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Secondary invasion: The bane of weed management

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ABSTRACT

Exotic plant invasions present a global threat to natural ecosystems, yet the efficacy of management efforts in mitigating invader impacts remains unclear. A rapidly emerging problem is that of secondary invasion — an increase in abundance of non-target exotics following treatment of targeted invasive plants. Here, we present a global literature review and meta-analysis directed at quantifying the magnitude of secondary invasion effects and identifying possible causes. Of 168 studies examining the efficacy of exotic plant management in terrestrial habitats, 29% quantified community responses sufficiently to evaluate secondary invasion. Meta-analysis of 60 cases from 38 studies showed that control efforts strongly reduced target invader abundance overall, but secondary invaders increased, with a mean effect size double what was found for native plants, which increased only weakly. Moreover, 89% of the secondary invaders identified were classified as noxious or invasive plants. Increases in secondary invaders were correlated with target invader reductions, but control method and target invader growth form failed to explain variation in secondary invader responses. These results suggest that target invader suppression is the key factor driving release of secondary invaders. However, management side effects, target invader legacy effects, provenance effects, and shifting environmental conditions may all facilitate secondary invasion. Invasive plant management often successfully suppresses target invaders, but the result is largely secondary invasion. Addressing this problem requires management strategies that anticipate and suppress secondary invaders while rapidly restoring native plants to fill the space vacated by the target weed. Accomplishing the latter will require improved re-vegetation techniques.

Contents

1. Introduction

Exotic plant invasions disrupt ecosystem services and cost the global economy billions of dollars annually (Mack et al., 2000; Pimentel et al.,

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2005; Sinden et al., 2005). A substantial portion of these costs arises from management efforts directed at suppressing invader abundance (Binns et al., 2001; Pimentel et al., 2005; Sinden et al., 2005). While it is important to control invasive plants and promote native biodiversity, overall efficacy of such management efforts is not clear. Ultimately, the intent of invasive plant control efforts in natural areas is not only to suppress target invaders but also to mitigate their impacts and promote community recovery (Denslow and D'Antonio, 2005; Hulme, 2006; Zavaleta et al., 2001). However, reviews of natural areas invasive plant management indicate that many studies evaluating control efforts do not quantify community-level response to control efforts, leaving us blind to the overall outcomes of management (Denslow and D'Antonio, 2005; Kettenring and Adams, 2011; Reid et al., 2009). This lack of community-level focus has been attributed to the fact that pest management originates from less complex agricultural ecosystems where reductions in pest abundance are linked more directly to proportional increases in desirable crop species (Pearson and Ortega, 2009). However, invasive plant management in natural ecosystems involves much greater complexity, and reducing pest abundance may not always directly translate to ecosystem recovery.

Numerous factors can inhibit ecosystem recovery following suppression of a dominant invader in natural areas. First, limited precision of management tools can result in direct negative effects of the tool itself on desirable ecosystem components (Dickens et al., 2015; Mason and French, 2007; Pearson and Ortega, 2009). For example, using broadleaf herbicides to control invasive forbs can suppress native forbs (Crone et al., 2009; Ortega and Pearson, 2011; Pokorny et al., 2010; Rinella et al., 2009). Second, ecosystem recovery may be deterred by legacy effects that persist following invader suppression, such as when an invader has altered soil properties, disturbance regimes, or reduced native propagule sources (D'Antonio and Vitousek, 1992; Magnoli et al., 2013; Seabloom et al., 2003). Third, provenance effects may favor invader over native recovery due to introduction filters that select for disturbance-adapted traits or release from natural enemies (Buckley and Catford, 2016; Liu and Stiling, 2006). Finally, shifting environmental conditions such as those driven by anthropogenic changes may favor exotics over natives in ways that impede native recovery (Bauer and Reynolds, 2015; MacDougall and Turkington, 2005). An additional obstacle to ecosystem recovery, potentially interrelated with those described above, is secondary invasion — the proliferation of non-target invaders following efforts to suppress dominant target invaders (Kettenring and Adams, 2011; Butler and Wacker, 2010; Pearson et al., 2016; Larson and Larson, 2010; Symstad, 2004). For example, large-scale suppression of spotted knapweed (*Centuarea stoebe*) across critical wildlife foraging areas of the Rocky Mountains resulted in substantial increases in the secondary exotic, cheatgrass (*Bromus tectorum*; Ortega and Pearson, 2010, 2011), the only invader in this ecosystem having greater impact on native plants than spotted knapweed (Pearson et al., 2016). Given that most ecosystems contain multiple species of invaders (Kuebbing et al., 2013), the threat of secondary invasion is a potentially ubiquitous problem requiring immediate attention.

Recent reviews of the invasive plant management literature suggest that secondary invasion may be widespread. Kettenring and Adams (2011) conducted a global review addressing a broad range of invasive plant management questions and noted that >25% of the studies reviewed found control efforts to promote invasion of secondary exotics. Reid et al. (2009) reviewed the scientific literature and conducted manager surveys to evaluate outcomes of invasive plant control efforts in Australia and reported that >50% of studies evaluating community responses to management demonstrated increases in non-target exotic plant species. Abella (2014) reported similar results for invasive plant control treatments conducted on United States National Park Service lands, finding increases in non-target exotics in 44% of studies despite lower prevalence of exotics in these protected ecosystems. Increasingly, studies that focus on quantifying community responses to invasive plant management are calling attention to secondary invasion (Dickens et al., 2015; Magnoli et al., 2013; Ortega and Pearson, 2011; Ruwanza et al., 2013; Saito and Tsuyuzaki, 2012; Skurski et al., 2013). Collectively, the evidence suggests that secondary invasion may present a significant barrier to restoration of natural areas threatened by invasive plants, yet we still know little about when and why it occurs.

Herein, we present results from a global review and meta-analysis of the invasive plant management literature directed at quantifying the extent of the secondary invasion problem and exploring its potential causes within terrestrial ecosystems. Our main objectives were to 1) quantify the overall effect of invasive plant control measures on secondary invader abundance, 2) determine whether the management approach employed, the type of invader targeted, or the type of secondary invader influenced the degree of secondary invasion, 3) evaluate how the response of the target invader and native plant community to management correlated with the degree of secondary invasion, and 4) offer guidelines for mitigating secondary invasion to promote the conservation of natural areas threatened by exotic plant invasions.

2. Materials and methods

2.1. Literature review

We searched Google Scholar (http://scholar.google.com) and ISI Web of Knowledge (http://apps.webofknowledge.com) to generate a database of publications assessing effects of invasive plant control treatments in terrestrial ecosystems as of October 2014, with no restriction on publication date. We used the following search terms: (“invasive plant” or “exotic plant” or “non-native plant” or “nonnative plant” or “introduced plant” or “weed”) AND (“control” or “biological” or “prescribed fire” or “herbicide” or “mechanical” or “remov*”). Articles were included in the database if they met the following basic criteria: 1) quantitatively examined invasive plant control treatments in natural, terrestrial ecosystems (no agriculture, greenhouse, or laboratory settings; no aquatic habitats), 2) targeted exotic plant invaders, and 3) were peer-reviewed. If multiple papers reported on the same research, we included only the most comprehensive paper (see evaluation criteria below). We also screened the references of included articles for other relevant publications. Each study meeting these basic criteria was then reviewed in detail to assess to what extent they met specific methodological criteria deemed sufficient to evaluate secondary invasion. These criteria were: 1) the effect on the target invader was quantified using a valid population-level metric (cover, biomass, density, or frequency), 2) the effect on at least one non-target invader was quantified using a valid population-level metric, and 3) the study design included a valid untreated control from which to evaluate treatment effects. For each study included, we also recorded descriptive information including the identity and growth form of the target species, the treatment method, the study region, and the ecosystem type. We used X^2 tests for homogeneity of variance to examine whether the proportion of studies with one or more methodological issues (failing to meet above criteria) varied among time periods defined by publication year or among the three most common invasive plant treatment methods, and whether the proportion of studies with each of the three methodological issues differed among the three most common treatment methods.

2.2. Meta-analysis

To quantify the overall response of secondary invaders to control efforts and relate this to the response of target invaders and native taxa, we conducted a meta-analysis using standard methodologies (Koricheva and Gurevitch, 2014; Osenberg et al., 1999; Rosenberg et al., 2000). This technique offers important advantages over ‘vote-counting methods’ which simply tally the proportion of studies with significant results. Not only do meta-analyses estimate the magnitude of effects, they also account for study quality, override statistical idiosyncracies of constituent papers, and have greater statistical power for detection of effects (Gurevitch and Hedges, 1999; Rosenberg et al., 2000; Stewart, 2010).

Our meta-analysis was restricted to the subset of studies from our review that 1) quantified abundance (cover, biomass, density, or frequency) of at least one non-target exotic, 2) had a valid control/treatment design (see criteria above), and 3) reported associated mean values. For each study, we obtained mean values and measures of variation (SD or SE) and sample size for each valid case comparing treated and control groups (see treatment categorization below). Data for up to three response variables were extracted directly from tables or from figures using Web Plot Digitizer software (http://arohatgi.info/WebPlotDigitizer/app). To represent the response of secondary invaders to treatment, we extracted abundance data for non-target exotic plants. If data were presented for multiple groups or species of non-target exotic plants, we used the species with the greatest increase in response to treatment, since secondary invasion by one species is sufficient to preclude successful management. We also extracted abundance data representing the response of target invaders, and in the 8% of studies that presented data separately for multiple target species or groups, we selected the invader most suppressed by treatment. Finally, we extracted abundance data representing the response of natives as a group. If data were presented separately by functional group, we summed the means and associated variances.

For the 16% of studies that reported more than one abundance metric for each response variable, we used only one metric to avoid interdependence issues (Gurevitch and Hedges, 2001), prioritizing according to how commonly the metrics were used across all studies as follows: cover > biomass > density > frequency. We included versions of these metrics that represented relative values, e.g., the proportion of the total cover represented by the response group. Where possible, we chose the same abundance metric to represent all response variables from a given study. Many studies reported data on the effects of multiple invasive plant treatments. In such cases, we extracted one mean per treatment type. We categorized treatments as follows: 'removal' – relatively selective treatments including biological control (one case only), pulling, cutting, and discrete applications of herbicide to only the target species; 'herbicide' – herbicide application across all plant taxa in treatment plots; 'herbicide mix'– plot-scale herbicide application (as above) in combination with another treatment method (usually fire but also mechanical or seeding treatments); 'mechanical'– mowing, raking, and/or disking; and 'other' treatment methods including fire ($n = 6$) grazing ($n = 2$) and seeding ($n = 1$) that were applied across treatment plots. For the 11% of studies that manipulated background ecological factors that did not represent invasive plant control treatments per se (e.g., nutrient levels, livestock access), we only considered results from non-manipulated plots.

Many studies included multiple versions of a given treatment type, for example, varying the type of herbicide, and/or the application rate or timing. For each treatment category defined above, we extracted data for the one version that was most effective at suppressing the target, as this is the common metric of invasive plant control success. In the few cases where the suppressive effect was equal among multiple treatment types, we then chose the one with bigger secondary response. If results were presented over multiple years, we used only the final year of data. If results were presented separately for different sites or regions, we chose the location with the highest baseline level of target invaders, as measured in control plots. If levels of target invaders were comparable among sites or regions or went unreported, we used data for the location with the highest baseline level of secondary invaders (i.e., in control plots). We opted not to pool data across locations given that results were sometimes variable in terms of the degree of target suppression effected and/or the degree of the secondary response, such that averaging responses across locations would have diluted patterns.

We used MetaWin v2.1 software to calculate effect sizes and conduct all meta-analyses (Rosenberg et al., 2000). We chose Hedges *d* as our effect size metric for all response variables, calculated for each treatment type, or case, per study. Hedges *d* is a unit free index that standardizes the difference in mean abundance between treated and control groups by accounting for variance and also corrects for any bias introduced by small sample sizes (Rosenberg et al., 2000). The largest effect sizes are derived from cases showing large differences in response between treated and control plots and low variability among plots. Zero *d* values signify no difference in the response between treated and control plots, while positive and negative *d* values imply a general trend for an increase and decrease, respectively. For the 8% of studies included in our meta-analysis that did not report variance metrics necessary for calculation of *d*, we used the method of Wolf and Guevara (2001) to estimate variance based on that reported in other relevant studies. Specifically, for each response variable and abundance metric, we doubled the largest reported standard deviation and assigned this value to all missing standard deviation data. This conservative procedure ensured that all cases reporting valid means were utilized while ensuring that estimated values were down-weighted in the meta-analysis. To summarize effects for each response variable, we calculated the weighted mean effect size (d_+) across relevant cases. To test whether mean values of d_+ differed significantly from zero (i.e., indicating significant effects), we assessed whether the 95% bootstrap-confidence interval (CI) of d_+ overlapped zero based on 999 iterations (Rosenberg et al., 2000). We also tested whether effects sizes across all cases were homogeneous using the Q_t statistic which represents total heterogeneity. A significant Q_t based on an X^2 test indicates that the variance among effect sizes is greater than that expected by sampling error alone (i.e., effect sizes are not equal across studies).

We used two types of mixed meta-analysis models to examine potential sources of heterogeneity among effect sizes. In all cases, we considered fixed factors of interest with the inclusion of an error term to account for random variation in effect sizes among studies (Rosenberg et al., 2000). Inspection of effect sizes plotted against the normal quantiles for each response variable revealed no deviation from normality (Rosenberg et al., 2000). Hence we used the parametric version of statistics testing for significance of fixed factors. Categorical models were used to compare effect sizes among types of 1) treatments, 2) target invaders, and 3) secondary invaders. Invader types were categorized by growth form as forbs, grasses, or woody species consisting of trees and shrubs. For analysis of secondary invader type, studies lumping non-target invaders across growth forms were excluded. We note that each study represented the response of a single secondary invader type given that we only included the species or group with the largest treatment response in our meta-analysis (even though multiple species or groups may have responded). To test whether mean effect sizes differed among categorical factors, we assessed the significance of the between-group heterogeneity statistic (Q_b) based on the X^2 distribution. To test for potential interactions among categorical factors, we conducted tests in a hierarchical fashion so that the effect of one factor was tested within each level of another factor (Koricheva and Gurevitch, 2014). Sample sizes limited the testing of all possible interactions, but we were able to consider those interactions that made the most ecological sense. Specifically, after testing each of the three factors separately for differences among categories, we isolated each target invader group and repeated the tests for differences by treatment type and secondary invader type, respectively. Categories with at least two cases were included in comparisons. We also explored variation in effect sizes by life cycle (annual or biennial vs perennial) of target and secondary invaders, but do not report results given that no patterns were apparent and sample sizes were small when examining interactions with other factors of interest.

To relate treatment effects among secondary invaders, target invaders, and natives, we used continuous models employing weighted least-squares regression (Rosenberg et al., 2000). These meta-regression models allowed us to test whether variation in effect sizes of one response variable correlated with effect sizes of a second response variable. We assessed the significance of the relationship, or slope term, using the model heterogeneity statistic (Q_m), as evaluated with the X^2 distribution. We calculated r^2 values for this term by dividing Q_m by Q_t (Myers and Harms, 2009). To assess whether the effect size for the focal response variable differed from 0 when the effect size of the second response variable was 0, we also assessed the significance of the intercept term based on the Z-score and a normal distribution. For the secondary invader effect, we screened for potential variation in the target invader effect by treatment type, target type and secondary invader type, respectively, by running separate models for each category except where sample sizes were limited ($n < 10$ for mechanical and other treatments, woody targets, woody secondary invaders). Slope estimates were comparable in magnitude and direction among testable categories, hence we present results only for overall tests conducted across categories. Due to sample size constraints, we could not examine whether the relationship between native effect sizes and other response groups varied among categories of interest.

We included data for multiple treatment types per study in meta-analyses to enable us to more comprehensively test for variation in effects by treatment type and other potential moderator variables. To assure that our conclusions were not sensitive to pseudoreplication, we re-ran our overall analysis that tested for significance of each response variable with the inclusion of only a single randomly selected effect size per study. The mean effect size for each response variable was similar to that obtained when all cases were included and the CIs overlapped between the reduced dataset and the whole dataset. As a consequence, we felt confident in including all the data in our analyses.

To aid in interpretation of our results, we tested for temporal changes in effect sizes, potentially indicative of publication bias or changes in methodology, management approaches, etc. (see Koricheva and Gurevitch, 2014). We found no evidence for temporal changes in effect sizes when we tested for variation by publication year for the secondary invader effect ($r^2 = 0.001$, $Q_m = 0.11$, $P = 0.7$, $n = 60$; slope $= 0.007$, SE $= 0.18$,), target invader effect ($r^2 = 0.002$, $Q_m = 0.01$, $P = 0.89$, $n = 54$; slope $= 0.004$, SE $= 0.03$), or native effect ($r^2 = 0.03$, $Q_m = 0.96$, $P = 0.33$, $n = 31$; slope $= 0.03$, SE $= 0.03$). Additionally, we estimated the fail-safe number, or the number of studies that would have to be added to change the results of the meta-analysis for the secondary invader response (Rosenberg et al., 2000). This number was 1301, indicating that the observed results can be treated as a reliable estimate of the true effect based on the criteria presented in Rosenberg (2005). As further indication that our results were robust to publication bias (i.e., differential publication of studies showing significant effects, potentially biasing against studies with smaller sample sizes; Rosenberg et al., 2000), effect sizes were not correlated with sample size (Spearman's rank $r = 0.03$, $P = 0.79$). Finally, we checked our meta-analysis against the quality criteria established by Koricheva and Gurevitch (2014) for ecological studies.

3. Results

3.1. Literature review

We compiled 168 studies satisfying basic criteria for inclusion in our review (Appendix A). These studies targeted 108 exotic plant species for control, of which 36% were shrubs or trees, 33% forbs, 23% grasses, and 7% vines. The most common targets were the perennial forbs *Centaurea stoebe* ($n = 13$ studies) and *Euphorbia esula* ($n = 13$), the annual forb *Centaurea solstitialis* ($n = 8$), the annual grass *Taeniatherum caput-medusae* ($n = 9$), and the shrubs *Tamarix* spp. ($n = 5$). In 86% of the 168 studies, a single species was the focus of control efforts. Studies used a variety of treatment methods, with 53% including multiple methods. Invasive plant treatments most commonly involved herbicide ($n = 95$), mechanical means ($n = 78$), and/or biological control ($n = 36$). Most studies (80%) were conducted in North America, with the remainder conducted in Australia/New Zealand (8%), Africa (5%), Europe (3%), South America (3%), and Asia (1%). Nearly half of studies (48%) were conducted in grasslands and prairies (including rangelands and abandoned agriculture with representative native vegetation), followed by forest/woodland (22%), riparian (12%), coastal dunes/scrub (8%), shrubland (7%), desert (3%), and alpine ecosystems (<1%).

Of the 168 studies included in our review, 71% ($n = 119$) had methodological limitations precluding evaluation of secondary invasion. Notably, the proportion of studies failing to meet criteria for evaluation of secondary invasion declined significantly in the most recent publication years assessed ($X^2 = 6.7$, df $= 2$, $P = 0.03$), as 56% of 41 studies published from 2010–2013 had methodological issues compared to 79% of 72 studies published from 2006–2009 and 70% of 54 studies published 1959–2005 (Fig. 1). The proportion of studies with methodological issues also varied significantly across the three most common treatment methods ($X^2 = 15.9$, df $= 2$, $P = 0.003$). Studies with methodological issues included 97% of 36 biological control studies in contrast to 62% of 78 studies employing mechanical methods and 66% of 69 herbicide studies. The most common methodological issue, associated with 56% ($n = 94$) of studies, was failure to quantify effects on secondary exotics using a valid abundance metric (cover, biomass, density, or frequency). About a third ($n = 33$) of these studies focused solely on the target species and did not measure the response of any other community components, whether secondary exotics or natives. The remaining two thirds of studies ($n = 62$) did measure at least one community component, yet did not distinguish abundance of secondary exotics. Most commonly, secondary exotics were lumped with natives ($n = 34$) or went completely unmeasured ($n = 17$). Other problems included lumping of secondary exotics with target exotics ($n = 6$), and measurement of species richness but not abundance of invaders, again with target and secondary exotics lumped ($n = 4$). Nearly a third ($n = 29$) of the 94 papers with limitations in their examination of secondary effects had additional methodological issues explained below.

The second most common methodological issue was study design, attributed to 24% ($n = 41$) of studies. Studies with design issues had no control group and simply followed trends in treated plots over time ($n = 27$), used uninvaded rather than invaded plots as controls ($n = 11$), or had no true replication to represent the control and/or treatment group ($n = 2$). Almost half ($n = 19$) of the 41 studies with design limitations had other methodological issues. The final methodological issue that we identified, associated with 11% ($n = 19$) of studies, failed to quantify target invader effects using a valid abundance metric. These studies either limited assessment of target invader effects to individual level performances measures or did not include any metrics of target control. All but one of these 19 studies had other methodological issues.

The proportion of studies with each of the three methodological issues varied among treatment types ($X^2 = 12.1$, df $= 4$, $P = 0.017$).

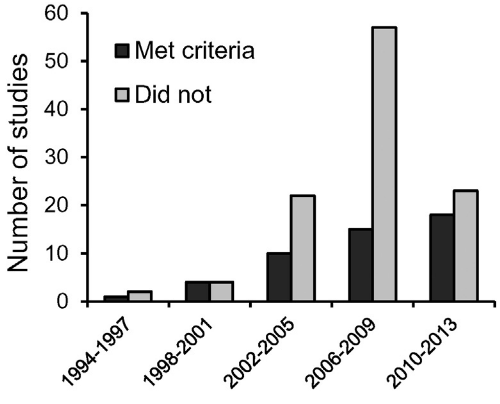

Fig. 1. Number of studies meeting vs not meeting criteria for evaluation of secondary invasion in a global review of invasive plant management research. Data not shown for studies published before 1994 ($n = 11$) or after 2013 ($n = 1$).

For studies involving herbicide and mechanical control, far more studies had limitations in quantification of secondary invaders (73% and 59%, respectively) versus study design (15% and 30%, respectively). In contrast, a similar proportion of biological control studies had limitations in quantification of secondary invaders and study design (47% vs 43%). For all three treatment types, target invader effects were ill-quantified in about 10% of studies.

3.2. Meta-Analysis

Of 168 papers meeting criteria for review, 38 (23%) met criteria for meta-analysis, which included adequate quantification of secondary invader abundance, valid study design, and presentation of mean values for treatment and control groups. This subset of studies targeted 33 species, and in 84% of cases, focused on a single species. Nearly 50% ($n = 18$) of the 38 studies included in meta-analysis presented data for multiple treatment types, with 78% of multi-treatment studies including two treatment types and the remainder three types. The set of 38 studies yielded 60 cases for which we calculated effect sizes comparing mean abundance in treated and control plots for up to three response groups: target invaders, secondary invaders, and native species, respectively.

Invasive plant control treatments significantly reduced abundance of target invaders (Fig. 2a), with a negative effect size in 94% of 52 cases. Effect sizes for target invaders exhibited significant variability among cases ($Q_t = 93.03$, df = 51, $P = 0.0003$). Furthermore, mean effect sizes differed significantly among the five treatment types tested ($Q_b = 9.32$, df = 4, $P = 0.05$). Although all treatment types significantly suppressed target invader abundance, mean effect sizes were about twice as large for removal, herbicide, and herbicide mix treatments as compared to mechanical and other treatments (Fig. 2a). However, effects of treatment on target invader abundance did not differ significantly among types of target invaders, as categorized by growth form ($Q_b = 2.75$, df = 2, $P = 0.25$; Table 1). We also found no evidence for an interaction between target invader type and treatment type. Although effects on target invader abundance did not differ significantly among treatment types when target grasses ($Q_b = 5.47$, df = 4, $P = 0.24$) and target forbs ($Q_b = 5.2$, df = 3, $P = 0.16$) were tested separately, mean effect sizes for treatment types followed the same pattern seen when all target invaders were tested together, with removal, herbicide, and herbicide mix treatments trending towards greater suppression as compared to mechanical and other treatments (Table B1). Variation by treatment type could not be assessed for woody targets due to sample size limitations ($n = 3$ of 4 cases employed removal methods).

Invasive plant control treatments significantly increased abundance of secondary invaders (Fig. 2b), with positive effect sizes in 75% of 60 cases. Effect sizes exhibited significant variability among cases ($Q_t = 91.58$, df = 59, $P = 0.004$). However, mean effect sizes did not differ significantly among the five treatment types tested ($Q_b = 3.75$, df = 4, $P = 0.44$; Fig. 2b). Similarly, effects of treatments on secondary invader abundance did not differ significantly among types of target invaders ($Q_b = 0.7$, df = 2, $P = 0.71$; Table 1). We also did not find evidence for an interactive influence of target invader type and treatment type on the response of secondary invaders in that effect sizes did not differ significantly among treatment types when target grasses ($Q_b = 3.51$, df = 4, $P = 0.48$) and target forbs ($Q_b = 0.42$, df = 3, $P = 0.94$) were tested separately (Table B2). Woody targets were not tested given that this group had little variation in the treatment type employed ($n = 8$ of 11 cases used removal methods).

Of the cases for which we had information on the growth form of the secondary invaders included in our meta-analysis, 54 documented the response of grasses or forbs to treatments and only 1 documented the response of woody taxa. Hence, only the first two groups of secondary invaders could be compared. When all types of target invaders were included in the analysis, there was no significant difference in the response of secondary invaders that were grasses ($d_+ = 0.5$, CI = 0.12 to 0.88, $n = 25$) vs forbs ($d_+ = 0.54$, CI = 0.29 to 0.83, $n = 29$; $Q_b = 0.03$, df = 1, $P = 0.86$). However, when target groups were considered separately, effects differed between secondary grasses and forbs, indicative of an interaction between the type of target invader and secondary invader. When grasses were the target of control efforts, secondary forb invaders had a stronger response than secondary grasses ($Q_b = 8.0$, df = 1, $P = 0.005$), with forbs increasing significantly ($d_+ = 0.82$, CI = 0.55 to 1.07, $n = 9$) but grasses did not ($d_+ = 0.03$, CI = −0.34 to 0.44, $n = 7$). Conversely, when forbs were the target invaders, secondary grasses trended towards a stronger response than secondary forbs ($Q_b = 2.61$, df = 1, $P = 0.1$), with grasses increasing significantly ($d_+ = 0.87$, CI = 0.41 to 1.33, $n = 15$) but forbs not ($d_+ = 0.37$, CI = −0.12 to 0.86, $n = 13$). For woody target invaders, there was no significant difference between the response of secondary grasses ($d_+ = -0.83$, CI = −2.59 to 1.31, $n = 3$) and forbs ($d_+ = 0.46$, CI = 0.05 to 0.9, $n = 7$; $Q_b = 2.51$, df = 1, $P = 0.11$), although sample sizes were limited.

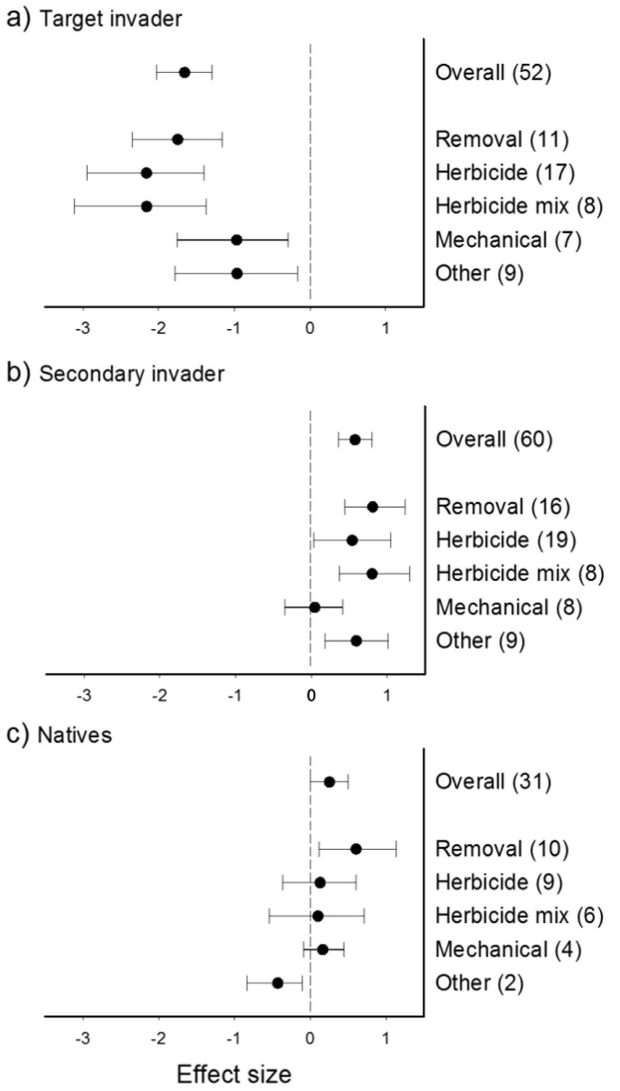

Fig. 2. Results of a meta-analysis quantifying effects of invasive plant control treatments on a) abundance of target invaders, b) secondary invaders, and c) native plants. Mean effect sizes (Hedges d_+) were calculated across all cases ('overall') and for differing treatment methods (see Methods). Mean effect sizes significantly differ from zero when their 95% confidence intervals (denoted by bars), do not bracket zero; negative values indicate lower abundance in treated plots, while positive values indicate higher abundance.

Invasive plant control treatments significantly increased abundance of native plants, with a positive effect size in 61% of 31 cases, although

Table 1
Results of meta-analysis comparing effects of invasive plant control treatments among three target invader types: grasses, forbs, and woody species. Summary statistics including mean effect sizes (Hedges d_+) are given for three response variables representing the abundance of target invaders, secondary invaders, and native plants, respectively. Negative mean effect sizes indicate that treated plots had on average lower abundance of the response variable, while positive effect sizes indicate higher abundance. A mean effect size significantly differs from zero when its 95% confidence interval does not bracket zero.

Target type	Target effect			Secondary effect			Native effect		
	n	d_+	95% CI	*n*	d_+	95% CI	*n*	d_+	95% CI
Grass	20	−1.34	−1.88 to −0.85	20	0.46	0.17 to 0.72	12	0.22	−0.13 to 0.58
Forb	28	−1.93	−2.60 to −1.41	29	0.67	0.38 to 0.99	14	0.13	−0.25 to 0.45
Woody	4	−1.41	−3.72 to −0.41	11	0.52	−0.22 to 1.29	5	0.72	0.0006 to 1.68

the mean effect size was small, with a confidence interval that nearly crossed 0 (Fig. 2c). Effect sizes for native abundance did not exhibit significant variability among cases ($Q_t = 34.35$, df = 30, $P = 0.27$), nor did mean effect sizes differ significantly among treatment types ($Q_b = 3.15$, df = 4, $P = 0.53$; Fig. 2) or among types of target invaders ($Q_b = 2.42$, df = 2, $P = 0.3$; Table 1).

3.2.1. Relationships among response variables

Across the 52 case studies with relevant data, the magnitude of the secondary invader effect increased significantly with the degree of target invader suppression effected by treatments (Fig. 3a; $Q_m = 20.7$, df = 1, $P < 0.0001$, $r^2 = 0.27$; slope = −0.24, SE = 0.05). Notably, the secondary effect did not deviate significantly from 0 when the target effect was 0 (intercept = −0.11, SE = 0.13, $P = 0.41$). These relationships were robust to removal of one extreme point ($Q_m = 13.84$, df = 1, $P = 0.0002$, $r^2 = 0.2$; slope = −0.23, SE = 0.06; intercept = 0.16, SE = 0.13, $P = 0.24$). In contrast, the degree of the secondary invasion was positively associated with the response of natives across 31 cases with relevant data (Fig. 3b; $Q_m = 5.01$, df = 1, $P = 0.025$, $r^2 = 0.09$; slope = 0.43, SE = 0.19), with a significant secondary effect even when the native effect was 0 (intercept = 0.61, SE = 0.15, $P = 0.0007$). However, when one extreme point was removed, the relationship between the response of secondary exotics and natives was no longer significant ($Q_m = 1.45$, df = 1, $P = 0.23$, $r^2 = 0.03$; slope = 0.25, SE = 0.21), with the secondary effect remaining significant in the absence of a native effect (intercept = 0.63, SE = 0.15, $P = 0.0003$). As seen with secondary exotics, treatment effects on native plant abundance increased with increased suppression of target invaders (Fig. 3c; $Q_m = 8.81$, df = 1, $P = 0.003$, $r^2 = 0.22$; slope = −0.18, SE = 0.06), and the native effect did not deviate significantly from 0 when the target effect was 0 (intercept = −0.19, SE = 0.17, $P = 0.24$). However, the relationship between native and target responses weakened substantially when we removed an extreme value ($Q_m = 2.39$, df = 1, $P = 0.12$, $r^2 = 0.07$; slope = −.12, SE = 0.08), and the native effect still did not deviate significantly from 0 in the absence of a target effect (intercept = −0.08, SE = 0.18, $P = 0.67$).

4. Discussion

Our literature review and meta-analysis indicate that secondary invasion presents a formidable barrier to the conservation of natural areas threatened by invasive plants. While our meta-analysis demonstrated strong reductions in the abundance of targeted invaders across studies, the general response across management approaches was a substantial increase in non-target exotic plants – secondary invaders – that corresponded with a weak increase in native plants. The mean effect size for secondary invaders was more than double that for natives, which was small in magnitude and bordered non-significance. Moreover, 89% of the secondary invaders pose significant risks to native ecosystems as indicated by their inclusion on noxious weed and invasive plant lists (Table B3). Collectively, these community-level outcomes suggest that invasive plant management efforts are not currently achieving significant conservation gains. To advance conservation of natural areas that are increasingly threatened by exotic plant invasions around the globe, we need to better understand and address the problem of secondary invasion.

So why does secondary invasion occur? Our meta-analysis supports the idea that secondary invaders respond to conditions of decreased competition and increased resource availability resulting from suppression of targeted invaders (Buckley et al., 2007; D'Antonio and Meyerson,

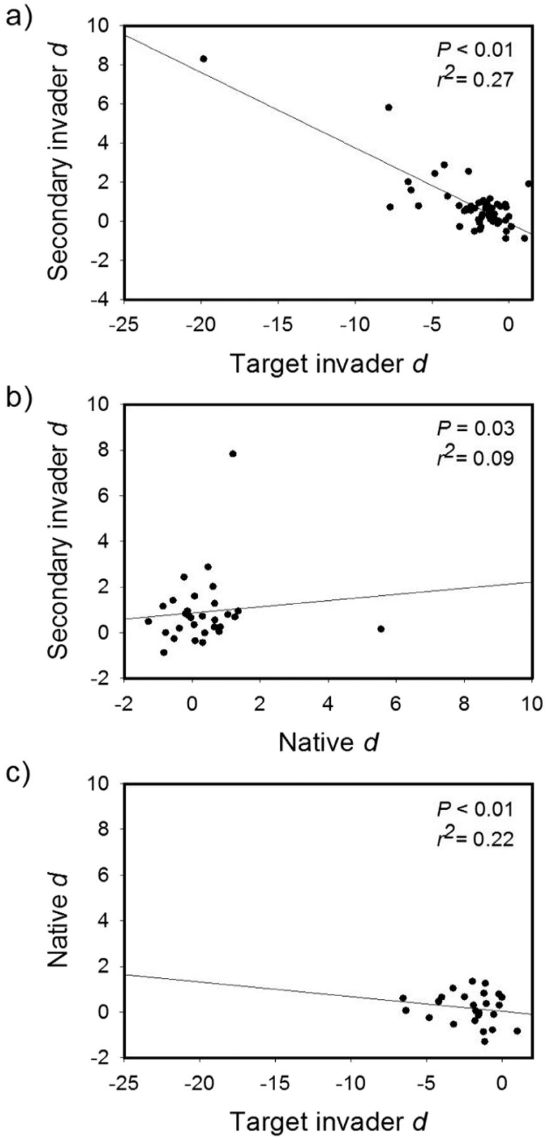

Fig. 3. Results of a meta-regression relating effects of invasive plant control treatments on abundance of target invaders, secondary invaders, and native plants. Each point represents one case study and the corresponding effect sizes (Hedges *d*) calculated for: a) secondary vs target invaders, b) secondary invaders vs natives, and c) natives vs target invaders. Negative effect sizes indicate lower abundance in treated plots, while positive values indicate higher abundance.

2002; Kettenring and Adams, 2011). Our analysis demonstrated that increases in secondary invader abundance correlated significantly with reductions in target invader abundance, a relationship documented in a few prior case studies (Ogden and Rejmánek, 2005; Ortega and Pearson, 2010; Symstad, 2004). We also found that management efforts did not significantly affect the abundance of secondary invaders when they failed to suppress the target invaders, suggesting that management tools did not generate substantial side effects independent of target invader control. All the management approaches that we evaluated effected target suppression and elicited secondary invasion, with more successful target suppression generally related to greater increases in secondary invaders. Indeed, while the average effect size for the increase in secondary invaders was moderate in magnitude across all studies ($d_+ = 0.57$, CI = 0.36 to 0.8, $n = 60$), the effect was large ($d_+ = 0.83$, CI = 0.56 to 1.11, $n = 36$) when less suppressive treatments were excluded from studies testing multiple control methods. In theory, controlling the target invader should allow ecosystem recovery (e.g., Smith and Van der Bosch, 1967), yet our results indicated that target invader suppression instead led to secondary invasion. So the question of why secondary invasion occurs is really a question of why exotics benefit more than natives following the control of a dominant invader.

An obvious prerequisite for secondary invasion is the presence of other exotic plants to exploit the space vacated by the target invader. Multiple invaders are becoming the norm in many terrestrial plant communities (Kuebbing et al., 2013; Pearson et al., 2016), thereby setting the stage for widespread secondary invasions. In ecosystems with multiple invaders, negative interactions among invaders are common, suggesting an important role of invader-invader competition (Kuebbing and Nuñez, 2015). Hence, the suppression of a dominant invader might be expected to release subordinate exotic competitors. However, native competitors should also be released. Likewise exotics are adept at exploiting disturbances (Davis et al., 2000), but both natives and secondary exotics should have access to the resources released via general treatment-related disturbances. So increased resource availability alone does not explain why exotics win out over natives following target invader control. Provenance could be sufficient to explain why exotics benefit more than natives following control efforts if the introduction process strongly favors exotic organisms that bear “weedy” traits or escape from natural enemies (Buckley and Catford, 2016; Pearson et al., 2014; Liu and Stiling, 2006; Ricciardi and Rasmussen, 1998; Keane and Crawley, 2002). However, additional factors that might help explain why exotics benefit more from target invader control include: treatment side effects, legacy effects of the target invader, and environmental shifts.

Analogous to treatments applied in human medicine, all invasive plant management actions have potential side effects (Pearson and Ortega, 2009). Side effects include unintended impacts on non-target ecosystem components such as soil compaction, direct damage to native plants, and indirect suppression of natives via altered food chains (Dickens et al., 2015; Mason and French, 2007; Rinella et al., 2009; Zavaleta et al., 2001). In short, invasive plant control is not simply precision removal of the target invader. Rather management actions represent a form of disturbance with positive and negative direct and indirect effects of varying strength on the target invader, non-target natives and exotics, and abiotic ecosystem components (Buckley et al., 2007; D'Antonio and Meyerson, 2002; Hobbs, 2007; Pearson and Ortega, 2009; Zavaleta et al., 2001). Understanding management outcomes and the extent to which they may favor secondary invaders over natives requires understanding how all of these dynamics play out.

We anticipated that more selective management strategies, those designed to affect only the target invader, would be less likely to facilitate secondary invaders by minimizing side effects. However, this expectation was not well supported across studies. For example, host specific biological control agents represent perhaps the most precise invasive plant management tool. While too few biocontrol studies met criteria for inclusion in our meta-analyses as an explicit category, numerous biocontrol studies documenting declines in target invaders have reported strong increases in secondary invaders (Butler and Wacker, 2010; Larson and Larson, 2010; Denslow and D'Antonio, 2005; Lesica and Hanna, 2004; Huffaker and Kennett, 1959). Similarly, in our meta-analysis, the most selective control method we evaluated, ‘removal’ (biological control, hand pulling, cutting, and/or specific application of herbicide to only the target invader), elicited strong increases in secondary invaders, whereas less selective methods tended towards smaller effects. Overall, target invader suppression appeared more important than precision of the management tool in driving secondary responses. This finding suggests that the size of the ‘hole’ left by target invader suppression is the most important factor determining secondary invader responses. Nonetheless, specific case studies show that side effects of management themselves can promote secondary invasion independent of target invader control (Firn et al., 2010; Olson and Wallander, 1998; Ortega and Pearson, 2010).

Due to treatment side effects, the specific control technique employed can play an important role in determining which taxa may be released following suppression of the target invader. Both non-target exotics and natives are susceptible to suppressive effects of treatment, but those that escape direct harm may take advantage of the new conditions created by control efforts. The reciprocal invader responses we observed, wherein control of a target forb was followed by greater increases in exotic grasses, or the opposite, illustrate how management tools may shift the balance among exotic (and/or native) functional groups within the community. In the most obvious example, many herbicides used to control invasive plants have limited selectivity in which they broadly suppress either monocots or dicots, leaving the non-susceptible group unharmed. Hence, use of a broadleaf herbicide to suppress a target invasive forb can also suppress non-target forbs, both native and exotic, while fueling the release of grasses (Skurski et al., 2013; Ortega and Pearson, 2010, 2011; Ogden and Rejmánek, 2005). Accordingly, if the prospective secondary invaders include grasses, then this management tool can trigger secondary invasion, a scenario depicted in many studies we reviewed (Sheley et al., 2006; Laufenberg et al., 2005; Symstad, 2004; Tyser et al., 1998; and references above); but if the prospective secondary invaders are forbs alone, a much less common scenario, the same treatment can impede secondary invasion (Goodall et al., 2010). While more selective tools like biological control focus suppression on the target invader, the resultant hole still allows for secondary invasion of those non-target exotics present if other measures are not deployed to counter their response. Increasing precision of management tools is critical to managing for increased plant biodiversity following invasion, but it will not resolve the secondary invasion problem.

Legacy effects arise when invaders alter conditions in ways that persist after the invader is gone (Cuddington, 2011). A few invasive plant control studies indicate that legacy effects on soil properties persisting after invader control can favor exotic over native recovery (Symstad, 2004; Yelenik et al., 2004). In the context of the novel weapons hypothesis (Callaway and Aschehoug, 2000), certain secondary exotics might be expected to benefit over natives in the presence of target invader legacies if the exotics share evolutionary history. Alternatively, given that such legacy effects by definition represent novel conditions within the community, secondary invaders might benefit over natives because they represent a broader range of traits. It is unclear how often legacy effects might promote secondary invasion, many exotics alter conditions in ways that can generate legacy effects (D'Antonio and Meyerson, 2002; D'Antonio and Vitousek, 1992; Jordan et al., 2008; Magnoli et al., 2013; Symstad, 2004; Yelenik et al., 2004). Invaders may also generate legacy effects by simply reducing native propagule sources via suppression of native plants over long time periods and broad spatial scales, a condition that can be addressed by reseeding native plants (Seabloom et al., 2003). Legacy effects that persist following invader control are likely an important factor contributing to secondary invasion.

Anthropogenic activities are rapidly changing our natural world via eutrophication, global climate change, altered disturbance regimes, etc. (Galloway et al., 2008; Schwartz et al., 2006; Vitousek et al., 1997). These shifts can benefit exotics over natives with the result that invaders may act as passengers rather than drivers of community change (MacDougall and Turkington, 2005). Such shifting environmental conditions could also help to explain why secondary invasion is such a common response to invasive plant control efforts (Hobbs, 2007; Firn et al., 2010). Recognizing when invaders are drivers versus passengers of community change is important, because when invaders are passengers the driving factors need to be managed to effect the desired long-term outcome, at least whenever this is possible.

Previous reviews of invasive plant management efforts have used vote-counting methods to highlight the problem of secondary invasion (Abella, 2014; Kettenring and Adams, 2011; Reid et al., 2009), but there have been no rigorous analyses examining the factors potentially influencing secondary invasion. Our meta-analysis is the first to quantify secondary invasion and relate its variability directly to suppression of the target invader. Nonetheless, there are a number of caveats to consider. Foremost is the fact that only a small proportion of studies actually quantified management outcomes sufficiently to evaluate secondary invasion, leaving us with limited sample sizes for addressing more complex questions. Furthermore, studies were skewed towards North America, reflecting the bias in research efforts directed at invasive species (Pyšek et al., 2008; Kettenring and Adams, 2011). We also note several factors affecting the estimation of secondary invader effect sizes in our meta-analysis. Studies included in our meta-analysis sometimes did not report the response of non-target exotics likely to be released by efforts to control target invaders, instead reporting data only for non-target exotics susceptible to treatment (e.g., Pokorny et al., 2010; Rinella et al., 2009; but see Skurski et al., 2013). Similarly, many studies reported the response of only a single non-target exotic (e.g., Aigner and Woerly, 2011; Firn et al., 2010; Sher et al., 2008; Symstad, 2004). As a result, we were forced to pick a single species or group to represent the response of secondary invaders even in the many studies where multiple species or groups increased following treatment. Accordingly, the effect size for the secondary response often represented only a subset of the exotic taxa released via control efforts (e.g., Enloe et al., 2005; Ruwanza et al., 2013; Saito and Tsuyuzaki, 2012; Wilson et al., 2008). Alternatively, in many other cases, studies presented data for non-target exotics as a single group, and hence, the effect size represented the net response across all constituent taxa (e.g., Andreu and Vilà, 2010; Butler and Wacker, 2010; Hendrickson and Lund, 2010; Loh and Daehler, 2008). Despite this variability, meta-analysis revealed an overarching pattern wherein at least some component of the non-target exotic community tended to increase markedly due to treatment. Such an increase in any one exotic taxon may have large negative ramifications for the community, particularly when the secondary invaders are recognized as invasive pests, as we found to be common (Table B3). In contrast, the native effect in our meta-analysis summarized the net response across constituent taxa in all cases, reflecting the nature of data reporting and that natives are generally desirable as a group.

Finally, we note that the magnitude of effect sizes estimated in our meta-analysis was likely affected by the limited post-treatment time window examined in most studies (median = 2 years, range 1–16 years). Secondary invader populations may build for years following treatment (e.g., Loh and Daehler, 2008; Ortega and Pearson, 2010, 2011; Skurski et al., 2013), but may also wain following factors such as re-invasion of the target invader or recovery of the native community. To address the longevity of secondary effects, future studies must evaluate responses over longer time spans, particularly beyond the typically restricted window of target invader suppression (e.g., Rinella et al., 2009). While spatial scale can also affect conclusions if research is conducted at small scales if management is conducted at larger scales, we found that the majority of studies included in our meta-analysis applied treatments at broad scales (57% of studies had treatment plots of at least 100 m^2). Meta-analysis offered no evidence that the magnitude of the secondary effect varied between studies conducted at broad versus smaller scales (plot size ≤30 m^2; $Q_b = 0.53$, df $= 1$, $P = 0.47$, $n = 58$).

Given the prevalence of secondary invasions, how can we avoid this problem? While there is a clear need to advance research efforts to better understand secondary invasion in the future, interim guidelines based on the best current information are needed to help mitigate this problem to restore weed-invaded ecosystems. Accordingly, we offer a simple dichotomous guide to management actions for reducing secondary invasion (Fig. 4). Future management must begin by evaluating communities for the presence of other exotics that may emerge as important secondary pests. In single invader ecosystems, weed management can focus on the target invader. However, these ecosystems are increasingly rare, and as the prospect for problematic secondary invaders increases, management strategies must become more sophisticated and complex, involving contingencies for suppressing prospective problematic secondary invaders (e.g., Firn et al., 2010). In all management scenarios, if the target species is known to have legacy effects that may inhibit natives or favor problematic exotics, efforts should be made to mitigate these effects as part of the treatment (e.g., Magnoli et al., 2013). Minimizing the size of the disturbance generated by management efforts in both space and time can help to reduce the opportunity for secondary invasion, e.g., by spot spraying in lieu of broadcasting herbicides and by targeting earlier stages of invasion (Ortega and Pearson, 2010, 2011; Pearson and Ortega, 2009; Pokorny et al., 2010; Skurski et al., 2013). In situations when the likelihood of promoting problematic secondary invaders is high and mitigation strategies for such invaders are lacking, the no action management alternative may be advisable.

Given that the hole created by suppression of the target invader appears to be a primary factor linked to secondary invasion, revegetation is a critical complementary tool for inhibiting secondary invasion and reinvasion by the target species to achieve overall restoration and biodiversity goals (Cutting and Hough-Goldstein, 2013). However, at present, revegetation efforts appear largely inadequate to address this problem (Kettenring and Adams, 2011). Of those studies meeting our criteria for evaluation of secondary invasion, only six tested for effects of seeding on the response of secondary invaders, with two of these studies reporting successful mitigation of secondary invasion (Enloe

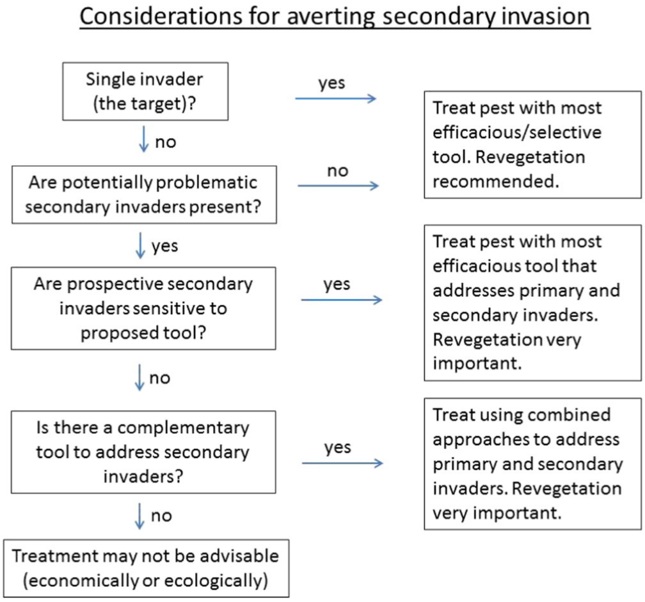

Fig. 4. Dichotomous guide to management actions for reducing the risk and severity of secondary invasion based on current rudimentary understandings from our meta-analysis and literature review.

et al., 2005; Sheley et al., 2006) and four studies reporting no effect (Endress et al., 2008; Pokorny et al., 2010; Stanley et al., 2011; Tyser et al., 1998). One obvious impediment is that reseeding efforts too commonly fail to effectively recruit seeded species (e.g., Hulet et al., 2010; Firn et al., 2010; Symstad, 2004; Wilson et al., 2008). New developments in reseeding technology offer promise in this regard (e.g., Madsen et al., 2012, 2014), but broad advances in revegetation technology are needed to take the next step in natural areas restoration (Bauer and Reynolds, 2015; Dickens et al., 2015). Succession and resilience theory both provide important frameworks that should be better integrated into weed management (Meiners et al., 2015; Chambers et al., 2014; Sheley et al., 2006; Luken, 1990).

5. Conclusion

Secondary invasion has arisen as the bane of weed management. Generally, the more successful the suppression of target invaders, the greater is the response of undesirable secondary invaders. This problem must be overcome to advance conservation and restoration of the many natural areas threatened by exotic plant invasions around the globe. Our review and meta-analysis highlights future research needed to address this problem. First, we found that few studies that examined invasive plant control in natural areas actually quantified exotic species responses within the community sufficiently to assess secondary invasion. Future research must go beyond quantifying the target invader's response to also evaluate how natives and secondary invaders respond to management actions. Beyond this, there is a need for research to elucidate the mechanisms favoring exotics over natives following management actions. Our findings suggest that four primary factors may facilitate secondary invasion and should be further explored: treatment side effects, target invader legacy effects, provenance effects, and shifting environmental conditions. If it turns out that the primary explanation for secondary invasion is that natural ecosystems are changing in ways that favor exotic species over natives, then natural areas conservation may need to consider less traditional approaches going forward (Hobbs et al., 2006; Hobbs, 2007). However, refining weed control tools to reduce side effects, neutralize invader legacies, and mitigate provenance advantages in conjunction with advancing restoration tools to fill the gap resulting from invader suppression, will go far towards improving invasive plant management and natural areas restoration.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2016.02.029.

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