RESEARCH ARTICLE

Can the Persistent Seed Bank Contribute to the Passive Restoration of Urban Forest Fragments After Invasive Species Removal?

Hannah Clements and Paulette Bierzychudek

ABSTRACT

Urban forest fragments are vulnerable to invasion by non-native species, and invaded forests are increasingly targeted for invasive species removals. Our goal was to determine the extent to which persistent seed banks can contribute to the recruitment of native forest species into urban forest fragments from which invasive plant species have been removed. In a greenhouse, we germinated seeds from soil samples from three forest fragments in Portland, Oregon, US. All sites had been invaded by *Hedera hibernica* (Irish ivy) and *H. helix* (English ivy), *Clematis vitalba* (virgin's bower), *Ilex aquifolium* (English holly), and *Prunus laurocerasus* (English laurel). At one site, these species had been removed three years prior to our study. Emergents represented 53 taxa, classified as: native forest species, native non-forest species, and non-native species. We observed few native forest species (5–12/site); 29–83% of samples contained these species, at median densities of 0–2 seeds/sample/site. Non-native species were more diverse (12–17/site), more frequent (75–89% of samples), and denser (median = 2–5 seeds/sample/site). *Clematis vitalba* seeds were especially abundant. Invasive removal had little effect on the persistent seed bank; however, the least-invaded site had the highest richness, frequency, and density of native forest species. The low richness and abundance of native forest species is not necessarily a concern, because many forest species do not form persistent seed banks. The annual seed rain can regenerate native species whose density has been diminished by invasive plant species and their removal. However, managers wishing to restore absent species should plan to follow removal efforts with active revegetation.

Keywords: emergent seedlings, ivy, native plant recruitment, non-native plant species

Restoration Recap

- Invasive species are common in urban forests and are often targeted for removal. We examined whether the persistent seed bank of three urban forests in the Pacific Northwest could contribute to restoring native forest species after invasive removal.
- The persistent seed bank contains some native forest species, but lacks many others, and also contains seeds of native non-forest species and non-native species.
- Not all native forest species produce dormant seeds, and many regenerate from annual inputs. However, desired forest species that are effectively absent, or not reproducing sexually, may require active replanting.
- The effect of invasive species on the seed bank will likely increase with time, so removal efforts should prioritize less-invaded sites where a richer native seed bank may still be present.

Urban natural areas provide many benefits (Elmqvist et al. 2015), including the preservation of biodiversity. However, because urban natural areas are typically small fragments embedded in a matrix of landscaped areas and disturbed ground, they are often heavily invaded by non-native plants (Duguay et al. 2007, Gavier-Pizarro et al. 2010). After the invasive species are removed, the native plant community may be sparsely vegetated and

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species-poor, because of decades of competition with aggressive invaders, and because removal efforts can sometimes adversely affect native species. Managers sometimes opt to engage in active revegetation of these areas, but this process is both expensive and laborious.

In more natural settings, plant communities recover from disturbances like fire, pest outbreaks, and windstorms passively, through the vegetative spread of survivors and the emergence of seedlings. Native seeds can come from surviving individuals within the disturbed area, from outside the boundaries of the disturbance, or from the persistent (sensu Thompson and Grime 1979) seed bank (Pakeman and Small 2005).

In urban natural areas, however, seeds of native species are unlikely to be transported into a fragment from outside its boundaries. If neighboring land contains only horticultural species or non-native species, the seed bank becomes particularly important for passive recovery. However, there are few studies of how the seed banks of invaded habitats are affected by species invasions and by the removal of those invasive species. Existing studies involve a limited number of invasive species, are of limited spatial extent, and have produced highly variable outcomes (reviewed in Gioria et al. 2012, 2014). Studies of the effects of invasions and of invasive removal on the seed banks of urban natural areas in particular are rarer still (but see Kostel-Hughes et al. 1998, Vidra et al. 2007, Overdyck and Clarkson 2012).

Understanding the potential of the seed bank to contribute to the restoration of urban natural areas is especially timely now. Growing awareness of the consequences of species invasions among land managers and citizens has inspired many efforts to restore invaded natural areas to a pre-invaded state (D'Antonio and Meyerson 2002, Andreu and Vilà 2011, Kettenring and Adams 2011, DiCicco 2014), though most management efforts are not described in the peer-reviewed scientific literature (Simberloff 2009). What kinds of management activities are required to achieve this goal? In particular, to what extent can managers expect the seed bank to contribute to the restoration of formerly-invaded areas? The abundance and identity of native species in the seed bank can help inform managers if passive recovery is likely, or whether active re-vegetation of desired species might be necessary.

We studied the potential of the persistent seed bank to contribute to the restoration of urban forest fragments after the removal of invasive plants in Portland, Oregon, US. Metropolitan Portland has a relatively high density of forested natural areas (Houck and Labbe 2007), but these are typically heavily invaded by non-native species, especially *Hedera helix* and *H. hibernica* (English and Irish ivy, respectively). We analyzed the persistent seed banks of three of these fragments. In one forest, invasive plants had been treated three years ago and were largely absent; in the other two, invasive species were widespread, but to differing degrees. To assess the potential of the seed bank to contribute to the restoration of the native forest community, we asked these questions:

1. What native forest species were present in each fragment? How abundant were seeds of these species?
2. What other species of seeds were present, and at what abundances?
3. Is there any evidence that removal of the invasive species affected the seed bank? For example, were seeds of the invasive species less frequent where invasive plant species were removed? Were seeds of native forest species more frequent?

Methods

Study Sites

We sampled the seed bank in three urban forests in southwest Portland, OR. All three sites are upland Douglas fir-maple forest, the most common pre-settlement plant community in the Portland area (Christy et al. 2009). This forest type is dominated by *Pseudotsuga menziesii* (Douglas fir) and *Acer macrophyllum* (bigleaf maple), with lower densities of *Tsuga heterophylla* (western hemlock), *Abies grandis* (grand fir), *Thuja plicata* (western red cedar), and *Alnus rubra* (red alder) (Christy et al. 2009). In these sites, the understory typically consists of high densities of *Polystichum munitum* (sword fern), along with a diverse shrub community whose most common species include *Oemleria cerasiformis* (Indian plum), *Symphoricarpos albus* (snowberry), and *Rubus parvifolius* (thimbleberry). *Hydrophyllum tenuipes* (waterleaf), *Claytonia sibirica* (miner's lettuce), *Galium aparine* (bedstraw), and *Trillium ovatum* (trillium) are the most common species in the herbaceous layer (Bureau of Sustainability 2016 and Bierzychudek, P., Lewis & Clark College, unpub. data). All three sites are surrounded by roads and residential development (Figure 1). The sites differ in the extent of non-native plant species invasion and in whether they have been subject to removal of the invasive species.

Our focal site (Figure 1) was the 59-ha River View Natural Area (RVNA), which was once heavily invaded by *H. helix* and *H. hibernica*, both on the ground and in the canopy, as well as by the non-native *Ilex aquifolium* (English holly) and *Prunus laurocerasus* (English laurel), at lower densities. Large woody vines of non-native *Clematis vitalba* (virgin's bower) bordered the site. In 2011, the woody stems of these species were cut and treated with triclopyr, and the ground *Hedera* was sprayed with glyphosate/triclopyr. While over 90% of sample plots contained one or more *Hedera* stems before treatment, *Hedera* was present in fewer than 20% of these plots by the time of our study three years later. Climbing stems of *Hedera*, present in over 50% of study plots before treatment, were absent in RVNA by the time of our study. The other invasive species experienced similar reductions (P. Bierzychudek, Lewis & Clark College, unpub. data).

We compared the seed bank of RVNA with that of two other sites where these invasive species were still present (Figure 1): the 40-ha southern part of Marquam Nature Park (MNP), and 3 ha of undeveloped forest on the Lewis & Clark College campus (LC) directly adjacent to RVNA. *Hedera* had likely invaded both RVNA and LC by the 1940s (S.D. Beckham, Lewis & Clark College, pers. comm.). The density of invasive species in LC was very similar to that in RVNA before treatment (P. Bierzychudek, Lewis & Clark College, unpub. data). MNP, by contrast, appeared to harbor lower densities of *Hedera* spp., *I. aquifolium*, *P. laurocerasus*, and *C. vitalba*, but we did not quantify the abundance of these species.

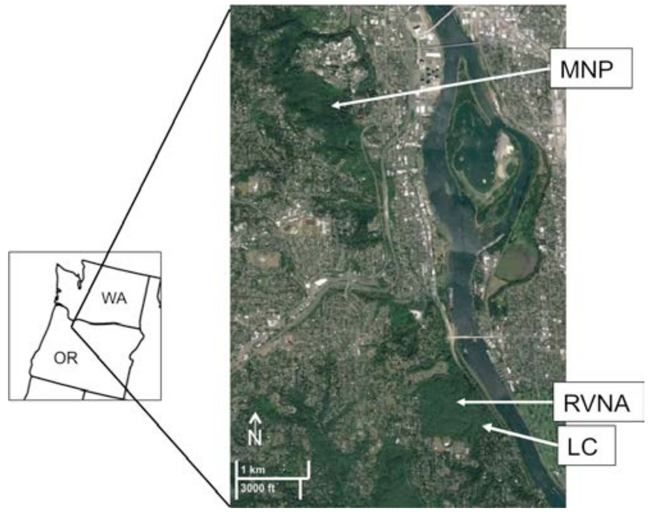

Figure 1. The three urban forests sampled in this study: River View Natural Area (RVNA), Marquam Nature Park (MNP), Lewis & Clark College campus (LC). Inset: Location of Portland, OR within the Oregon-Washington region.

Sampling and Seedling Emergence Protocols

To determine the contents of the persistent seed bank we used the seedling emergence method (Gross 1990). We collected soil samples in October-November 2014 from 90 locations in the focal forest, RVNA. We selected sampling locations by stopping along trails every 20 m, and walking left or right for a randomly-chosen distance of 5–20 m and remaining at least 5 m from trails or forest edges. We avoided steep slopes and riparian areas to avoid trampling these sensitive areas. We used the same protocol and inter-sample distance to select 40 sample locations in MNP and 24 in the much smaller LC site.

In each sampling location we removed the leaf litter and took three cylindrical soil cores of 5-cm diameter and 10-cm depth. We pooled the three cores and refrigerated them until early December 2014, then placed them in a growth chamber for 11 weeks of cold stratification. Samples experienced 10-hr "days" at 10°C and 65% RH and 14-hr "nights" at 4°C and 85% RH (Baskin and Baskin 2014). To simulate burial in the soil, the growth chamber was unlit during both "days" and "nights."

After stratification we transferred the samples to a heated greenhouse. We loosened soil clumps and spread 600 mL of each sample (~ ½ the sample volume, representing a sample area of ~ 30 cm^2) in a 1 cm layer over 700 mL of sterile potting soil (Black Gold, Sun Gro Horticulture, Agawam, MA) in an 8.5 × 7.8 × 2.9-cm plastic tray, perforated to permit drainage. We randomized container locations on greenhouse benches, interspersed with 11 control trays of sterile potting soil. We watered the containers as needed to keep the soil moist. We counted and identified emerging seedlings for six months, by which time no new seedlings had emerged for several weeks. We observed individuals until they had reached the flowering stage and/or developed mature foliage characteristics.

We classified emergents by species and placed each one into one of three ecological categories: native forest species, native species associated with habitats other than forest (hereafter non-forest species), and non-native species. For analyses by species or ecological category, we excluded seedlings whose identity was uncertain. Only 0.3% of individuals could not be identified to at least the genus level. Our authority for species identifications and origins was the Oregon Flora Project (www.oregonflora.org/index.php). To determine a taxon's ecological category, we relied on habitat information in the image collection of the University of Washington herbarium (biology.burke.washington.edu/herbarium/imagecollection.php?), Kozloff (2005), Pojar and MacKinnon (2004) and the Portland Plant List (Bureau of Sustainability, 2016).

Data Analysis

We recorded each species' frequency (presence/absence in each sample) and density (the number of seedlings of that species/sample). Density values for each species and ecological category were typically highly skewed to the right, so we report medians and ranges rather than means. Because several pairs of very similar native and non-native species or subspecies were present in our samples, 11% of the individuals could not be placed in an ecological category and were excluded in analyses involving ecological categories.

Some of our sites were sampled more heavily than others, making it difficult to compare the species composition of the sites in conventional ways. In order to compare the species richness of native forest species among sites given this difference in sample number, we created species rarefaction curves (Gotelli and Colwell 2001) that include 95% confidence clouds. When these clouds do not overlap, differences between sites are significant at the $p < 0.05$ level. We used a similar approach to determine the adequacy of our sampling protocol for detecting those species that were present. We performed our analyses in R (version 3.1.2, R

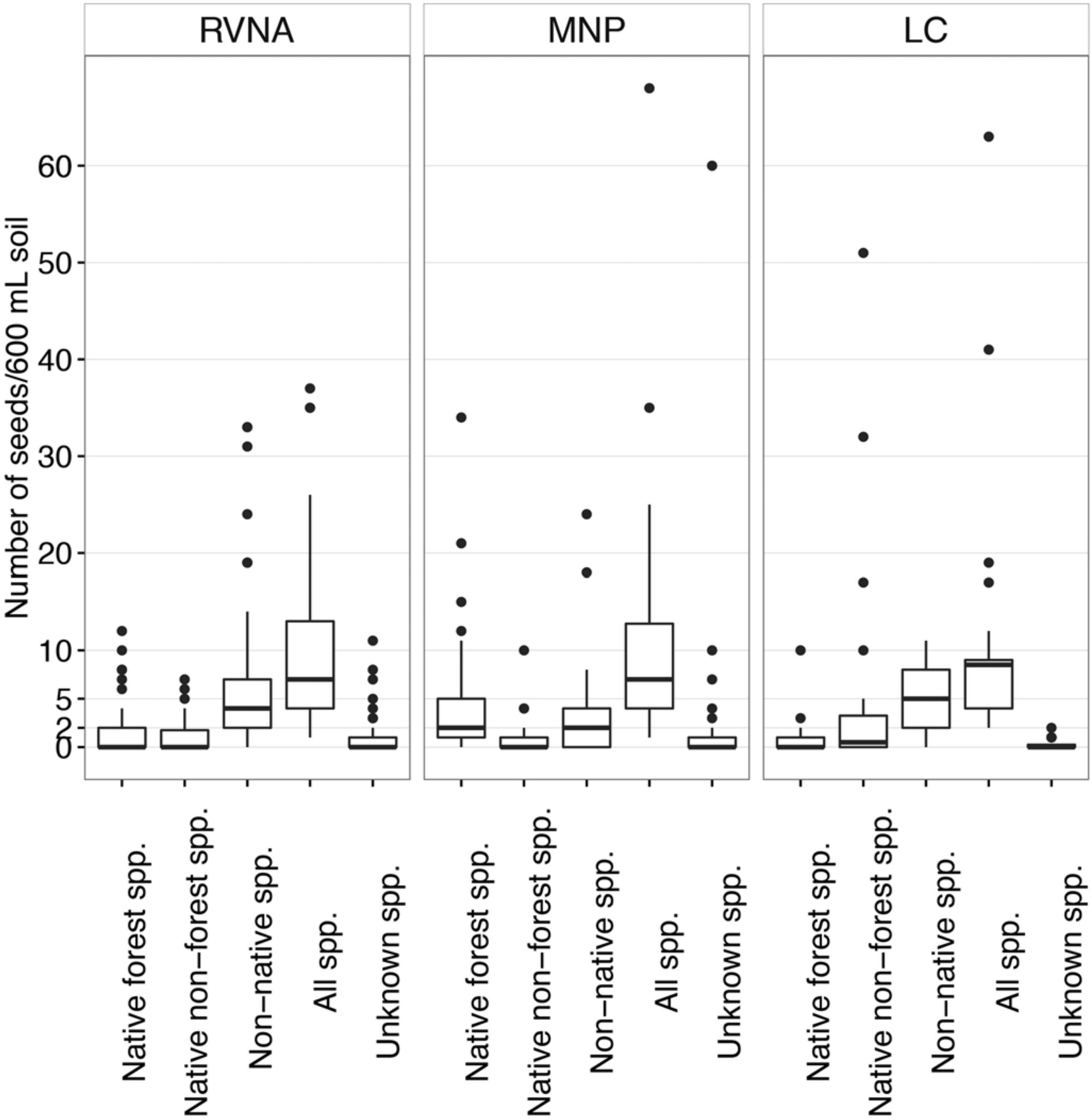

Figure 2. Density of emergents of different ecological categories per 600-mL sample from each site. Horizontal bar = median, box encloses IQR, whiskers represent data extremes that are within 1.5 IQR, dots = outliers. RVNA, N = 90; MNP, N = 40; LC, N = 24. River View Natural Area (RVNA), Marquam Nature Park (MNP), Lewis & Clark College campus (LC).

Foundation for Statistical Computing, Vienna, Austria, www.R-project.org/). To create the rarefaction curves, we used the R package "vegan" (Oksanen et al. 2015).

Results

A total of 1555 individuals representing 53 taxa emerged from the 154 samples. No control trays contained any emergents. At least one seedling (median = 7, range 1–68) emerged from every 600 mL soil sample, and the total number of emergents per sample was similar in all three forests (Figure 2).

We were able to identify 50 of the 53 taxa to at least the genus level. Of these 50, only 15 (30%) were native forest species (Table 1). An additional six (12%) were native species from non-forest habitats. At least 25 species (50%) were non-native. There were six additional taxa whose native/non-native status we could not determine. The sites

Table 1. Alphabetical list of species represented among the emergents of the three sites. Freq = proportion of samples in which a particular species was present (± SE). Density = median number of seeds/30 cm^2 × 10 cm sample (range). RVNA forest, N = 90; B: MNP forest, N = 40; C: LC forest, N = 24. River View Natural Area (RVNA), Marquam Nature Park (MNP), Lewis & Clark College campus (LC).

Species	Ecological category	RVNA freq	RVNA density	MNP freq	MNP density	LC freq	LC Density
Acer macrophyllum	forest	0	0	0.03 (± 0.03)	0 (0–1)	0	0
Agrostis exarata	nonforest	0.08 (± 0.03)	0 (0–2)	0.08 (± 0.04)	0 (0–10)	0	0
Alnus rubra	forest	0.03 (± 0.02)	0 (0–1)	0	0	0	0
Arabidopsis thaliana	non-native	0	0	0.03 (± 0.03)	0 (0–1)	0	0
Buddleja davidii	non-native	0	0	0.03 (± 0.03)	0 (0–1)	0	0
Campanula scouleri	forest	0	0	0	0	0.08 (± 0.06)	0 (0–1)
Cardamine sp.	omitted	0.06 (± 0.02)	0 (0–5)	0.08 (± 0.04)	0 (0–3)	0.08 (± 0.06)	0 (0–1)
Carex leptopoda	forest	0.01 (± 0.01)	0 (0–1)	0.05 (± 0.03)	0 (0–1)	0	0
Centaurium erythraea	non-native	0.01 (± 0.01)	0 (0–1)	0.13 (± 0.05)	0 (0–22)	0	0
Cirsium arvense	non-native	0.04 (± 0.02)	0 (0–1)	0.08 (± 0.04)	0 (0–1)	0.13 (± 0.07)	0 (0–1)
Cirsium vulgare	non-native	0.04 (± 0.02)	0 (0–1)	0.03 (± 0.03)	0 (0–1)	0	0
Claytonia sibirica	forest	0.16 (± 0.04)	0 (0–5)	0.03 (± 0.03)	0 (0–1)	0	0
Clematis vitalba	non-native	0.73 (± 0.05)	2 (0–31)	0.15 (± 0.06)	0 (0–4)	0.75 (± 0.09)	1 (0–9)
Deschampsia sp.	nonforest	0.01 (± 0.01)	0 (0–1)	0	0	0	0
Epilobium ciliatum	nonforest	0.38 (± 0.05)	0 (0–7)	0.23 (± 0.07)	0 (0–2)	0.42 (± 0.1)	0 (0–51)
Erechtites minima	non-native	0	0	0.03 (± 0.03)	0 (0–1)	0	0
Galium sp.	nonforest	0.02 (± 0.02)	0 (0–1)	0	0	0	0
Geranium robertianum	non-native	0	0	0.03 (± 0.03)	0 (0–1)	0	0
Geum sp.	omitted	0.01 (± 0.01)	0 (0–1)	0.08 (± 0.04)	0 (0–7)	0.08 (± 0.06)	0 (0–1)
Hypericum perforatum	non-native	0.01 (± 0.01)	0 (0–1)	0	0	0.17 (± 0.08)	0 (0–6)
Juncus bufonius	omitted	0.17 (± 0.02)	0 (0–11)	0.1 (± 0.05)	0 (0–58)	0.08 (± 0.06)	0 (0–1)
Juncus effusus subsp. *pacificus*	nonforest	0.04 (± 0.02)	0 (0–6)	0.08 (± 0.04)	0 (0–2)	0.13 (± 0.07)	0 (0–17)
Lactuca muralis	non-native	0.04 (± 0.02)	0 (0–1)	0	0	0.08 (± 0.06)	0 (0–3)
Lactuca serriola	non-native	0.01 (± 0.01)	0 (0–1)	0	0	0.08 (± 0.06)	0 (0–1)
Lapsana communis	non-native	0.01 (± 0.01)	0 (0–10)	0.03 (± 0.03)	0 (0–1)	0	0
Luzula parviflora	forest	0.04 (± 0.02)	0 (0–3)	0.13 (± 0.05)	0 (0–1)	0	0

Table 1., *continued*

Species	Ecological category	RVNA freq	RVNA density	MNP freq	MNP density	LC freq	LC Density
Medicago polymorpha	non-native	0	0	0.03 (± 0.03)	0 (0–1)	0	0
Mitella caulescens	forest	0.01 (± 0.01)	0 (0–2)	0	0	0	0
Oenothera biennis	non-native	0	0	0	0	0.04 (± 0.04)	0 (0–3)
Oxalis corniculata	non-native	0.33 (± 0.05)	0 (0–7)	0.35 (± 0.08)	0 (0–3)	0.25 (± 0.09)	0 (0–5)
Paulownia tomentosa	non-native	0.1 (± 0.03)	0 (0–29)	0.05 (± 0.03)	0 (0–1)	0.04 (± 0.04)	0 (0–1)
Phacelia nemoralis	forest	0	0	0.03 (± 0.03)	0 (0–1)	0	0
Plantago major	non-native	0	0	0.03 (± 0.03)	0 (0–1)	0	0
Pseudognaphalium stramineum	nonforest	0.03 (± 0.02)	0 (0–1)	0.05 (± 0.03)	0 (0–2)	0	0
Ranunculus repens	non-native	0.01 (± 0.01)	0 (0–1)	0	0	0	0
Ranunculus uncinatus	forest	0	0	0.03 (± 0.03)	0 (0–1)	0	0
Ribes sanguineum	forest	0.02 (± 0.02)	0 (0–1)	0.08 (± 0.04)	0 (0–1)	0	0
Rubus bifrons	non-native	0.2 (± 0.04)	0 (0–3)	0.38 (± 0.08)	0 (0–5)	0.46 (± 0.1)	0 (0–4)
Rubus parvifolius	forest	0.16 (± 0.04)	0 (0–4)	0.43 (± 0.08)	0 (0–5)	0.04 (± 0.04)	0 (0–3)
Rubus sp.	omitted	0.11 (± 0.03)	0 (0–2)	0.13 (± 0.05)	0 (0–2)	0	0
Rubus ursinus	forest	0.06 (± 0.02)	0 (0–9)	0.15 (± 0.06)	0 (0–5)	0.08 (± 0.06)	0 (0–1)
Rumex obtusifolius	non-native	0.01 (± 0.01)	0 (0–1)	0	0	0	0
Sagina procumbens	non-native	0	0	0.03 (± 0.03)	0 (0–3)	0	0
Sambucus sp.	forest	0.03 (± 0.02)	0 (0–1)	0.13 (± 0.05)	0 (0–5)	0.04 (± 0.04)	0 (0–1)
Senecio sylvaticus	non-native	0.01 (0.01)	0 (0–1)	0.05 (± 0.03)	0 (0–1)	0	0
Sonchus oleraceus	non-native	0.02 (± 0.02)	0 (0–1)	0	0	0.04 (± 0.04)	0 (0–1)
Stellaria crispa	forest	0.03 (± 0.02)	0 (0–3)	0.03 (± 0.03)	0 (0–1)	0	0
Tolmiea menziesii/Tellima grandiflora	forest	0.1 (± 0.02)	0 (0–11)	0.28 (± 0.07)	0 (0–33)	0.08 (± 0.06)	0 (0–10)
Trifolium repens	non-native	0.02 (± 0.02)	0 (0–10)	0.1 (± 0.05)	0 (0–7)	0.08 (± 0.06)	0 (0–1)
Verbascum thapsus	non-native	0.01 (± 0.01)	0 (0–1)	0	0	0.04 (± 0.04)	0 (0–2)
Unknown grass	unknown	0	0	0	0	0.04 (± 0.04)	0 (0–1)
Species E	unknown	0.01 (± 0.01)	0 (0–2)	0	0	0	0
Species I	unknown	0.01 (± 0.01)	0 (0–1)	0	0	0	0

differed somewhat in their richness of native forest species; we observed a total of 12 native forest species from MNP samples, 11 from RVNA, and 5 from LC (Figure 3). While the difference in native forest species richness between MNP and RVNA may seem small, it is important to recognize that we sampled less intensively at MNP. The species rarefaction curves (Figure 3), which account for differences in sampling intensity at these sites, show that the richness of native forest species at MNP is significantly higher than that at RVNA and LC, and that this difference would be predicted to increase with a greater sampling effort at MNP. There is no significant difference between RVNA and LC in the richness of native forest species, though there is the suggestion that a greater sampling intensity at LC might ultimately reveal that RVNA is more species-rich.

All three sites produced emergents from all three ecological categories, native forest species, native non-forest species and non-native species. However, the sites differed in the relative abundance of these categories. At RVNA and LC, non-native species were the most frequent emergents, occurring in nearly 90% of the samples (Figure 4). At RVNA and LC, native forest species and native non-forest species were about equally frequent, occurring in 30–50% of samples (Figure 4). By contrast, at MNP, native forest species were the most frequent emergents, occurring in 82.5% of samples. Non-native species were somewhat less frequent at MNP (< 75% of samples), and native non-forest species occurred in only about 40% of the MNP samples (Figure 4).

Density patterns showed similar trends (Figure 2). At both RVNA and LC, the density of non-native emergents per sample (median = 4 and 5 at RVNA and LC, respectively) was approximately five times greater than those from the other two categories. However, at MNP, seeds of forest natives and of non-natives were similarly dense (median = 2 seeds/sample).

While the relative abundance of forest and non-native species differed among sites, the identities of the species represented were similar. Figure 4 displays the species that occurred in at least 10% of samples in at least one of the sites. The most frequent forest herbs were C. *sibirica*, *Tolmiea menziesii* (piggyback plant), and *Tellima grandiflora* (fringecup), related species whose nonflowering individuals cannot be reliably distinguished. Common woody species were *R. parvifolius*, *Rubus ursinus* (dewberry) and *Sambucus* spp. (red and blue elderberry). *C. sibirica* was the only one of these not occurring at all of the sites; it was absent from the LC samples. Many other species occurred less frequently (Table 1). All of the trees and most of the woody shrubs occurring in the aboveground community at these sites, such as *O. cerasiformis* and *S. albus*, were absent from our samples. Two herbs that were common in the understory, *H. tenuipes* and *T. ovatum*, were also absent from our samples.

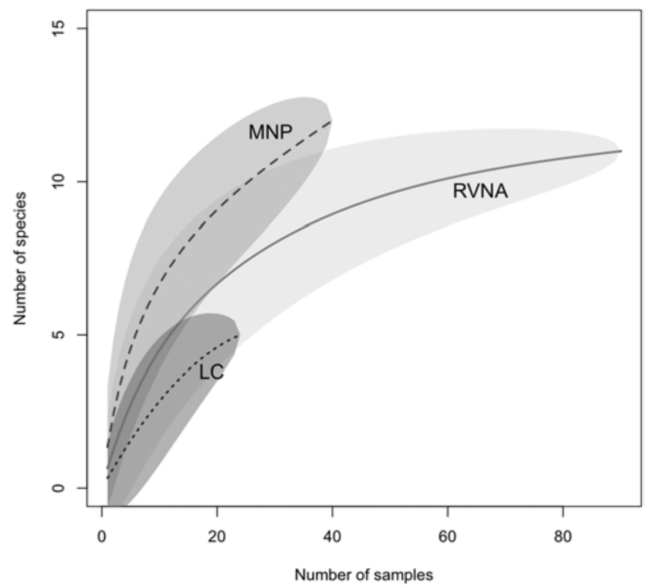

Figure 3. Rarefaction curves for the richness of native forest species at each site. Gray clouds represent 95% confidence intervals. Non-overlapping clouds indicate the existence of significant differences at $p < 0.05$. River View Natural Area (RVNA), Marquam Nature Park (MNP), Lewis & Clark College campus (LC).

The most frequent non-native species by far was *C. vitalba*, which occurred in ~ 75% of the RVNA and LC samples, and in ~ 15% of the MNP samples. Other frequent non-native species were *Rubus bifrons* (Himalayan blackberry), *Oxalis corniculata* (yellow wood sorrel), *Trifolium repens* (white clover), and *Hypericum perforatum* (St. John's wort). Many other non-native species occurred less frequently; we observed 17 non-native species from RVNA and MNP samples and 12 from LC samples (Table 1). Though all sites had medium-heavy *Hedera* cover either at the time of sampling or only a few years previously, no *Hedera* seedlings emerged from any samples. We also did not observe any emergents of two other taxa that were removed from RVNA, *I. aquifolium* and *P. laurocerasus*.

Rarefaction analysis suggests that we captured most of the common species in the seed banks of these three sites, but that there are other, less frequent, species present that we missed, particularly at MNP. None of the curves (Figure 5) reached a plateau, but all three are decelerating, which indicates that additional samples would add new species at a slower rate. However, there is no reason to expect that data from these less-frequent species would change the broad patterns we describe here, except for reported levels of species richness.

Discussion

These results provide several insights about the effects of invasive removal on the persistent seed bank. Because our different conditions (invasive species present vs. removed)

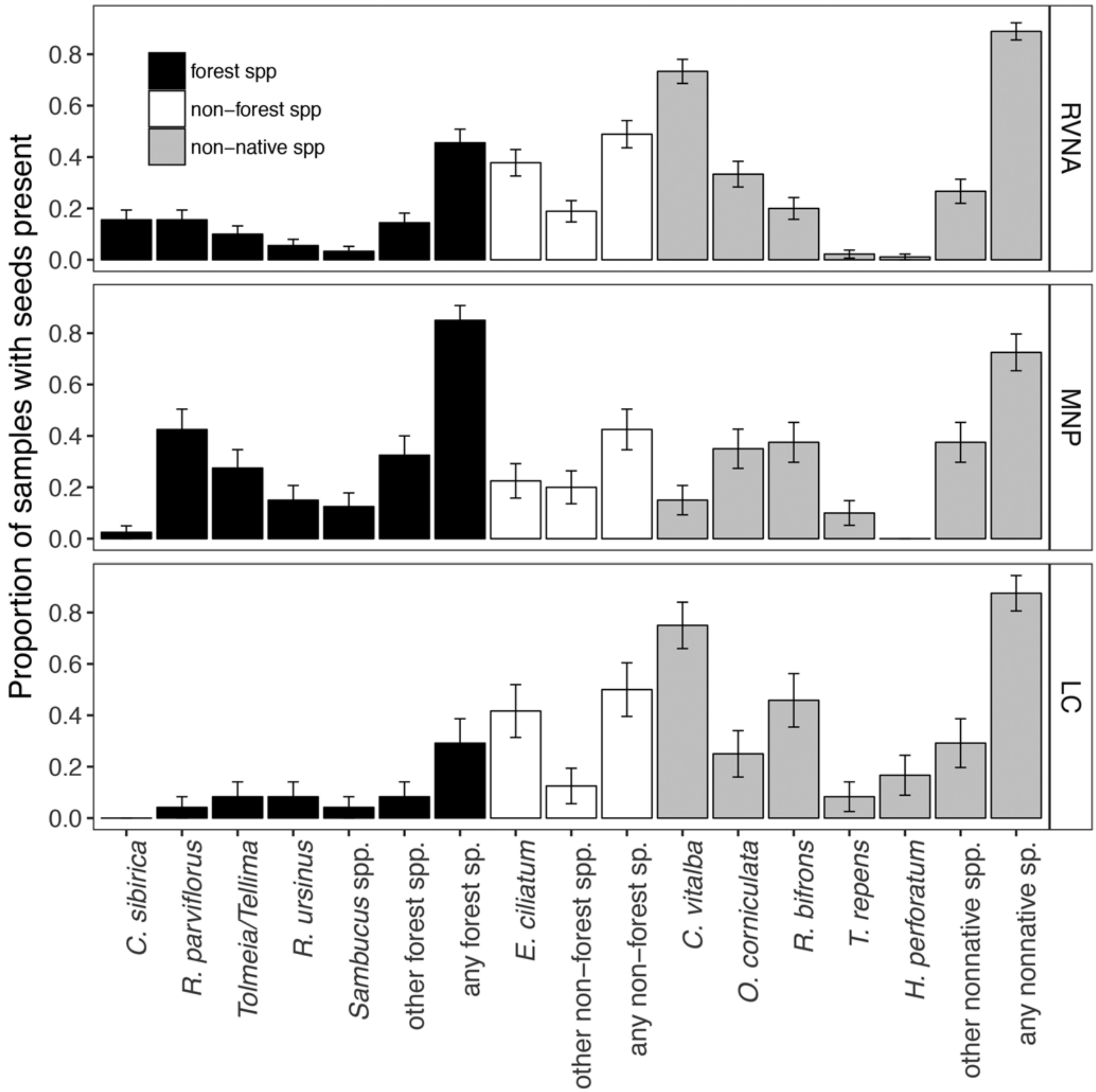

Figure 4. The frequency of emergents of common species and of different ecological categories in each site. Bars represent the proportion of samples containing emergents from a particular species or category ± one se. RVNA, N = 90; MNP, N = 40; LC, N = 24. River View Natural Area (RVNA), Marquam Nature Park (MNP), Lewis & Clark College campus (LC).

were not replicated, we cannot draw definitive conclusions about the effects of invasive removal. However, it is notable that we observed only minor differences between the seed banks of LC (where invasive species were present at high density) and of RVNA (where invasive species had been removed). RVNA's seed bank did contain more *C. sibirica* seeds than the other forests; this annual native forest herb increased rapidly after invasive species were removed (P. Bierzychudek, Lewis & Clark College, unpub. data). Overall, however, the removal of invasive species has not had a large effect on RVNA's seed bank. There were no clear differences in the richness of native forest species between RVNA and LC. Three years after invasive control, non-native emergents were still more frequent at RVNA than were emergents of native species, just as they were at LC.

These non-native emergents were predominantly *C. vitalba*. The wind-dispersed seeds of *C. vitalba* were present in most samples in RVNA and LC, as well as in some of the MNP samples. The other three invasive plant

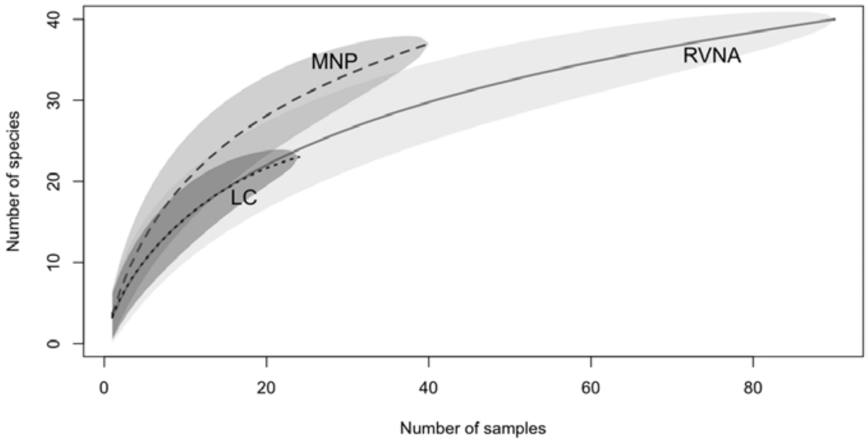

Figure 5. Rarefaction curves for each site for all species observed in the samples. Gray clouds represent 95% confidence intervals. River View Natural Area (RVNA), Marquam Nature Park (MNP), Lewis & Clark College campus (LC).

taxa that were removed at RVNA, *Hedera* spp., *I. aquifolium*, and *P. laurocerasus*, were not detected in the seed bank of any of the sites. Under a closed canopy, *Hedera* spp. spread vegetatively and produce seeds only when the vines can climb trunks to reach higher light levels. In addition, neither *Hedera* spp. nor *I. aquifolium* seeds possess the deep dormancy required for persistence in the seed bank (Thompson et al. 1997). The third absent species, *P. laurocerasus*, rarely produces fruit in the dark interior of the forest.

The greatest difference we observed was not between RVNA, the site where invasive species were removed, and those where they remained intact. Instead, it was between the seed bank of MNP, the less-invaded site, and those of the other two sites. MNP had greater richness and higher abundance of native forest species. It also had fewer non-native species and a lower density of non-native seeds. Variation between MNP and the other sites in slope, elevation, and the nature of the matrix may underlie some of these differences, but MNP's more native-rich seed bank may also reflect the lower density of invasive species in its plant community and/or a shorter history of invasion. Because MNP is similar to the other sites in degree of human use and the presence of deer, these factors are unlikely contributors to the observed differences.

While the density of seeds/sample we observed is comparable to seed bank densities in non-urban, non-fragmented forests (Kellman 1970, Kramer and Johnson 1987, Pickett and McDonnell 1989), only a few native forest species were well-represented, and they occurred in relatively few samples. The richness of native forest species we observed in the seed banks of these sites was only one-third that of the aboveground plant community at RVNA (P. Bierzychudek, Lewis & Clark College, unpub. data). Many of the species represented in the seed bank were either non-natives or native species typically associated not with forests but with disturbed ground or earlier successional stages (Bureau of Sustainability 2016).

However, the paucity of native species in these urban forest seed banks does not necessarily lead to the conclusion that they have limited potential to contribute to the recovery of the native forest community. Even non-fragmented, non-urban forest seed banks contain relatively low numbers of forest herb and tree species (Kellman 1970, Pickett and McDonnell 1989, Bossuyt and Honney 2008) and relatively high numbers of non-native species (Halpern et al. 1999, Leckie et al. 2000, Stark et al. 2006, Andreu et al. 2009) or of native species that are early-successional or disturbance-associated (Pickett and McDonnell 1989). In general, the similarity between the standing vegetation of forests and the species composition of their persistent seed banks is low (Pickett and McDonnell 1989, Kostel-Hughes et al. 1998, Halpern et al. 1999, Hopfensberger 2007, Bossuyt and Honnay 2008). Instead of being present in persistent seed banks, many long-lived forest species have alternative regeneration strategies (Pickett and McDonnell 1989). For example, many tree species produce abundant seeds every year; those with episodic seed production, e.g., *A. macrophyllum*, persist as seedling or sapling banks (Plotkin et al. 2013). Many forest herbs have stolons, corms, or bulbs that allow them to persist and spread; sexual reproduction by these species can be relatively uncommon and still suffice for replacement (Bierzychudek 1982, Leckie et al. 2000).

The species whose scarcity in the seed bank is most concerning are the woody shrubs that typically make up the forest understory. These species rarely flower or set fruit in the dark forest interior, so they are not present even in the transient seed bank. Notably, the only two native forest shrubs well-represented in our samples were *R. parvifolius* and *Sambucus* spp. These bird-dispersed species are common components of seed banks in many urban (Kostel-Hughes et al. 1998, Vidra et al. 2007) and non-urban forests (Kellman 1970, Halpern et al. 1999, Leckie et al. 2000, Andreu et al. 2009), presumably because they can reproduce in light gaps and forest edges and be carried into the forest interior by birds.

Invasive removal requires a large commitment of time and resources, and does not often lead to increases in native plant cover (Kettenring and Adams 2011). Compared to larger, non-urban forests, small forest fragments embedded in an urbanized matrix have limited re-establishment routes. In forested natural areas in the Pacific Northwest that experience invasive removal, some herbaceous and bird-dispersed woody species can be expected to recruit from the persistent seed bank. Most trees can be expected to regenerate via the annual seed production of canopy individuals. But many forest species, particularly shrubs, will not regenerate passively, and the restoration of these native forest species may require active re-vegetation.

The frequency of *C. vitalba* seeds in the seed bank may also be seen as a cause for concern in these forests. It may take many years for these seeds to disappear from the seed bank. However, despite its abundance in RVNA, *C. vitalba* has so far not successfully reinvaded this site, though small seedlings have been observed (personal observation). As a species typically found in light gaps and along forest edges, the potential for its re-invasion may be limited to those specific high-light microhabitats, which will need to be closely monitored.

Finally, our finding that MNP's seed bank contained the highest frequency of native species, and the highest richness of native forest species, suggests that invasive species' effects on the seed bank may increase with the degree and duration of the invasion. Because a forest in the early stages of invasion will have experienced fewer reductions in the richness and density of its native species, restoration may require less intervention in such sites and may be more successful. For this reason, treatment of invasive species in lightly-invaded sites should perhaps be prioritized over treatment of sites where an invasion is further advanced.

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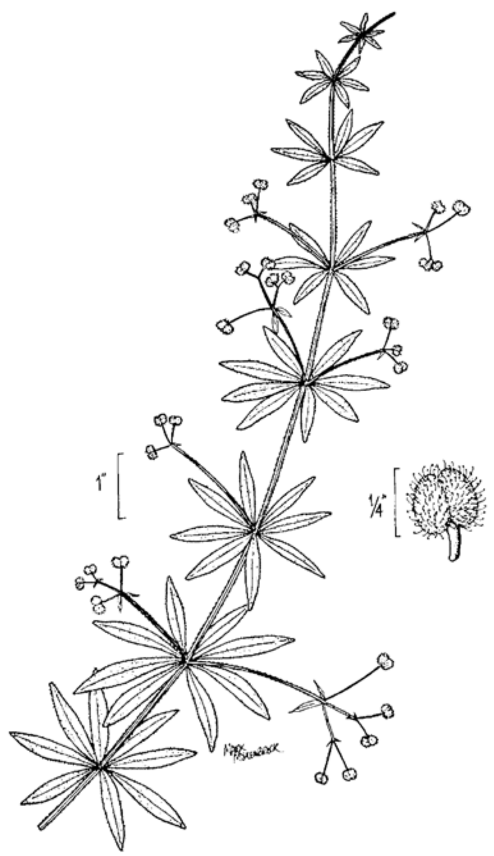
Hannah Clements, Department of Biology, Lewis & Clark College, Portland, OR 97219. Current address 19704 21st Ave NW, Shoreline, WA 98177.

Paulette Bierzychudek (corresponding author), Department of Biology, Lewis & Clark College, Portland, OR 97219, bierzych@lclark.edu.



Galium aparine. **USDA-NRCS PLANTS Database.** ***Wetland Flora: Field Office Illustrated Guide to Plant Species.*** **NRCS National Wetland Team.**