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Incipient Invasion of Urban and Forest Habitats in New Hampshire, USA, by the Nonnative Tree, *Kalopanax septemlobus*

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We analyzed the recent (< 25 yr) spread in New Hampshire, USA, of the exotic tree *Kalopanax septemlobus*, native to Asia. The invasion was likely initiated by a single tree planted ca. 1972. Our objective was to assess the viability of the invasion, especially in light of the small propagule size. We tallied, mapped, aged, and measured the height and growth of *K. septemlobus* individuals at two sites, the University of New Hampshire campus (UC) and Thompson Farm (TF), both in Durham. We found over 3,800 plants at UC and 270 at TF in < 120 ha (296 ac) total area. Plant age ranged from 0 to 22 yr, and UC plants were as far as 775 m (2,543 ft) from the purported parent tree. Annual height growth was comparable to midtolerant native trees. Plants occurred in both open and forested habitats, and the mean level of photosynthetically active radiation incident on understory plants was 4 to 6% of full sun. The large population size, shade tolerance, rapid height growth, and ability to sprout from damaged stems suggest potential for *K. septemlobus* to invade and persist in forests, the most common natural ecosystem in the northeastern United States. We further suggest that small propagule size, likely a single tree, has not prevented *K. septemlobus* from initiating a spatially extensive and vigorous population. *Kalopanax septemlobus* has been planted as an ornamental in the northeastern United States, and prevention of region-wide invasion might depend on removal of these trees, even when they occur as single individuals.

Nomenclature: Castor-aralia, *Kalopanax septemlobus* (Thunb.) Koidz.

Key words: Age structure, biological invasion, exotic tree, propagule pressure, shade tolerance.

Little research has been done on the earliest stages of exotic tree invasions. One obvious reason is that most invasions are not detected until they are well developed. Even when early detection occurs, researchers can be reluctant to allocate time and effort to relatively small, young, exotic populations whose existence might be quickly terminated by demographic, environmental, or genetic stochasticity (Shaffer 1987), or Allee effects (Courchamp et al. 2008). Such reluctance might be more likely when invaders are trees, whose spread can be slowed by delayed reproduction (Frappier et al. 2003; Larkin 2012; Richardson et al. 1994; Wangen and Webster 2006; Webster et al. 2006).

Yet much may be learned from studies of incipient tree invasions. Although the most important inference might be the potential impact of the invasion (e.g., Vanhellemont et al. 2010; Wangen and Webster 2006; Zenni and Simberloff 2013), such studies might also suggest invasion pattern and process. For example, mapping of exotic *Acer platanoides* L. coupled with tree ring analysis allowed inferences to be made about lag times, spread rates, tolerance of suppression, and roles of roads and disturbances in facilitating spread (Wangen and Webster 2006; Wangen et al. 2006; Webster et al. 2005). Langdon et al. (2010) used young *Pinus contorta* Douglas *ex* Loudon plantations in Chile to describe spatial patterns of dispersal, and data from a 70-yr-old *Ficus carica* L. invasion in California allowed Holmes et al. (2014) to estimate spread rates and identify intrinsic limits to spread, including shade tolerance and pollinator availability.

Study of incipient tree invasions might also shed light on the role of propagule pressure in invasion success. Vanhellemont et al. (2009) attributed a less aggressive *Prunus serotina* Ehrh. invasion in Belgium, in part, to low connectivity to seed sources. Studying recruitment around isolated, 45-yr-old *Pinus* plantations in Brazil, Zenni and Simberloff (2013) found that the number of colonizing

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Management Implications

Castor-aralia (*Kalopanax septemlobus*) is capable of spreading via seed from planted individuals to urban and natural forest landscapes in southeastern New Hampshire. The invaded forest types, eastern white pine and sugar maple–beech–red oak, are common in the northeastern United States. Although the impact of castor-aralia on North American communities and ecosystem processes is not yet known, colonization of forest understories and rapid height growth there suggest it is capable of competing with economically important native plants. At present, early detection coupled with rapid removal is a sensible strategy.

Because a single castor-aralia individual is capable of seed production, even small populations and isolated individuals should be eradicated. The large potential dispersal distance and success of seedlings in human-influenced habitats means that even isolated plants in urban environments, including those at urban arboretums, should be removed. Data on age and size of first reproduction are limited, but generally trees must be > 20 cm in diameter at breast height or in their second decade of life before they produce seed. Consequently, in populations of diverse age and size, trees exceeding these values should have first priority for removal. The long juvenile period also means that once all trees have been removed from a site, a second round of control need not occur for ca. 10 yr.

No data on herbicide effects are available for castor-aralia, but plants can be killed by uprooting. The ability of cut plants to produce root and butt sprouts, however, means that removal of entire plants including major roots is essential.

individuals (propagule number) and the number of source populations (propagule diversity) were positively related to a species' invasion success. The recent spread in North America of *Pyrus calleryana* Decne., coupled with historical information about its introduction, allowed Culley and Hardiman (2007) to identify cultivar diversity as enabling invasion of this sexually self-incompatible species. Such findings are important because propagule pressure is emerging as a fundamental variable in invasion biology (Colautti et al. 2006; Simberloff 2009; Lockwood et al. 2005).

Here we analyze the recent spread of the exotic tree *Kalopanax septemlobus* (Thunb.) Koidz. (Araliaceae), commonly known as castor-aralia, in New Hampshire, USA. A single *K. septemlobus* seedling was planted on the University of New Hampshire (UNH) campus in Durham between 1971 and 1975. We are unaware of any other planted *K. septemlobus* in Durham or adjacent towns. In 2007, seedlings of this species were observed on campus and in forested portions of the UNH-owned Thompson Farm ca. 3 km (1.9 mi) away. Further reconnaissance revealed multiaged populations at both sites, prompting the research reported here.

The unusual circumstance of an invasion potentially attributable to a single "parent" tree compelled us to use demographic and distributional data to make inferences about the viability of the invasion and the possibly limiting role of propagule size. Our specific objectives were to: (1) describe the spatial distribution, age structure, and height growth of the two *K. septemlobus* populations; (2) characterize the colonized habitats, including light levels in the understory of the invaded forest; and (3) assess the potential for further persistence and spread.

We document here for the first time the invasive potential of *K. septemlobus* in the northeastern United States. Although our work was partly motivated by the opportunity to study an incipient tree invasion, it was also driven by growing concern about the effects of over 20 woody invasive species already present in eastern North American forests (Webster et al. 2006). Early detection and rapid response in the case of *K. septemlobus* might prevent yet another exotic plant, with potentially negative effects on forest ecosystems, from burdening natural resource managers.

Materials and Methods

Species Description. Native to China, Korea, and Japan (Sakaguchi et al. 2012), *Kalopanax septemlobus* is a broadleaf, deciduous forest tree capable of reaching > 30 m in height and > 1.5 m in diameter (Iida and Nakashizuka 1998). In its native forests, *K. septemlobus* is intermediate in shade tolerance (Iida and Nakashizuka 1998) and forms a persistent seedling bank (Abe et al. 2002) that is released by formation of canopy gaps (Abe et al. 1995, 2002; Masaka et al. 2012). Flowers are protandrous hermaphrodites requiring a pollen vector, either bees (Fujimori et al. 2006b) or wind (Jung et al. 2003). The bird-dispersed seeds are contained within fleshy blue drupes that ripen in the fall (Iida and Nakashizuka 1998).

Kalopanax septemlobus was introduced to the United States in 1865 for use as an ornamental (Pijut 2008), a use that continues today (e.g., Dirr 2009). Although its distribution and invasive status in the United States have not been documented in the peer-reviewed literature, other sources indicate that *K. septemlobus* has been widely planted (e.g., North American Invasive Species Council 2014), and one source states that a major arboretum "…distributed the plant to schools across the country in 1972 …" (Swearingen et al. 2010). The latter program might account for the tree planted in Durham, NH. *Kalopanax septemlobus* is listed by several nonpeer-reviewed sources as invasive in North America (e.g., Ochs and Fellows 2010) and seedlings have been reported from disturbed forest in Michigan (Reznicek et al. 2011). However, *K. septemlobus* is not included in the recently updated global database of invasive alien trees and shrubs (Rejmánek and Richardson 2013).

Site Description. Research was conducted at two sites, the University of New Hampshire (UNH) campus and the

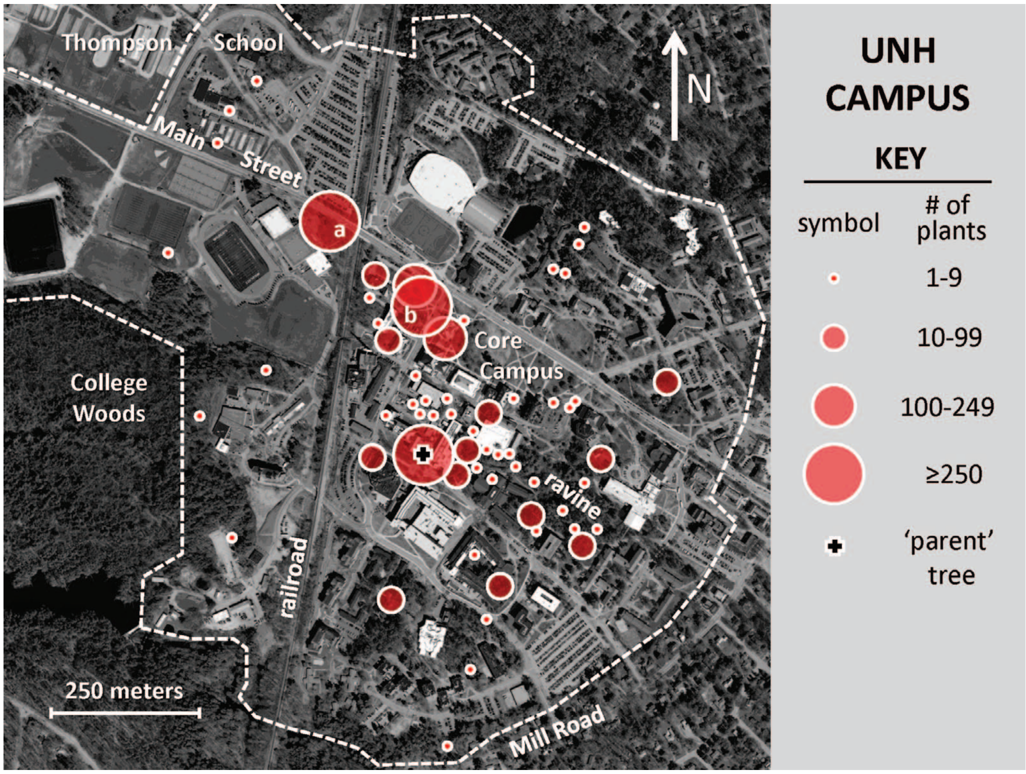

Figure 1. Aerial image (spring 2010) of University of New Hampshire campus, Durham, NH, showing locations and approximate numbers of individuals of *Kalopanax septemlobus*. Location of purported parent tree is denoted with a cross. Large numbers of first-year seedlings (0-yr-old) are found at "a" and "b". Dashed line indicates limit of intensive search for *K. septemlobus* plants. (Color for this figure is available in the online version of this paper.)

UNH-owned Thompson Farm, both in Durham, southeastern New Hampshire. By the Köppen system, Durham's climate is classified as Dfb (warm summer continental). Mean annual precipitation of 1,169 mm (46.0 in) is evenly distributed throughout the year and with ca. 10% as snow; mean annual temperature is 8.9 C (48.0 F) (National Oceanic and Atmospheric Administration 2013). Soils are inceptisols on glacial till, outwash, or marine sediment (Vieira and Bond 1973).

Data Collection and Analysis: Campus. The UNH campus was surveyed for *Kalopanax septemlobus* in 2011 and 2012, with $>$ 96% of all tallied plants found and measured in 2011. The purported parent tree, located as shown on the map in Figure 1, served to center our campus survey. We censused shrub and tree plantings, flower beds, gravel borders adjacent to buildings, and unmanaged woodlands. Lawns were not formally surveyed because frequent mowing precluded establishment of *K. septemlobus*. The survey was initially limited to ca. 550-m radius from the parent tree because few if any plants were found beyond 400 m. The exception was to the northwest, where high plant density at 500 m caused us to extend the search to ca. 900 m (Figure 1).

Each small ($<$ 400 m^2 [4,306 ft^2]) planting, flower bed, or woodland patch was systematically searched for *K. septemlobus*. Large forest patches ($>$ 400 m^2) were censused by walking a set of parallel transects 5 m apart. Two areas ("a" and "b" in Figure 1), each $<$ 1,000 m^2, had such high *K. septemlobus* densities that we chose to sample them with randomly located 1 by 1 m quadrats rather than census. Total *K. septemlobus* density and density of each age class in these areas were then extrapolated from the plot data.

Each plant encountered was excavated or its roots were severed below ground. We recorded height (using a metric tape) from the stem base to the tip of the terminal bud and determined location using a handheld GPS receiver (GARMIN GPS 12 or GPS 60 CSx, Garmin Ltd.). As UNH gardeners cut back unwanted woody plants during periodic maintenance, we noted whether or not each *K. septemlobus* stem had been cut. Any other stem damage was also noted.

In the lab, the age of each plant was estimated from a count of its wood rings. Each stem base was sliced in cross-section with a sharp knife, and the number of wood rings counted with the aid of a magnifier. *Kalopanax septemlobus* is ring-porous so annual rings are distinct. Seeds of *K.*

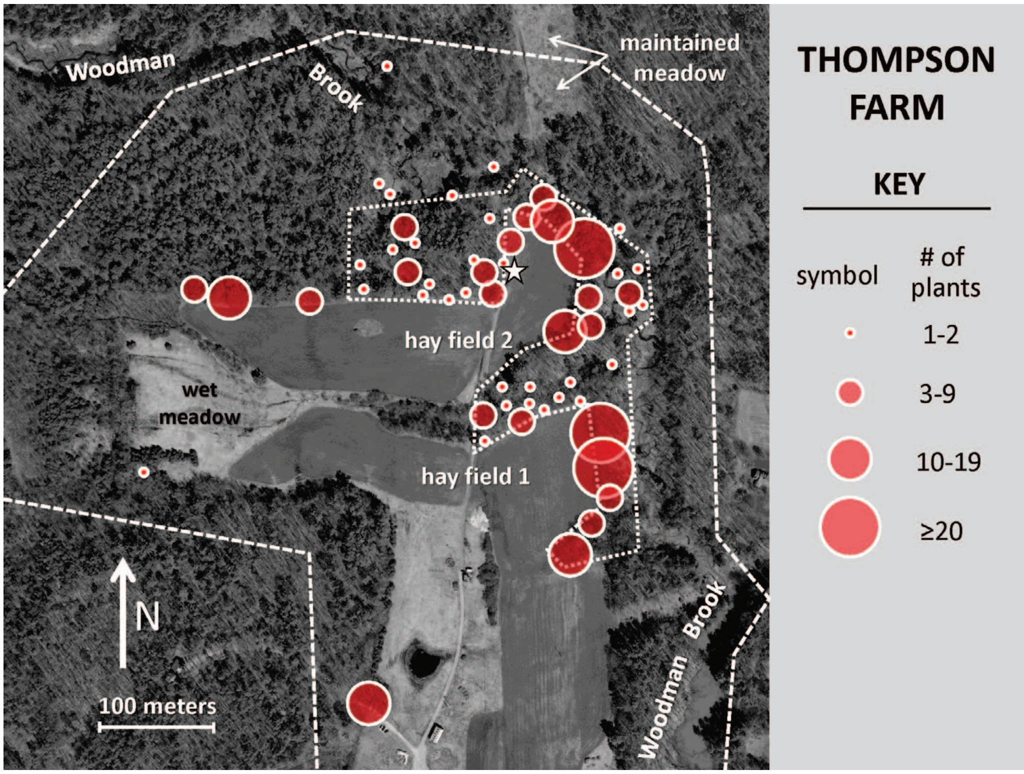

Figure 2. Aerial image (spring 2010) of the Thompson Farm, University of New Hampshire, Durham NH, showing locations and approximate numbers of individuals of *Kalopanax septemlobus*. Coarsely dashed line indicates limit of intensive search for *K. septemlobus* plants. Finely dashed line circumscribes area sampled for characterization of forest type. The star indicates the location of a log landing cut from the forest in 2008. (Color for this figure is available in the online version of this paper.)

septemlobus germinate in May, and thus a plant's age (the number of complete yr lived) cannot be incremented until a full year has passed from the previous May. Because our ring counts were made in summer or fall after a new ring had been initiated but after only a portion of the plant's radial growth for the year had been completed, plant age was estimated by subtracting 1 from the number of rings. Thus, plants in their first year of life were "0 yr olds," plants in their second year were "1 yr olds," etc.

To see how much of the variation in plant height could be explained by age, we ran linear, least squares regression of height of undamaged plants on plant age. Height was log$_e$-transformed to normalize the data. Regressions were run (in JMP Pro 11, SAS Institute) with different transformations of age (log, square root, square, and Arrhenius) and the model with lowest corrected Akaike information criterion (AICc) was considered the "best" model (Burnham and Anderson 2002).

Data Collection and Analysis: Thompson Farm. Field reconnaissance in June 2011 allowed a rough circumscription of the *K. septemlobus* population at Thompson Farm (Figure 2). Most plants were found north and east of the large hay fields located in the south-central portion of the property (Figure 2). Plants were found only in the forest and at forest-meadow edges. No plants were found in the managed hayfields, which are cut or tilled at least once a year, so these were not examined further. Forest and edge areas of Thompson Farm were surveyed from September 2011 to August 2012 using parallel transects, 10 m apart. Typically, transects ran perpendicular from the forest-hayfield edge and extended at least 100 m beyond the last encountered *K. septemlobus* individual. Surveyors continuously moved 5 m to the left or right of the transect in order to maximize the probability of detecting *K. septemlobus*. Each *K. septemlobus* individual encountered was measured and located as described for campus plants (see above), except that at Thompson Farm we also estimated annual height growth in 2011 by measuring the vertical distance between bud scale scars of 2010 and 2011.

To see how much of the variation in total plant height in 2011 and annual height growth in 2011 could be explained by age, we ran linear, least squares regressions (in JMP Pro 11) of these two variables (undamaged plants only) on plant age. Height and growth were both log$_e$-transformed and we tested the same transformations of age as were used in the analysis of the campus plants (see above). The model with lowest AICc was considered the "best" model (Burnham and Anderson 2002).

We characterized the forest in which *K. septemlobus* had established using twelve, 200 m^2 circular plots placed at fixed distances along parallel transects. Sampling was confined to the area where *K. septemlobus* density exceeded ca. 30 plants ha^{-1} (area circumscribed by the fine dotted line in Figure 2). Within each plot we identified and measured diameter at breast height (dbh) of all trees ≥ 10 cm dbh. We determined relative basal area of each tree species per plot and used these data in cluster analysis (Ward minimum variance method with Euclidean distance; SYSTAT 13, SYSTAT Software, Inc.) to group plots and identify forest types.

Light in the Invaded Forest Understory. To assess the quantity of photosynthetically active radiation (PAR) received by *Kalopanax septemlobus* plants in the forest understory, we estimated PAR incident on the crowns of 26 understory *K. septemlobus* individuals at Thompson Farm in 2012. First, all plants were divided into two groups: those within 5 m of the forest edge and those in the forest interior, ≥ 5 m from the forest edge. The latter plants were patchy in distribution, and 21 patches were identified. One plant was randomly chosen from each patch. In addition, five edge plants (within 5 m of the forest edge) were haphazardly chosen. Selected plants were separated by at least 10 m. On 3 d in August 2012 and at various times before and after solar noon on those days, we used a Sunfleck PAR Ceptometer (Decagon Devices, Inc.) to estimate PAR on a horizontal surface within the volume occupied by the crown of each plant (the actual plant crown was moved aside during measurement). Percent PAR transmitted was estimated by dividing each crown measurement by a PAR value obtained at the same time in an open field no more than 200 m away using a LI-COR 185 quantum sensor (LI-COR®, Inc.). Values of percent PAR transmitted were averaged for each plant. Total PAR and percent open sky were estimated using hemispherical photographs obtained using a Nikon CoolPix 950 digital camera with Nikon fisheye converter lens FC-E8 (Nikon Corporation). Photos were taken from the approximate center of each crown during twilight on September 12 and 13, 2012, and analyzed with Gap Light Analyzer software (Frazer et al. 1999). A one-way ANOVA on arcsin transformed values was used to compare interior and edge plants as to (1) % PAR measured by Ceptometer and (2) % PAR and (3) % open sky estimated from photographs.

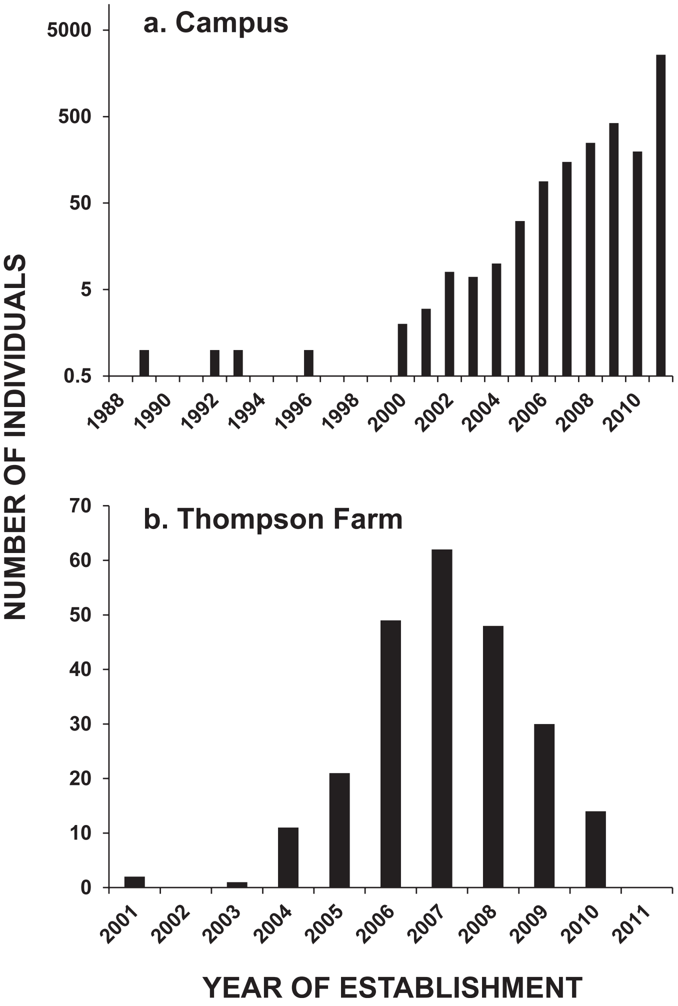

Figure 3. Age structures of the *Kalopanax septemlobus* populations on (a) the University of New Hampshire campus and (b) Thompson Farm, Durham, NH. Note log scale of vertical axis in (a) and differences in ranges of yr on horizontal axes in (a) and (b).

Results

Population Structure: Campus. We estimated a total population of 3,803 *Kalopanax septemlobus* individuals over ca. 100 ha within the surveyed portion of the UNH campus. Most of these (2,597) were first-year seedlings (0-yr-olds) and 1,206 were 1 or more yr old. Plants ranged in age from 0 to 22 yr (ages of plants collected in 2012 were converted to 2011 ages by subtracting 1). The number of individuals per age class declined exponentially from the "0 yr olds" to the 11-yr-old cohort, which established in the year 2000 (Figure 3a). Only four individuals were ≥ 15 yr old and the oldest of these was 22 (i.e., in its 23rd year), having germinated in 1989 (Figure 3a).

Densities of *K. septemlobus* generally declined with distance from the purported parent plant (Figure 4), with the most remote individuals located 775 m (ca. 0.5 mi) away (Figure 1). *K. septemlobus* abundance did not decline evenly away from the parent, but had anomalous high densities at 200 to 300 m and 450 to 500 m (Figures 1 and 4), likely a consequence of habitat availability patterns. Considering only plants ≥ 1 yr old, 56%, were found in

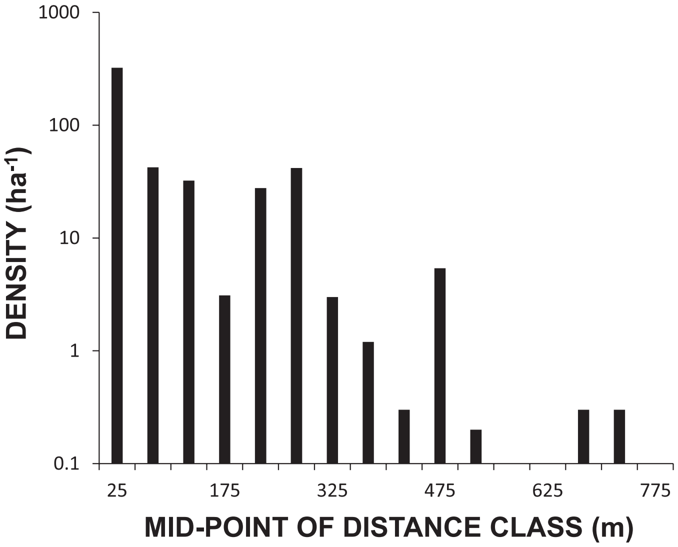

Figure 4. Density of *Kalopanax septemlobus* ≥ 1 yr old vs. distance from the purported parent plant on the University of New Hampshire campus, Durham, NH. Distance is expressed as midpoints of 50-m-wide concentric rings centered on the parent plant.

shrub and tree plantings. Twenty-five percent grew adjacent to buildings in strips of gravel or other unconsolidated material. The edge and interior of unmanaged woods provided habitat for 19% of the plants, and less than 1% grew in annually maintained flower beds.

Age classes differed in distribution across the study area. Seedlings (0-yr-old) were much more common than older plants in gravel or planted borders adjacent to buildings and in a wooded strip north of the Field House ("a" in Figure 1). The four oldest plants (15- to 22-yr-old) were found in unmanaged woodlands, and two of these were located in eastern white pine (*Pinus strobus* L.)-hardwood stands in the University's College Woods, a forest reserve west of campus. All of the other plants ≥ 10 yr old were found within the 0.2 ha shrub and tree planting that also contained the parent tree.

Over 29% of the plants ≥ 1 yr old showed evidence that their stem bases had been cut with a sharp tool. Some plants had been cut more than once. Plants that had survived cutting had one or more butt or root sprouts. We saw no evidence on cut or uncut plants of vegetative stem production via rhizomes or stolons. Moreover, none of the plants we examined, except the purported parent tree, showed any evidence of sexual reproduction.

Population Structure: Thompson Farm. We found 270 *K. septemlobus* individuals over ca. 20 ha within the surveyed portion of the Thompson Farm (Figure 2); 93 were found in 2011 and 177 in 2012. We pooled plants from both yr and examined the population's age structure using 2011 ages (ages of plants collected in 2012 were converted by subtracting 1). Our survey encountered no seedlings (0-yr-old), although there were 14 1-yr-old plants. Numbers of plants increased with age until 4 yr (62 individuals) and declined at higher ages (Figure 3b); maximum age was 10 yr. Plants at Thompson Farm were located in forests or at forest edges adjacent to hay meadows or wetlands (Figure 2). The highest density of plants occurred in the forest surrounding the eastern end of hayfield 2 (Figure 2). Plant density declined unevenly west and south from this area.

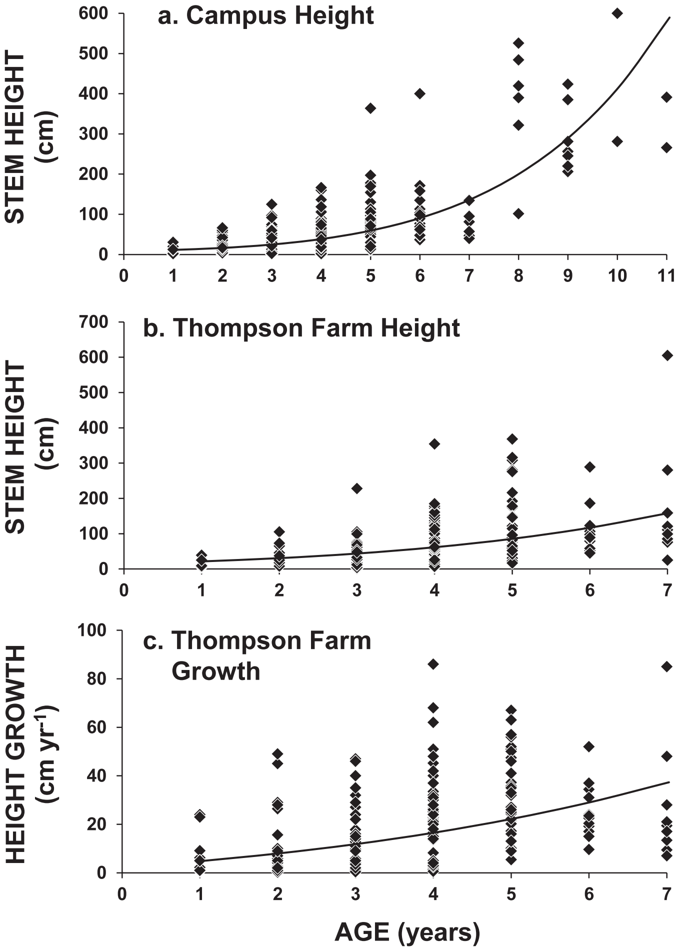

Figure 5. Height and height growth of *Kalopanax septemlobus* by age (year) at two sites in Durham, NH. (a) Height of 533 plants on the University of New Hampshire campus. *Height* = exp (−1.119 + 2.252 ($\sqrt{Age}$)); R^2 = 0.589. (b) Height of 194 plants on the Thompson Farm. *Height* = exp (0.6084 + 1.683 ($\sqrt{Age}$)); R^2 = 0.344. (c) Annual height growth of 184 plants on the Thompson Farm. *Height growth* = exp (0.1930 + 1.268 ($\sqrt{Age}$)); R^2 = 0.179. Height, growth, and age of all plants at both sites measured in 2011.

Height and Height Growth. On the UNH campus, undamaged and uncut plants ranged in height (in 2011)

Table 1. Photosynthetically active radiation (PAR, expressed as percent of full sun) and percent open sky associated with *Kalopanax septemlobus* plants in the forest interior and edge at Thompson Farm, Durham, NH. Actual PAR measured using quantum sensors; estimated PAR and percent open sky estimated from canopy photographs. F and P from one-way analysis of variance on arcsin-transformed data.

	Location			
	Edge	Interior	$F_{1,24}$	P
Number of plants	5	21	—	—
Actual PAR (%)	9.38	4.11	4.48	0.045
Estimated PAR (%)	7.8	5.99	1.78	0.195
Open sky (%)	10.6	5.55	28.14	< 0.0001

from a few cm to 641 cm (ca. 21 ft). Older plants tended to be taller, but individuals of a given age varied greatly in height (Figure 5a). Eight-yr-old plants, for example, ranged in height from 101 to 526 cm. When height in 2011 ($\log_e$ transformed) was regressed on ages 1 to 9 (individuals with age > 9 were excluded due to small sample size per age group), age accounted for only 59% of the variation in height ($n = 487$; $\log_e(Height) = -1.112 + 2.252(\sqrt{Age})$; $F = 102.1_{1,485}$; $P < 0.0001$).

At Thompson Farm, the 2011 height of undamaged and uncut plants ranged from a few cm to 605 cm (ca. 20 feet). As was the case on campus, older plants tended to be taller than younger ones, but plants of a given age varied greatly in height (Figure 5b). For example, 7-yr-old plants ranged from 25 to 605 cm; even 3-yr-old plants ranged from 5 to 228 cm (Figure 5b). In the regression of $\log_e$-transformed height on ages 1 to 7 (individuals with age > 7 were excluded due to small sample size per age), age accounted for only 34% of the variation in height ($n = 194$; $\log_e(Height) = 0.6084 + 1.683(\sqrt{Age})$; $F = 102.1_{1,192}$; $P < 0.0001$).

At Thompson Farm, annual height growth of undamaged and uncut plants in 2011 ranged from 0.3 to 86 cm, with over 25% of plants adding 30 cm or more, and 8% adding ≥ 50 cm. Older plants tended to have greater height growth (Figure 5c), but there was much variation within age classes. In the one-way analysis of variance of $\log_e$-transformed growth on age classes 1 to 7 (individuals with age > 7 were excluded due to small sample size per age), age accounted for only 18% of the variation in height growth ($n = 184$; $\log_e(Height) = 0.1930 + 1.268(\sqrt{Age})$; $F_{1,182} = 41.0$; $P < 0.0001$).

Light in the Invaded Forest Understory. Actual measurements of % PAR transmitted to a horizontal surface and estimates of % total PAR transmitted from hemispherical canopy photographs indicated that *K. septemlobus* plants ($n = 21$) growing in the forest interior received, on average, 4 to 6% incident PAR (Table 1), with some individual plants exposed to $< 4\%$. Based on canopy photos, forest interior plants were also exposed, on average, to $< 6\%$ open sky. Plants within 5 m of the forest edge ($n = 5$) received greater PAR and had more open sky than interior plants, but edge/interior differences were significant only for actual PAR and percent open sky (one-way ANOVA on arcsin transformed values, Table 1).

Forest Composition at Thompson Farm. Cluster analysis, based on tree relative basal area (RBA), divided plots into two groups (Table 2). Groups were relatively distinct; the first division occurred at a Euclidean distance of 0.74 and the next division did not occur until 0.38. Plots in cluster 1 were dominated by *Pinus strobus*, with no other tree species exceeding 10% RBA. Plots in cluster 2 had little *P. strobus*, supporting instead a mixed deciduous forest of *Quercus rubra* L., *Acer saccharum* Marshall and *A. rubrum* L., and *Fagus grandifolia* Ehrh.

Table 2. Mean relative basal area per plot (200 m^2) of tree species (stems $\geq$ 10 cm diameter at breast height) in two clusters identified using Ward minimum variance method with Euclidean distance. Attributes used in clustering were basal areas of tree species (stems $\geq$ 10 cm diam). Data from Thompson Farm, Durham, NH.

	Number of plots	*Pinus strobus*[a]	*Quercus rubra*	*Fagus grandifolia*	*Acer saccharum*	*Acer rubrum*	Other (11 spp)
Cluster 1	7	0.64	0.09	0.04	0.01	0.05	0.16
Cluster 2	5	0.04	0.31	0.18	0.19	0.11	0.18

[a] *Pinus strobus*, eastern white pine; *Quercus rubra*, northern red oak; *Fagus grandifolia*, American beech; *Acer saccharum*, sugar maple; *Acer rubrum*, red maple.

Discussion

Individuals of the nonnative tree, *Kalopanax septemlobus*, have spread and established—without direct human intervention—in anthropogenic and natural habitats in southeastern New Hampshire. Plants have established under diverse conditions, including forest understory. They can exhibit rapid height growth and some have reached ages and sizes approaching reproductive maturity (Fujimori et al. 2006b and see below).

Kalopanax septemlobus plants on the University of New Hampshire campus are almost certainly progeny of a single seedling intentionally planted ca. 1971 to 1975. Two lines of evidence support the notion that this individual is the progenitor of the campus population: (1) the lack of any other mature and reproductive *K. septemlobus* individual on campus and in adjacent areas, and (2) the central location of this tree relative to the younger *K. septemlobus* individuals we mapped. Of course, for the planted tree to be the sole parent to the campus population it would have to be sexually self-compatible and, indeed, *K. septemlobus* individuals are hermaphrodites with some degree of self-compatibility (Fujimori et al. 2006b). Given that the oldest offspring we found established in 1989, the parent tree apparently became reproductive < 20 yr after it was planted.

We do not know how the Thompson Farm population originated. We have not found a candidate "parent tree" at this site; in fact, the oldest plants were only 10 yr old. Two observations, however, support the hypothesis that a parent tree once existed at this site and is now gone. First, the population had a central area of high density (northeast of hayfield 2, Figure 2) with scattered clumps and isolated individuals outside of this area. A parent tree located in the high density area would be consistent with this distribution. Second, the population age structure suggests that the source of seeds began production no later than 2001, and ceased in 2011 (and probably earlier, given multiyear seed dormancy in *K. septemlobus*; see Iida and Nakashizuka 1998); this pattern is consistent with a parent tree that reached reproductive age before 2001 and then died within 10 yr. Such a tree might have been located in a patch of young forest that was cleared in 2008 (marked by the star in Figure 2). Death of this tree in 2008, coupled with seed dormancy, would explain the smaller numbers of trees < 5 yr old in the population. The hypothesized Thompson Farm parent tree would likely have been an early offspring of the campus tree (3 km away), although, while extremely unlikely, it could have been the result of long-distance dispersal from some more remote parent. An alternative hypothesis for the Thompson Farm population is that it arose directly from numerous seeds dispersed from the planted campus tree by birds. It is unclear, however, why birds would disperse seeds year after year to the same confined area of Thompson Farm. It is also conceivable that seeds were deposited in a single dispersal event and annual germination from a long-lived seed bank was responsible for the multiaged population.

Inferences from research on early stages of invasion will be limited if the study does not last long enough to determine whether or not populations will become self-sustaining (Simberloff 2009). Although we have not demonstrated that our *K. septemlobus* populations are self-sustaining, in what follows we use data on seed dispersal, age structure and longevity, shade tolerance, and potential for successful sexual reproduction to make tentative inferences about population viability.

Population spread from the parent tree on the UNH campus likely resulted from bird dispersal. Birds disperse *K. septemlobus* in its native range (Iida and Nakashizuka 1998), and the great distances from the parent to the more remote offspring (at least 775 m and 3 km if the Thompson Farm population was initiated by the campus plant) are consistent with endozoochory (Vittoz and Engler 2007).

The age structure of the campus population, with few individuals ≥ 15 yr, and younger age classes geometrically greater than older ones, results in part from a relatively high annual rate of offspring mortality primarily due to removal by gardeners. Although many plants survived the gardener's shears (and some survived several cuts), it is likely that death caused by pulling or repeated cutting precluded the occurrence of older plants in managed habitats. That the oldest plants (15 to 22 yr) on campus all occurred in unmanaged forest is consistent with this hypothesis. We did not see evidence that any of these older plants were yet sexually reproductive, but assuming that trees 20 yr old (above) or 20 cm dbh (Fujimori et al. 2006b) can produce seeds, maturity of these plants might be close at hand.

That some *K. septemlobus* at the campus site and most at Thompson Farm were found under a forest canopy—with those at Thompson Farm persisting with as little as 4 to 6% full sunlight—suggests moderate shade tolerance. Moreover, that some understory plants > 4 yr old at both sites were adding just a few cm of height growth annually suggests an ability to withstand prolonged suppression. These observations agree with those made on *K. septemlobus* in its native range, where shade tolerance is reported as "intermediate" (Iida and Nakashizuka 1998) and persistent populations of slow-growing seedlings occur in the understory (Abe et al. 2002).

Although *K. septemlobus* can maintain slow growth under suppression, some of our understory *K. septemlobus* plants, presumably those exposed to higher levels of PAR, showed annual height growth rates comparable to, and often greater than, those of native, intermediately tolerant tree species. Hibbs (1982) reported that midtolerant saplings of *Betula alleghaniensis* Britton, *B. lenta* L., and *Quercus rubra* growing in canopy gaps in Massachusetts grew up to 50 cm yr^{-1}. In fact, 8% of our *K. septemlobus* growing in forest edge or interior exceeded that rate. Several of our open-grown plants showed remarkably rapid growth, reaching 600 cm (ca. 20 ft) in just 8 to 11 yr. If Lamarque et al. (2011) are correct that growth rate is the best predictor of invasiveness in exotic trees, *K. septemlobus* might have a bright future in the northeastern United States.

Our results indicate that *K. septemlobus* can disperse, establish, grow, and persist in forests, the most common natural ecosystem in the northeastern United States. Invaded forests on the UNH campus had mixed canopies of various native trees, whereas invaded forests at Thompson Farm were of two distinct types, eastern white pine and mixed hardwoods. These latter forest types are widespread at low elevations throughout New England (Griffith et al. 2009), and thus the potential habitat for *K. septemlobus* is extensive.

Although our demographic and shade tolerance data suggest that *K. septemlobus* could spread widely and persist in the area's forests and suburban habitats, additional population growth and spread will depend on the production of viable offspring. Conceivably, such viability could be limited by inbreeding depression. Given the limited gene pool represented by a single *K. septemlobus* individual and its offspring, inbreeding is certain. For two reasons, however, we doubt that inbreeding depression will be strongly limiting. First, the large number and especially the remarkable vigor of plants on the UNH campus, all of which were presumably derived from self-pollination of the planted tree, indicate that inbreeding effects were small in this first generation. Second, *K. septemlobus* population structure in its native range has likely favored plants tolerant of inbreeding. Despite a vast native range and high level of overall genetic diversity (Jung et al. 2003; Sakaguchi et al. 2012), local populations, especially in Korea and China, tend to be small and scattered (Fujimori et al. 2006a,b; Jung et al. 2003; Sakaguchi et al. 2012). Small, isolated populations tend to experience inbreeding and are likely to purge deleterious recessive alleles (Keller and Waller 2002), reducing inbreeding depression. Consistent with reported *K. septemlobus* population structure in its native range, inbreeding coefficients (F_{is}) from wild populations in Japan (F_{is} = 0.117 to 0.138, Sakaguchi et al. 2011) and Korea (F_{is} = 0.221 to 0.418, calculated from Jung et al. 2003) are consistent with low to moderate levels of inbreeding. Several other studies have suggested that genetic stochasticity may not always limit the spread of exotic species (e.g., Dlugosch and Parker 2008; Facon et al. 2011; Pujol et al. 2009). A population genetics study of planted and invasive *K. septemlobus* populations in North America would be worthwhile.

A growing literature shows that invasion success generally increases with propagule size, number, and diversity (Colautti et al. 2006; Lockwood et al. 2005; Simberloff 2009), with single propagules often failing to initiate invasion (e.g., Zenni and Simberloff 2013). Large propagule size might be necessary, for example, in sexually self-incompatible species such as *Pyrus calleryana*, where individuals from more than one cultivar must be present to assure seed production (Culley and Hardiman 2007). Although propagule pressure is surely a major driver of some invasions, there are a few cases where it is relatively unimportant (e.g., Mata et al. 2013; Nuñez et al. 2011; Tobin et al. 2013; Yeates et al. 2012) and there are instances where one or a few individuals have initiated invasions (cited in Simberloff 2009). On the UNH campus, a single exotic tree has produced a large population with potential for further spread and with unknown ecological and economic effects. Without denying the predictive power of large propagule size, we suggest that it would be unwise for forest managers to routinely ignore small propagules. Thus, given that *K. septemlobus* has been planted as an ornamental in the eastern United States (e.g., Dirr 2009), prevention of region-wide invasion could depend on removal of these trees, even when they occur as single individuals.

We have provided the first documentation of the invasive character of *Kalopanax septemlobus*. Although a definitive statement about the viability of the *K. septemlobus* invasion would be premature, the apparent wide dispersal of seeds, distribution of individuals across diverse habitats, presence of individuals ≥ 20 yr old, high rates of height growth, and tolerance of shade indicate that *K. septemlobus* was well established in our study area. Successful self-pollination and the possibility of limited inbreeding depression are also consistent with the notion that this species could spread and persist in the northeastern United States, despite small propagule size. We do not know how the addition of *K. septemlobus* to northeastern forests would affect community structure and ecosystem properties, but this topic deserves investigation.

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Literature Cited

Abe M, Izaki J, Miguchi H, Masaki T, Makita A, Nakashizuka T (2002) The effects of sasa and canopy gap formation on tree regeneration in an old beech forest. J Veg Sci 13:565–574

Abe S, Masaki T, Nakashizuka T (1995) Factors influencing sapling composition in canopy gaps of a temperate deciduous forest. Vegetatio 120:21–32

Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. 2nd edn. New York: Springer-Verlag. 480 p

Colautti RI, Grigorovich IA, MacIsaac HJ (2006) Propagule pressure: a null model for biological invasions. Biol Invasions 8:1023–1037

Courchamp F, Berec L, Gascoigne J (2008) Allee Effects in Ecology and Conservation. Oxford, UK: Oxford University Press. 272 p

Culley TM, Hardiman NA (2007) The beginning of a new invasive plant: a history of the ornamental callery pear in the United States. BioScience 57:956–964

Dirr MA (2009) Manual of Woody Landscape Plants: Their Identification, Ornamental Characteristics, Culture, Propagation, and Uses. Champaign, IL: Stipes Publications. 1325 p

Dlugosch KM, Parker IM (2008) Invading populations of an ornamental shrub show rapid life history evolution despite genetic bottlenecks. Ecol Lett 11:701–709

Facon B, Hufbauer RA, Tayeh A, Loiseau A, Lombaert E, Vitalis R, Guillemaud T, Lundgren JG, Estoup A (2011) Inbreeding depression is purged in the invasive insect *Harmonia axyridis*. Curr Biol 21: 424–427

Frappier B, Lee TD, Olson KF, Eckert RT (2003) Small-scale invasion pattern, spread rate and lag-phase behavior of *Rhamnus frangula* L. For Ecol Manag 186:1–6

Frazer GW, Canham CD, Lertzman KP (1999) Gap Light Analyzer (GLA). Imaging Software to Extract Canopy Structure and Gap Light Transmission Indices from True-Colour Fisheye Photographs. Users Manual and Program Documentation. Version 2.0. Burnaby, British Columbia, Canada: Simon Fraser University, and Millbrook, NY: The Institute of Ecosystem Studies. 36 p

Fujimori N, Kenta T, Kond T, et al. (2006a) Microsatellite loci for a sparsely distributed species, *Kalopanax pictus* (Araliaceae) in Japanese temperate forests. Mol Ecol Notes 6:468–469

Fujimori N, Samejima H, Kenta T, Ichie T, Shibata M, Iida S, Nakashizuka T (2006b) Reproductive success and distance to conspecific adults in the sparsely distributed tree *Kalopanax pictus*. J Plant Res 119:195–203

Griffith GE, Omernik JM, Bryce SA, Royte J, Hoar WD, Homer JW, Keirstead D, Metzler KJ, Hellyer G (2009) Ecoregions of New England. (map with text) Reston, VA: United States Geological Survey. 1 p

Hibbs DE (1982) Gap dynamics in a hemlock–hardwood forest. Can J For Res 12:522–527

Holmes KA, Greco SE, Berry AM (2014) Pattern and process of fig (*Ficus carica*) invasion in a California riparian forest. Invasive Plant Sci Manag 7(1):46–58

Iida S, Nakashizuka T (1998) Spatial and temporal dispersal of *Kalopanax pictus* seeds in a temperate deciduous forest, central Japan. Plant Ecol 135:243–248

Jung SD, Huh HW, Hong JH, Choi JS, Chun HS, Bang KH, Huh MK (2003) Genetic diversity and population structure of *Kalopanax pictus* (Araliaceae). J Plant Biol 46:255–262

Keller LF, Waller DM (2002) Inbreeding effects in wild populations. Trends Ecol Evol 17(5):230–241

Lamarque LJ, Delsoz S, Lortie CJ (2011) Tree invasions: a comparative test of the dominant hypotheses and functional traits. Biol Invasions 13:1969–1989

Langdon B, Pauchard A, Aguayo M (2010) *Pinus contorta* invasion in the Chilean Patagonia: local patterns in a global context. Biol Invasions 12:3961–3971

Larkin DJ (2012) Lengths and correlates of lag phases in upper-Midwest plant invasions. Biol Invasions 14:827–838

Lockwood J, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. Trends Ecol Evol 20: 223–228

Masaka K, Sato H, Kon H, Fukuchi M (2012) Demographic and height growth response of native broad-leaved deciduous tree saplings to overhead canopy release in a coastal *Pinus thunbergii* forest in Hokkaido, northern Japan. J For Res 17:421–431

Mata TM, Haddad NM, Holyoak M (2013) How invader traits interact with resident communities and resource availability to determine invasion success. Oikos 129:149–160

National Oceanic and Atmospheric Administration (2013) National Climatic Data Center. http://www.ncdc.noaa.gov/. Accessed February 21, 2013

North American Invasive Species Council (2014) Castor aralia, *Kalopanax septemlobus* (Thunb.) Koidz. http://naisn.org/profile.html?sub=28071. Accessed July 5, 2014

Nuñez MA, Moretti A, Simberloff D (2011) Propagule pressure hypothesis not supported by an 80 year experiment on woody species invasion. Oikos 120:1311–1316

Ochs D, Fellows, M (2010) Attacking invasive species. Parks and Rec Business, September 2010:12–15

Pijut PM (2008) *Kalopanax septemlobus* (Thunb. ex A. Murr.) Koidz. castor-aralia. Pages 618–619 *in* Bonner FT, Karrfalt RP, eds The Woody Plant Seed Manual. Agriculture Handbook 727. Washington, DC: U.S. Department of Agriculture, Forest Service

Pujol B, Zhou SR, Vilas JS, Pannell JR (2009) Reduced inbreeding depression after species range expansion. Proc Natl Acad Sci USA 106:15379–15383

Rejmánek M, Richardson DM (2013) Trees and shrubs as invasive alien species—2013 update of the global database. Divers Distrib 19: 1093–1094

Reznicek AA, Voss EG, Walters BS (2011) Michigan Flora Online. *Kalopanax septemlobus*. University of Michigan. http://michiganflora.net/species.aspx?id=191. Accessed October 4, 2014

Richardson DM, Williams PA, Hobbs RJ (1994) Pine invasions in the southern hemisphere: determinants of spread and invasibility. J Biogeogr 21:511–527

Sakaguchi S, Qiu Y-X, Liu Y-H, Qi X-S, Kim S-H, Han J, Takeuchi Y, Worth JRP, Yamasaki M, Sakurai S, Isagi Y (2012) Climate oscillation during the Quaternary associated with landscape heterogeneity promoted allopatric lineage divergence of a temperate tree *Kalopanax septemlobus* (Araliaceae) in East Asia. Mol Ecol 21: 3823–3838

Sakaguchi S, Takeuchi Y, Yamasaki M, Sakurai S, Isagi Y (2011) Lineage admixture during postglacial range expansion is responsible for the increased gene diversity of *Kalopanax septemlobus* in a recently colonised territory. Heredity 107:338–348

Shaffer ML (1987) Minimum viable populations, coping with uncertainty. Pages 69–86 *in* Soule ME, ed Viable Populations for Conservation. Cambridge UK: Cambridge University Press

Simberloff D (2009) The role of propagule pressure in biological invasions. Annu Rev Ecol Evol Syst 40:81–102

Swearingen J, Slattery B, Reshetiloff K, Zwicker S (2010) Plant invaders of mid-Atlantic natural areas. 4th edn. Washington, DC: National Park Service and U.S. Fish and Wildlife Service. 168 p

Tobin PC, Turcotte RM, Snider DA (2013) When one is not necessarily a lonely number: initial colonization dynamics of *Adelges tsugae* on eastern hemlock, *Tsuga canadensis*. Biol Invasions 15: 1925–1932

Vanhellemont M, Verheyen K, De Keersmaeke L, Vandekerkhove K, Hermy M (2009) Does *Prunus serotina* act as an aggressive invader in areas with a low propagule pressure? Biol Invasions 11: 1451–1462

Vanhellemont M, Wauters L, Baeten L, Bijlsma R-J, De Frenne P, Hermy M, Verheyen K (2010) *Prunus serotina* unleashed: invader dominance after 70 yr of forest development. Biol Invasions 12: 1113–1124

Vieira FJ, Bond RW (1973) Soil survey of Strafford County, New Hampshire. Washington DC: U.S. Department of Agriculture Soil Conservation Service. 96 p

Vittoz P, Engler R (2007) Seed dispersal distances: a typology based on dispersal modes and plant traits. Bot Helv 117:109–124

Wangen SR,Webster CR (2006) Potential for multiple lag phases during biotic invasions: reconstructing an invasion of the exotic tree *Acer platanoides*. J Appl Ecol 43:258–268

Wangen SR, Webster CR, Griggs JA (2006) Spatial characteristics of the invasion of *Acer platanoides* on a temperate forested island. Biol Invasions 8:1001–1012

Webster CR, Jenkins MA, Jose S (2006) Woody invaders and the challenges they pose to forest ecosystems in the eastern United States. J For 104:366–374

Webster CR, Nelson K, Wangen SR (2005) Stand dynamics of an insular population of an invasive tree, *Acer platanoides*. For Ecol Manag 208:85–99

Yeates AG, Schooler SS, Garono RJ, Buckley YM (2012) Biological control as an invasion process: disturbance and propagule pressure affect the invasion success of *Lythrum salicaria* biological control agents. Biol Invasions 14:255–271

Zenni RD, Simberloff D (2013) Number of source populations as a potential driver of pine invasions in Brazil. Biol Invasions 15:1623–1639

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