes in species composition, savanna patch structure, and ecosystem resilience. Using a previous study in urban savanna patches, we measured change through 10 years and compared it to relative management efforts in each patch. We hypothesized that higher invasive species removal would lead to maintenance or improvement in composition, structure, and resilience of these threatened communities, implying that passive restoration post-removal was effectively achieving ecosystem conservation goals.

2 | MATERIALS AND METHODS

2.1 | Site description

Garry oak savannas are highly diverse, forb-dominated communities with a sparse overstory of Garry oak (*Quercus garryana*) and Douglas fir (*Pseudotsuga menziesii*). Climate is sub-Mediterranean, with wet winters and significant summer drought (MacDougall, 2005). Much of the remaining savanna fragments are scattered in urban and rural areas, secondary coastal Douglas fir forests, and agricultural areas (Fuchs, 2001).

This study was conducted in the northern portions of the savanna range on Vancouver Island, British Columbia. The region was historically characterized by extensive First Nations management activity, with regular fire maintaining the open savanna canopy structure (Pellatt & Gedalof, 2014; Pellatt, McCoy, & Mathewes, 2015). As European settlement advanced, much of the savanna extent was quickly lost to land use change. The loss of fire, however, has also proven to be a persistent threat to remnant savanna patches (Barlow, 2017), as native trees and shrubs lead to canopy closure and eventual conversion to woodland (Dunwiddie & Bakker, 2011).

Other than land use change, one of the largest current threats to these Garry oak savanna communities is the diverse suite of invasive species (Dunwiddie & Bakker, 2011; Shackelford, Standish, Ripple, & Starzomski, 2018) such as Scotch broom (*Cytisus scoparius*), Himalayan blackberry (*Rubus armeniacus*), and laurel-leaved daphne (*Daphne laureola*). These woody species create closed canopies that fundamentally alter the structure of the ecological community (Clements, 2013). Local urban parks are some of the most prominent remaining savanna patches, and they are managed primarily to combat invasion through hand-pulling and

limited use of chemical control methods. We chose 23 parks with historical data on plant species composition and abundance (Bennett, Vellend, Lilley, Cornwell, & Arcese, 2013; Lilley & Vellend, 2009). Garry oak savannas are naturally patchy, and few parks are entirely savanna. Within parks, we focused on savanna patches less than 10 ha, as patches larger than 10 ha are rare and tend to be dramatically larger. Seven parks had multiple patches within our size limit; in these parks, we surveyed two randomly selected patches each for a total of 30 individual patches (Supporting Information S1).

2.2 | Restoration metrics

2.2.1 | Ecosystem structure: woody encroachment

The open canopy structure of the savanna community is a primary goal in ecosystem conservation and restoration efforts. Much of the native diversity requires high access to sunlight and cannot compete when woody encroachment reduces light availability (Clements, 2013). The combination of native encroachment and exotic woody species invasion causes serious concern for savanna persistence. Thus, we measured loss in savanna area to woody encroachment for each of the surveyed patches as one restoration metric. Using 2016 aerial photographs, we estimated patch boundaries based on vegetation density. We ground-truthed boundaries during field surveys, using a GPS to mark necessary adjustments based on canopy cover and characteristic species. Patch area lost to woody encroachment was estimated by comparing these boundaries to the 2007 boundaries estimated using the same methods (Lilley & Vellend, 2009).

2.2.2 | Ecosystem diversity: native species richness and turnover

Garry oak savannas in British Columbia represent a national hotspot of native plant diversity, with close to 10% of the total listed Species at Risk for Canada occurring in less than 2000 ha of savannah (i.e.,70 listed plant species (Clements, 2013)). Persistence of native species in these ecosystems is also a key conservation metric. To track changes in native species richness, we repeated the 2007 surveys of Lilley and Vellend (2009). We ran parallel transects 25 m apart across the patch extent and recorded all vascular plant species. Garry oak savannas undergo dramatic compositional shifts between seasons. To capture the full suite of plant species, we conducted two surveys in 2017, one in spring (10 April–4 May) and a second in summer (29 May–24 June). The previous patch-level surveys were completed in spring and summer 2007. In addition to native species richness, we examined community turnover, measured as species replacements between the first and second timepoint (Anderson et al.,

2011), as a potential restoration metric. This was calculated as the proportion of species either gained or lost relative to the total number of species observed across both time periods (Hallett et al., 2018). Though high or low turnover may not be an inherent measure of restoration success, understanding how management corresponds with community changes can give insight into overall management impacts.

2.2.3 | Ecosystem resilience: functional redundancy and response diversity

One challenge of monitoring high-level outcomes like ecological resilience to disturbances is choosing which metrics to measure (Duelli & Obrist, 2003). Resilience is an abstract ecosystem characteristic that is notoriously difficult to quantify (Standish et al., 2014). One common suggestion is to monitor proxies of resilience – concrete attributes thought to correlate closely with resilience (Bennett, Cumming, & Peterson, 2005). Functional redundancy (Walker, 1992) and response diversity (Elmqvist et al. 2003) are two such proxies. Current theory suggests that a resilient ecosystem will have many species within primary ecological functions (functional redundancy), enabling fluctuations in one population to be compensated by another (Pillar et al., 2013). As a resilience proxy, functional redundancy is necessarily paired with response diversity – the diversity of response types within a single function. If redundancy is high but all species respond negatively to disturbance, the compensatory dynamics are lost (Mori, Furukawa, & Sasaki, 2013). Thus, the combination of high functional redundancy and high response diversity within a single function is hypothesized to make that function resilient to disturbance and change (Elmqvist et al. 2003; Mori et al. 2013). Though they have not yet been used in restoration contexts, both are measurable aspects of communities dependent on species presence and so make good candidates to quantify resilience for this study.

Defining functional redundancy and response diversity requires specifying relevant plant functional traits, in our case with respect to resilience to ecosystem-relevant disturbance. Additionally, there must be a clear distinction of response and effect traits. We defined effect traits as those traits that impact biogeochemical processes in the system, such as growth rates or lifeform (Cornelissen et al., 2003; Lavorel & Garnier, 2002). Response traits are traits that shape a species response to disturbance (Lavorel & Garnier, 2002; Suding et al., 2008), usually captured by regeneration habits like dispersal or seed size. We also included known environmental tolerances to capture the window of conditions within which species could respond neutrally or positively to shifting regional conditions, which are predicted to shift towards increasing summer drought and climatic warming (Hamann & Wang, 2006). Woody invasion, climate shifts, and increasing pressure from other non-native

species result in an ecosystem undergoing a variety of pressures. Thus, we captured a wide variety of traits relevant to community response to short- (e.g., growth rate and seed weight) and long-term disturbance (e.g., dispersal method and clonal reproduction). We collected 22 traits over 304 species from online trait databases such as the Seed Information Database through Kew Gardens and the United States Department of Agriculture (Supporting Information S2 for details and sources). We were missing more than three traits for only 4% of species.

Functional redundancy is most often measured within individual functional groups. To define functional groups, we used the FD package (Laliberté, Legendre, & Shipley, 2014) in R (R Core Team, 2017). Functional group classifications were created using Ward's minimum variance clustering on the trait dissimilarity matrix (Legendre & Legendre, 2012). Because we had mixed classes of variables (continuous, categorical, and ordinal) as well as some missing values, distance matrices were computed as a Gower dissimilarity matrix (Podani, 1999). Ward's clustering of Gower dissimilarities tends to result in roughly equally-sized functional groups if the species are evenly distributed within the trait space (Legendre & Legendre, 2012). To define functional groups, we used only effect traits of the full set of compiled traits (see Supporting Information S2 for trait designations). We defined the number of groups based on a visual inspection of the clustering dendrogram (Aubin, Ouellette, Legendre, Messier, & Bouchard, 2009). Clusters were computed using Principal Coordinates Analysis (PCoA), a method requiring Euclidean distance matrices. Thus, we corrected our Gower's distance matrix using the Cailliez correction method (Cailliez, 1983).

Once classification was complete, we recorded the functional group for each species. A few of the groups were composed either entirely of non-native species or of non-native species and one native. We considered these groups as functional groups not indigenous to the historical Garry oak savanna system and excluded them from subsequent calculations. For all other individual groups in each patch, functional redundancy was measured as the total number of recorded species (Laliberté et al., 2010; Walker, 1992). Our response variable was the proportional change in redundancy from 2007 to 2017. This variable was closely tied with changes in site-level species richness, but split by, and taking into consideration, individual ecosystem functions.

Rather than focusing on individual functional groups for response diversity, we instead calculated response diversity of the full understory communities. In general, these understory communities are the most altered component, which in turn threatens the structure of Garry oak savannas through recruitment failure and species loss. Response diversity for all understory species was calculated as the multivariate functional dispersion of represented species in response trait space

(Laliberté & Legendre, 2010). This represents a different set of traits than those used to calculation functional groups and thus captures a different trait-based attribute of ecosystem dynamics. The functional dispersion is an average distance of each species to the centroid of the response trait space of all species, meaning that it is little influenced by the number of species, ensuring independence of response diversity from redundancy. Gower dissimilarity matrices were used and corrections for non-Euclidean distances were made prior to dispersion calculations (Anderson, 2006). Our response variable was the proportional change in response diversity from 2007 to 2017.

2.3 | Predictor variables

We met with managers at each park and discussed the amount of time and resources invested in invasive species control within each patch for the last 10 years. Only one patch had management activities beyond species removal and the location of the action was isolated to a fenced-off area at the patch boundary. We categorized management effort as one of four levels – none, low, medium, and high. A patch had no management if the organization did none and we found no evidence of community intervention, low management if the organization did no formal management, but we found management evidence (e.g., old piles of pulled plants), medium if the organization applied irregular invasive species control, and high if consistent, annual invasive species removal occurred. Removal efforts in all patches involved hand-pulling invasive species individuals. Local managers do not use herbicide or mechanical methods, and we found no evidence that these methods had been used. Thus, 'high' management between sites is relatively uniform, involving targeted, annual removal of key invaders by local community volunteers.

We had three other predictor variables: patch area in the 2007 surveys or area lost between 2007 and 2017, connectivity, and surrounding road density. For area lost to woody encroachment, we used the 2007 area of the patch. For all other response variables, we used the amount of patch area lost. Connectivity and road density were determined previously (Lilley & Vellend, 2009). Road density was calculated as the length of roads per unit area within a 1 km radius of the patch edge. Connectivity (C_i) was calculated as a distance-weighted sum of the area of surrounding savanna patches:

$$C_i = \sum_{i \neq j} \exp(-\alpha d_{ij}) A_j$$

where A_j is the area of patch j (in m^2), d_{ij} is the minimum edge-edge distances between patches i and j, and α represents the influence of distance on biotic connectivity (Moilanen & Nieminen, 2002), that is, species' distance-dependent dispersal range. For grassland species, $\alpha = .002$ is

TABLE 1 Model results for each conservation goal (listed on the left, with the metric listed in the second column)

Ecosystem trait	Response variable	Model	Goodness of fit
Structure	Change in area	− Management − **0.05*Road density** − **0.05*Patch area (2007)** − Mng:Rds	.34
Native diversity	Change in native species richness	+ Management + Road density + Connectivity + Lost area + Mng:Rds	.43
Composition	Species turnover	− Management + Road density + **0.25*Connectivity** + 0.2*Lost area − Mng:Rds	.33
Resilience	Functional redundancy	+ Management + Road density + **0.06*Connectivity** + Lost area − Mng:Rds + **Group**	.21
Resilience	Response diversity	− Management − Road density + Connectivity + Lost area − Mng:Rds	.19

Note: All predictors were standardized prior to modeling except invasive species management. Predictors shown in bold and underlined were significant at $\alpha = .05$; underlined only were significant at $\alpha = .1$; coefficients are only given for significant predictors, though direction of relationship (positive or negative) is included for all. Goodness of fit values for change in area, change in native diversity, and change in response diversity are adjusted-R^2; for turnover (Gamma distribution) proportion deviance explained; for functional redundancy, the marginal R^2 (Nakagawa & Schielzeth, 2013).

likely a realistic estimate of migration range (Verheyen, Vellend, Van Calster, Peterken, & Hermy, 2004), representing migration in which medium-long distance dispersal events are not rare. With the exception of the ordinal variable management level, we standardized all predictors by subtracting the mean and dividing by the standard deviation for effect-size comparison.

2.4 | Statistical analysis

Area change, change in native species richness, and change in response diversity were fit with linear models of each response against their set of predictors (see Table 1 for full model specifications). To check for violations of linear model assumptions, we looked for outliers using Cook's distance calculations (Cook, 1977). In the one instance where case Cook's distance exceeded 1, the model was fit with and without the outlier to understand its overall influence on model predictions.
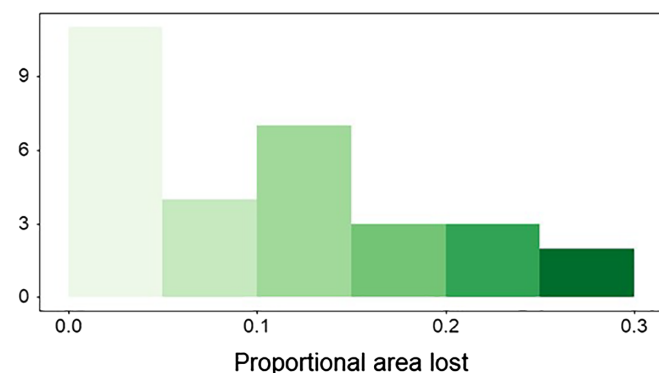
Additionally, we used Shapiro-Wilks tests (Shapiro & Wilk, 1965) to check that residual values were normal for all models. Species turnover was between 0 and 1. Thus, we fit a generalized linear model with a Gamma distribution (Zuur, Ieno, Walker, Saveliev, & Smith, 2009) for turnover. Change in functional redundancy within groups was modeled with a mixed effects model, where site was used as a random effect and group was used as a fixed effect. All calculations and analyses were conducted in R (R Core Team, 2017).

3 | RESULTS

3.1 | Ecosystem structure: woody encroachment

On average, meadow patches lost around 11% of their 2007 area, with only 20% of the patches maintaining their boundaries between 2007 and 2017 (Figure 1).
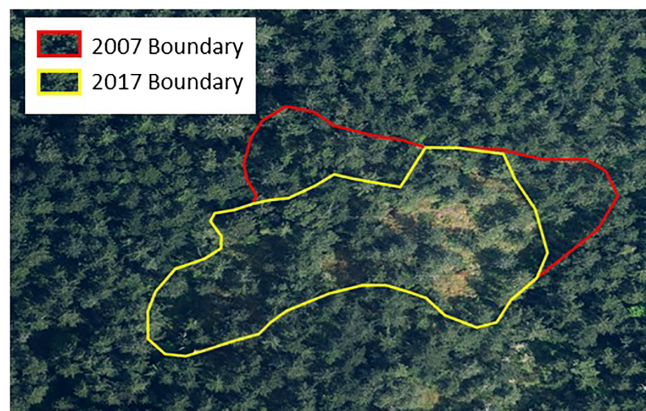

FIGURE 1 Histogram of proportional area lost from 2007 to 2017 in each patch (left) and illustration of canopy closure (right). In the right panel, the delineated 2007 boundary (red) has been overlaid on an aerial photo from 2017. The new 2017 boundary (yellow) was estimated from aerial imagery and ground-truthed at the patch-level
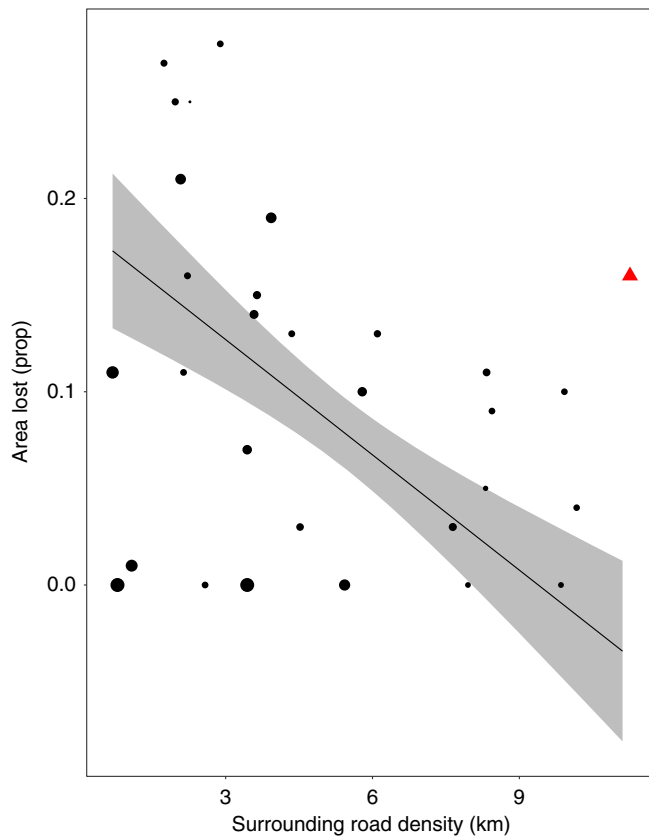
FIGURE 2 Model results for patch area lost to woody encroachment. Black points represent raw data, where the *y*-axis is the proportion of area lost between 2007 and 2017, and each point is sized relative to the 2007 area of the patch. Model predictions (black line with standard error in grey) show that the amount of area lost decreases as surrounding road density (length of roads within 1 km radius area around patch) increases, shown here as a standardized *x*-axis. The red point represents the outlier patch removed during the analysis

FIGURE 3 Model results for functional redundancy (marginal $R^2 = 0.21$). The model predicts a positive relationship between changes in functional redundancy and patch connectivity ($p = .02$), shown here as a unitless standardized *x*-axis. Each functional group was included individually in the model. Here, points represent the average change in redundancy for all groups within a patch, with the standard deviation as error bars

The amount of area lost was negatively related to surrounding road density ($p = .02$; Table 1) and original patch size ($p = .01$; Table 1). Those patches that had lower surrounding road density or were smaller in 2007 had the highest levels of canopy closure (Figure 2). There was one outlier site that was removed to ensure the model met assumptions of residual normality. Removal of the outlier did not change the direction or relative strength model coefficient estimates. Residuals for the model were normally distributed, though small amounts of positive skew were found when residuals were plotted against the road density predictor.

3.2 | Ecosystem diversity: native species richness and total turnover

Changes in native species richness were generally positive, with only 20% of patches showing species declines. Species turnover was variable, with anywhere from 25 to 50% of species within each patch either being gained or lost between
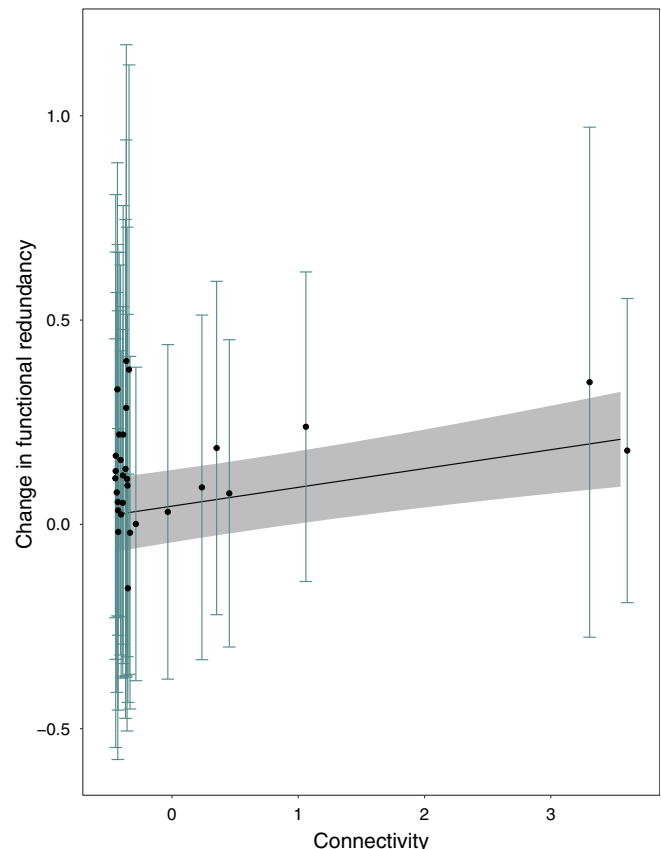
timepoints. Though no significant predictors were found for changes in native species richness (Table 1), species turnover was positively related to connectivity ($p = .047$; Table 1) and less significantly, though still positively related to size of patch ($p = .08$; Table 1).

3.3 | Ecosystem resilience: functional redundancy and response diversity

We found 31 unique functional groups, six of which could be considered nonnative functions in which all species, or all but one species, were nonnative species. Supporting Information S3 details each group, including a brief description of the functional effect traits that shape it, species lists, and origin of each species. Changes in functional redundancy were generally positive, with only three sites averaging decreased redundancy across all groups. Four functional groups tended to have higher increases, all of which were characterized by moderate to fast growing forb species. The

only other model predictor significantly related to changes in redundancy was connectivity, where increased connectivity was related to increased redundancy (Figure 3). On average, changes in response diversity were weakly negative, and no significant predictors were found (Table 1).

4 | DISCUSSION

Overall, we found that both native species richness and ecosystem resilience were relatively stable or increasing for most of the Garry oak patches we surveyed. However, structural changes in the form of canopy closure by native and non-native species were fairly widespread. We found little statistical relationship between invasive species management and canopy closure, or management and any of the other ecosystem metrics we tested. Rather, landscape context in the form of ecological connectivity and road density surrounding each patch had the most consistent relationships with ecological changes through time. Given that the main motivation behind much of the Garry oak invasive species management is to maintain the open canopy against aggressive exotic woody species (Costanzo et al., 2011), the missing links between management level and patch area changes imply different management tactics are required to affect desired restoration goals. Successful restoration in these systems may require replication of key lost habitat-forming processes like ground fire.

The main driver of structural changes was a combination of non-native and native shrub species invading into the otherwise open meadow. Several sites without management showed high cover by Scotch broom (*Cytisus scoparius*) and Himalayan blackberry (*Rubus armeniacus*), while several sites with management showed canopy closure by snowberry (*Symphoricarpos albus*) and wild rose (*Rosa* sp.). Thus, there was little to no relationship between management efforts and structural shifts. Our measure of management effort was qualitative: it was captured by four broad categories. In this management setting, our metric was appropriate because it allowed comparisons among sites: actions are undertaken by a similar type of volunteer between sites, that is, local community members who have been managing these sites for more than the decade under study, using the same techniques, that is, hand pulling of key invasive species. However, other details of management were not captured in our metric (e.g., history of management, biomass of weeds removed), and more complex issues of site history and setting were also missed. This may reduce the statistical significance of our management metric, emphasizing the need even in local community settings such as these to quantify as many aspects of management wherever possible without limiting resources to the management effort itself.

Road density was the strongest predictor of woody encroachment, with higher road density related to lower patch area loss. Sites with low road density were generally nested within a forest-rural matrix, where borders of the patch were surrounded by native woodland with understories characterized by species like snowberry. Globally, many ecosystems undergoing native woody encroachment evolved under different habitat-forming processes of fire and grazing regimes than they currently experience (e.g., Parr, Lehmann, Bond, Hoffmann, & Andersen, 2014; Twidwell, Fuhlendorf, Taylor, & Rogers, 2013). Similarly, Garry oak savannas were actively managed with fire by local First People to limit Douglas fir expansion (Bjorkman & Vellend, 2010). The urban setting may impact canopy closure processes in Garry oak savannas by surrounding each patch with infrastructure, effectively removing the border of native woodland and limiting encroachment fronts. Road density may also be positively associated with visitation and recreational use of the Garry oak savannas, potentially leading to increased trampling of encroaching vegetation.

There was stable or increasing species richness and ecological resilience over the 10-year-period. The 2017 survey followed a particularly good rainfall and flowering year and might have led to increased species germination or visibility. Variability in species appearance between sites, however, supports site-level trends independent of climatic conditions. For ecological resilience, as measured by functional redundancy, patch connectivity was the most important predictor, with evidence of increasing connectivity supporting stable or increasing resilience. Connectivity has been found to maintain native species populations (Damschen, Haddad, Orrock, Tewksbury, & Levey, 2006), enable biotic and abiotic flow between patches (Lundberg & Moberg, 2003), and ensure access to refugia and specialized habitat (e.g., Dorenbosch, Verberk, Nagelkerken, & van der Velde, 2007; Keith, McCaw, & Whelan, 2002). The connectivity considered here is a distance-weighted sum of surrounding area that is Garry oak savanna. Higher levels of nearby savanna likely encourage propagule dispersal between patches (Rudnick et al., 2012). The relationship between redundancy and connectivity was likely driven in part by the relationship between species richness and functional redundancy but these two metrics track ecologically distinct responses (see Supporting Information S4 for an analysis of how outcomes for species richness and functional redundancy differ). Functional groups that consistently gained species, for example rapidly growing woody species, had high rates of wind dispersal and thus likely benefitted from increased connectivity. This finding was corroborated by significant positive relationship with species turnover, where higher connectivity related to higher species turnover at the patch-level. As a manageable landscape attribute, connectivity seems to be one of the most generalizable resilience mechanisms, both in this study and in others (e.g., Shackelford et al., 2017).

Invasive species management was not significantly related to any ecosystem-wide metric studied here, implying

8 of 11 | WILEY— Conservation Science and Practice
A Journal of the Society for Conservation Biology
SHACKELFORD ET AL.

that benefits derived from invasive species control, particularly plant species control, may need to be complemented by other restoration actions. Additionally, our metrics are primarily built on species presence within entire patches and may not capture the most responsive native ecosystem components. Though invasive plants have been globally linked with consistent declines in native production and reproduction (Vilà et al., 2011), they have not yet been linked with local extinctions (Gurevitch & Padilla, 2004) and removal does not consistently increase native species richness (Kettenring & Adams, 2011). Thus, alternative restoration metrics may provide more insight into the ecosystem-level effects of invasive species removal. Our most potentially applicable response metric was woody species encroachment, which is likely to be a direct measure of an ecosystem-level benefit. The lack of relationship between management and encroachment was due to the presence of native species encroachment, highlighting that sole focus on invasive species control may be too narrow a tactic. Management aimed at maintaining an open canopy structure would likely need to expand control measures beyond exotic species.

Passive restoration, however, often is founded in the cessation of the primary threat (Holl & Aide, 2011; Zahawi, Reid, & Holl, 2014). In some of these patches, the primary threat is likely to be invasion by exotic woody species (Costanzo et al., 2011). Given that we had no prior data on invasive species coverage, or the amount of biomass removed annually, we could not capture the pressure of invasion on each individual patch. This somewhat confounds our management measurement, where we could not parse apart increased effort focused on areas under greatest pressure. Overall, we measured ecosystem maintenance at the patch level, where individual metrics changed on average from less than 1% (native species richness) to 6% (response diversity). It is possible, though not tested here, that invasive species management is required for ecosystem maintenance in some of the highly invaded patches, but that active restoration after control is required for ecosystem improvement. Targeted restoration experimentation and monitoring is needed to fully explore the dynamics between invasive species, management, and ecosystem-level changes.

The influence of landscape context on ecosystem dynamics was broadly supported in our models (i.e., goodness of fit 0.19 to 0.43), yet Garry oak savannas are complex ecosystems that have evolved under a variety of environmental conditions and human interventions. Within even the limited spatial scope of Vancouver Island, differences in soil depth from site to site likely influence the amount and type of woody encroachment (Erickson & Meidinger, 2007) and heterogeneous grazing pressure between patches may variably alter species recruitment (Gonzales & Arcese, 2008). These factors are rarely measured on the landscape or

incorporated into active community restoration planning. Additionally, fire plays a deeper role in ecosystem development than merely maintaining open canopies (Kozlowski & Ahlgren 2012), and its reinstatement may be necessary for ecological improvement at any location that relied historically on fire disturbance regimes. Regional management has begun the experimental use of fire on remote island sites. Though the primary pressure on most Gulf Island patches is not woody invasion, preliminary results will provide important insights into species recruitment and patch-level recovery dynamics. In other North American systems, however, the reintroduction of fire alone has not resulted in a transition back to open-canopy herbaceous cover (Briggs et al. 2005). Thus, though fire may be essential to achieving desired ecosystem-level outcomes, the inclusion of shrub removal and invasive species control is likely to remain a pivotal component moving forward. Given the value that urban savanna patches represent both to the community to the remaining extent of Canadian Garry oak (Costanzo et al., 2011), effective urban Garry oak restoration may be the key leverage point in Garry oak conservation more widely. Ultimately, invasive species control in urban patches may need to be conducted in coordination with broader understanding of relevant pressures within each patch and active restoration practices like species reintroductions, grazing exclusion, and the reestablishment of fire or fire-like disturbances.

CONFLICT OF INTERESTS

The authors have no conflict of interests to declare in this work.

AUTHOR CONTRIBUTION

N.A.S. led the field work, analysis, and writing. S.M.M. assisted with field work, data collection and organization for trait databases, and analysis. J.R.B. and P.L.L. led field work and provided feedback on experimental design and

ETHICAL STATEMENT

All authors and contributors to this work have followed the Committee on Publication Ethics (COPE) code of conduct and ethics.

ORCID

Nancy Shackelford https://orcid.org/0000-0003-4817-0423

REFERENCES

Anderson, M. J. (2006). Distance-based tests for homogeneity of multivariate dispersions. *Biometrics*, *62*, 245–253.

Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., … Swenson, N. G. (2011). Navigating the multiple meanings of β diversity: A roadmap for the practicing ecologist. *Ecology Letters*, *14*, 19–28.

Aubin, I., Ouellette, M.-H., Legendre, P., Messier, C., & Bouchard, A. (2009). Comparison of two plant functional approaches to evaluate natural restoration along an old-field—Deciduous forest chronosequence. *Journal of Vegetation Science*, *20*, 185–198.

Barlow, C. M. (2017). *Garry oak ecosystem stand history in southwest British Columbia: Implications for restoration, management and population recovery*. Vancouver, Canada: Master of Resource Management, Simon Fraser University.

Bennett, E. M., Cumming, G. S., & Peterson, G. D. (2005). A systems model approach to determining resilience surrogates for case studies. *Ecosystems*, *8*, 945–957.

Bennett, J. R., Vellend, M., Lilley, P. L., Cornwell, W. K., & Arcese, P. (2013). Abundance, rarity and invasion debt among exotic species in a patchy ecosystem. *Biological Invasions*, *15*, 707–716.

Bjorkman, A. D., & Vellend, M. (2010). Defining historical baselines for conservation: Ecological changes since European settlement on Vancouver Island, Canada. *Conservation Biology*, *24*, 1559–1568.

Bolton, R. M., & Brooks, R. J. (2010). Impact of the seasonal invasion of *Phragmites australis* (Common Reed) on turtle reproductive success. *Chelonian Conservation and Biology*, *9*, 238–243.

Briggs, J. M., Knapp, A. K., Blair, J. M., Heisler, J. L., Hoch, G. A., Lett, M. S., et al. (2005). An ecosystem in transition: Causes and consequences of the conversion of mesic grassland to shrubland. *Bioscience*, *55*, 243.

Buckley, Y. M., Bolker, B. M., & Rees, M. (2007). Disturbance, invasion and re-invasion: Managing the weed-shaped hole in disturbed ecosystems. *Ecology Letters*, *10*, 809–817.

Cailliez, F. (1983). The analytical solution of the additive constant problem. *Psychometrika*, *48*, 305–308.

Clements, D. R. (2013). Translocation of rare plant species to restore Garry oak ecosystems in western Canada: Challenges and opportunities. *Botany*, *91*, 283–291.

Cook, R. D. (1977). Detection of influential observation in linear regression. *Technometrics*, *19*, 15–18.

Cordell, S., Ostertag, R., Michaud, J., & Warman, L. (2016). Quandaries of a decade-long restoration experiment trying to reduce invasive species: Beat them, join them, give up, or start over? *Restoration Ecology*, *24*, 139–144.

Core Team, R. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Cornelissen, J. H. C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D. E., … Poorter, H. (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, *51*, 335–380.

Costanzo, B., Eastman, D., Engelstoft, C., Gorman, M., Hebda, R. J., Hook, F., et al. (2011). *Restoring British Columbia's Garry oak ecosystems: Principles and practices*. Victoria, BC: Garry Oak Ecosystems Recovery Team.

Damschen, E. I., Haddad, N. M., Orrock, J. L., Tewksbury, J. J., & Levey, D. J. (2006). Corridors increase plant species richness at large scales. *Science*, *313*, 1284–1286.

de Lange, W. J., & van Wilgen, B. W. (2010). An economic assessment of the contribution of biological control to the management of invasive alien plants and to the protection of ecosystem services in South Africa. *Biological Invasions*, *12*, 4113–4124.

Dorenbosch, M., Verberk, W., Nagelkerken, I., & van der Velde, G. (2007). Influence of habitat configuration on connectivity between fish assemblages of Caribbean seagrass beds, mangroves and coral reefs. *Marine Ecology Progress Series*, *334*, 103–116.

Duelli, P., & Obrist, M. K. (2003). Biodiversity indicators: The choice of values and measures. *Agriculture, Ecosystems & Environment*, *98*, 87–98.

Dunwiddie, P. W., & Bakker, J. D. (2011). The future of restoration and management of prairie-oak ecosystems in the Pacific northwest. *Northwest Science*, *85*, 83–92.

Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B. H., et al. (2003). Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment*, *1*, 488–494.

Erickson, W. R., & Meidinger, D. V. (2007). *Garry oak (Quercus garryana) plant communities in British Columbia: A guide to identification*. British Columbia: Ministry of Forests and Range, Forest Science Program.

Fuchs, M. A. (2001). *Towards a recovery strategy for Garry Oak and associated ecosystems in Canada: Ecological assessment and literature review* (No. Technical Report GBEI/EC-00-030). Environment Canada, Canadian Wildlife Service, Pacific and Yukon Region.

Gaertner, M., Holmes, P. M., & Richardson, D. M. (2012). Biological invasions, resilience and restoration. In J. van Andel & J. Aronson (Eds.), *Restoration ecology: The new frontier* (pp. 265–280). Chichester, UK: Wiley-Blackwell.

Gonzales, E. K., & Arcese, P. (2008). Herbivory more limiting than competition on early and established native plants in an invaded meadow. *Ecology*, *89*, 3282–3289.

Gurevitch, J., & Padilla, D. K. (2004). Are invasive species a major cause of extinctions? *Trends in Ecology & Evolution*, *19*, 470–474.

Hallett, L., Avolio, M. L., Carroll, I. T., Jones, S. K., MacDonald, A. A. M., Flynn, D. F. B., … Jones, M. B. (2018). codyn: Community dynamics metrics, R package version 2.0.2. https://doi.org/10.5063/F1N877Z6

Hamann, A., & Wang, T. (2006). Potential effects of climate change on ecosystem and tree species distribution in British Columbia. *Ecology*, *87*, 2773–2786.

Hazelton, E. L. G., Downard, R., Kettenring, K. M., McCormick, M. K., & Whigham, D. F. (2018). Spatial and temporal variation in brackish wetland seedbanks: Implications for wetland restoration following Phragmites control. *Estuaries and Coasts*, *41*, 68–84.

Higgs, E. S. (2003). *Nature by design: People, natural process, and ecological restoration*. Cambridge, MA: MIT Press.

Holl, K. D., & Aide, T. M. (2011). When and where to actively restore ecosystems? *Forest Ecology and Management*, *261*, 1558–1563.

Keith, D. A., McCaw, W. L., & Whelan, R. J. (2002). Fire regimes in Australian heathlands and their effects on plants and animals. In *Flammable Australia: The fire regimes and biodiversity of a continent* (pp. 199–237). Cambridge, England: Cambridge University Press.

Kettenring, K. M., & Adams, C. R. (2011). Lessons learned from invasive plant control experiments: A systematic review and meta-analysis. *Journal of Applied Ecology*, *48*, 970–979.

Kozlowski, T. T., & Ahlgren, C. E. (Eds.). (2012). *Fire and ecosystems*. New York, NY: Academic Press.

Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, *91*, 299–305.

Laliberté, E., Legendre, P. & Shipley, B. (2014). *FD: Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology*, R package version 1.0-12.

Laliberté, E., Wells, J. A., Declerck, F., Metcalfe, D. J., Catterall, C. P., Queiroz, C., et al. (2010). Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecology Letters*, *13*, 76–86.

Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the holy grail. *Functional Ecology*, *16*, 545–556.

Legendre, P., & Legendre, L. F. J. (2012). *Numerical ecology*. Oxford, UK: Elsevier.

Lilley, P. L., & Vellend, M. (2009). Negative native–exotic diversity relationship in oak savannas explained by human influence and climate. *Oikos*, *118*, 1373–1382.

Lundberg, J., & Moberg, F. (2003). Mobile link organisms and ecosystem functioning: Implications for ecosystem resilience and management. *Ecosystems*, *6*, 0087–0098.

MacDougall, A. S. (2005). Responses of diversity and invasibility to burning in a northern oak savanna. *Ecology*, *86*, 3354–3363.

Mack, R. N., Simberloff, D., Mark Lonsdale, W., Evans, H., Clout, M., & Bazzaz, F. A. (2000). Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications*, *10*, 689–710.

McDonald, T., Gann, G. D., Jonson, J., & Dixon, K. W. (2016). *International standards for the practice of ecological restoration—Including principles and key concepts*. Washington, DC: Society for Ecological Restoration.

Meyer, J.-Y., & Fourdrigniez, M. (2011). Conservation benefits of biological control: The recovery of a threatened plant subsequent to the introduction of a pathogen to contain an invasive tree species. *Biological Conservation*, *144*, 106–113.

Miller, B. P., Sinclair, E. A., Menz, M. H. M., Elliott, C. P., Bunn, E., Commander, L. E., … Stevens, J. C. (2017). A framework for the practical science necessary to restore sustainable, resilient, and biodiverse ecosystems. *Restoration Ecology*, *25*, 605–617.

Miller, J. R., & Hobbs, R. J. (2007). Habitat restoration—Do we know what we're doing? *Restoration Ecology*, *15*, 382–390.

Moilanen, A., & Nieminen, M. (2002). Simple connectivity measures in spatial ecology. *Ecology*, *83*, 1131–1145.

Mori, A. S., Furukawa, T., & Sasaki, T. (2013). Response diversity determines the resilience of ecosystems to environmental change. *Biological Reviews*, *88*, 349–364.

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*, 133–142.

Parr, C. L., Lehmann, C. E. R., Bond, W. J., Hoffmann, W. A., & Andersen, A. N. (2014). Tropical grassy biomes: Misunderstood, neglected, and under threat. *Trends in Ecology & Evolution*, *29*, 205–213.

Pellatt, M. G., & Gedalof, Z. (2014). Environmental change in Garry oak (*Quercus garryana*) ecosystems: The evolution of an eco-cultural landscape. *Biodiversity and Conservation*, *23*, 2053–2067.

Pellatt, M. G., McCoy, M. M., & Mathewes, R. W. (2015). Paleoecology and fire history of Garry oak ecosystems in Canada: Implications for conservation and environmental management. *Biodiversity and Conservation*, *24*, 1621–1639.

Perring, M. P., Standish, R. J., Price, J. N., Craig, M. D., Erickson, T. E., Ruthrof, K. X., et al. (2015). Advances in restoration ecology: Rising to the challenges of the coming decades. *Ecosphere*, *6*, 1–25.

Pillar, V. D., Blanco, C. C., Müller, S. C., Sosinski, E. E., Joner, F., & Duarte, L. D. S. (2013). Functional redundancy and stability in plant communities. *Journal of Vegetation Science*, *24*, 963–974.

Podani, J. (1999). Extending Gower's general coefficient of similarity to ordinal characters. *Taxon*, *48*, 331–340.

Rudnick, D., Ryan, S. J., Beier, P., Cushman, S. A., Dieffenback, F., Epps, C., et al. (2012). The role of landscape connectivity in planning and implementing conservation and restoration priorities. *Issues in Ecology*, *16*, 1–16.

SER. (2004). *SER international primer on ecological restoration*. Tucson, AZ: Society for Ecological Restoration International Science & Policy Working Group.

Shackelford, N., Standish, R. J., Ripple, W., & Starzomski, B. M. (2018). Threats to biodiversity from cumulative human impacts in one of North America's last wildlife frontiers. *Conservation Biology*, *32*, 672–684.

Shackelford, N., Starzomski, B. M., Banning, N. C., Battaglia, L. L., Becker, A., Bellingham, P. J., … Standish, R. J. (2017). Isolation predicts compositional change after discrete disturbances in a global meta-study. *Ecography*, *40*, 1256–1266.

Shapiro, S. S., & Wilk, M. B. (1965). An analysis of variance test for normality (complete samples). *Biometrika*, *52*, 591–611.

Simberloff, D., Martin, J.-L., Genovesi, P., Maris, V., Wardle, D. A., Aronson, J., … Vilà, M. (2013). Impacts of biological invasions: What's what and the way forward. *Trends in Ecology & Evolution*, *28*, 58–66.

Standish, R. J., Hobbs, R. J., Mayfield, M. M., Bestelmeyer, B. T., Suding, K. N., Battaglia, L. L., … Thomas, P. A. (2014). Resilience in ecology: Abstraction, distraction, or where the action is? *Biological Conservation*, *177*, 43–51.

Suding, K. N., & Hobbs, R. J. (2009). Threshold models in restoration and conservation: A developing framework. *Trends in Ecology & Evolution*, *24*, 271–279.

Suding, K. N., Lavorel, S., Chapin, F. S., Cornelissen, J. H. C., Díaz, S., Garnier, E., et al. (2008). Scaling environmental change

through the community-level: A trait-based response-and-effect framework for plants. *Global Change Biology*, *14*, 1125–1140.

Twidwell, D., Fuhlendorf, S. D., Taylor, C. A., & Rogers, W. E. (2013). Refining thresholds in coupled fire–vegetation models to improve management of encroaching woody plants in grasslands. *Journal of Applied Ecology*, *50*, 603–613.

Verheyen, K., Vellend, M., Van Calster, H., Peterken, G., & Hermy, M. (2004). Metapopulation dynamics in changing landscapes: A new spatially realistic model for forest plants. *Ecology*, *85*, 3302–3312.

Vilà, M., Espinar, J. L., Hejda, M., Hulme, P. E., Jarošík, V., Maron, J. L., … Pyšek, P. (2011). Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, *14*, 702–708.

Walker, B. H. (1992). Biodiversity and ecological redundancy. *Conservation Biology*, *6*, 18–23.

Zahawi, R. A., Reid, J. L., & Holl, K. D. (2014). Hidden costs of passive restoration. *Restoration Ecology*, *22*, 284–287.

Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York, NY: Springer Science & Business Media.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

How to cite this article: Shackelford N, Murray SM, Bennett JR, Lilley PL, Starzomski BM, Standish RJ. Ten years of pulling: Ecosystem recovery after long-term weed management in Garry oak savanna. *Conservation Science and Practice*. 2019;1:e92. https://doi.org/10.1111/csp2.92