

Long term dynamics of *Rosa multiflora* in a successional system

Stephen E. Banasiak · Scott J. Meiners

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Abstract Long term studies of invasion dynamics are critical in developing a more complete understanding of the factors that influence species spread. To address this issue, the dynamics of the non-native invasive plant, *Rosa multiflora*, were examined using a 40-year record of successional change. The roles of biotic and abiotic factors in regulating *R. multiflora* invasion were also assessed. The invasion showed an initial 9-year time lag, followed by a 20-year period of population expansion and an ultimate decline as succession progressed. During all phases of *R. multiflora*'s invasion, there was continuous turnover within plots. Rainfall during the previous season was found to increase *R. multiflora* colonization during population expansion while tree species inhibited the invader's growth. During expansion and decline of *R. multiflora*, common associated species were often positively or negatively correlated with changes in *R. multiflora* cover. Though early population dynamics were regulated by propagule pressure, the major influence on *R. multiflora* late in succession was canopy closure. Although the invasion of this species was largely self-limiting in this

system, the species is likely to persist within late successional systems and may require management intervention.

Keywords Abiotic limitation · Deciduous forest · Old field succession · Population dynamics · Propagule pressure · *Rosa multiflora*

Abbreviations

BSS Buell-Small Succession Study

Introduction

Due to accidental, deliberate, or indirect introduction, an estimated 4,500 non-native plant species have become established in the United States (Devine 1998). Estimated economic damage for these species is \$20 billion annually (US Department of Interior 2003). Non-native invasive plants reduce the complexity and structure of invaded areas through the suppression of native species (Woods 1993; Luken and Thieret 1996; Wyckoff and Webb 1996; Hutchinson and Vankat 1997; Meiners et al. 2001). Non-native species are a major threat to biodiversity, second only to habitat destruction (Wilcove et al. 1998) and also have detrimental effects on the reestablishment of native species (Bellemare et al. 2002). Despite these well-known threats, there is a real need for long term

S. E. Banasiak
Homewood-Flossmoor High School, District 233,
999 South Kedzie Ave., Flossmoor, IL 60422, USA

S. J. Meiners (✉)
Department of Biological Sciences, Eastern Illinois
University, Charleston, IL 61920, USA
e-mail: sjmeiners@eiu.edu

studies to fully understand the many factors that influence the spread and impact of non-native invasive species in natural systems (Luken and Thieret 1996; Parker et al. 1999; Byers et al. 2002).

Most introductions of non-native species can be attributed to human actions (Sakai et al. 2001) and some of the strongest promoters of invasion are anthropogenic habitat disturbances (Lundgren et al. 2004). However, not all promoters of invasion are directly human associated as resource availability (Burke and Grime 1996; Davis et al. 2000) and propagule pressure (Drake and Lodge 2006) are often key factors in invasion. Colonizing species tend to have a limited window of expansion and growth based on the environment and successional stage of the recipient community (Gross 1980; Bartha et al. 2003; Yurkonis et al. 2005) and the window for colonization may be different even among similar species (Rankin and Pickett 1989). Therefore, we might expect similar limitations to exist for invasive non-native species.

Knowledge of the factors that control the population dynamics of invaders in succession is important for understanding overall community dynamics, habitat management, and environmental restoration. In forest communities, non-native shrubs and trees have greater cover near edges (Hunter and Mattice 2002; Lundgren et al. 2004). However, non-native species often develop dense vegetative cover at the edges, decreasing light and inhibiting their own establishment deeper into the forest (Brothers and Spingarn 1992). Other studies have also shown that closed canopy vegetation generally prevents the colonization of plant species (Bartha et al. 2003). This suggests that invasions into late successional systems, with continuous plant cover, should be relatively limited.

Non-native invasive species often alter species richness within invaded communities (Woods 1993; Wyckoff and Webb 1996; Hutchinson and Vankat 1997; Meiners et al. 2001). At the same time, areas of greater species richness are more often invaded than species poor areas (Robinson et al. 1995; Wisser et al. 1998; Levine and D'Antonio 1999; Lonsdale 1999; Huebner and Tobin 2006). While at community-wide scales, species richness and factors such as propagule supply make diverse communities more likely to be invaded, diversity may enhance community resistance at neighborhood scales (Levine 2000) acting as a regulator of invasibility (Knops et al. 1999; Levine

and D'Antonio 1999; Kennedy et al. 2002). These seemingly contradictory results may be caused by variation in how individual invaders respond to species richness and how they impact communities. There are many potential controlling factors that interact to regulate invasibility for each invader, making generalizations across a community impossible (Meiners et al. 2004), further emphasizing the need for detailed, long term studies on individual invaders to clarify these interactions.

To better understand invasion processes, this study focused on the long term dynamics of the invasive non-native, *Rosa multiflora* during secondary succession. *Rosa multiflora* is native to eastern Asia, where it is considered a mid-successional species within disturbed grasslands (Numata 1974). The species was actively promoted and spread throughout North America for its utility as a living fence, to reduce soil erosion, and for benefits to wildlife (Steavenson 1946; Hill 1983), but it quickly became a management concern because of its ability to spread and proliferate (Evans 1983). *Rosa multiflora* has become a major conservation issue in many states, with 31 states reporting it as invasive by 2006 (USDA Forest Service 2006).

Several characteristics make *R. multiflora* an invader of a wide variety of habitats. *Rosa multiflora* is an erect branching shrub with prickles on the branches and petioles. It is semi-evergreen, photosynthesizing during the winter when deciduous forest canopies are open, allowing light penetration (Robertson et al. 1994). *Rosa multiflora* is pollinated by generalist insect pollinators (Jesse et al. 2006) and its seeds are bird dispersed; however the species can also reproduce vegetatively (Szafoni 1991). *Rosa multiflora* seeds can remain viable in the soil for over 20 years (USDA Forest Service 2006).

Within invaded regions, *R. multiflora* can have varying rates of success and impacts on the native community. *Rosa multiflora* can be quite successful in invading riparian areas, thickets, and woodlands but is much less successful in mature forests where the amount of light is greatly reduced (Robertson et al. 1994). However, *R. multiflora* has been found to be one of the more prominent alien species to extend deep into forests due to its broad seed dispersal (Brothers and Spingarn 1992). In herbaceous communities, *R. multiflora* invasion results in reduced species richness through the suppression of local colonization rates (Yurkonis et al. 2005).

Rosa multiflora affects tree regeneration in a much more complex way. While tree seed predation is increased around shrubs generating an overall negative affect on forest regeneration (Meiners and LoGiudice 2003), *R. multiflora* may also enhance the survival and performance of tree seedlings once established (Meiners and Martinkovic 2002).

To investigate long term invasion dynamics, *Rosa multiflora* was examined in a permanent plot study of abandoned agricultural land in the New Jersey Piedmont. This species was chosen as a focal species due to its pervasiveness throughout the study site's successional history and its status as a regionally problematic species. With continuous data collection extending back to field abandonment, the study site provides a unique opportunity to follow the spread of and controls on *R. multiflora* invasion during succession from agricultural field to forest. These data were used to: (1) document the fine scale temporal dynamics of invader spread and decline, (2) determine community and population level controls on invasion, and (3) assess the influence of abiotic factors on invasion dynamics.

Methods

Study site and data collection

The data collected on the invasion and establishment of *R. multiflora* were taken from a long term, experimental study of successional dynamics within abandoned agricultural land in the Piedmont region of New Jersey (40°30' N, 74°34' W), the Buell-Small Succession Study (BSS). Initiated in 1958, the study consists of 10 agricultural fields abandoned in pairs over a period of 8 years (Buell et al. 1971; Pickett 1982). Fields range from 0.5 to 1 ha and were distributed across a fairly level site with uniform silt loam soils (Ugolini 1964). Fields experimentally differed in season of abandonment (autumn or spring), last crop (hay field or row crops) and final plowing regime (plowed or intact vegetation) to assess the impact of different disturbance legacies on succession (Myster and Pickett 1990). Eight of the fields are directly adjacent to an old growth mixed-oak forest. Within each field, 48 permanently marked 0.5 × 2.0 m plots were established immediately after abandonment. The 48 plots are arranged in a regular

pattern which varies somewhat with the shape of the fields. In each year (alternate years since 1979), the percent cover of all species present in each plot was recorded with the assistance of a sampling frame. These data included both understory plants and estimates of coverage for the forest canopy, when present. This study represents the longest continuous data set of post-agricultural successional change known.

Data analysis

Data analyses were restricted to years 0–40 as there was not complete replication across all fields past this period due to variation in year of abandonment. Furthermore, it is around this age that rose rosette disease had begun to appear within the site (first observed in 1999, Meiners SJ personal observation). Rose rosette disease is native to North American roses and has also begun to infect *R. multiflora* populations, leading to population declines in many areas (Epstein et al. 1997; Amrine 2002). While this disease may ultimately speed the decline of *R. multiflora* at the research site, its limited occurrence after year 40 would make conclusions difficult, and so this period was eliminated from analysis. As fields were abandoned over an 8-year period, data analyses involving time were conducted on field age rather than calendar year. All analyses were conducted using SPSS 13.0 (SPSS Inc., Chicago, IL).

Changes in the prevalence of *R. multiflora* were summarized across all 10 fields using the average cover per plot and percent frequency within each field. To maintain even replication among fields, data collected in alternate years were condensed into two-year intervals (e.g. data from years 39 to 40 were condensed into one sample). To explore those temporal changes in more detail, plot colonization and extinction rates were also calculated for each field. Data collected in alternate years were adjusted to reflect annual colonization and extinction rates (e.g. two colonization events over 2 years were coded as one in each year). Net change in plot occupancy (colonizations–extinctions) was also calculated. While the BSS data do not follow individual plants to allow direct measure of population change, we use plot occupancy as an estimate of these rates.

To understand biotic and abiotic limitations on the growth and decline of *R. multiflora*, two temporal windows of the BSS data were examined. These

windows were determined based on *R. multiflora* cover and selected to represent periods of population expansion (years 18–28) and decline (years 32–40). This analysis generates two roughly equivalent window lengths, comparable to other analyses utilizing the BSS data (e.g. Yurkonis et al. 2005).

Plant community controls on the spread of *R. multiflora* were assessed with multiple regression models for the change in *R. multiflora* cover for the windows 18–28 and 32–40. For each plot, the change in cover of *R. multiflora* during each time frame ($T_2 - T_1$) was related to several factors. To assess the impacts of individual species on change in *R. multiflora*, the cover of the 10 most abundant resident species at the beginning of the each period (years 18 and 32) were included in the model. Species richness, total tree cover, and total plot cover at the beginning of each period were also included to assess community level controls on plant performance. For this analysis, data from all 10 fields were pooled. All regression models were run forwards, backwards and stepwise, though all converged on the same final model for both periods. Multicollinearity was not a problem in this analysis as variance inflation ratios were consistently 1.236 or less. Besides the species directly tested, other less common species may have important positive or negative effects on *R. multiflora*. However, these species did not appear in sufficient numbers to produce statistically valid tests.

Average rainfall during the summer (June through August) for years 1957 to 2005 was determined and the percent deviation of each growing season from that mean was calculated using data from the New Brunswick, NJ weather station (NOAA). Deviation from average rainfall was correlated with the number of plot colonization and extinction events within each field. This analysis was done for years 9–28, the entire period over which *R. multiflora* was expanding in the site. This analysis was repeated using the prior year's growing season rainfall.

Results

Successional dynamics

Two years after abandonment, the first of the fields were colonized by *R. multiflora* with fields being invaded within 6–7 years on average (Fig. 1).

Overall, *R. multiflora* had an extended lag period when invading a newly abandoned field, a rapid growth and invasion period, and an eventual decline as succession continued towards a forested system. During the initial lag period, *R. multiflora* cover averaged less than 4% until the field reached an age of 9 years when *R. multiflora* cover began to increase sharply until age 28, when the mean plot cover was almost 30%. Even at the population peak, individual plot cover varied dramatically, ranging from 0% to 100%. After a four-year plateau at this peak, *R. multiflora* coverage declined each consecutive year to an average of 20% by year 40 (Fig. 1a). Frequency showed largely the same temporal response as cover, with several differences. A lag period, with a smoother transition into the growth phase extended until a peak of nearly 75% frequency was reached at age 32 (Fig. 1b). As with cover, a decrease followed year 32, but it was a more gradual decline.

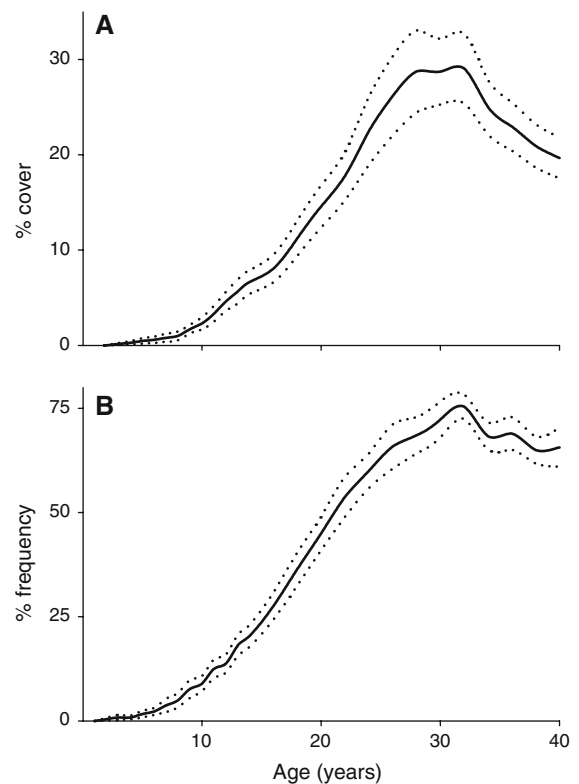


Fig. 1 Changes in the cover (a) and frequency (b) of *R. multiflora* during succession in the 10 BSS fields. Data presented are averages of the 10 fields. Dotted lines represent \pm SE

Colonization and extinction

Colonization rates started very low after abandonment but increased linearly until a maximum was reached in year 19 (Fig. 2a). After this peak, plot colonization decreased, leveling off at around three colonization events per field each year. Extinction events had a more consistent and gradual increase over time, but had a similar lag in the beginning, when the population was low (Fig. 2b). The net annual change in the number of plots occupied by *R. multiflora* (colonization–extinction) was positive and increasing until year 19, at which point net colonization decreased, although it remained positive. Extinction events exceeded colonization events in most years after age 32 (Fig. 2c).

Constraints on *Rosa* growth and expansion

Tree cover was very low for the first 10 years after abandonment and then experienced a sharp exponential increase in growth until age 30 when the rate of increase slowed down (Fig. 3). After 40 years of succession, total tree cover averaged 93% per plot. Increases in tree cover and *R. multiflora* cover were remarkably similar for the first 18 years. After this time period, tree cover continued to increase at a much greater rate than *R. multiflora* cover.

From years 18 to 28, change in *Rosa multiflora* cover was significantly associated with several factors (Table 1, $F_{5,474} = 16.37$, $P < 0.001$, $R^2 = 0.15$). *Acer rubrum* and *Juniperus virginiana* cover were inversely related to changes in *R. multiflora* cover, while *R. multiflora* was positively associated with *Lonicera japonica* and *Aster pilosus* (Table 1). Initial species richness was also positively associated with increases in *R. multiflora* cover over this time period. The remaining species included in the regression model, *Cornus florida*, *Euthamia graminifolia*, *Fragaria virginiana*, *Hieracium caespitosum*, *Poa pratensis*, *Solidago juncea*, and *Toxicodendron radicans* did not show an association with *R. multiflora* growth. Surprisingly, during this stage of succession total cover was not associated with changes in *R. multiflora* cover.

For the regression model of years 32–40, when the *R. multiflora* population was in decline, change in *R. multiflora* cover was significantly associated with several species and community metrics. Though the

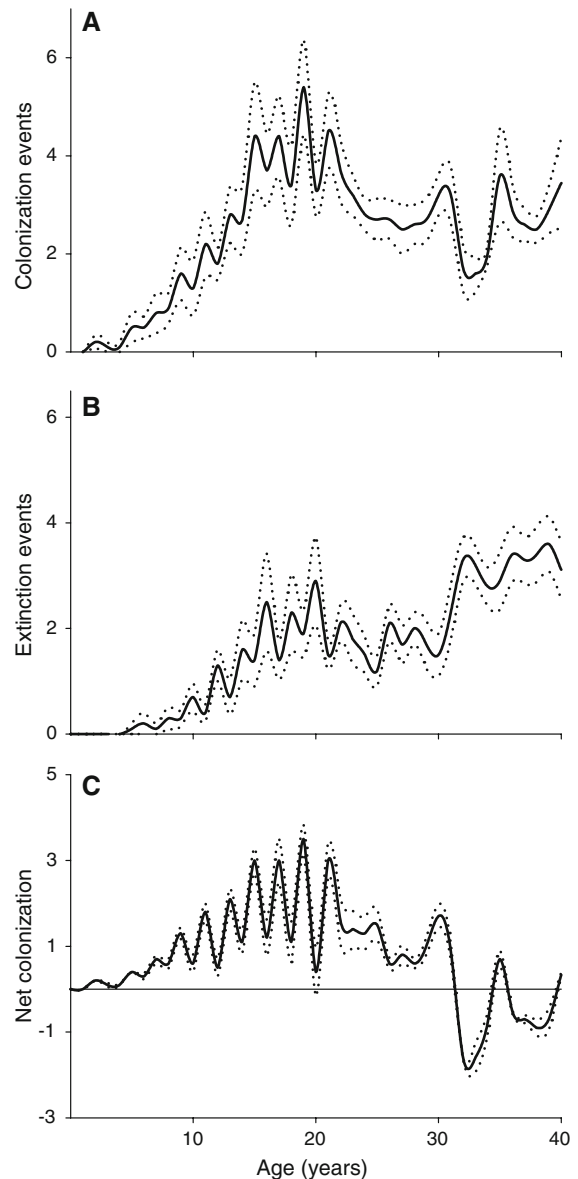


Fig. 2 Mean colonization (a), extinction (b) and net colonization rates (c) for the 10 study fields over 40 years. Reference line for net colonization rate indicates no net change in the population. Dotted lines in each panel represent \pm SE

overall population trend was for decreasing *R. multiflora* cover, the species persisted or even increased in cover in many individual plots during this period. Change in *R. multiflora* cover ($T_2 - T_1$) was positively associated with *Acer rubrum*, *Cornus florida*, *Juniperus virginiana*, *Solidago rugosa*, and *Toxicodendron radicans* (Table 1). As when *R. multiflora* cover was increasing, species richness was positively

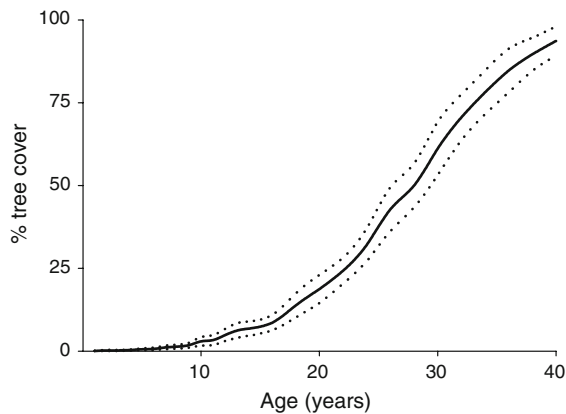


Fig. 3 Changes in total percent cover of trees in each plot over 40 years of succession. Data presented are averages of the 10 fields. Dotted lines represent \pm SE

Table 1 Multiple regression analysis of the common resident species and community attributes associated with change in *R. multiflora* cover for the period of population increase (years 18–28) and population decline (years 32–40)

Model term	β	SE	<i>P</i>
Population growth			
Intercept	-7.623	6.105	0.212
Richness	1.451	0.388	<0.001
<i>Lonicera japonica</i>	0.164	0.057	0.004
<i>Acer rubrum</i>	-0.262	0.098	0.008
<i>Juniperus virginiana</i>	-0.696	0.177	<0.001
<i>Aster pilosus</i>	0.995	0.208	<0.001
Population decline			
Intercept	-3.702	6.416	0.564
Richness	1.031	0.25	<0.001
Total cover	-0.191	0.027	<0.001
<i>Juniperus virginiana</i>	0.142	0.06	0.019
<i>Acer rubrum</i>	0.194	0.047	<0.001
<i>Toxicodendron radicans</i>	0.223	0.073	0.002
<i>Cornus florida</i>	0.159	0.049	0.001
<i>Solidago rugosa</i>	0.495	0.125	<0.001

See text for factors not retained in the analyses

associated with the change in *R. multiflora* cover. The only negative influence on *R. multiflora* cover was total cover of all species within each plot. *Acer negundo*, *Eupatorium rugosum*, *Junglans nigra*, *Lonicera japonica*, and *Parthenocissus quinquefolia* were common resident species but were not associated with change in *R. multiflora* cover during this period of decline.

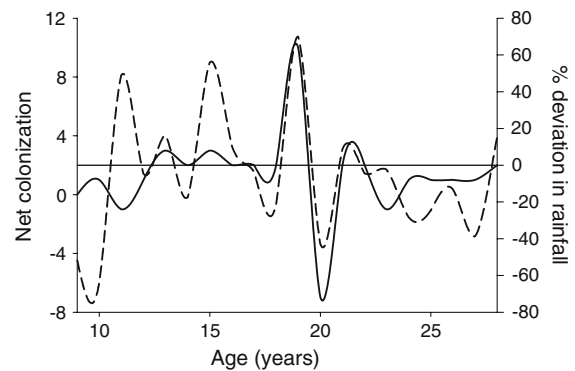


Fig. 4 An example of previous year's rainfall (dashed line) on net colonization rates (solid line) during population expansion of *R. multiflora*. Rainfall data presented as % deviation from the long-term average. The data shown are from one of the 10 fields. Reference line represents zero net colonization

The strongest association between the dynamics of *R. multiflora* and precipitation was with summer rainfall (June–August) of the previous year (Fig. 4). The number of colonization events during the period of expansion were positively correlated with the previous summer's deviation from average rainfall for all fields ($R = 0.162$, $P = 0.022$). Extinction events were negatively correlated with the previous summer's deviation from average summer rainfall ($R = -0.176$, $P = 0.013$). Net colonization rates (annual colonization–extinction) were also positively correlated with the previous summer's rainfall ($R = 0.260$, $P < 0.001$). Colonization, extinction, and net colonization were not correlated with the current year's rainfall (all $P > 0.33$).

Discussion

The long term dynamics of *R. multiflora* revealed a variety of controls on fine scale turnover that resulted in the overall population change. Early in the invasion, propagule pressure and those factors directly influencing propagule pressure, appear to be the dominant mechanisms that determine population expansion. However, population regulation switched from biotic to abiotic limitation as a forest canopy developed on the site and reduced light levels. Details of the lag time, population expansion, and population decline are addressed individually below.

Lag phase, years 0–9

Rosa multiflora exhibited a lag phase of 9–10 years before the population began to increase dramatically, even though the species appeared as early as year 2 in some fields. Competition from early successional plants and limited seed dispersal are the two most likely factors generating this time lag. At the BSS study site, *R. multiflora* was found to be one of the top three bird dispersed seeds in mid-successional habitats (McDonnell 1986), suggesting seed production and bird dispersal would not be limiting factors for *R. multiflora* expansion once established. However, the behavior of bird dispersers may be limiting within early successional habitats. Taller vegetation that act as perches recruit significantly more bird dispersed seedlings around their base (McDonnell 1986), so the amount, location, and patterns of these perch sites would effect initial dispersal. As these perch sites would be limited early in succession, dispersal of *R. multiflora* may have been limited despite its abundance in the surrounding landscape at the time of abandonment.

As the fields aged, propagule pressure would have increased as both the number of perch sites increased and *R. multiflora* shrubs within the fields became reproductive, leading to an increase in population growth rates (Deering and Vankat 1999). In addition, the change from a lag to a growth phase may reflect increased microsite availability coupled with increasing propagule pressure (Huebner and Tobin 2006). During the growth phase there would have been high turnover of early successional plants, providing sites for seedling recruitment (Prach et al. 1993; Myster and Pickett 1994). While biotic and abiotic controls may have also been important in determining the temporal extent of the lag phase, the small number of occupied plots did not statistically allow for adequate tests.

Population expansion, years 9–28

Rosa multiflora rapidly increased in cover to become one of the most dominant plants in the study site, with the average cover per plot near 30% (range 0–100%). It is during this population expansion that rainfall was found to have its strongest control on *R. multiflora* dynamics. Rainfall in the previous year increased *R. multiflora* colonization and decreased extinction while the current year's rainfall was not correlated

with dynamics. It appears that rainfall increased seed production, so that seed availability the following year would be greater, increasing colonization rates. These results further suggest that propagule pressure was crucial in regulating this invasion. The linkage of colonization rates with rainfall may be a time delayed example of the fluctuating resource availability theory of invasion (Davis et al. 2000), where greater water availability enhanced reproduction of the invader in 1 year, increasing its propagule pressure in the next. Greater rainfall may have also increased the over-winter survival of established plants, leading to net increases in the population.

Several species and community properties were important regulators of *R. multiflora* dynamics during the second half of the growth phase (years 18–28). Most notably, *R. multiflora* cover increased more in plots with higher species richness but was inhibited by the trees *Acer rubrum* and *Juniperus virginiana*. During the same period, *R. multiflora* growth was positively associated with *Aster pilosus* and *Lonicera japonica*. It has been previously found that *Lonicera japonica* decreases *R. multiflora* colonization rates within heavily invaded plots (Yurkonis and Meiners 2004), yet during the period of 18–28 years post-abandonment, there was a positive correlation with *L. japonica* cover, perhaps due to the climbing nature of both species. While total tree cover was not associated with *R. multiflora* cover, shading from two of the more abundant species in the site were associated with reduce cover of *R. multiflora*. The study site was largely susceptible to *R. multiflora* colonization and growth until canopy closure became limiting.

Population decline, years 32–40

The balance between plot colonization and extinction events never shifted towards net extinction until year 32, when *R. multiflora* cover also began to decrease. Most likely, shade associated with canopy closure was the dominant limiting factor later in succession (Robertson et al. 1994). As tree cover approached 90% across the site, *R. multiflora* was well on the decline. The increased number of plots available to *R. multiflora* late in succession did not lead to an increase in colonization, even temporarily, further suggesting that lack of light played a large role in the decrease of *R. multiflora*. During

population decline, rainfall was no longer linked with population dynamics. In general, older forests tend to produce lower exotic plant abundances due to low light levels produced by the canopy and understory strata (Robertson et al. 1994).

As trees became the main contributor to overall cover, it is surprising that *R. multiflora* cover was not associated with total tree cover during population decline. This is most likely due to differential influences of individual tree species on *R. multiflora*. During this decline, several tree species were positively correlated with changes in *R. multiflora* cover where the species was better able to persist or even expand. The tree species which influenced *R. multiflora* growth appear associated with higher subcanopy light levels or with the ability of *R. multiflora* to climb and reach higher light levels. *Juniperus virginiana* has a narrow, conical canopy, allowing light penetration to the understory. *Rosa multiflora* tends to climb on *Acer rubrum* and *Cornus florida*, allowing it to expand once in the full sun of the canopy. Since *J. virginiana* and *A. rubrum* both inhibit *R. multiflora* during population expansion, this suggests that *R. multiflora* initially has difficulty initially establishing near these species, but can persist once established near them.

During both population growth and decline, *R. multiflora* abundance was positively associated with species richness. This positive correlation between invasive species and richness (Levine and D'Antonio 1999; Robinson et al. 1995; Wisser et al. 1998; Lonsdale 1999) and specifically with *R. multiflora* (Meiners et al. 2004) has been noticed in previous studies. It appears that species rich areas are very susceptible to invasion, either due to resource abundance, openness, or other properties of species rich areas. While the positive association is likely associated with open areas and a lack of shading during population decline, the cause of the positive association between *R. multiflora* and species richness before trees dominated is not clear. This relationship is particularly interesting as *R. multiflora* reduces local species richness in this system (Yurkonis et al. 2005).

Persistence in forested habitats

Although *R. multiflora* is successful in invading established forests, it does not become dominant as

it does in abandoned agricultural fields. Non-native shrubs, including *R. multiflora*, have greater cover near edges as these areas tend to share characteristics with disturbed habitats (Brothers and Spingarn 1992; Hunter and Mattice 2002; Lundgren et al. 2004). The success of *R. multiflora* in invading established and older forests is poor compared to its invasiveness in riparian forests, edges and other more open habitats (Robertson et al. 1994; USDA Forest Service 2006). Mature forests may also possess a multilayered structure consisting of shade tolerant species, which further reduces light availability (Robertson et al. 1994; Luken 2003). Within the study site, *R. multiflora* was present in successional areas and neighboring woods as well as along thickets and roadsides at the beginning of the study. Despite this availability within the landscape, *R. multiflora* showed no signs of becoming aggressive within the old growth forest of the site (Ambler 1965). More recent observations of the old growth forest continue to show sporadic *R. multiflora* individuals, (Meiners SJ personal observation). This species will most likely persist at edges, where it is successful regardless of successional stage due to the high light and seed availability (Ambler 1965; Robertson et al. 1994; Brothers and Spingarn 1992). It seems likely that this invader will persist at low levels within these forests, periodically expanding to capitalize on openings within the forest canopy.

Conclusions

Detailed documentation of *R. multiflora* population dynamics at this site has yielded several interesting results. Despite the severity and apparent permanence of this invasion at its peak, there was constant population turnover during all stages of the invasion. This turnover should provide opportunities for resident species to persist during the invasion, but also shows the ability of *R. multiflora* populations to rebound following disturbances. The increased growth of *R. multiflora* in species rich plots suggests that beyond shading, there is little ability of the recipient plant community to resist this invasion and that invasion impacts on the community may be strong (Meiners et al. 2001). In sites such as this, where succession proceeds unimpeded to a forested system, *R. multiflora* invasions should be limited by

shading. In closed canopy forests, *R. multiflora* should remain manageable if canopy disturbances are minimized. However, canopy opening events, particularly those preceded by relatively wet years, may allow the population to expand again. However, if *R. multiflora* were to become abundant enough to reduce tree establishment in successional areas, the species may arrest succession at the shrub stage (Fike and Niering 1999).

Long term studies of pervasive non-native invaders offer great understanding of their role within communities as well as a greater comprehension of the biotic and abiotic factors that influence their populations. The shift from biotic to abiotic limitation during the invasion suggests that management strategies may also need to shift based on the phase of the invasion. While not all studies can be as lengthy and detailed as the data presented here, any measures of population dynamics, however limited, can dramatically improve our understanding of invasion and should be incorporated into monitoring schemes. This information can be critical to tailoring management and containment strategies as well as to setting management priorities.

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