

To list or not to list: using time since invasion to refine impact assessment for an exotic plant proposed as noxious

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Abstract. Methods that allow rapid and robust evaluation of plant invader impacts are needed to identify problematic species before they become too widespread to effectively manage. While observational data can be readily gathered to identify negative relationships between invading and native species, these patterns are not necessarily indicative of invader impact and may instead reflect the legacy of past conditions influencing invasibility. We augmented standard observational methods by using local-scale time-since-invasion information in conjunction with rapidly gathered plant abundance data to evaluate potential impacts of common buckthorn (*Ramnus cathartica*), a woody exotic in the early stages of invasion in Montana, USA. This species occurred as scattered populations of limited distribution and was proposed for listing as a state noxious weed, but empirical information on ecological impacts in the region was lacking. We recorded cover of understory and overstory plants across gradients of buckthorn invasion at 12 riparian sites representing five river drainages throughout the state. Uninvaded plots were located proximal to invaded plots at each site. Time since invasion per plot was approximated by aging buckthorn plants via annual rings. We found strong negative correlations between cover of native plants and buckthorn. In addition, buckthorn overstory cover increased with time since invasion, while native overstory cover decreased with invasion time, consistent with an impact scenario wherein the progression of invasion and associated increases in invader abundance suppressed native taxa. Although environmental factors that simultaneously promoted the increase of invaders and the decline of natives over time could have produced patterns mimicking invader impact, such a mechanism would have been more likely to manifest at broad scales to affect both uninvaded and invaded plots at a site. Our approach of using local-scale time-since-invasion data to examine temporal signatures strengthened inferences made from standard observational methods and provided key input to support the listing of an emerging invader as a noxious weed in Montana. These results suggest that rapid empirical assessments of plant communities that consider time since invasion could be used to more confidently evaluate invader impacts and better inform the listing process for noxious and other regulated species.

Key words: common buckthorn; exotic shrub; invader impact; invasive plant; Montana; noxious weed listing; *Ramnus cathartica*; time since invasion.

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INTRODUCTION

Noxious weed and regulated invasive plant lists are a principal means for prioritizing

management of the many plants introduced to natural systems. However, the process for listing species can be subjective and is often not based on quantification of invader impacts (McGeoch

et al. 2012, Quinn et al. 2013, Pearson et al. 2016, Vanderhoeven et al. 2017; but see Carboneras et al. 2018). Quantification of invader impacts should be a key step in prioritizing management efforts (Parker et al. 1999, Hulme et al. 2013, Kumschick et al. 2015, Sofaer et al. 2018), including the decision to list a species as noxious or otherwise regulated. While prevalent invaders are often assumed to have ecological impact, quantification of these impacts is typically lacking, in part largely due to methodological challenges (Barney et al. 2013, Hulme et al. 2013, Pearson et al. 2016, Tekiela and Barney 2017). Waiting until an invader becomes widespread to recognize impacts is disadvantageous given that management is most effective at earlier stages of invasion when relatively few sites are occupied (Higgins et al. 2000, Simberloff et al. 2013, Epanchin-Niell 2017). Better tools are needed to evaluate invader impacts, particularly to identify problematic invaders before they become prevalent at broad scales.

Observational studies are the most common method used to evaluate plant invader impacts (Stricker et al. 2015). One advantage of these studies is that they consider cumulative effects on native communities exerted over relatively long time scales whereas experimental approaches typically address only short-term responses (Stricker et al. 2015, D'Antonio and Flory 2017, Flory et al. 2017, Tekiela and Barney 2017). In observational studies, negative correlations between invader and native abundance measured at local scales are assumed to represent invader impacts, that is, direct or indirect consequences of invasion. However, it can be difficult to distinguish causes from effects of increased invader abundance; that is, negative local-scale relationships between invader and native abundance may reflect patterns of invasibility and/or invader impacts (Ortega and Pearson 2005, Stricker et al. 2015, Pearson et al. 2016). In the former case, invaders may simply be favored by conditions associated with reduced native abundance such as disturbance and/or increased resource availability (Stohlgren et al. 1998, Davis et al. 2000, Sokol et al. 2017, Pearson et al. 2018). Not surprisingly then, correlations between invader and native abundance are used to infer impact in some studies (reviews in Vilà et al. 2011, Hulme et al. 2013, Stricker et al. 2015)

and invasibility in others (Stohlgren et al. 1999, Knight and Reich 2005, Mills et al. 2012). Yet relationships between invader and native abundance may be the product of either or both processes (MacDougall and Turkington 2005, Ortega and Pearson 2005, Bauer 2012, Sokol et al. 2017). More generally, variation in ecological factors affecting invader success (e.g., disturbance, resource availability) may confound, obscure, or alter relationships attributable to invader impact (Didham et al. 2007, Kumschick et al. 2015, Sokol et al. 2017, Mueller et al. 2018).

Recent studies have made headway in addressing some of the methodological issues affecting evaluation of invader impacts via observational data (Thiele et al. 2010, Barney et al. 2013, 2015, Pearson et al. 2016). However, it remains a challenge to distinguish patterns of invader impact from those reflecting invasibility, even if care is taken during study design to select invaded and uninvaded locations with similar background conditions (Barney et al. 2013, 2015, Kumschick et al. 2015). When examining local-scale relationships between invaders and native species, insight may be gained by accounting for ecological covariates potentially affecting abundance of both taxa (Bauer 2012, Mueller et al. 2018). For example, the presence of multiple invaders and their potential interactive effects on native abundance can be accounted for in statistical models (Pearson et al. 2016). However, conditions measured during surveys may not reflect important factors relevant at the time of invasion. In particular, past disturbances and associated resource pulses that might have favored invaders over natives may no longer be detectable, and hence, negative relationships between invader and native abundance may reflect the legacy of past conditions rather than impacts of the invader accrued over time (Pearson et al. 2016). As such, in most observational studies, we still lack assurance that negative local-scale relationships between invader and native abundance are indeed indicative of invader impact rather than reflecting variation in ecological factors promoting invasion.

One potential way to mitigate this problem is to incorporate data on time since invasion when evaluating impacts of plant invaders at local scales. The magnitude of invader impacts should generally change over time as a function of

invader abundance (Dostál et al. 2013, Flory et al. 2017, Sofaer et al. 2018; but see D'Antonio and Flory 2017). While time series data relevant to invader impacts are seldom available (Stricker et al. 2015, D'Antonio and Flory 2017, Flory et al. 2017), spatially explicit time-since-invasion data, that is, chronosequences, can be derived for a given point in time, t , in particular for woody invaders that are readily aged (Hartman and McCarthy 2007), but also via aerial imagery (Mitchell et al. 2011, Dostál et al. 2013). Such time-since-invasion data could be related to local-scale plant community data collected at time t to specifically test for temporal signatures consistent with invader impact. For example, in the simple scenario where invader abundance and associated impacts build over time, local-scale variation in invader abundance at time t should align positively with time since invasion, while native abundance at time t should align negatively not only with invader abundance but also with time since invasion. Notably, the measured gradient of native abundance would not be expected to align negatively with time since invasion if it represented variation in invasibility present prior to invasion rather than a product of invader impacts. While it is still possible that background factors that simultaneously promote the increase of invaders and the decline of natives over time could produce patterns mimicking those expected under the impact scenario above (MacDougall and Turkington 2005), such a mechanism would be less likely to manifest at local scales, particularly if precautions were taken via study design (see *Discussion*). Time since invasion has seldom been considered in studies of plant invader impacts (Dostál et al. 2013, Stricker et al. 2015, D'Antonio and Flory 2017), yet such information could improve interpretation of local-scale patterns measured via observational methods. Quantitative tools allowing more confident evaluation of invader impacts could also aid in prioritizing management of plant invaders, including the listing of regulated species.

Herein, we present a case study where we used local-scale time-since-invasion information in conjunction with rapidly gathered plant community data to evaluate potential ecological impacts of the invader, common buckthorn (*Ramnus cathartica*), in time to inform the noxious

weed listing process for this species in Montana, USA. Common buckthorn is a woody plant native to Europe and western Asia that heavily invades natural systems in the northeast and northern Midwest of the USA (Knight et al. 2007), where it has been declared a noxious weed in several states. While buckthorn is also found in the arid west of North America, it had not been recognized as problematic in this region, where it remained largely unstudied. In Montana, buckthorn exists in riparian habitats as scattered populations of limited broad-scale distribution reflecting a legacy of horticultural plantings and possibly early stages of invader expansion. It was proposed for listing as a state noxious weed in January 2016, with the decision period scheduled for the next noxious weed listing hearing one year later. In the interim, our objective was to gather field data and conduct a robust assay of buckthorn's potential ecological impacts for use in the hearing. To do so, we used the recommended approach of examining local-scale native plant abundance across gradients of invader abundance (Barney et al. 2015, Mueller et al. 2018, Sofaer et al. 2018), while exploiting the woody nature of buckthorn to age plants and thereby consider temporal signatures associated with time since invasion. We also built on recent work to account for the potential impact of other invaders present in plots (Pearson et al. 2016). Finally, to assess possible effects of buckthorn on understory species, we controlled for heterogeneity in another important ecological variable, native overstory cover (Tuttle et al. 2016). Using this combined approach, we considered the response of both herbaceous and woody plant species to buckthorn invasion.

METHODS

During the 2017 growing season, we sampled 12 riparian sites invaded by common buckthorn across four study areas distributed throughout Montana, USA (Appendix S1: Fig. S1, Table S1). The study areas were located near Missoula (Clark Fork and Bitterroot River drainages), Helena (Missouri River drainage), Bozeman (Gallatin River drainage), and Billings (Yellowstone River drainage). Sites within each study area were separated by >0.5 km ($\bar{x} = 6.8$ km $\pm$ standard error [SE] of 0.9 km). Within each site,

conditions including vegetation type and management history were similar aside from the gradient of buckthorn invasion. All sites were riparian habitats dominated by broadleaf tree and shrub species, though species composition varied, with common native species including cottonwoods and aspens (*Populus angustifolia*, *P. deltoides*, *P. tremuloides*, and *P. trichocarpa*), chokecherry (*Prunus virginiana*), roses (*Rosa* spp.), and snowberry (*Symphoricarpos albus*). Common exotic woody species in addition to the focal invader included Tartarian honeysuckle (*Lonicera tatarica*), white willow (*Salix alba*), crack willow (*Salix fragilis*), and Russian olive (*Elaeagnus angustifolia*). Native herbaceous species were primarily forbs, with more common species including false Solomon's seal (*Smilacina stellata*) and catchweed bedstraw (*Galium aparine*). Exotic herbaceous species were dominated by grasses, including Kentucky bluegrass (*Poa pratensis*), quackgrass (*Agropyron repens*), and smooth brome (*Bromus inermis*), while common exotic forbs were hound's tongue (*Cynoglossum officinale*), common dandelion (*Taraxacum officinale*), and Canada thistle (*Cirsium arvense*).

At each site, we conducted sampling within 10 × 10 m plots that were either invaded or uninvaded by buckthorn. All plots within a site were separated by a minimum distance of 25 m between centroids. Invaded plots were centered within 5 m of a mature buckthorn individual (i.e., with evidence of past or current reproduction) to increase the likelihood that sufficient time had passed for impacts to accrue, and a cross section of the focal buckthorn, the largest diameter individual in the plot, was cut at breast height to allow age estimation. In an effort to assure that uninvaded and invaded plots represented similar background conditions at each site, we located uninvaded plots by walking in a random direction from each invaded plot to the first location free of buckthorn canopy (>1.3 m tall) within the vegetation type characterizing the site. Given heterogeneity in invasion levels within each site, invaded and uninvaded plots could generally be located proximal to each other and were spatially intermixed rather than clustered by invasion status. We attempted to balance the number of uninvaded and invaded plots at each site to assure robust representation of uninvaded conditions,

but this was not possible at several sites with more widespread buckthorn establishment (Appendix S1: Table S1).

Plots were divided into four 5 × 5 m quadrats, and plants were sampled in each of three vertical layers per quadrat. We estimated percent cover of each woody species in the mid-story (1.3–3 m) and upperstory (>3 m), respectively. In addition, within each of two systematically identified quadrats per plot, we centered a 1 × 1 m microplot to quantify cover of both woody and herbaceous species in the understory (<1.3 m). We chose cover to represent abundance of each group given that this metric translates more directly to biomass than stem counts, particularly when multiple taxa are considered (see Pearson et al. 2016). For analyses, we summed cover across taxa according to their origin (native or exotic) for (1) woody species other than buckthorn in each vertical layer and (2) herbaceous understory species. In addition, given that woody species cover was sparse in the midstory relative to upperstory layer, particularly for native species ($\bar{x} = 3.1 \pm 0.8\%$ vs. $\bar{x} = 17.8 \pm 3.2\%$), we summed these layers together to collectively represent the overstory. These continuous cover variables were incorporated into the models described below. In the laboratory, we sanded cross-sections of focal buckthorn stems down to 320 grit and counted annual growth rings to estimate age, representative of time since invasion (Hartman and McCarthy 2007).

Statistical analyses

We used generalized linear mixed effects models in SAS version 9.4 for analyses (PROC GLIMMIX; SAS Institute 2013). Because all response variables were positively skewed, we specified a lognormal distribution with the addition of a small constant to account for zeroes. Denominator degrees of freedom were allowed to fluctuate according to the influence of random factors via the Satterthwaite method (SAS Institute 2013). Given significant heterogeneity in buckthorn invasion levels among the quadrats defining each 10 × 10 m plot, data were analyzed at the scale of the quadrat (or embedded microplot) while accounting for potential covariance in the response within plots via a random factor as relevant.

We first ran a series of models following current methods for assessing potential invader impacts (see Pearson et al. 2016). In these models, we used data from both invaded ($n = 80$) and uninvaded plots ($n = 49$) to test for relationships between native cover response variables and buckthorn cover while accounting for cover of background community components potentially affecting the response (e.g., other exotics). If buckthorn invasion negatively impacted native species, we expected native cover variables to decline with increasing buckthorn cover. Buckthorn cover and background cover variables were treated as fixed factors in models, with study area, site, and plot included as random factors. The first model tested for a relationship between native woody overstory cover and buckthorn overstory cover while controlling for overstory cover of other exotic woody species. Two subsequent models examined the response of native understory cover (woody and herbaceous species, respectively) using the same structure as the first but with the addition of terms to account for understory cover of buckthorn, understory cover of other exotics (woody and herbaceous invaders, respectively), and overstory cover of native woody species (Tuttle et al. 2016). We also ran a parallel model to assess the collective response of native and exotic herbaceous species (total herbaceous cover) given that cover of the former was relatively sparse. We did not include interactions between variables representing buckthorn and other exotics in models given that these extra terms did not substantively improve models; similarly, extra terms accounting for non-linear relationships between response variables and buckthorn cover variables were not well supported (Appendix S2: Tables S1–S2; Pearson et al. 2016). For simplicity, we did not consider interactions between variables representing understory and overstory conditions.

We ran a second set of models to examine variation in both buckthorn and native species cover as a function of time since invasion, measured via buckthorn annual ring counts. This analysis used data from the subset of invaded quadrats containing a focal buckthorn ($n = 1$ per plot), which yielded sufficient sample size for consideration of overstory but not understory responses (focal buckthorn plants did not necessarily fall in the same quadrats wherein understories were

sampled). We expected that buckthorn overstory cover would increase with time since invasion if the measured gradient of buckthorn abundance represented successive points in the invasion process, that is, the progression of invasion, rather than solely reflecting variation in ecological factors driving invader success (e.g., native species abundance, resource availability, disturbance, etc.). In addition, we expected that native overstory cover would decrease with time since invasion if indeed buckthorn invasion and associated increases in invader abundance impacted native species. While such a temporal signature would not definitively prove that the invader impacted native species, alternate mechanisms for such a pattern were less plausible (see *Discussion*). The first model treated overstory cover of buckthorn as the response and time since invasion as a fixed factor, with study area and site included as random factors. The second model followed the same structure, with native woody overstory cover as the response and the addition of other exotic overstory cover as a fixed factor. Hence, this model paralleled the model used to test for potential impacts of buckthorn on native overstory cover except that the buckthorn cover term was replaced with time since invasion. Addition of the interaction between time since invasion and other exotic overstory cover did not improve the model, and inclusion of terms representing a non-linear relationship between response variables and time since invasion was also not well supported; these terms were therefore omitted (Appendix S2: Table S3).

For presentation of results in figures, we output least squares means, that is, predicted marginal means, associated with the models described above (LSMEANS statement, PROC GLIMMIX; SAS Institute 2013). This allowed us to depict relationships between community response variables and buckthorn invasion (cover variables or time since invasion) while controlling for background model parameters (e.g., cover of other exotics found in plots and random factors) and non-normality of response variables. To compute least squares means, SAS defaults to mean levels for model parameters (i.e., cover variables and time since invasion in our models) unless specific values are given. For the first set of models examining potential impacts of buckthorn invasion, we obtained least

squares means at each of four specified levels of buckthorn overstory cover (0%, 20%, 40%, 60%, and 80% cover) to represent the measured gradient and held background cover variables representing other exotics at their mean level given that they did not vary significantly with buckthorn overstory cover (other woody overstory: $F_{1, 505} = 3.3$, $P = 0.068$; other woody understory: $F_{1, 178} = 1.1$, $P = 0.3$; herbaceous understory: $F_{1, 232} = 2.5$, $P = 0.12$). To obtain least squares means for understory responses, we had to account for two additional model parameters that did vary significantly with buckthorn overstory cover: buckthorn understory cover, which had a positive relationship ($F_{1, 227} = 46.9$, $P < 0.0001$), and native overstory cover, which had a negative relationship (see *Results*). Hence, with each increasing level of buckthorn overstory cover specified, we also specified an increasing level of buckthorn understory cover and a decreasing level of native overstory cover, based on the modeled relationships with buckthorn overstory cover. For the second set of models examining variation in overstory cover of either buckthorn or native species in relation to time since invasion, we obtained least squares means for four specified time points (at intervals of 10 yr) to represent the measured gradient. In the latter case, we held overstory cover of other woody exotics at the mean level across years given that this variable was not significantly correlated with time since buckthorn invasion ($F_{1,72} < 0.1$, $P = 0.96$). All least squares means were back-transformed from the log scale in SAS for presentation.

RESULTS

Our first set of models testing for potential impacts of buckthorn on riparian communities revealed negative relationships between native woody species and buckthorn (see Table 1 for details). Both overstory and understory cover of native woody species varied negatively with overstory buckthorn cover ($P < 0.02$), with levels reduced by >50% over the invasion gradient (Fig. 1a). Native woody species responses were also negatively correlated with overstory cover of other exotic woody species ($P < 0.01$). In addition, native woody understory cover varied negatively with understory cover of both

buckthorn and exotic herbaceous species ($P \leq 0.001$).

Herbaceous understory species similarly showed negative relationships with buckthorn invasion (see Table 2 for details). Total herbaceous cover, which was dominated by exotic species, varied negatively with both overstory and understory buckthorn cover ($P < 0.03$), with levels falling >60% over the gradient of buckthorn invasion (Fig. 1b). Native species comprised a small proportion of the total herbaceous cover and showed a trend toward a negative relationship with overstory buckthorn cover ($P = 0.073$; Fig. 1b), also correlating negatively with overstory cover of other exotics ($P = 0.017$). Both total and native herbaceous cover varied negatively with increasing native woody overstory cover ($P < 0.02$).

Our second set of models considered temporal patterns associated with buckthorn invasion to inform interpretation of observed relationships between cover of native species and buckthorn (see Table 3 for details). In this analysis, overstory cover of buckthorn varied positively with time since invasion ($P < 0.0001$; Fig. 2), suggesting that the measured gradient of buckthorn abundance represented the progression of invasion. In addition, overstory cover of native woody species varied negatively with time since invasion ($P = 0.038$; Fig. 2), consistent with the scenario wherein the progression of invasion and associated increases in invader abundance impacted native taxa.

DISCUSSION

Methods that allow rapid and robust evaluation of ecological impacts of plant invaders are needed in order to identify problematic species before they become too widespread to effectively manage. While observational data can be quickly gathered to identify negative relationships between invading and native species, interpretation of such patterns is limited by the correlational nature of the data. In particular, negative local-scale relationships may reflect patterns of invasibility rather than invader impacts (Ortega and Pearson 2005, Stricker et al. 2015, Pearson et al. 2016). Our case study of the woody invader, common buckthorn, suggests that interpretation of these relationships may be bolstered by

Table 1. Relationships between cover of native woody species and the exotic invader, common buckthorn (*Rhamnus cathartica*), assessed via generalized linear mixed models controlling for cover of background covariates in the overstory (OS; midstory and upperstory combined) and understory (US) of riparian communities in Montana, USA.

Covariate	Native woody OS				Native woody US			
	β	<i>F</i>	df	<i>P</i>	β	<i>F</i>	df	<i>P</i>
Buckthorn OS	−0.008	22.2	490	<0.0001	−0.014	5.5	237	0.019
Other exotic woody OS	−0.019	49.7	488	<0.0001	−0.021	7.0	240	0.009
Buckthorn US					−0.029	10.5	220	0.001
Other exotic woody US					0.023	0.6	222	0.449
Exotic herbaceous US					−0.018	16.4	250	<0.0001
Native woody OS					0.001	0.1	248	0.745

Note: A lognormal distribution was specified for analyses, and parameter estimates (β) are given on the log scale.

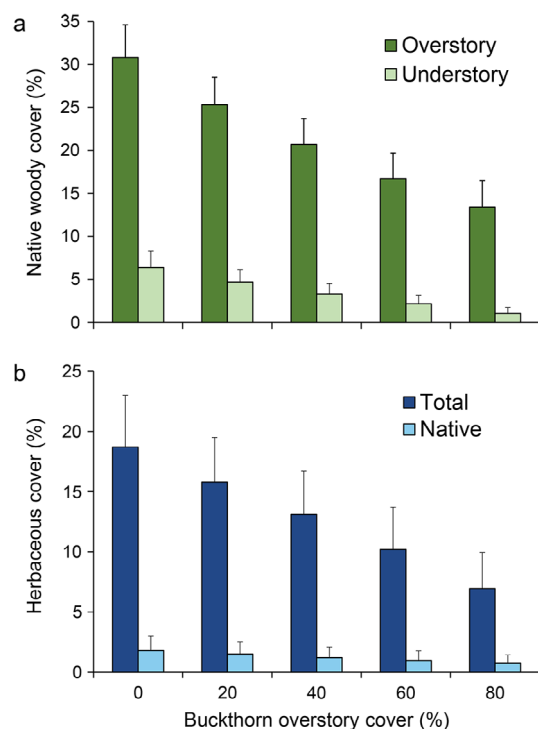


Fig. 1. Cover (least squares means + standard error) of (a) native woody species and (b) herbaceous understory species in relation to overstory cover (midstory and upperstory combined) of the exotic invader, common buckthorn (*Rhamnus cathartica*), in riparian communities of Montana, USA. Note that responses control for cover of background covariates included in generalized linear mixed models.

consideration of time-since-invasion data. This species was proposed for listing as a noxious weed in Montana, USA, in the early stages of invasion when it existed as scattered populations

of limited distribution. Although buckthorn was reported to impact plant communities in wetter regions of the northeastern and midwestern United States (Knight et al. 2007, Klionsky et al. 2011, Waller et al. 2016), little empirical information existed for our region. We found strong negative correlations between abundance of native plants and buckthorn, as measured at local scales across 12 riparian sites in four study areas within the state. In addition, gradients in plant abundance aligned with time since invasion in a manner consistent with invader impacts. Notably, required data were gathered in time to inform the noxious weed listing process, and this species was added to the Montana Noxious Weed List (Montana Department of Agriculture 2019). These results suggest that rapid empirical assessments of plant communities that include time-since-invasion information could be used to more confidently evaluate invader impacts and better inform the listing process for noxious and other regulated species.

Negative local-scale correlations between native and invader abundance are often used to identify apparent impacts of plant invaders in observational studies (Stricker et al. 2015). Current approaches incorporate safeguards to help ensure that measured relationships are driven by invader impacts rather than confounding factors that might mimic impact. In particular, uninvaded plots that appear to have similar background conditions as invaded plots are included in analyses to serve as a baseline for native abundance in the absence of invasion (Barney et al. 2013, 2015, Kumschick et al. 2015, Pearson et al. 2016). However, the fact remains that without

Table 2. Relationships between cover of herbaceous understory species and the exotic invader, common buckthorn (*Rhamnus cathartica*), assessed via generalized linear mixed models controlling for cover of background covariates in the overstory (OS; midstory and upperstory combined) and understory (US) of riparian communities in Montana, USA.

Covariate	Total herbaceous US				Native herbaceous US			
	β	F	df	P	β	F	df	P
Buckthorn OS	−0.01	5.8	240	0.017	−0.011	3.3	228	0.073
Other exotic woody OS	0.005	0.9	228	0.346	−0.021	5.8	229	0.017
Buckthorn US	−0.015	5.0	225	0.026	−0.008	0.6	208	0.435
Other exotic woody US	−0.021	0.9	228	0.346	0.01	<0.1	232	0.765
Exotic herbaceous US					<0.001	<0.1	247	>0.999
Native woody OS	−0.011	12.3	251	<0.001	−0.011	6.1	241	0.015

Note: A lognormal distribution was specified for analyses, and parameter estimates (β) are given on the log scale.

Table 3. Relationships between cover variables and time since invasion of the exotic shrub, common buckthorn (*Rhamnus cathartica*), assessed via generalized linear mixed models controlling for cover of other exotic woody species in the overstory (OS; midstory and upperstory combined) of riparian communities in Montana, USA.

Covariate	Buckthorn OS				Native woody OS			
	β	F	df	P	β	F	df	P
Time since invasion	0.046	31.9	74	<0.0001	−0.017	4.4	76	0.039
Other exotic woody OS	<0.001	<0.1	63	0.939	−0.015	4.0	53	0.052

Note: A lognormal distribution was specified for analyses, and parameter estimates (β) are given on the log scale.

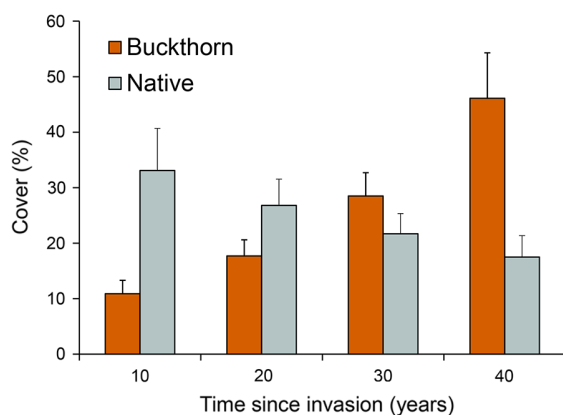


Fig. 2. Cover (least squares means + standard error) of the exotic invader, common buckthorn (*Rhamnus cathartica*), and native woody species in relation to time since invasion in the overstory (midstory and upperstory combined) of riparian communities of Montana, USA. Note that responses control for cover of other exotic woody species included as a covariate in generalized linear mixed models.

pre-invasion data, we cannot be sure that conditions prior to invasion were comparable across the present invasion gradient. Of particular concern is the possibility that pre-invasion decrements in native abundance and/or covarying factors such as disturbance favored the establishment and proliferation of invaders in a subset of plots to produce a negative correlation between native and invader abundance (Stohlgren et al. 1998, Sokol et al. 2017, Pearson et al. 2018). In this scenario, decrements in native abundance measured in invaded vs. uninvaded plots would primarily reflect pre-invasion differences in invasibility. Alternatively, in the impact scenario, invasion and associated increases in invader abundance drive declines in native abundance to produce the measured decrements in invaded plots. Notably, while both scenarios can generate negative correlations between taxa, only the impact scenario is predicted to generate temporal changes in native abundance coinciding with invasion processes.

To better interpret negative local-scale correlations between native and invader abundance in our case study of common buckthorn, we augmented established methods for assessing invader impacts by considering temporal patterns associated with invasion. First, we minimized background variation in conditions by sampling plant abundance in uninvaded plots located proximal to invaded plots at each study site. In addition, we estimated time since invasion per plot by aging buckthorn plants via annual ring counts. Models testing for local-scale correlations between native and buckthorn cover accounted for cover of background community components (e.g., other exotics) potentially affecting responses. This analysis revealed negative relationships potentially indicative of buckthorn impacts, but also possibly driven by invasibility gradients present prior to invasion. To distinguish between these potential mechanisms, we ran a second set of models relating plant community variables to time since invasion data. We found that buckthorn overstory cover (midstory and upperstory cover combined; see *Methods*) varied positively with time since invasion, suggesting that the measured invasion gradient represented successive points in the invasion process, that is, the local-scale progression of invasion, rather than solely reflecting variation in ecological factors driving invader success. Moreover, we found that native overstory cover varied negatively with time since invasion, consistent with an impact scenario wherein local-scale decrements in native abundance build over time as a function of invader abundance (Dostál et al. 2013, Flory et al. 2017, Sofaer et al. 2018).

It is possible that background factors simultaneously promoting the increase of the focal invader and the decline of natives over time could produce patterns that mimic those expected under the impact scenario. However, such factors would have to act at local scales to trigger the demise of native species coincident with invasion. In our study, buckthorn cover varied substantially within sites as a function of time since invasion, with invasion apparently progressing from multiple foci therein. Native cover was higher in uninvaded plots relative to plots with increasing buckthorn cover, and the longer a particular plot had been invaded, the greater the

decrement in native abundance. While environmental change (e.g., related to climate, altered disturbance regimes, or habitat fragmentation) can differentially suppress native vs. invading species (MacDougall and Turkington 2005, Didham et al. 2007, Bauer 2012), such forces would be more likely to act at broad scales to trigger declines in native abundance measurable across a site (assuming consistent community type etc.) vs. at fine scales in alignment with invasion processes in space and time. Factors such as disease or herbivory could act differentially within a site to suppress native abundance in a subset of plots and thereby favor invaders therein, but these processes would have to prevail over sufficient time scales to maintain declines in native abundance that coincide with local-scale invasion patterns. While the invasion of other more potent plant species could represent such a process, local abundance of other invaders can be controlled for in models, and in the case of our system, cover of these invaders was not correlated with focal invader cover or the timing of its invasion. The confounding influence of chronic disturbance factors may be more relevant in systems with broader-scale variation in invasion patterns, for example, where periodic flooding simultaneously promotes the loss of native abundance and the proliferation of invaders to mimic temporal signatures associated with impact. Study designs that locate uninvaded plots proximal to invaded plots, ideally within the same sites, can help reduce the influence of such background factors (Thomaz et al. 2012, Barney et al. 2015, Pearson et al. 2016). While the analytical goal is to quantitatively isolate invader impacts from those attributable to environmental drivers, we note that these forces can certainly have interactive effects on native species (e.g., back-seat driver model; Bauer 2012), and mechanistic knowledge of such interactions will be key to effective management (Didham et al. 2007, Johnson et al. 2015, Sokol et al. 2017).

Using time since invasion data to test for temporal signatures consistent with invader impact worked well in our study system, but how applicable might this approach be in other cases? Our focal invader appeared to follow the simple scenario of increasing local abundance over time, which could have in part reflected its rather recent invasion. The mean age of focal buckthorn

plants per plot was 25.5 ± 1.1 yr (range 7–45 yr), which is not long relative to the age when this species first reproduces (7 yr in our study) and to age spans of woody species in general (Schweingruber and Poschlod 2005). Notably, while this time frame was sufficient to allow the building of populations at local scales, with a range of invasion ages present within sites (Appendix S1: Table S1), the broad-scale distribution of this species was still limited, consistent with typical timelines for the invader establishment phase preceding the phase of rapid expansion to new sites (Williamson et al. 2009, Aikio et al. 2010, Blackburn et al. 2011). Populations of potent invaders are generally assumed to increase over time (Barney et al. 2013), but population growth may eventually attenuate due to many factors (Ricciardi et al. 2013, Yelenik and D’Antonio 2013, Flory et al. 2017). In our study, local-scale increases in buckthorn overstory cover appeared to be sustained over the measured invasion time span (Fig. 2), with some weak evidence for an eventual slowing of population growth (Appendix S2: Table S3). Few studies have examined invader impacts over time, but most show that impact levels generally track invader abundance regardless of the latter’s particular trajectory (Mitchell et al. 2011, Dostál et al. 2013, Flory et al. 2017). This pattern is in line with theory linking local-scale competitive effects to biomass (Parker et al. 1999, Pearson et al. 2016, Sofaer et al. 2018). Notable exceptions include cases where invaders exert impact by altering soil properties or ecosystems processes (D’Antonio and Flory 2017). Based on these understandings, use of time-since-invasion data to assay invader impacts holds promise under the likely prevalent scenario where impacts and abundance are coupled at local scales.

Incorporation of time-since-invasion data may improve impact assessments for a wide range of invasive species. These data can be readily obtained for many woody species via annual ring counts (Schweingruber and Poschlod 2005, Hartman and McCarthy 2007). In fact, >40% of all species classified as invasive globally fall in this group (Hulme et al. 2013), yet their ecological impacts are understudied relative to other lifeforms, in part due to methodological challenges (Stricker et al. 2015, Mueller et al. 2018). The potential utility of our approach also extends

beyond woody invaders, as time-since-invasion data can be obtained from aerial imagery (Mitchell et al. 2011, Dostál et al. 2013). Importantly, regardless of how these data are derived, the spatial resolution must be sufficient to allow evaluation of local-scale patterns given that invader impacts typically accrue at this scale. While invasion ecology is increasingly recognizing the need to consider time since invasion in studies of invader impact, research examining local-scale patterns, including linkages to invader abundance over time, will be particularly informative (Mitchell et al. 2011, Flory et al. 2017, Sofaer et al. 2018). Observational studies addressing these questions through chronosequences are far more practical than experimental studies, particularly for long-lived woody invaders, but conclusions must be tempered by the correlational nature of the data (see Mueller et al. 2018). Longer-term studies, as feasible, will provide further insight into the dynamics of invader impacts (Thomaz et al. 2012, D’Antonio and Flory 2017, Sofaer et al. 2018).

Our approach of using time since invasion data to test for temporal signatures consistent with invader impact strengthened inferences made from standard observational methods. These results provide empirical evidence of buckthorn’s ecological effects in western North America and served as key input to support the listing of this species as a noxious weed in Montana. Ecological impact is only one consideration in the regulation of invasive species, albeit an important one that often receives inadequate attention in state noxious weed listing processes (Quinn et al. 2013). Quantitative methods for assessing ecological impact are needed to increase the robustness of regulation decisions and direct management strategies toward mitigation of risks posed by invasive species (Barney et al. 2015, Pearson et al. 2016, Sofaer et al. 2018). Reliance on perception of risk or subjective criteria produces a bias toward the listing of conspicuous invaders in the late stages of invasion—when distribution is widespread and management is difficult and more costly (Quinn et al. 2013, Simberloff et al. 2013, Epanchin-Niell 2017). Our method allowed a rapid and more robust assessment of the ecological impacts of an exotic plant relatively early in the invasion process and holds promise for improving how

these taxa are prioritized for regulation and management.

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