Pictures of an Invasion: English Holly (Ilex aquifolium) in a Semi-Natural Pacific Northwest Forest

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Abstract

English holly (*Ilex aquifolium*) is an increasingly common invader of west-side Pacific Northwest forests, but little site-scale information exists about the pattern and processes of this invasion. We comprehensively surveyed English holly in an 8.4 ha area of invaded forest at St. Edward State Park (WA), a largely native forest in the Seattle metropolitan area. We measured, mapped, aged, and removed all holly ≥ 1 cm basal diameter or > 1 m from the nearest sampled holly, and used these data to characterize the invading population and the course of the invasion. Holly in our sample (n = 466 known-age plants; 55.5 stems ha^{-1}) ranged in age from 1 to 46 years. Trees ≥10 years old appeared to have very low mortality rates and exhibited accelerating rates of size increase and biomass accumulation with age. Native vegetation was greatly reduced under holly canopy. Our spatial and age data indicate that holly is proliferating and spreading rapidly at two scales: contiguous, primarily vegetative, expansion of tree clumps, and long distance dispersal via seed. Spread by both mechanisms appears to be accelerating, with population and canopy area both increasing approximately exponentially, with doubling times of approximately 6 and 5 years respectively. Projecting past spread patterns forward suggests that holly has the potential to soon become a prominent species both in number and canopy extent, likely at the expense of native plant diversity and forest structure. Based on these results, we offer recommendations for holly management in forested areas in the region.

Keywords: invasion ecology; invasive species; dendrochronology; English holly; *Ilex aquifolium*

Introduction

The spread of non-native species is emerging as one of the greatest threats to biodiversity (Wilcove et al. 1998, Primack 2010). Invasive non-natives can have diverse and far-reaching effects on native ecosystems, including the elimination of native species and alteration of physical structure and ecological processes (examples in Lockwood et al. 2007). Invasive plants pose a particularly serious threat to natural areas (Cronk and Fuller 1995, Reichard and White 2001, Zhao et al. 2013). In the Pacific Northwest, as elsewhere, non-native plants are increasingly invading natural areas, displacing native plant species and reducing habitat quality for native animal species (examples in Boersma et al. 2006, Reichard 2007). A critical need in developing effective management of invasives is a better understanding of the pattern and process of their spread (Parker and Reichard 1998, Lockwood et al. 2007).

English holly (*Ilex aquifolium*), native to Eurasia and northern Africa, is an increasingly common invader of Pacific Northwest wildlands (Olmsted 2006). It is a small-to-medium-sized (up to 23 m height in its native range [Peterken and Lloyd 1967]) dioecious evergreen tree that can reproduce both vegetatively and from seed. In its native range it occurs in diverse plant communities, sometimes forming dense, nearly single-species stands (Peterken and Lloyd 1967). Holly was introduced to the Pacific Northwest in 1869 as an ornamental plant (Olmsted 2006), and has been grown commercially in the region from the late 1800s to the present (Wieman 1961, Zika 2010). It apparently first became naturalized in the 1950s (Zika 2010). Although the invasiveness of holly in the Pacific Northwest has only recently been recognized by ecologists (Jones and Reichard 2009) and is largely unstudied, it is well known to land managers. English holly is classified as a "Weed of Concern" in King County, Washington, and has been identified as the most abundant non-native tree species in Seattle's city parks (King County 2006). It is on the Washington State

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Noxious Weed Control Board's list of plants to be monitored for possible inclusion on the State Noxious Weed list (NWCB 2010), and is on the List of Exotic Plants That Threaten Wildlands in California, with "Alert" status as a species with the potential to invade new ecosystems (CalEPPC 2006, 2011).

Little information exists about holly's effects on native Pacific Northwest species and ecosystems (Jones et al. 2010). It may suppress or displace native species through a variety of possible mechanisms, including shading (demonstrated in its native range; Morgan 1987) and nutrient competition (Rietkerk and Francis 2003). It also appears to have the capacity to become a dominant forest plant that could alter native forest structure in novel ways (King County 2006) by forming a persistent thicket-like evergreen sub-canopy tree layer, a structural element with no analogue in the region's native forest. As one of the few invasive plants apparently able to colonize closed-canopy Pacific Northwest forest (Gray 2005), holly may have the potential to transform the region's native forests on a large scale.

Despite the seriousness of English holly's possible effects on native ecosystems, little is known about the pattern and process of the holly invasion in the Pacific Northwest, a situation that has impeded holly management efforts (Steven Burke, King County, personal communication). The present study addresses this lack of knowledge by using a large sample of known-age holly to quantify parameters of holly population growth and spread in a Pacific Northwest forest. Our research questions included: What is the current state of holly in the forest—its population size, age structure, and morphological characteristics? What have been the past pattern and rate of numeric increase and spatial spread since the beginning of the invasion? And finally, what are the implications of past spread for the future of holly in the forest? As holly appears to be broadly invasive across many west-side Northwest forests (King County 2006; Robert Fimbel, Washington State Parks, personal communication; Gregario Teague, Bureau of Land Management, personal communication), results of this study may help inform management of holly in wildland forests of diverse ownerships throughout the region.

Study Area

Our study area was located in Saint Edward State Park, site of a substantial area (~120 ha) of largely native forest situated in a suburban matrix near Seattle WA (Figure 1). Since it was logged in the late 1800s (NPS 2006), most of the park has been relatively undisturbed, resulting in the current maturing successional forest dominated by native tree species of large size (Smith 2006). With its relatively intact native flora (Smith 2006) and mid-to-late successional condition, the forest is characterized as "high quality Pacific Northwest forest" (Green et al. 2013), and is typical of much of Washington's west-side low elevation forest (western hemlock zone, *sensu* Franklin and Dyrness 1988), nearly all of which was logged in the late 1800s or early 1900s and is in various stages of natural succession (Franklin and Dyrness 1988). As one of the closest such forests to Seattle, and with high levels of use by the public (Washington State Parks 2008), the park likely provides many Seattle area residents with their first and most frequent experiences of a natural forest ecosystem (Smith 2006; Mohammad Mostafavinassab, Washington State Parks, personal communication).

The study area consisted of an 8.4 ha area of forest in the Park contiguous with forest to the east and west, and bordered on the north by a residential neighborhood and an elementary school playfield, and on the south by a road and grass sports fields. The vegetation in the study area is mixed evergreen and deciduous forest characterized as an *Alnus rubra/Polystichum munitum* community (Chappell 2006), a common forest type in western Washington (Smith 2006). The canopy is mostly dominated by large red alder (*A. rubra*) and bigleaf maple (*Acer macrophyllum*), with substantial but variable amounts of Douglas-fir (*Pseudotsuga menziesii*), western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*). The shrub layer is substantial, primarily consisting of deciduous species such as salmonberry (*Rubus spectabilus*) and Indian plum (*Oemleria cerasiformis*), as well

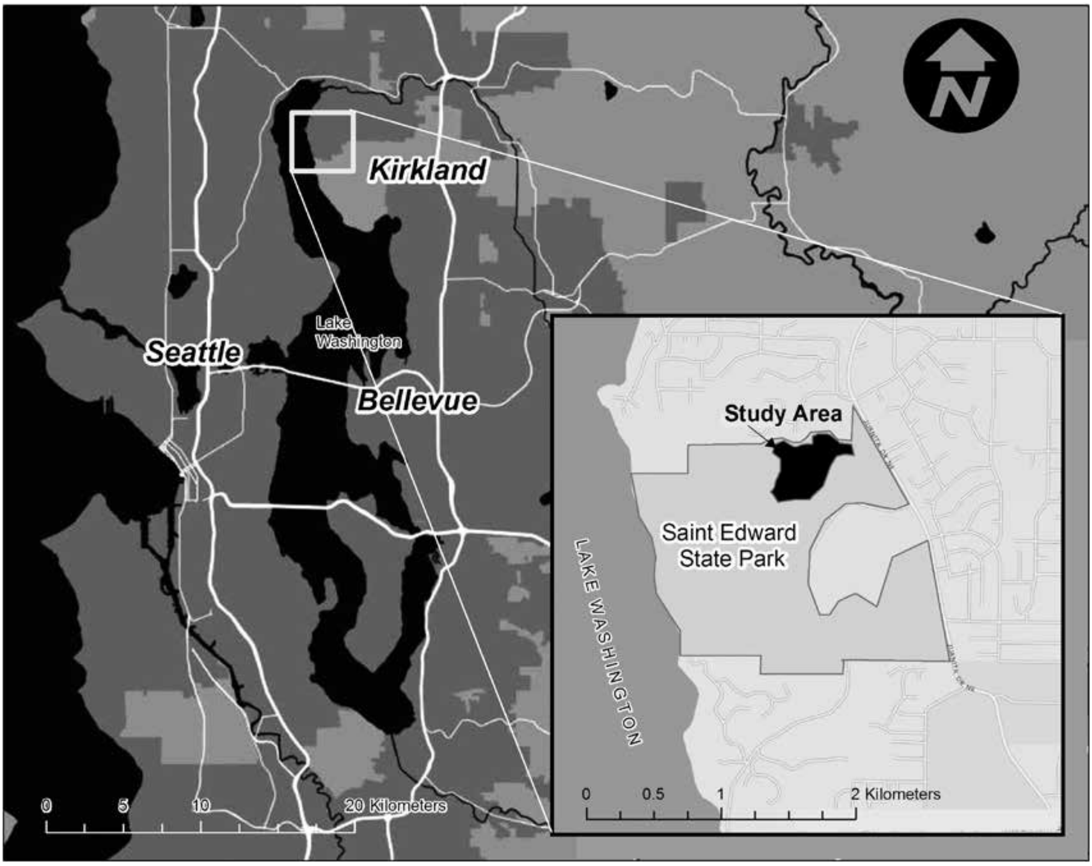

Figure 1. St. Edward State Park study area and environs. The park is dominated by primarily native semi-mature forest, and is surrounded on three sides by suburban residential development. North of the park and our 8.4 ha study area is a residential neighborhood, with most homes constructed in the 1950s to the 1980s, and an elementary school and grounds established in 1957.

as lower growing evergreen species such as salal (*Gaultheria shallon*), Oregon grape (*Mahonia nervosa*), sword fern (*Polystichum munitum*), and native blackberry (*Rubus ursinus*).

Management goals for St. Edward State Park include preserving and enhancing the native old-growth characteristics of the park's forests and controlling invasive non-native species (Washington State Parks 2008). Invasion by non-natives is one of the chief threats to the ecological condition of the park and the native biodiversity found there, and English holly is the most widespread invasive plant species present (Smith 2006); however, no systematic attempt has been made to control holly in the park, and no prior holly removal had occurred in our study area.

Methods

We surveyed the study area for English holly in the winter and spring of two successive years: February 4–April 20, 2011 (6.1 ha) and February 1–May 14, 2012 (2.3 ha). To find all holly plants, teams of two to five investigators searched the entire study area systematically, walking in a line 2–10 m apart, depending on vegetation conditions. Most deciduous vegetation had not leafed out at the time of our searches, and holly, with its distinctive and evergreen foliage, was highly conspicuous. To check the thoroughness of our surveys, we systematically searched areas we had previously surveyed. In those searches, and in many additional opportunistic visits, we found only one small holly plant (0.4 m tall) that was missed in our survey 11 months earlier, when it would presumably have been smaller. We conclude that we found nearly all holly in our study area, and all holly ≥ 0.5 m tall.

We determined the location of each holly plant using a handheld GPS unit (Trimble Juno SB; estimated error after differential correction < 3 m) or, if the plant was within 25 m of a previously located plant, we determined location based on distance and bearing from the already located plant using a meter tape and hand-held compass (estimated error < 1m). For each holly plant located, we used a meter stick to measure height (or length of central leader if tree was bent over) and mean canopy diameter (average of maximum and minimum horizontal extent). We used dial calipers to measure mean trunk diameter at ground level (to nearest 1 mm). We also recorded presence of berries (sampling period was within the time of year when holly berries are present in Washington).

At the site of many of the larger holly trees, numerous small holly sprouts were present under the holly canopy or nearby. We included in our sample all of these sprouts that had a basal stem diameter ≥ 1cm or were farther than one meter from a sampled plant. This allowed us to map the extent of the area occupied by holly. The remaining sprouts (i.e., those < 1 cm basal diameter and ≤ 1 m from a sampled plant) were not sampled; we estimated their numbers to the nearest 10 at each site and removed them by uprooting. At each holly tree or holly clump (group of trees with continuous canopy) sampled in 2012 we also visually estimated percent cover (to nearest 5%; consensus value among two or three investigators) of native evergreen and woody vegetation in the area beneath holly canopy and in the adjacent area within 5 m of holly cover.

In 2012 we also determined whether sampled trees originated from seed or vegetative spread. This determination could be made for 246 of the 251 trees sampled that year based on root structure and root connections with other trees (n = 235), age (oldest tree in a clump; n = 7), or distance from nearest conspecific (n = 4).

We removed all holly in our sample by uprooting when possible, pulling by hand or using a weed wrench (Weed Wrench Company, Grants Pass, OR). For trees too large to uproot (n = 45), we cut the trunk at ground level using a chainsaw or bow saw. Following cutting, we immediately treated the cut surface of a sample (n = 29) of the stumps with 18% glyphosate herbicide (Roundup Concentrate Plus; Monsanto), widely used for wildland invasive control (Tu et al. 2001).

We cut and collected a ground-level cross section of the stem of each plant in our sample. After the cross-sections had dried for at least two months, we sanded them with 80 grit sandpaper followed by 150 and 220 grit, and examined them under a dissecting scope and with a hand lens, counting annual growth rings (Schweingruber et al. 2013) to determine plant age.

Locations and ages of sampled holly were entered in a GIS and mapped using ArcMap 10 (ESRI 2011). The spatial data were projected into State Plane coordinate system (Washington North FIPS 4601), using a Lambert Conformal Conic Projection, based on the North American Datum of 1983. We used ESRI's imagery service to identify an aerial image of the area, and used a 2009 AEX 0.3 m resolution RGB composite as a background layer for the mapped locations. We mapped holly density using a point density function that calculated the number of holly plants within a 100 x 100 m neighborhood around each 1 m^2 in the study area. To assess the spatial distribution of holly trees at different scales we used a multi-distance spatial cluster analysis technique (Ripley's K function). The K function, referred to as L(d), is defined as:

$$L(d) = \sqrt{\frac{A\sum_{i=1}^{n}\sum_{j=1, j\neq i}^{n} k_{i,j}}{\pi n(n-1)}}$$

where *L(d)* is the value of K within a circular neighborhood with radius *(d)*, *n* is the total number of points in the distribution, *A* is the total study area and $k_{i,j}$ is a weighting factor equal to one when the distance between locations *i* and *j* is less than *d* and zero otherwise (Ripley 1981; Mitchell 2005). All other statistical methods followed Zar (1999). Size-age and population and area change regressions were carried out using SPSS statistics software (SPSS 2009).

TABLE 1. Number, density, age, and size of English holly in St. Edward State Park study area; complete sample, ≥ 10 yr old, and < 10 yr old trees. Trees sampled in 2011 and 2012.

Sample	N	Density (ha^{-1})	Age (yrs)* avg (SD)	Age (yrs)* range	Basal diam. (cm) avg (SD)	Basal diam. (cm) range	Height (m)** avg (SD)	Height (m)** range	Crown diam. (m)** avg (SD	Crown diam. (m)** range
All	466	55.5	8.7 (8.3)	1–46	2.0 (3.4)	0.1–35.0	1.6 (1.2)	0.1–18.0	0.7 (1.1)	0.1–10.5
≥ 10 yrs	150	17.9	18.6 (7.8)	10–46	4.7 (4.9)	0.8–35.0	3.5 (2.7)	0.5–18.0	1.7 (0.5)	0.3–10.5
< 10 yrs	316	43.6	4.4 (2.3)	1–9	0.7 (0.4)	0.1–2.9	0.8 (0.6)	0.1–3.0	0.3 (0.2)	0.1–1.3

* Age could not be determined for 3 small individuals.

** Trees for which height (n = 12) or canopy diameter (n = 8) was not determined are excluded from averages for those measures.

Results

The Invading English Holly Population

We located, sampled, and removed a total of 466 holly trees in our 8.4 ha study area, a density of 55.5 trees ha^{-1} (Table 1). In addition to the sampled trees, we removed approximately 650 small sprouts growing under larger sampled trees. These unsampled sprouts (basal diameter < 1 cm and ≤1 meter from a sampled tree) were likely very young; average age of sampled trees in this size range (basal diameter < 1 cm) was 3.62 years (SD 2.09, n = 262). Five (1.9%) of the sampled trees with basal diameter < 1 cm were ≥ 10 years old (all aged 10–12 years). Number of sprouts (mean = 13, SD 23) under a tree or group of trees was positively correlated with age of the oldest tree in the group ($r^2 = 0.49$, $P < 0.001$, n = 35).

We found no dead holly trees in our study area, despite the fact that holly bark is distinctive and leaves remain attached long after death of the plant, making dead holly trees easily recognizable (see Discussion). All sampled holly plants except one appeared to be healthy, with deep green foliage showing little evidence of disease or herbivory. Twenty (4.3%) of the sampled trees showed damage from falling trees or limbs: four had broken trunks, and 16 were bent over and pressed to the ground or nearly so. All but one of these 20 had healthy-looking foliage. Most of the bent-over trees showed rooting from limbs that had been brought into contact with the ground. Three trees located near a trail had been previously cut by park personnel and were sprouting vigorously. The only holly tree in our sample that did not appear healthy was a 16 year-old tree with sparse, yellow-green foliage. It had been pinned to the ground by a large fallen tree, apparently for several years.

The holly population in our study area ranged in age from 1–46 years (Table 1), and was dominated by young trees (Figure 2). The oldest tree established in 1966. Within the general pattern of increasing numbers since initial establishment, annual establishment rate varied, with anomalously low and high numbers in some years (Figure 2). Of the 98 trees in the study area that were 15 years or older (i.e., expected to be of reproductive age; Peterken and Lloyd 1967), only 14 (14%) had berries, a significant departure from the expected 50:50 sex ratio (Peterken and Lloyd 1967, Kay and Stevens 1986; Chi-square goodness of fit, $\chi^2 = 25.0$, df = 1, $P < 0.001$). Of the 246 trees in the 2012 sample for which reproductive mode of origin could be determined, 193 (78%) originated vegetatively from holly roots or branches, and 53 (22%) originated from seed. Number of trees originating from seed varied by year, but generally increased since the start of the invasion (Figure 3a), resulting in a steep increase in the cumulative number of seed-originated trees (Figure 3b).

All measures of tree growth—basal diameter, height, and canopy diameter—were strongly positively correlated with age, and size-age curves for all three measures became progressively steeper with age (Figure 4). Consistent with these patterns, among the oldest trees in our sample (≥ 30 years; n = 17), average annual growth ring width over the last five years was substantial (mean = 0.31 cm, SD 0.14) and significantly greater than the annual average for the previous five years (mean = 0.26 cm, SD 0.17; paired t-test, $t = 2.84$, df = 16, $P <$

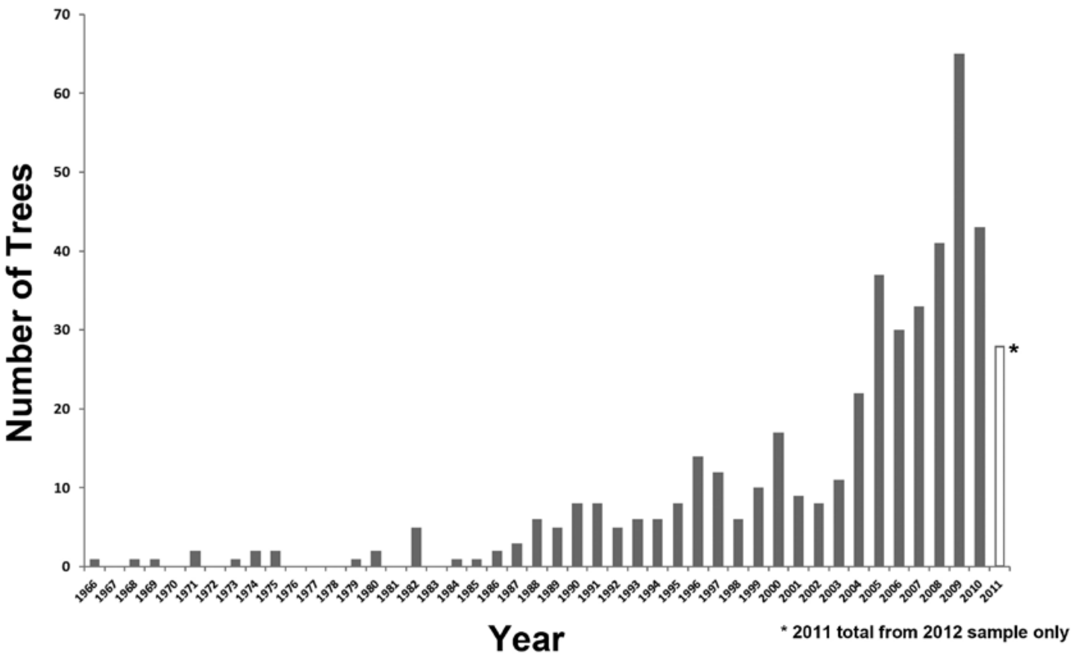

Figure 2. Year of establishment of English holly (n = 463) in St. Edward State Park study area. Data collected in 2011 and 2012. Three small sampled trees for which age was not determined are excluded. Young trees are under-represented due to incomplete sampling of small sprouts under sampled trees (see text).

0.05), indicating that the growth rate of even the oldest trees in our sample was still increasing. The oldest holly plant in the study area, a large multi-trunked tree, had the greatest stem diameter (35.0 cm) and canopy diameter (10.5 m). The second oldest tree (43 years) was the tallest (18 m), six meters taller than the next tallest tree.

Native vegetation was much sparser under holly canopy than in the surrounding area. At the 33 sites where we compared vegetation cover under and adjacent to holly canopy, an average of 79% (SD 24) of the area under holly was devoid of native evergreen and woody vegetation, versus 36% (SD 22) in the adjacent area (paired t-test on arcsine-transformed values; t = 10.08, df = 32, $P < 0.001$). Substantial areas with no native vegetation occurred under large holly clumps. Under the largest clump in our study area, holly sprouts constituted the only ground cover over a 60 m^2 area.

Holly Dispersion and Spread

Holly was widely distributed across the study area (Figure 5). Stem density varied, and was highest (292 stems ha^{-1}) in the northwestern portion of the study area near an area of residential development. Other high density areas were located near the elementary school play field to the northeast and adjacent to the road and grass sports fields along the southern edge of the study area. The overall spatial distribution of holly was highly clustered over spatial scales ranging from 0 to 100 m (Figure 6a), a pattern that would be even more pronounced if the 650 small sprouts within 1 m of our sampled trees were included. Trees that originated from seed were widely distributed as well, with some located more than 25 m from other seed-originated holly (Figure 7). Seed-established trees were also significantly clustered (Figure 6b), although to a lesser degree than the whole sample.

Holly clumps consisted of trees of different ages and appeared to result from one or more founder trees producing additional nearby individuals (Figure 8). Most of the trees within clumps, including the unsampled sprouts, originated vegetatively

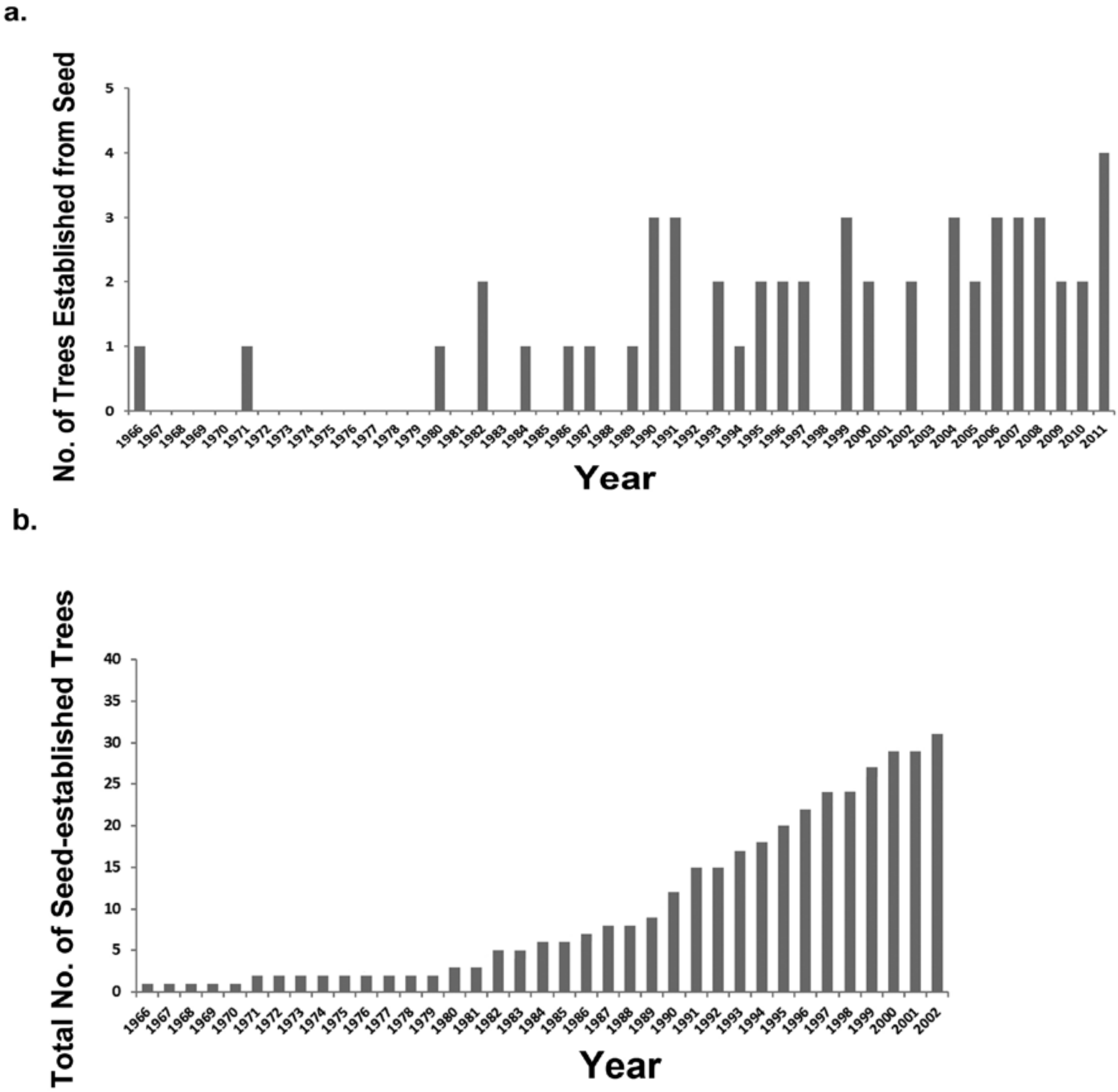

Figure 3. Establishment of English holly from seed in the 2012 study area (2.3 ha) in St. Edward State Park. a) Year of establishment of all sampled holly resulting from seed (n = 53). Establishments in the most recent years are likely under-represented because of incomplete sampling of small sprouts under sampled trees. b) Cumulative number of holly resulting from seed (n = 31), 1966 to 2002. Years after 2002 excluded because of incomplete sampling of small trees.

and had root systems that were connected to older trees. Clumps appeared to spread generally outward from the oldest trees. We also observed linear expansion of clumps resulting from the fall of a dead tree or limb onto a holly tree. When the holly was thus pressed lengthwise along the ground, its branches formed vertically standing trees, and rooting occurred from branches in contact with the ground.

Discussion

Characteristics of the Invading Holly Population

In less than 50 years English holly appears to have proliferated from initial introduction to become a significant component of the forest at St. Edward Park, with a density of more than 55 stems ha^{-1} (excluding the 650 small sprouts [77 ha^{-1}] grow-

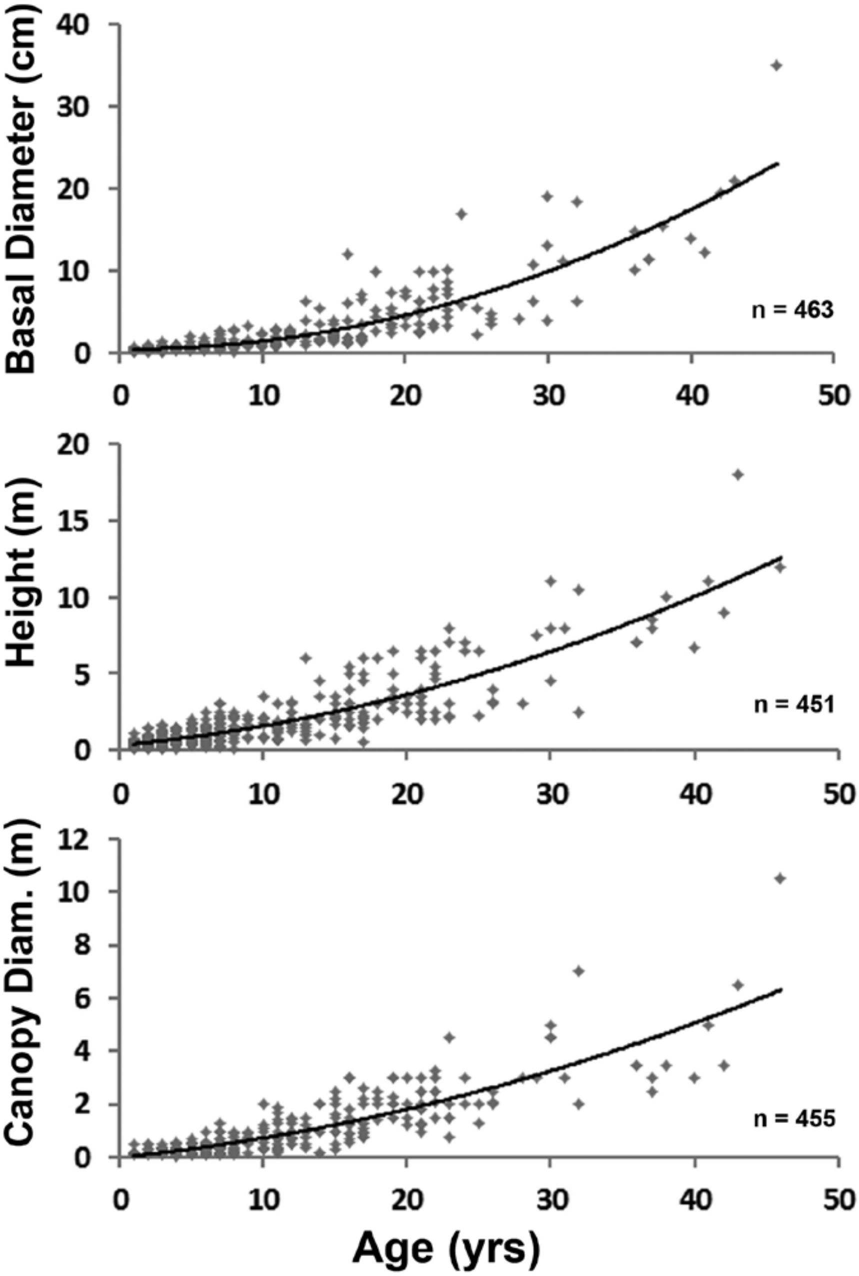

Figure 4. English holly size by age in St. Edward Park study area. Quadratic equation curve fit: a) mean basal diameter ($y = 0.011x^2 – 0.014x + 0.520$; $r^2 = 0.79$; $P < 0.001$; $F_{2, 460} = 933.6$, $P < 0.001$); b) height $y = 0.004x^2 – 0.089x + 0.314$; $r^2 = 0.77$; $P < 0.001$; ($F_{2, 448} = 771.3$, $P < 0.001$); c) mean canopy diameter ($y = 0.002x^2 – 0.055x + 0.008$; $r^2 = 0.77$; $P < 0.001$; $F_{2, 452} = 714.5$, $P < 0.001$). Trees that were not aged (n = 3) excluded. Trees missing a size measurement excluded from graph of that measure (height, $n = 12$; canopy diameter, $n = 8$). All regression lines remained upward curving and r^2 values were virtually unchanged (0.00–0.01 difference) with the largest outlier removed.

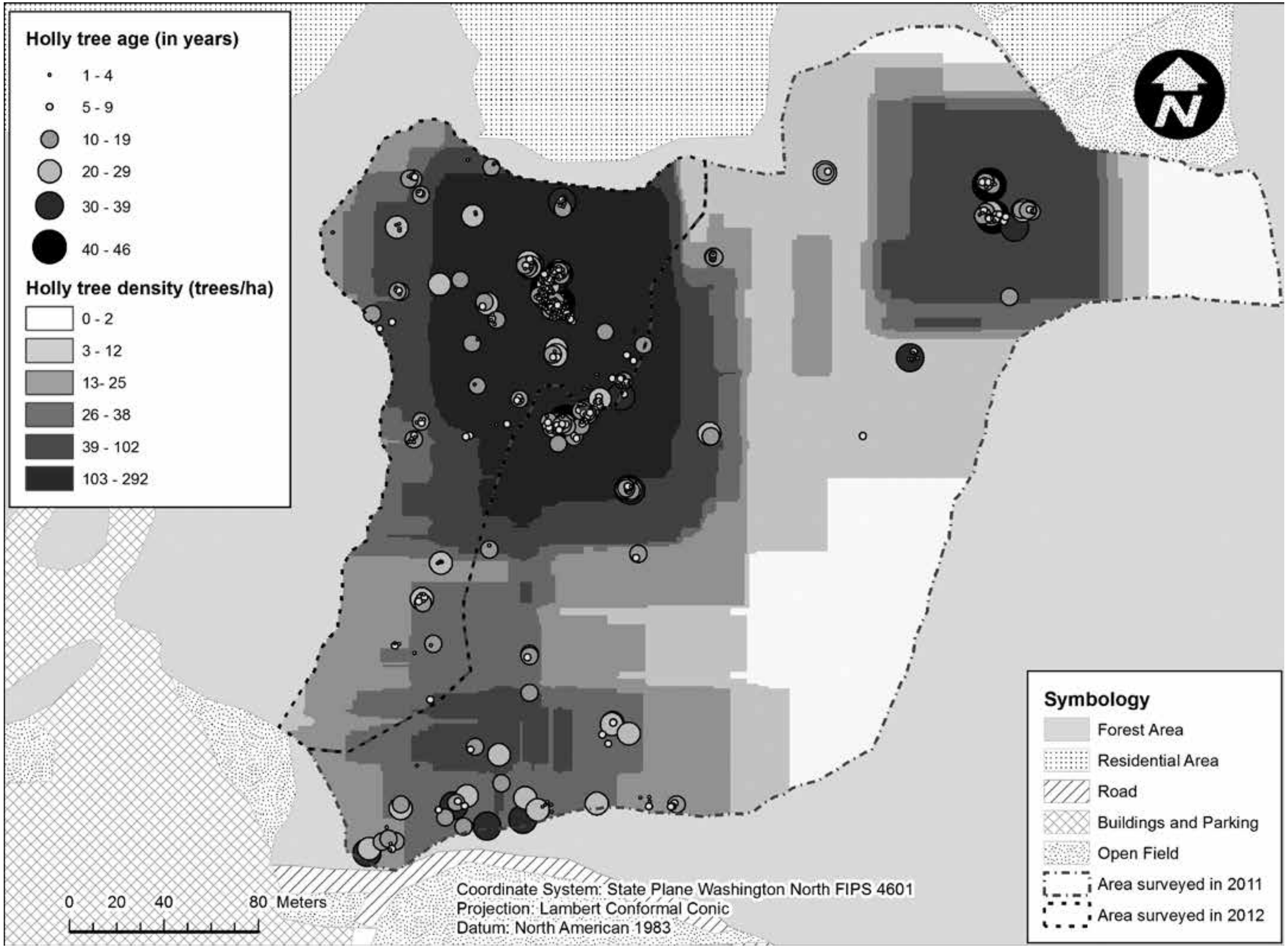

Figure 5. Location, age, and density of all (n = 466) English holly sampled in the St. Edward Park study area. Ages of 3 trees that could not be determined were modeled based on basal diameter-age relationship (modeled ages = 4, 8, and 9 years). Density, categorized in equal-area quantiles, was determined using a focal operation totaling the number of trees within a 1 ha neighborhood of each 1 m^2 in the study area.

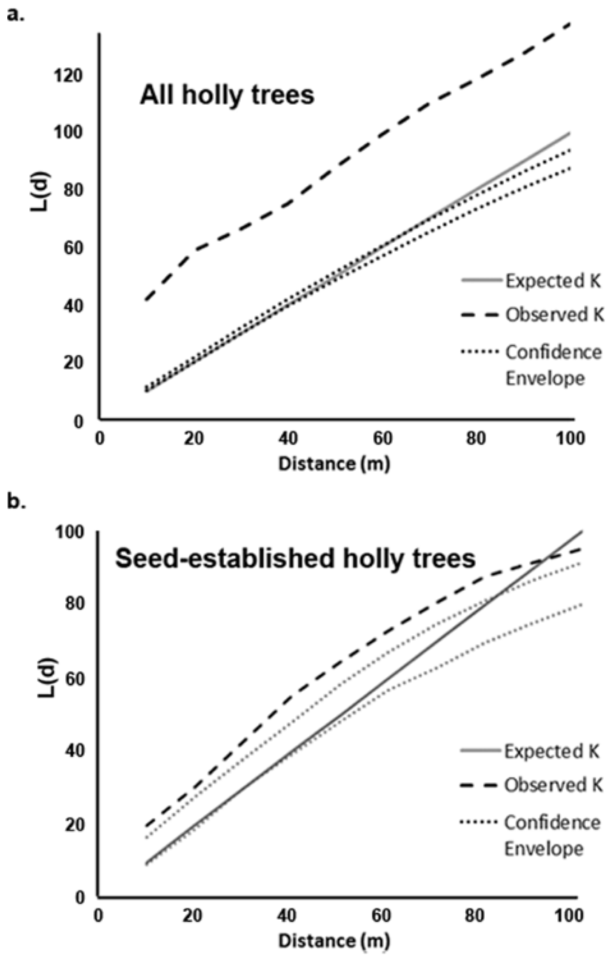

Figure 6. Multi-distance spatial cluster analysis for a) all sampled holly (n = 466), and b) seed-established holly (n = 53) in St. Edward Park study area, showing a strongly clustered pattern at scales of 0–100 m, both for all holly and seed-established holly. Observed K > expected K indicates a distribution more clustered than random at that distance. Observed K outside confidence envelope indicates departure from random at that distance is statistically significant ($P < 0.05$).

ing under larger trees). The population is growing rapidly as a result of high rates of establishment and very low rates of mortality of established trees (see below).

Relative to holly's maximum age (> 250 yrs; Peterken and Lloyd 1967), the population at St. Edward Park is young. In its native range, following a period of slow growth in the initial years following germination, holly grows rapidly for several decades before slowing (Peterken 1966, Peterken and Lloyd 1967). In our sample, three measures of tree size were strongly positively correlated with age, and growth curves for all three measures became progressively steeper with age. This, along with increasing annual growth ring width in the oldest trees, indicates that the holly in St. Edward Park—even the oldest individuals—are still at a stage of accelerating biomass accumulation. Sizes of trees ≥ 10 years old in our sample (basal diameter: 4.7 cm avg., 35 cm max.; height: 3.5 m avg., 18 m max.) were far below maxima observed in English holly in its native range (> 64 cm dbh, 23 m height; Peterken and Lloyd 1967), suggesting that holly trees in St. Edward Park have the potential for considerable further size increase.

The proliferation of small holly sprouts and the marked reduction of native shrub and ground cover under holly trees in our study area indicate that holly profoundly alters native vegetation. The effects appear to increase with tree age, as holly canopy deepens, sprouts proliferate, and the tree-sprout assemblage becomes more thicket-like. Negative effects of English holly on native tree seedling abundance are also reported in holly's native range (Morgan 1987).

The small proportion of mature trees in our study area that had berries suggests the possibility of a skewed sex ratio. Reports of holly's sex ratio in its native range differ, with some studies indicating an even sex ratio (Peterken and Lloyd 1967, Kay and Stevens 1986), and others finding that males outnumber females in some populations (Richards 1988, Obeso et al. 1998). As berry production in holly appears to depend not only on age (Peterken and Lloyd 1967), but also on size and light conditions (Richards 1988), mature trees without berries may not be reliably assumed to be male. Given the implications of sex ratio for holly dispersal and, hence, management, the sex ratio of holly invading Northwest forests merits further investigation.

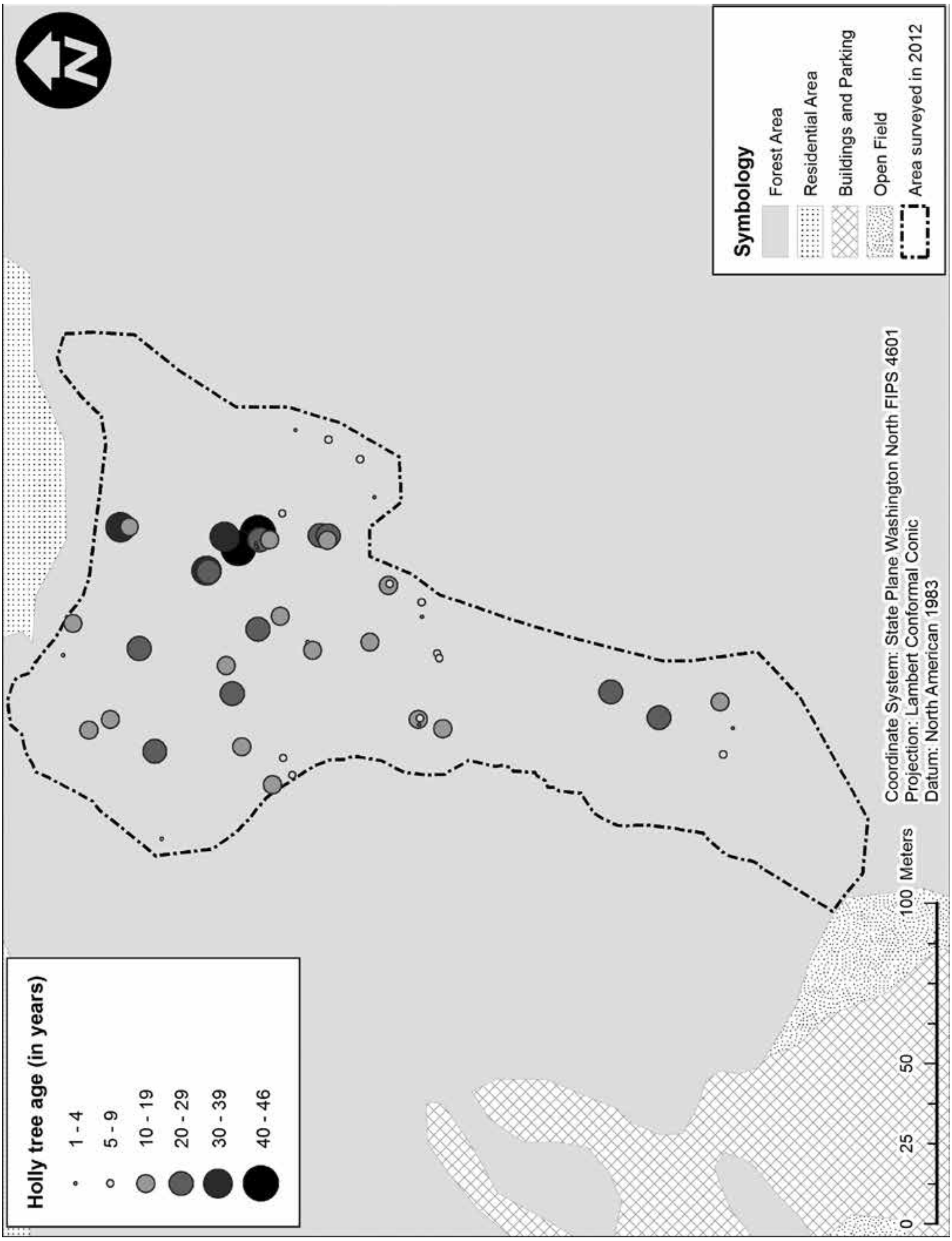

Figure 7. Location and age of seed-established English holly ($n = 53$) in the 2012 St. Edward Park sample area. Tree origin (seed versus vegetative) determined in 2012 only.

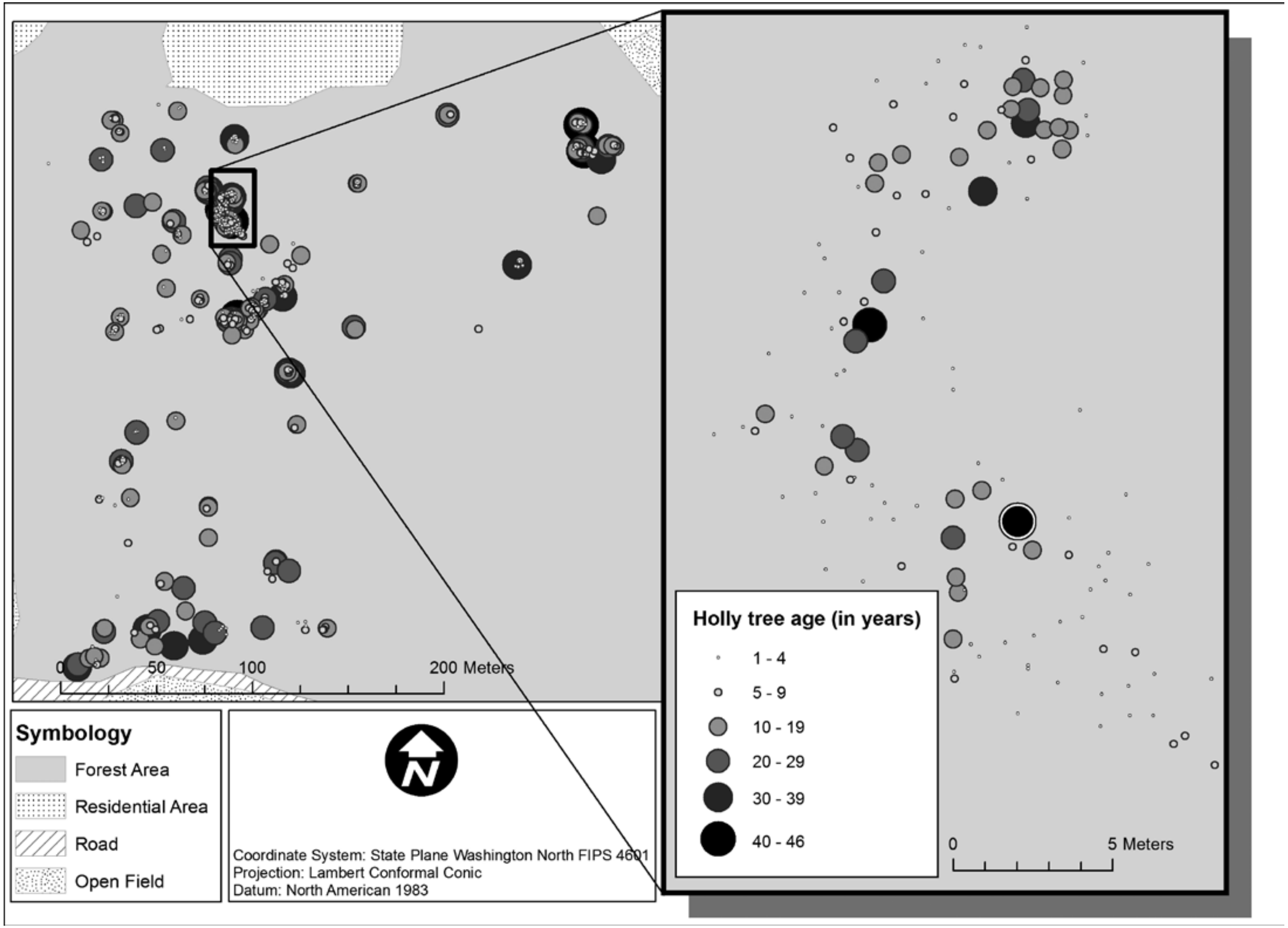

Figure 8. English holly dispersion and age in the largest (n = 131 sampled trees) holly clump in the St. Edward Park study area. Oldest tree (46 years) indicated by ring. Approximately 280 additional unsampled small (basal diameter < 1 cm) sprouts were present under the canopy of trees in the clump. Ground and shrub layer vegetation cover in the clump was > 99% English holly.

With more than three quarters of the sampled holly in our 2012 study area originating from roots and branches of older trees, it is clear that vegetative spread is responsible for most of the invading population's growth. Nonetheless, the capacity for long-distance spread via animal-dispersed seed makes seed-originated holly an important component of the invasion, accounting for all spread into unoccupied habitat. The number of yearly seed establishment events has generally increased since the start of the invasion, and the total number of seed-originated holly trees has increased sharply as the holly population in the area has grown. However, annual variability in seed establishment (Figure 3a) suggests that rate of establishment from seed is not solely a function of the number of trees in the area, and may be influenced by many factors, including weather (Peterken 1966, Peterken and Lloyd 1967), seed predator (García et al. 2005, Zika 2010) and disperser populations (Arrieta and Suárez 2005, Martinez et al. 2008, Zika 2010), herbivory (Peterken 1966, Obeso and Fernández-Calvo 2002), and pollen availability (Coller and Ticknor 1983).

The spatial distribution of holly in the park is a product of both long-distance seed dispersal, probably via birds (Zika 2010), resulting in widely spaced clump locations; and localized vegetative spread and perhaps some seedfall (Peterken 1966, Arrieta and Suárez 2005) leading to outward spread of clumps. Both processes appear to be active; young individuals resulting from seed—potential founders of future clumps—were found far from other holly trees, and nearly all existing clumps included very young individuals, indicating ongoing expansion of clumps.

Although we cannot be certain of the origin of the holly invasion, the year of establishment of the oldest tree in our sample (1966) is consistent with initiation of invasion by animal-dispersed seed from landscape plantings at residences in the surrounding area. Development of much of the residential neighborhood north of St. Edward Park began in the 1950's (King County Recorders Office 2013), and berry producing holly was a popular ornamental plant by 1960 (Wieman 1961). Large holly trees are currently common in the neighborhood (personal observation).

Holly Population Change and Spread

Our comprehensive tree age and location data can provide a detailed depiction of the course of the English holly invasion at the St. Edward study area, provided that the mortality rate of invading holly is low. Long-lived trees are expected to exhibit a U-shaped mortality pattern, with low mortality in the period after the youngest ages and before senescence (Harcombe 1987, Runkle 2000). Mortality rates during this stage are particularly low in shade tolerant (Lorimer et al. 2001) and rapidly growing (Wyckoff and Clark 2002) trees, such as the holly in our study area. Moreover, in the course of two years of surveys during which 150 holly trees ≥ 10 years old were sampled, we found only one that appeared unhealthy, and we found no dead trees, despite the distinctive bark and persistence of leaves which make dead holly readily identifiable. Out of a sample of 25 trees (age range: 2–46 years) that we cut or uprooted in 2012 and revisited 11–13 months later, 24 (96%), including the one unhealthy tree we found, still had attached dead leaves. We conclude that sizeable holly trees that had died within a year—and likely longer—prior to our surveys would have been observed. Based on the absence of dead individuals, the near-absence of unhealthy individuals, and substantial and increasing growth in the oldest trees, we surmise that the mortality rate of holly ≥ 10 years old in the study population is very close to zero.

Assuming negligible mortality of 10–70 year old holly, we were able to use our record of tree ages to model holly population change in the study area since the start of the invasion and into the future. Biological invasions are typically characterized by a three stage pattern of population change: an initial period of slow or negligible increase (a lag period) when negative processes associated with small populations retard growth, followed by an expansion phase of rapid increase, and finally a period of slowing or cessation of growth (Mack et al. 2000, Radosevich et al. 2003, Arim et al. 2006, Zhao et al. 2013). During the expansion phase, populations may increase exponentially (Pysek and Prach 1993, Wangen and Webster 2006), and the area occupied may increase linearly (Wangen and Webster 2006) or exponentially (Shigesada and Kawasaki 1997, Radosevich 2003).

Growth of the population of ≥ 10-year-old holly in our study area showed a lag period of approximately 14 years following the occurrence of the first 10-year-old individual in 1976. During this interval less than one additional 10-year-old tree occurred per year on average. The slow population growth in this period, typical of woody perennial invasives (Petit et al. 2004), may have been a product of the time required for holly to reach reproductive maturity, pollen limitation, or other factors limiting seed production or dispersal.

The lag period was followed by a marked shift to rapid, approximately exponential growth beginning around 1990, when the population increased from 13 trees ≥ 10 years old to 154 in 2012 (four 9-year-old trees sampled in 2011 included), a doubling time of approximately six years (Figure 9a). The small departure from the exponential model in the most recent years may be due to undercounting of younger trees, as we estimate that approximately 1.9% (n = 12) of the 650 unsampled sprouts were 10–12 years of age and are "missing" from the sample population of trees ≥ 10 years of age (see Results). At the current rate of exponential growth, the number of trees ≥ 10 years old in the study area would have grown (absent the removal of trees in this study) from the current 154 (18 ha^{-1}) to 580 (69 ha^{-1}) in 10 years, and to 3500 (417 ha^{-1}) in 25 years. Because mortality of ≥ 10 year-old holly, while low, is probably greater than 0, we also modeled population growth assuming 2% annual mortality. This model indicates a doubling time of approximately 7.5 years and predicts that the number of ≥ 10 year old trees would have grown to approximately 1100 (131 ha^{-1}) in 25 years. Based on the large proportion of trees < 10 years old in our sample (68%, not including unsampled sprouts), the total number of holly plants of all ages would likely be several times the number of ≥ 10 year old trees.

Increase of holly canopy cover (Figure 9b) also followed an approximately exponential trajectory after 1990, and was even more rapid (doubling time approximately 5 years) than growth of tree numbers because of the compounding effect of increasing tree size with age. From near non-existence before 1990, holly cover had expanded to occupy 0.6% of the study area by 2012 (Figure 10). At this rate, holly would cover more than 2% of the study area in 10 years, more than 15% in 25 years, and more than 50% in less than 35 years. Given the tendency of holly to exclude native shrubs and ground cover, this increase would cause substantial loss of native vegetation.

At the densities and aerial extent predicted by these models, holly would be a prominent species in the forest. For example, at 15% cover, holly would account for the second most cover of any canopy species in the *Alnus rubra/Polystichum munitum* forest community type that characterizes the study area (Smith 2006), exceeding common species such as Douglas-fir and Bigleaf maple. It would account for the second- or third-most cover of all canopy species in most representative associations of western hemlock forest (Franklin and Dyrness 1988).

The precise values predicted by population and cover models must be treated with caution. While exponential models closely fit the data, other models (e.g., steeply increasing logistic, and quadratic models) fit the data nearly as well. Moreover, these future projections do not consider density-dependent factors that are likely to eventually limit population increase (Mack et al. 2000; Radosevich et al. 2003). Unfortunately, the point in the invasion process at which those factors will become limiting is unknown. English holly forms dense single-species thickets in its native range (Peterken and Lloyd 1967, Arrieta and Suárez 2005), and we observed such thickets in our study area (Figure 8), suggesting that limiting factors may not exert strong effects until very high densities are reached. In the absence of information on the limits of holly expansion, we can only say that the record of holly proliferation and canopy growth in our study area indicates a recent invasion that is proceeding rapidly, and that

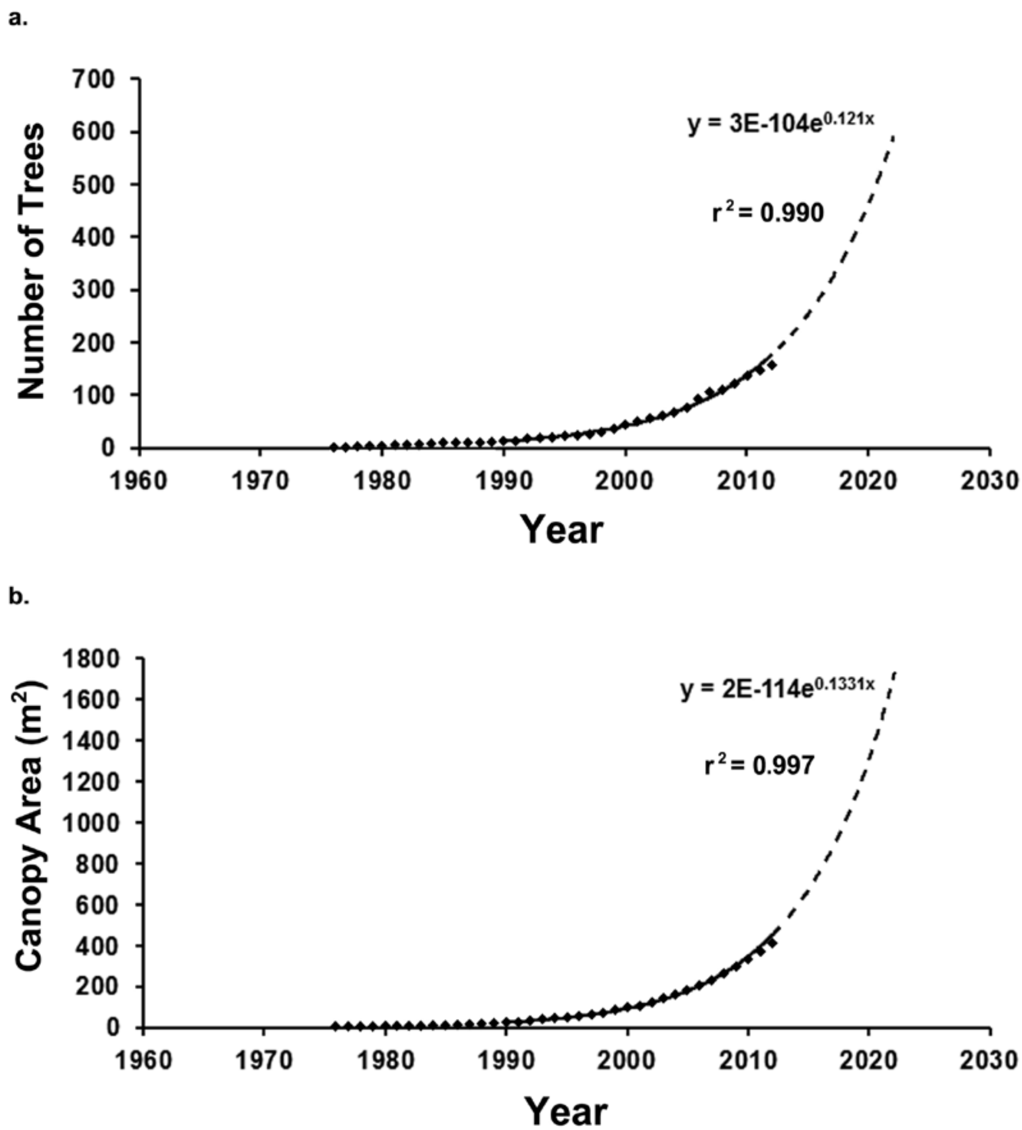

Figure 9. Proliferation and spread of ≥ 10 year old English holly trees at St. Edward Park study area from beginning of the invasion to 2012 (points), and projected to 2022 (dashed line). Exponential curve fit from 1990: a) Number of trees ($F_{2,21}$ = 2116.3.0, P < 0.001); b) Total area covered by holly canopy ($F_{2,21}$ = 6783.4, P < 0.001). Canopy area in past years derived from canopy-age relationship (see Figure 4c.).

projections of future growth suggest the likelihood of rapid transformation of the largely native forest at St. Edward Park to a plant community in which English holly is a prominent, and perhaps eventually dominant, species.

The degree to which results of this study are generalizable to other western hemlock zone forests in the Pacific Northwest merits investigation. Anecdotal reports suggest holly is increasing rapidly in many locations (Smith 2013, Steven Burke, personal communication). While conditions in our study area are typical of many forests in the region, the landscape context of the site is characterized by more intense anthropogenic influence, including residential landscaping, than forests farther from metropolitan areas. The rate of

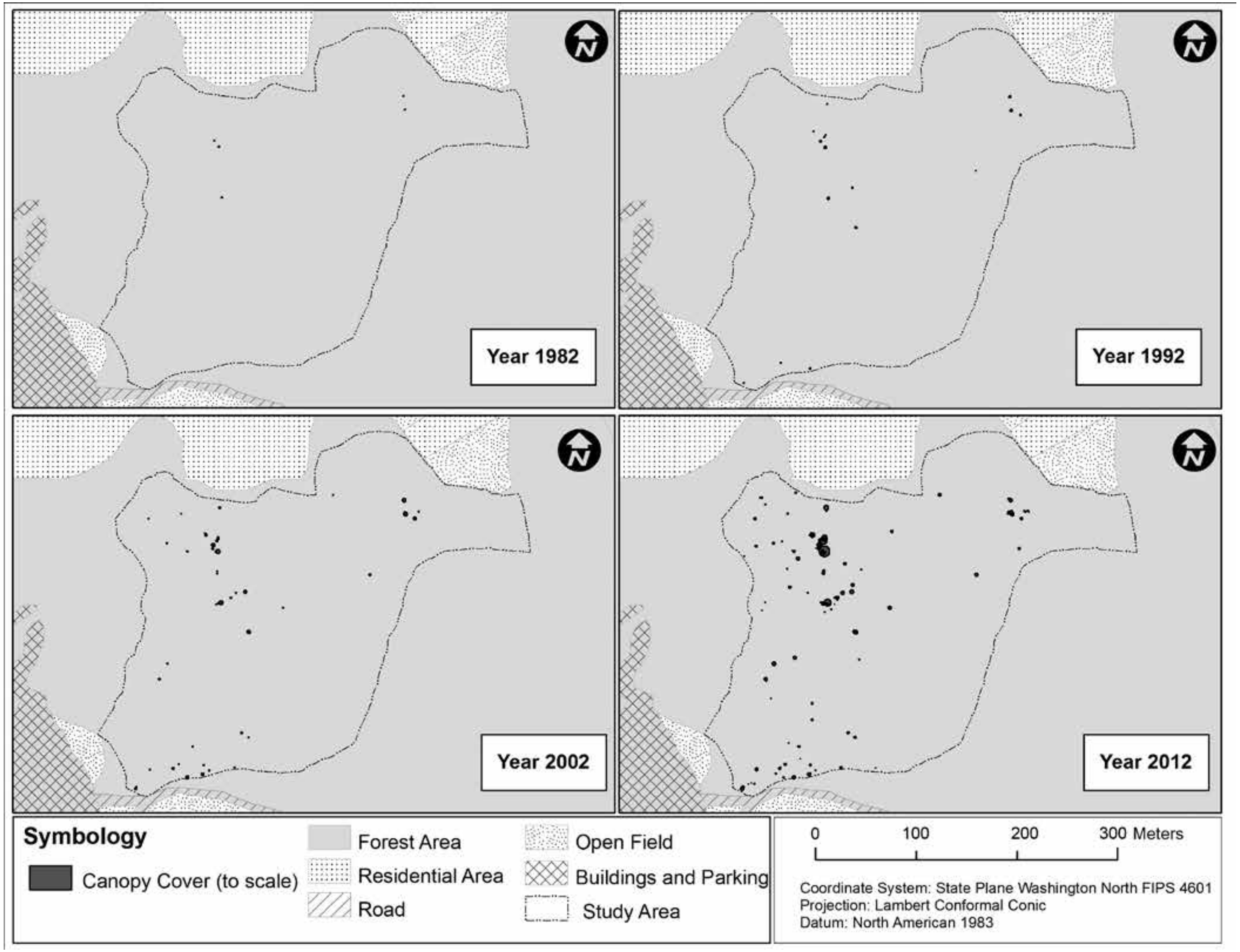

Figure 10 a-d. Past and current spatial extent of English holly canopy of ≥ 10 year old trees in St. Edward Park study area at 10 year intervals. Canopy area increased from 4 m^2 in 1982 to 482 m^2 by 2012. Past canopy area modeled from canopy diameter-age relationship (see Figure 4c).

holly proliferation in forests with less propagule pressure–especially undisturbed or old-growth forest—is of particular conservation interest.

Management Recommendations

Designation of English Holly as a Noxious Weed

The results of this study clearly demonstrate the invasive character of English holly in Pacific Northwest forests. Formal designation as a noxious weed (e.g., listing as a Class C noxious weed by the Washington State Noxious Weed Control Board) would assist in controlling the species by expanding management options and regulatory control.

Immediate development and implementation of a plan for holly control in Pacific Northwest west-side wildland forests

In Pacific Northwest forests managed for natural ecosystem processes and native biodiversity, control or elimination of English holly is an appropriate management goal. While widespread, holly is still at a level that is amenable to control in at least some forests (e.g., St. Edward State Park). Our projections suggest that delaying action for just a few years will result in large numbers of additional holly trees and added difficulty of removal due to increasing tree size. A holly control plan should be developed and control measures undertaken while control is still a feasible management option. Large female (berry-producing) trees are especially important to remove. Control efforts should be concentrated first in areas most susceptible to invasion. Spatially explicit modeling of invasion risk could help identify invasion-prone areas (Jones et al. 2010). It is likely that a control plan will require modification as more information about the holly invasion becomes available.

Holly Control on Adjacent Lands

As the original source of holly in wildlands is probably seed from nearby human-dominated landscapes, and these landscapes are likely to be a continuing seed source, reduction of that seed source would be beneficial in slowing the invasion (Reichard and White 2001). Opportunities for reducing the prevalence of berry-producing holly on human-occupied lands near wildlands (e.g., residential neighborhoods), and education of the local public about the invasiveness of holly should be pursued. The graphical and map products of this study (e.g., Figures 5, 7–10) can be adapted by land management agencies to communicate the negative effects of this and other invasive species to the public (Mack et al. 2000).

Additional Research on English Holly Invasion Ecology

Additional research is needed to address several remaining questions that are critical to better understanding the English holly invasion and to developing an effective management response. Topics in need of investigation include the vulnerability to invasion of different forest locations and types, particularly mature forest; effects of holly on native species; effectiveness of various control methods; and possible factors, including forest management practices, that promote or limit holly spread.

Conclusions

From initial establishment in the forest of St. Edward Park less than 50 years ago, English holly has quickly increased in both numbers and area occupied. The distribution pattern and ages of holly trees indicate rapid proliferation by both seed and vegetative spread. If current rates of increase continue, holly could be a major component of the park's forest in less than 25 years. Given the negative effects holly appears to have on native vegetation, this increase would likely have substantial impacts on the park's forest, native floral diversity, and perhaps habitat value.

All experience with invasive species indicates that the earlier an invasion is addressed, the greater the likelihood of successful control (Rejmanek 2000, McNeely et al. 2003). While it is widespread, holly in St. Edward State Park appears to still be at a level that is amenable to control. Our future projections suggest that delaying control for even a few years will result in a substantial increase in number of holly trees. Moreover, because the holly is at an age of rapid size increase, increasing canopy area and difficulty of removal are expected to compound the effects and management challenges presented by the increase in numbers. An immediate management response is recommended, along with a significant research effort that can inform holly management.

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