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Community-level consequences of invasion: impacts of exotic clonal plants on riparian vegetation

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Abstract Biological invasions by exotic species are occurring at exceptional rates and spatial scales worldwide and are increasingly recognized as key forms of global environmental change. Despite this growing prominence, surprisingly few ecological studies have quantified the impacts of exotic taxa on the plant communities they invade, and this is especially evident in riparian ecosystems. Along the Russian River in northern California, we used both comparative and experimental studies to investigate the influence of two exotic clonal plant species—giant reed (*Arundo donax*) and blue periwinkle (*Vinca major*)—on the composition of riparian plant communities. Our results indicate that *Arundo* invasion was associated with significantly lower richness of native perennial plant species on stream banks and floodplains, whereas there was no relationship on gravel bars. Additional research showed that plots invaded by *Arundo* and *Vinca*, both individually and collectively, exhibited significantly lower native and exotic species richness and abundance of both established plants and seedlings than uninvaded plots. Finally, after 2 years, experimental reductions of

Arundo biomass via cutting and herbicide resulted in significantly increased native plant species richness and abundances of both established plants and seedlings, while having no effects on other exotics. In summary, our results indicate that *Arundo* and *Vinca* have strongly negative effects on diverse components of a riparian plant community, which must be addressed via effective control and restoration efforts.

Keywords *Arundo donax* · Biological invasions · Clonal plants · Community effects · Riparian plant communities · *Vinca major*

Introduction

Biological invasions are occurring at unprecedented rates and spatial scales throughout the world, and are increasingly viewed as critical forms of global environmental change (Drake et al. 1989; Vitousek et al. 1996; D'Antonio 2000; Mack et al. 2000; Mooney and Hobbs 2000; Ruiz and Carlton 2003; Hulme 2006; Lockwood et al. 2007; D'Antonio et al. 2007). Indeed, Wilcove et al. (1998) found that non-native species are second only to habitat loss as the leading cause of species endangerment in the USA. Although the growing prominence of invasive species has stimulated a wealth of research on diverse topics (see reviews by Parker et al. 1999; Mack et al. 2000;

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Pimentel et al. 2000; Sakai et al. 2001 and others), numerous investigators have pointed out that there is a shortage of quantitative studies that assess the impacts of exotic taxa on the plant communities they invade (Parker et al. 1999; Alvarez and Cushman 2002; Hulme 2003). Furthermore, as noted by multiple authors (see Parker et al. 1999; Alvarez and Cushman 2002; Hulme and Bremner 2006; Truscott et al. 2008), most of the studies that quantify community-level impacts of plant invaders involve non-experimental comparisons, which make it difficult to understand definitively the community-level impacts of these human-caused additions. For example, a review by Levine et al. (2003) found that 90% of the studies purporting to document community-level effects of plant invaders were entirely non-experimental. Such correlative studies of invader impacts have substantial merit but are most useful when combined with and compared to community data from experimental studies.

Although infrequently examined, different components of a plant community will likely vary greatly in their responses to invasion by exotic plant taxa. For example, native and exotic plant species may differ in their capacity to co-exist with a dominant invader and response to its reduction or removal from an area. In addition, examining the response of native and exotic taxa at different life history stages—especially seedlings—should provide insight about the degree to which a particular invader has influenced plant communities and how systems will respond to its reduction or removal.

Riparian ecosystems are especially prone to invasion by exotic plants, probably due in large part to the intense disturbance regimes that they experience (Planty-Tabacchi et al. 1996; Stohlgren et al. 1998; Hood and Naiman 2000; Quinn et al. 2007; Vila et al. 2007). Using a mixture of correlative and/or experimental techniques, a handful of studies have shown that invaders can reduce plant species richness in these communities (Hulme and Bremner 2006; Maskell et al. 2006; Truscott et al. 2008). In addition, due to their capacity to exploit ephemeral resources and patchy substrates, exotic plant taxa that reproduce clonally have been especially successful at invading disturbance-prone riparian environments (Baker 1986; Prach and Pysek 1994; Pysek 1997). However, despite their success, very little attention has focused on the influence of clonal invaders on

riparian plant communities. One exception is a study by Alvarez and Cushman (2002), which used comparative and experimental approaches to document that invasion by a South African clonal vine reduced plant species richness and diversity in two types of riparian habitats.

In this paper, we summarize results from comparative and experimental studies that address the influence of two clonal exotic plant species—giant reed (*Arundo donax*) and blue periwinkle (*Vinca major*)—on riparian plant communities in northern California. Although these two plant species are widespread throughout many riparian areas of North America, we are aware of no studies that have evaluated their impacts on resident plant communities. Given this absence, we conducted field research to address the following questions: (1) Does the abundance of *Arundo* differ among three riparian zones (gravel bars, stream banks and floodplains), and is the richness of native woody plant species reduced by *Arundo* in each of these zones? (2) Do plant communities invaded by *Arundo* and *Vinca*—separately and together—differ in the richness of native and exotic plant species and the abundance of established plants and seedlings compared to communities lacking these invaders? and (3) How does experimental reduction of *Arundo* abundance and biomass affect the richness of native and exotic plant species and the abundance established plants and seedlings? This research will provide insight about how different components of riparian plant communities—those varying in geographic origin and life stages—respond to invasion by two dominant clonal perennials. Focusing on such issues will be critical for developing a predictive framework for understanding community responses to invasion.

Study system

Giant reed or cane (*Arundo donax*; Poaceae; hereafter referred to as *Arundo*) is a large-statured perennial grass native to Asia (Polunin and Huxley 1987) that has invaded extensive areas of wetland and riparian habitat in North America, especially California, Texas and the southeastern U.S. (Bell 1997; Dudley 2000). It has also become widespread in southern Africa, North Africa, the Middle East, Australia and South America (see Boose and Holt 1999). *Arundo*

relies exclusively on vegetative reproduction and disperses rapidly through riparian systems during floods via stems and rhizomes (Bell 1997; Boose and Holt 1999; Dudley 2000; Decruyenaere and Holt 2001, 2005; Khudamrongsawat et al. 2004; Quinn et al. 2007). At our three study sites in northern California, *Arundo* colonizes areas that are inhabited by a wide range of native and exotic plant species.

Blue Periwinkle (*Vinca major*; Apocynaceae; hereafter referred to as *Vinca*) is a perennial semi-evergreen vine native to Europe and northern Africa that has been introduced to many continents for its medicinal and ornamental qualities. In the United States, this species has escaped cultivation and become widespread throughout much of California, Washington and Oregon, as well as numerous southeastern states. *Vinca* has a prostrate growth form, readily forms dense and extensive mats on the forest floor and spreads rapidly into new areas predominantly through vegetative reproduction (Dudley 1998; Drewitz 2000). At our study sites in northern California, *Vinca* colonizes the understory environments of riparian forests and co-occurs with a wide range of native and exotic plant species.

All three sites used in our study were located in the Alexander Valley on the main stem of the Russian River in Sonoma County, California, USA. Two of our study sites—adjacent to Choteau and Clos du Bois Vineyards—were located in the lower Alexander Valley, separated by approximately 3000 m. The third site—adjacent to Hidden Springs Vineyard—was approximately 18 km upstream of these sites. All sites were characterized by a riparian corridor that was at least 200 m wide and included a substantial floodplain area with mature riparian vegetation. Common exotic species included Himalayan blackberry (*Rubus discolor*), fennel (*Foeniculum vulgare*), and wild plum (*Prunus domestica*), whereas common natives included box elder (*Acer negundo*), California black walnut (*Juglans hindsii*), California blackberry (*Rubus ursinus*), California wild rose (*Rosa californica*), blue elderberry (*Sambucus mexicana*), coyote bush (*Baccharis pilularis* var. *consanguinea*), poison oak (*Toxicodendron diversilobum*), snowberry (*Symphoricarpos albus*), Santa Barbara sedge (*Carex barbarae*), mugwort (*Artemisia douglassii*) and western spice bush (*Calycanthus occidentalis*). A complete list of all plant species encountered at our three study sites is shown in Appendix 1.

Methods

Arundo abundance and effects within three riparian zones

In the spring of 1997, we initiated a study in the riparian habitat adjacent to Choteau Vineyards to evaluate (a) the degree to which *Arundo* abundance differed among gravel bar, stream bank and floodplain zones and (b) the characteristics of plant communities in *Arundo*-invaded and un-invaded areas in each of these zones. We established 30 40 × 40 m plots stratified across the three major riparian zones: the floodplain (4–6 m above the low-flow channel), the stream bank (2–4 m above the low-flow channel), and gravel bars (0–2 m above the low-flow channel). In each of these zones, we haphazardly located our plots in areas that were either invaded or uninvaded by *Arundo*.

During April of 1997, we sampled the vegetation in these invaded and uninvaded plots. In each of our 30 plots, we first quantified the total number of perennial plant species present and then determined the number of *Arundo* stems occurring in 10 randomly selected 1 m² patches in all invaded plots. We measured the area of all *Arundo* clumps in each plot and estimated per-plot stem abundance by multiplying stem number per m² by total plot area.

Comparison of plant communities invaded by *Arundo* and *Vinca*

To evaluate the influence of *Arundo* and *Vinca* invasion on plant communities, individually and jointly, we established 80 2 × 2 m plots distributed among 10 blocks adjacent to Clos du Bois Vineyards in the spring of 1999 (we used blocks to control for any underlying spatial variation that existed in the study area). Plots in each block were located in floodplain areas that were dominated by mature riparian forest. We chose to use 4 m² plots because preliminary data suggested that this size was best for capturing the distinctive fine-scale vegetation patches that occurred at our sites. We matched plots within blocks for elevation, slope, light levels and riparian forest structure and composition. We positioned our plots within four different patch types (with two replicates per type per block): (1) invaded by *Arundo* but not *Vinca*, (2) invaded by *Vinca* but not *Arundo*,

(3) invaded by both *Arundo* and *Vinca*, and (4) invaded by neither *Arundo* nor *Vinca*. The number of *Arundo* stems in *Arundo*-invaded plots averaged 63.18 (± 4.23 SE), whereas the number of *Vinca* stems in *Vinca*-invaded plots averaged 359.57 (± 38.57 SE).

We sampled all plots in June of 1999 to evaluate the association between these two invasive taxa and various characteristics of the plant community. We counted all plants in every plot (including *Arundo* and *Vinca* stems, if present), distinguishing between seedlings and established plants. We defined seedlings as those plants that had grown from seeds during the previous 6 months (i.e., first-year seedlings), whereas we defined established plants as all plants that were not seedlings.

Community responses to *Arundo* reduction

In the summer of 1998, we established a field experiment adjacent to Hidden Springs Vineyard to document the response of plant communities to *Arundo* reduction. We established 12 4 m² plots distributed randomly among six blocks of two in a mature floodplain riparian forest that was heavily invaded by *Arundo* (we used blocks to control for any underlying spatial variation that existed in the study area). We cut all *Arundo* stems at the study site within 10 cm of the ground in June of 1998, and allowed them to re-grow for 2 months prior to initiating the experiment. This was done because *Arundo* forms such dense, tall stands that plot establishment in this environment was virtually impossible without an initial clearing of the site (K. A. Gaffney and J. H. Cushman, personal observation). For each plot, we counted all *Arundo* stems and measured their diameters and lengths in August of 1998. We then randomly selected one plot in each block to receive a cutting and herbicide manipulation to reduce *Arundo* abundance and left the other plot unmanipulated to serve as a control. In August 1998, we cut all *Arundo* stems in manipulation plots and immediately applied herbicide (100% glyphosate) to them. After these initial manipulations, we re-cut all *Arundo* stems and applied herbicide every month during the following growing season, which for *Arundo* was between May and October 1999. We severed underground rhizome connections at the perimeter of all plots at the beginning of the

experiment, and at monthly intervals thereafter in order to prevent resource sharing with *Arundo* stems outside of the plot.

We determined the effectiveness of our manipulations in June 1998 and July 2000 by first quantifying *Arundo* stem abundance in each plot and estimating *Arundo* biomass as follows. We randomly sampled 40 *Arundo* stems, measured each of their heights and diameters 2 cm from the ground, dried them at 70°C for 72 h, and weighed them. Because *Arundo* diameter is remarkably consistent throughout the length of its stem (Spatz et al. 1997), we used diameter and length to estimate stem volume. Dry biomass was then regressed on stem volume for each of the sampled stems, and the relationship was found to be quite strong ($y = 4.77 + 0.26x$; $P < 0.0001$; $R^2 = 0.87$). With this equation, we then generated estimates of *Arundo* biomass per plot from stem abundance, diameter and height.

In June 1998 and July 2000, we also documented the community responses to these manipulations by determining the abundance of all native and exotic plant species and individuals in each plot, distinguishing between seedlings and established plants in all cases as described previously.

Statistical analyses

We analyzed all data from the comparative and experimental studies using the JMP 7 statistical program (SAS Institute, Cary, North Carolina, USA). In order to evaluate the association between *Arundo* stem density and position within the riparian corridor, we used a one-way ANOVA, with riparian zone (gravel bar, stream bank, and floodplain) as the grouping factor and *Arundo* stem number as the response variable. We also evaluated community patterns using a two-way ANOVA, with invasion status (*Arundo* present/absent) and riparian zone as the grouping factors and perennial species richness as the response variable. In both cases, we used Tukey HSD post-hoc tests ($\alpha = 0.05$) to compare means for the three riparian zones.

To assess the influence of *Arundo* and *Vinca* invasion on riparian floodplain communities, we first performed a three-way MANOVA, with *Arundo* status (present/absent), *Vinca* status (present/absent), and block (1–6) as the grouping factors and species richness, seedling abundance and the number of

individual established plants for both native and exotic taxa as the response variables. We treated block as a random effect in all of these analyses. Prior to analysis, we log-transformed all data to equalize variances. For all MANOVAs with significant invasion status main effects, we proceeded with separate “protected” ANOVAs on each of the six response variables using the same three grouping factors. As discussed by Scheiner (2001), this approach is an effective method for addressing potential correlations among multiple dependent variables (see Alvarez and Cushman 2002; Cushman et al. 2004). Because, the *Arundo* × *Vinca* interaction terms were significant for all three response variables, we again used Tukey HSD post-hoc tests ($\alpha = 0.05$) to compare all four treatment combinations.

We analyzed data from the *Arundo*-reduction experiment using two separate two-way MANOVAs, with *Arundo* treatment (control vs. repeated cutting followed by herbicide) and block (1–6) as the grouping factors. Block was treated as a random effect in all analyses and we were unable to calculate treatment × block interaction terms because our experiment did not have replication within block. Relative change ($\ln[2000/1998]$) in *Arundo* stem number and biomass were the response variables for the first MANOVA and relative change in native and exotic species richness, seedling abundance and number of individual established plants were the response variables for the second MANOVA. If the *Arundo* main effect in a MANOVA was significant, we again proceeded with separate “protected” ANOVAs (*sensu* Scheiner 2001) on each response variable, as described previously.

Results

Arundo abundance and effects within three riparian zones

At the Choteau Vineyard site, abundance of *Arundo* stems varied significantly among the three riparian zones (Fig. 1a; $F_{2,12} = 92.58$, $P < 0.001$). Post-hoc tests indicated that all three zones differed significantly from each other, with stream banks having the greatest density, gravel bars having the lowest density, and flood plains having intermediate density.

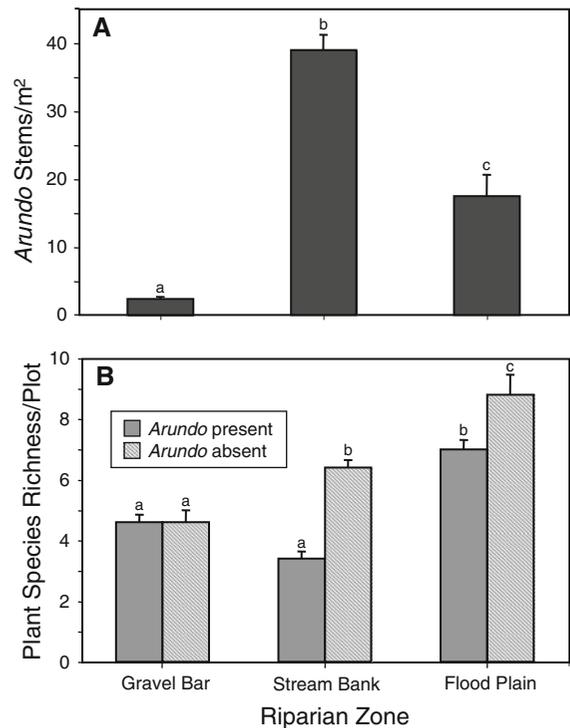


Fig. 1 Mean (± 1 SE) number of *Arundo* stems per m² (a) and native perennial species richness per plot (b) at three riparian zones (gravel bars, stream banks and floodplains) within a riparian corridor of the Russian River adjacent to Choteau Vineyards. Letters above bars correspond to the results of post-hoc tests

Invasion by *Arundo* was associated with significant reductions in the richness of perennial plant species, all of which were native (Fig. 1b; $F_{1,24} = 26.18$, $P < 0.0001$). Species richness also varied significantly among riparian zones ($F_{2,24} = 45.41$, $P < 0.0001$), and we also detected a significant interaction between *Arundo* invasion and riparian zone ($F_{2,24} = 7.77$, $P = 0.0025$). Subsequent post-hoc tests showed that *Arundo* invasion was associated with significantly lower richness of perennial plant species in stream-bank (47% lower) and flood-plain zones (21% lower) but not gravel bars (Fig. 1b).

Comparison of plant communities invaded by *Arundo* and *Vinca*

At the Clos Du Bois Vineyard site, results from a three-way MANOVA indicated that *Arundo* and *Vinca* invasion was associated with significant reductions in seedling abundance, plant species richness

and the number of individual established plants for both native and exotic taxa (*Arundo*: $F_{6,35} = 157.78$, $P < 0.0001$; *Vinca*: $F_{6,35} = 42.96$, $P < 0.0001$). Subsequent protected ANOVAs revealed that, in all but one case, plots invaded by *Arundo* and those invaded by *Vinca* had significantly reduced richness of native and exotic plant species (Table 1a, Fig. 2a and b), abundance of established native plants (Table 1b; Fig. 2c), and abundance of native and exotic seedlings (Table 1c; Fig. 2e and f). The only exception to this pattern was for the abundance of established exotic plants, which did not vary significantly with *Arundo* invasion (Table 1b; Fig. 2d). In addition, we detected significant *Arundo* \times *Vinca* interaction terms for all of these six response variables (Table 1). Post-hoc tests indicated that species richness and individual abundance of established plants and seedlings was greatest in plots free

of both *Arundo* and *Vinca*, and usually lowest in plots invaded by *Arundo* and *Vinca*, both singly and together (see Fig. 2). Thus, once one invader was present in the system, adding the second invader had little additional effect on the community.

Community responses to *Arundo* reduction

Results from a two-way MANOVA indicated that the *Arundo* treatment at our Hidden Springs Vineyard site had a large and significant overall effect on relative change in *Arundo* biomass and stem abundance ($F_{2,4} = 50.53$, $P = 0.0014$). Subsequent protected ANOVAs showed that repeated cutting and herbicide application significantly reduced stem abundance ($F_{1,5} = 12.90$, $P = 0.0157$) and biomass ($F_{1,5} = 46.64$, $P = 0.001$) of *Arundo* in plots (Fig. 3).

Results from a second MANOVA revealed that our *Arundo* treatment had a significant overall effect on relative change in native and exotic vegetation ($F_{6,5} = 13.57$, $P = 0.0058$). Specifically, the reduction of *Arundo* abundance and biomass caused by repeated cutting and herbicide application led to significant increases in native plant species richness ($F_{1,5} = 44.58$, $P = 0.0011$; Fig. 4a), established plant abundance ($F_{1,5} = 17.61$, $P = 0.0085$; Fig. 4b) and seedling abundance ($F_{1,5} = 30.29$, $P = 0.0027$; Fig. 4c). In contrast to these results for native taxa, *Arundo* reductions had no effect on exotic plant species richness ($F_{1,5} = 0.003$, $P = 0.96$), seedling abundance ($F_{1,5} = 0.52$, $P = 0.50$), and established plant abundance ($F_{1,5} = 0.14$, $P = 0.72$; Fig. 4).

Table 1 Results from three-way ANOVAs evaluating the influence of *Arundo donax* (present, absent), *Vinca major* (present, absent) and block on native and exotic plant species richness as well as the abundance of established plants and seedlings

Source	Natives			Exotics	
	df	F	P	F	P
a. Plant species richness					
<i>Arundo</i>	1,9	386.63	<0.0001	36.48	<0.0001
<i>Vinca</i>	1,9	150.44	<0.0001	39.69	<0.0001
Block	9,4.8	3.54	0.3556	1.85	0.2656
<i>Arundo</i> \times <i>Vinca</i>	1,49	55.46	<0.0001	53.25	<0.0001
<i>Arundo</i> \times Block	9,49	0.79	0.6273	0.73	0.6806
<i>Vinca</i> \times Block	9,49	0.60	0.7902	1.57	0.1521
b. Number of established plants					
<i>Arundo</i>	1,9	43.55	<0.0001	0.01	0.9122
<i>Vinca</i>	1,9	63.47	<0.0001	18.51	0.0020
Block	9,4.8	3.15	0.1381	2.82	0.2222
<i>Arundo</i> \times <i>Vinca</i>	1,49	27.19	<0.0001	9.68	0.0031
<i>Arundo</i> \times Block	9,49	1.37	0.2279	0.78	0.6389
<i>Vinca</i> \times Block	9,49	0.71	0.6987	0.96	0.4857
c. Number of seedlings					
<i>Arundo</i>	1,9	392.46	<0.0001	77.82	<0.0001
<i>Vinca</i>	1,9	167.35	<0.0001	86.40	<0.0001
Block	9,4.8	2.05	0.2233	10.40	0.4431
<i>Arundo</i> \times <i>Vinca</i>	1,49	110.16	<0.0001	60.60	<0.0001
<i>Arundo</i> \times Block	9,49	1.63	0.1320	0.43	0.9118
<i>Vinca</i> \times Block	9,49	0.73	0.6792	0.80	0.6209

Discussion

Our research suggests that both *Arundo donax* and *Vinca major* are causing substantial changes to the composition of riparian plant communities. Comparative and experimental studies at three different sites in northern California indicated that invasion by *Arundo* was associated with large reductions in native plant species richness as well as the number of native seedlings and established individuals (Figs. 1, 2, and 4). In contrast, the response of exotic plant taxa to *Arundo* invasion was more variable, with significant, but less pronounced, reductions detected for these three variables in a comparative study and no effects

Fig. 2 Mean (± 1 SE) plant species richness (a, b), the number of individual established plants (c, d) and seedling abundance (e, f) per plot for both native and exotic taxa as a function of the presence or absence of *Arundo donax* and *Vinca major* within a riparian flood plain along the Russian River adjacent to Clos de Bois Vineyard. Letters above bars correspond to the results of post-hoc tests

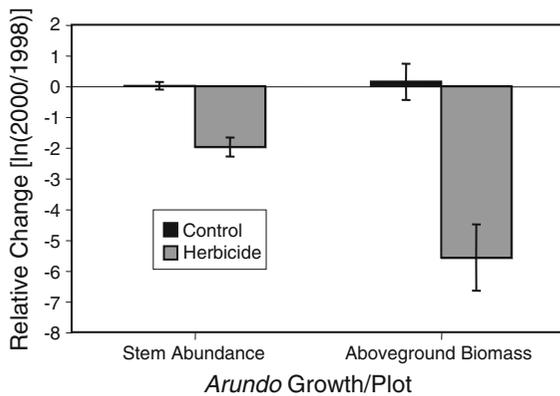
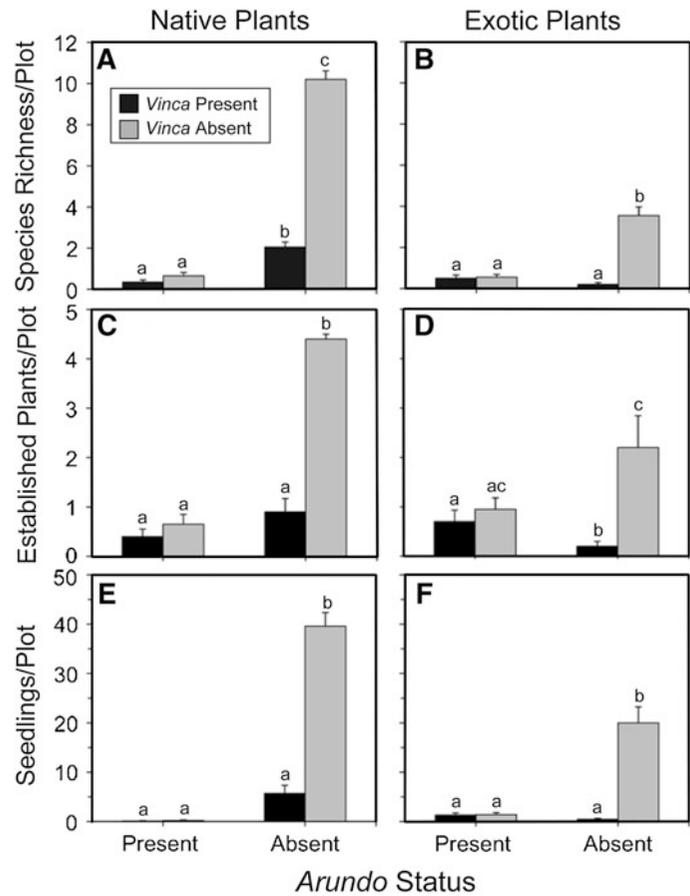


Fig. 3 Mean (± 1 SE) relative change (ln 2000/1998) in *Arundo* stem abundance (a) and aboveground dry biomass (b) per plot in response to an *Arundo*-reduction manipulation (cutting followed by herbicide versus no manipulation) within a floodplain riparian forest adjacent to Hidden Springs Vineyard

found in an experimental study. In addition, a comparative study revealed that invasion by *Vinca* was associated with similar findings—lower native plant species richness, abundance and seedling recruitment, as well as exotic species richness and seedling abundance (Fig. 2).

Our findings for *Arundo* and *Vinca* corroborate those from other community-level studies of plant invasions in riparian systems. For example, Alvarez and Cushman (2002) found that a clonal invader (Cape ivy, *Delairea odorata*) from South Africa reduced species richness, diversity and seedling recruitment of both native and exotic plant taxa in two types of riparian habitats in northern California. Similarly, Hulme and Bremner (2006) documented that the invasive forb *Impatiens glandulifera* native to the western Himalayas decreased plant species richness, species diversity and seedling abundance in

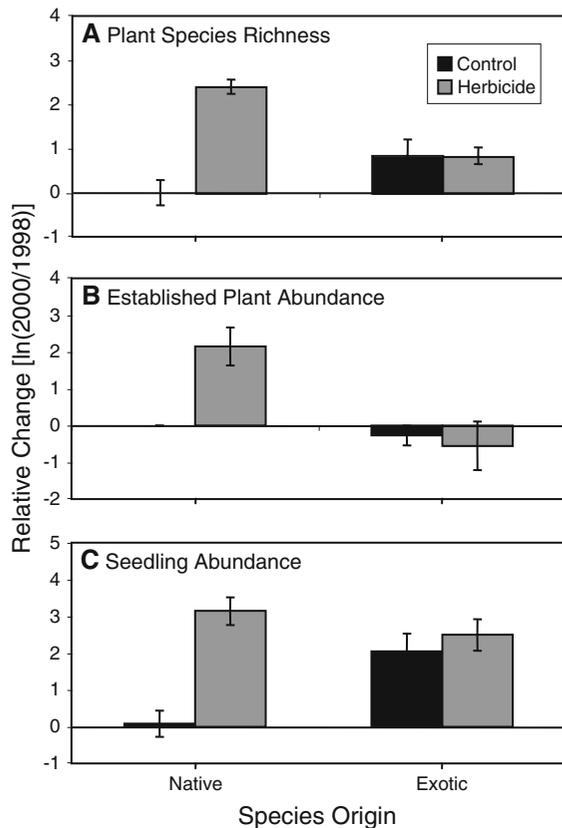


Fig. 4 Mean (± 1 SE) relative change (ln 2000/1998) in plant species richness (a), number of individual established plants (b) and seedling abundance (c) per plot for both native and exotic taxa in response to an *Arundo*-reduction manipulation (cutting followed by herbicide versus no manipulation) within a floodplain riparian forest adjacent to Hidden Springs Vineyard

riparian communities in northeast England. Truscott et al. (2008) also found that another widespread invasive forb, *Mimulus guttatus*, reduced plant species richness of riparian areas in Scotland, as well as altered species evenness and community composition. Collectively, these findings highlight the major impacts that plant invaders can have on riparian communities worldwide.

We hypothesize that *Arundo* and *Vinca* caused significant community-level effects because they are superior competitors in riparian areas. Both species propagate clonally, exhibit rapid growth and come to dominate the vegetation of riparian corridors. These traits are similar to those of Cape ivy and *Mimulus* discussed previously (Alvarez and Cushman 2002; Truscott et al. 2008). These characteristics enable

invaders to compete effectively for limiting resources such as light, water and nutrients in riparian habitats. Indeed, as demonstrated by several researchers, clonal integration may increase the invasion success of exotic taxa, allowing them to more effectively exploit patchy light, nutrient and moisture resources than their non-clonal neighbors (Alpert 1999; Meyer and Schmid 1999; Pennings and Callaway 2000).

Arundo and *Vinca*'s influences on the plant community may be due to factors other than, or in addition to, their ability to reproduce asexually. For example, the large effects of *Arundo* may result from its rapid photosynthetic (Rossa et al. 1998) and growth rates (Quinn et al. 2007), which collectively allow it to capture resources more effectively than other riparian species (see Quinn and Holt 2008). Indeed, *Arundo* is one of the fastest growing plants in the world (Perdue 1958) and has been shown to be an aggressive competitor within its introduced range (Quinn et al. 2007). *Vinca* also exhibits rapid growth rates and commonly forms extremely dense mats on the forest floor, which can greatly reduce the ability of other plant species to colonize areas that have been invaded by this vine (D'Antonio and Haubensak 1998). *Arundo* and *Vinca* may also represent "novel life forms" (*sensu* Vitousek 1986) in riparian areas. Several researchers have suggested that exotic taxa with life forms and strategies different from those in the native community may be more successful as invaders (Vitousek 1986; Alpert et al. 2000) and have greater impacts on the community (see Cushman 1995). *Arundo* is clearly a different life form than is typical of riparian communities in California (see Quinn and Holt 2008). There are very few native riparian grasses in our study system, and those that do exist—such as *Leymus triticoides*—are relatively rare specialists and quite small in stature compared to *Arundo*. *Vinca* also represents a novel life form in our system, as we know of no other species that form such low-growing, space-monopolizing mats on the floor of riparian forests.

As mentioned previously, the majority of studies that evaluate the community impacts of invasive plant species are non-experimental. Our study presents both comparative and experimental data for *Arundo*, and we were encouraged to see that we obtained fairly similar results for these two approaches, especially for native plant taxa. However, our experiment did not control for any disturbances that might have occurred due to *Arundo* removal. Although such procedural controls

are important and commonly performed (see D'Antonio et al. 1998; Alvarez and Cushman 2002), we did not feel they were necessary in our case because we did not disturb the soil when removing *Arundo*. Instead, we cut stems near ground level and painted herbicide on them. Thus, we are confident that the effects we observed were due to the absence of *Arundo* rather than an artifact arising from the way we removed this invader.

In contrast to *Arundo*, the data for *Vinca* are entirely correlative, and we thus need to evaluate hypotheses for why the presence of *Vinca* was associated large differences in the plant community. We hypothesize that these observed patterns were due to *Vinca* itself rather than this species preferentially colonizing patches of riparian understory that had low species richness and reduced abundance of individual plants. This is because the floodplain site where our studied occurred had a consistently flat topography and homogeneous soils and light levels (Gaffney 2002). Thus, the abiotic environment was quite homogeneous and would be unlikely to support vegetation patches that varied widely in plant species richness and abundance (with *Vinca* preferentially colonizing the low-richness, low-abundance patches).

When the dominance of a tenacious exotic plant is reduced, one possible outcome is that the focal invader will be replaced by a suite of different invaders rather than or in addition to a wealth of natives. For example, the experimental study of Cape Ivy mentioned previously showed that removal of this exotic clonal vine led to significant increases in seedling abundance and plant species richness of exotic taxa in both riparian and coastal scrub habitats (Alvarez and Cushman 2002). A striking result of our experiment is that only native species richness and abundance increased significantly in response to *Arundo* reduction, whereas exotics did not. We hypothesize that this difference results from predictable variation in the predominant mode of reproduction for the two groups—native plants at this site reproduced primarily by seed and exotic taxa

reproduced primarily through asexual means (Gaffney 2002). Thus, native plant species were able to respond rapidly to *Arundo* removal due to an influx of seeds whereas exotic did not have sufficient time to clonally colonize removal plots (Appendix 1).

Although biological invasions are occurring at an unprecedented geographic scale and have stimulated an international research effort, there are surprisingly few quantitative studies that address the impacts of exotic taxa on the plant communities they invade (Parker et al. 1999; Hulme 2003). Research that examines the response of native and exotic taxa at different life history stages should be especially critical for understanding the degree to which invaders influence plant communities and how systems will respond to control efforts. Here, we have explored the impacts of two clonal invaders in riparian systems and show that *Arundo* and *Vinca* reduce native plant species richness as well as the number of native seedlings and established individuals. The influence of these two invaders on exotic richness, abundance and recruitment was more variable but our experimental results for *Arundo* showed that exotic taxa did not increase after invader removal. Together, these clonal invaders represent a serious threat to the biological integrity of riparian ecosystems in California and elsewhere, one that must be addressed via effective control and restoration techniques.

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Appendix 1 Plant species encountered at three study sites (Choteau Vineyards, Clos Du Bois Vineyards, Hidden Springs Vineyards) along the Russian River in northern California

Scientific name	Common name	Origin	Life history
<i>Acer macrophyllum</i>	Big leaf maple	Native	Perennial
<i>Acer negundo</i>	Box elder	Native	Perennial

Appendix 1 continued

Scientific name	Common name	Origin	Life history
<i>Aesculus californica</i>	California buckeye	Native	Perennial
<i>Allium vineale</i>	Wild garlic	Exotic	Perennial
<i>Alnus rhombifolia</i>	White alder	Native	Perennial
<i>Anagallis arvensis</i>	Pimpernel	Exotic	Annual
<i>Artemisia douglassii</i>	Mugwort	Native	Perennial
<i>Arundo donax</i>	Giant reed	Exotic	Perennial
<i>Asclepias curassavica</i>	Milkweed	Exotic	Annual
<i>Avena fatua</i>	Wild oats	Exotic	Annual
<i>Baccharis pilularis</i>	Coyote bush	Native	Perennial
<i>Baccharis salicifolia</i>	Mulefat	Native	Perennial
<i>Brassica nigra</i>	Black mustard	Exotic	Annual
<i>Brassica rapa</i>	Field mustard	Exotic	Annual
<i>Bromus diandrus</i>	Ripgut brome	Exotic	Annual
<i>Calycanthus occidentalis</i>	Western spice bush	Native	Perennial
<i>Capsella bursa-pastoris</i>	Shepherd's purse	Exotic	Annual
<i>Carduus pyncocephala</i>	Italian thistle	Exotic	Annual
<i>Carex barbarae</i>	Santa Barbara sedge	Native	Perennial
<i>Centaurea calcitrapa</i>	Purple star thistle	Exotic	Annual
<i>Centaurea solstitialis</i>	Yellow star thistle	Exotic	Annual
<i>Chenopodium album</i>	Lamb's quarters	Exotic	Annual
<i>Conium maculatum</i>	Hemlock	Exotic	Annual
<i>Cyperus eragrostis</i>	Nut sedge	Exotic	Annual
<i>Dipsacus sativa</i>	Teasel	Exotic	Annual
<i>Epilobium ciliatum</i>	Willow herb	Exotic	Annual
<i>Eremocarpus setigerus</i>	Doveweed	Native	Perennial
<i>Foeniculum vulgare</i>	Fennel	Exotic	Annual
<i>Gallium murale</i>	Tiny bedstraw	Exotic	Annual
<i>Heteromeles arbutifolia</i>	Toyon	Native	Perennial
<i>Hordeum murinum</i>	Farmer's foxtail	Exotic	Annual
<i>Juglans hindsii</i>	Black walnut	Native	Perennial
<i>Lomatium caruifolium</i>	Lomatium	Native	Perennial
<i>Lonicera involucrata</i>	Twinberry	Native	Perennial
<i>Melilotus albus</i>	White sweet clover	Exotic	Annual
<i>Plantago lanceolata</i>	English plantain	Exotic	Annual
<i>Polypogon monspeliensis</i>	Annual beardgrass	Exotic	Annual
<i>Populus fremontii</i>	Fremont cottonwood	Native	Perennial
<i>Prunus domestica</i>	Wild plum	Exotic	Perennial
<i>Quercus agrifolia</i>	Coast live oak	Native	Perennial
<i>Quercus lobata</i>	Valley oak	Native	Perennial
<i>Raphanus sativus</i>	Radish	Exotic	Annual
<i>Rorippa palustris</i>	Cress	Exotic	Annual
<i>Rosa californica</i>	California wild rose	Native	Perennial
<i>Rubus procerus</i>	Himalayan blackberry	Exotic	Perennial
<i>Rubus ursinus</i>	California blackberry	Native	Perennial

Appendix 1 continued

Scientific name	Common name	Origin	Life history
<i>Rumex crispus</i>	Curly dock	Exotic	Annual
<i>Salix exigua</i>	Sandbar willow	Native	Perennial
<i>Salix laevigata</i>	Red willow	Native	Perennial
<i>Salix lasiandra</i>	Yellow willow	Native	Perennial
<i>Salix lasiolepis</i>	Arroyo willow	Native	Perennial
<i>Sambucus mexicana</i>	Blue elderberry	Native	Perennial
<i>Scrophularia californica</i>	California bee plant	Native	Annual
<i>Solanum americanum</i>	Nightshade	Exotic	Annual
<i>Symphoricarpos albus</i>	Snowberry	Native	Perennial
<i>Taraxacum officinale</i>	Dandelion	Exotic	Annual
<i>Toxicodendron diversilobum</i>	Poison oak	Native	Perennial
<i>Umbellularia californica</i>	California bay laurel	Native	Perennial
<i>Vinca major</i>	Blue periwinkle	Exotic	Perennial
<i>Vitis californica</i>	California wild grape	Native	Perennial
<i>Xanthium spinosum</i>	Cocklebur	Exotic	Annual

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