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The persistence of invasive populations of kudzu near the northern periphery of its range in New York City determined from historical data[1,2]

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Abstract. In 1989, Edward Frankel recorded the distribution of *Pueraria montana* var. *lobata* (kudzu) in and around New York City, motivated by the concern that kudzu was extending its range northward from the southeastern USA, where it is an aggressive invasive species. Understanding species persistence is important in determining the dynamics of the distribution of invasive species as they spread, particularly since harsh environmental conditions at the periphery of a species range might result in frequent extinctions. Long-term species persistence data are difficult to obtain; the Frankel (1989) data thus represent a valuable contribution to documenting population persistence. In this study, we were able to identify unambiguously 22 of Frankel's original 34 sites of kudzu in the New York City metropolitan area. After more than 20 yr, we found only 32% of kudzu populations persisted in and around New York City. In contrast, we used herbarium records to identify 19 sites in Georgia and South Carolina where *P. montana* var. *lobata* was documented to occur in the same approximate time period as Frankel's data, and found that 95% of these populations persisted. Even accounting for the difference between urban and rural sites, populations of *P. montana* var. *lobata* go extinct more often near the periphery of the range than at the core of the invasion.

Key words: extinction, invasive species, range edge, range periphery, urban population

Pueraria montana var. *lobata* (Willd.) Maesen & S. Almeida (Ward 1998), kudzu, is a primarily clonally reproducing perennial vine introduced from east Asia to North America in the late 19th century. Kudzu has been widely reportedly as being first introduced at the 1876 Centennial Exposition in Philadelphia (Mitich 2000); however, early accounts show that kudzu was sold as an ornamental shade plant (Piper 1909, Winberry and Jones 1973) by a well-known nursery in Manhattan as early as 1855 (Lindgren *et al*. 2013). Records of established *P. montana* var. *lobata* populations in New York City date to 1900 (Frankel 1989).

Since its first introduction to the USA, kudzu was planted extensively in the southeastern USA to mitigate soil erosion (Pieters 1932, Miller and Edwards 1983, Alderman 2004). Kudzu is now considered a harmful invasive species (Forseth and Innis 2004), with a current primary distribution in the southeastern USA, extending north into New York and west to east Texas and Kansas (Forseth and Innis 2004, Li *et al*. 2011). Reports of the location of the northern range limit of the species on the North American East Coast are variable and range from Pennsylvania, New Jersey, Massachusetts, and Maine (Snyder 1987) to Nova Scotia, Canada (Shurtleff and Aoyagi 1977).

Kudzu is such an iconic invasive plant that in the 1980s it was hailed in the popular press as "the vine that ate the South" (McGourty 1982) and concern grew that the species would continue its expansion further northward (Frankel 1989, Sasek and Strain 1990). Considering that growth and spread of kudzu might increase due to global warming, Frankel (1989) warned that kudzu had the potential to increase its range further into the northeastern USA. Frankel (1989) reported the locations of all known populations of *P. montana* var. *lobata* in the New York City metropolitan area.

Pueraria montana var. *lobata* can withstand environmental conditions currently present in the northeastern USA (Mitich 2000; Forseth and Innis 2004; Frye, Hough-Goldstein, and Kidd 2012), and empirical studies show that kudzu is not limited by low temperature in southern Ontario (Coiner 2012). However, theoretical models suggest that the distribution of kudzu is likely limited

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by fall and winter temperatures (Sasek and Strain 1990; Bradley, Wilcove, and Oppenheimer 2010). As CO_2 levels and winter temperatures rise, the range of kudzu is expected to expand northward (Sasek and Strain 1990; Bradley, Wilcove, and Oppenheimer 2010; Follak 2011).

Detailed species' distribution data are important for understanding a variety of basic ecological and evolutionary dynamics (Wright 1940, Andrewartha and Birch 1954, Brown 1984), but the challenges of global climate change (Parmesan 1996) and invasive species (Mainali *et al*. 2015) have made species' distribution and persistence data much more urgently needed to model and predict changes in species' distributions (Elith and Leathwick 2009, Wallace and Bargeron 2014).

Modeling and predicting changes in a species' distribution requires an understanding of what happens at the geographic margins of its range (Soule 1973). Peripheral, or marginal, populations often exist in suboptimal habitat with different environmental conditions than those in the center of the range (Hoffmann and Blows 1994, Holt and Keitt 2000, Hardie and Hutchings 2010). Populations at the periphery of a species' range are at an increased probability of going extinct (Soule 1973, Reed 2005) due to harsher environmental conditions, smaller populations sizes (Vucetich and Waite 2003), and perhaps less genetic diversity (Shumaker and Babble 1980; Eckert, Samis, and Lougheed 2008). The persistence (individuals of a species living in a certain location continuously over a given amount of time) of peripheral invasive populations is also important because these populations create stepping stones for increased gene flow between invasive populations, which may facilitate the spread of the species (Holt and Gomulkiewicz 1997; Alleaume-Benharira, Pen, and Ronce 2006).

Although data on native species' persistence are often available at large spatial and temporal scales, those data are rarely available for invasive species (Pergl *et al*. 2012). Furthermore, the range of invasive species based solely on a current census would be overestimated if populations at the periphery of the range are dynamic, with frequent extinction and recolonization (Pergl *et al*. 2012). Thus, the dataset Frankel (1989) created is unusual and valuable because it provides a historical reference of the distribution of an important invasive species. A contemporary census would document the persistence of this invasive species.

In order to understand the dynamics of kudzu near the periphery of its range, we revisited Frankel's (1989) sites in 2011 to record whether *P. montana* var. *lobata* has persisted in the New York metropolitan area over 22 yr. As a contrast, we used herbarium records to estimate the persistence of kudzu populations over a similar time span at the core of kudzu's range in the southeastern USA.

Methods. Frankel (1989) recorded the presence of 34 populations of *P. montana* var. *lobata* in the New York City metropolitan area, but only 22 of these had unambiguous site descriptions, such as street addresses or persistent landmarks. We could not unambiguously identify the remaining 12 sites because of a lack of sufficient descriptions of the site and, therefore, we could not census those sites. We did visit the identifiable 22 sites in October 2011 and recorded kudzu as being present if we could find any individual plants within 200 m of the described location (Supplemental Material, Table S1). At each site, we visually assessed the existence of suitable habitat, defined as any soil-covered surface, even if this surface was disturbed or on the edge of an impervious surface.

In July 2012, we investigated the persistence of *P. montana* var. *lobata* at the core of its range in the southeastern USA by obtaining 60 herbarium records dated earlier than 1992 from the University of Georgia Herbarium and Clemson University Herbarium. From these 60 records, we were able to identify unambiguously 19 collection locations. We resurveyed these 19 sites using the same methods employed for the New York City sites. The mean time since the date of the herbarium record to our census of the site was 33.9 yr (range: 21 to 42 yr, Supplemental Material, Table S2). We statistically compared the difference in persistence between these core populations and the New York sites using a χ^2 test.

We recorded GPS coordinates at all sites (Supplemental Material, Table S1, S2), and designated sites as either "urban" or "rural" according to US Census definitions. We considered sites as urban if they occurred within the 2012 TIGER/Line Shapefiles Urban Areas, defined as densely developed territory with over 50,000 people, or rural if they were not included within an urban area (Census Bureau 2011). We statistically compared the persistence of populations within urban and rural areas within and among regions using single degree of freedom comparisons χ^2 tests.

Results. In the New York City metropolitan area, we positively identified *P. montana* var. *lobata* at 7 of the 22 (32%) sites where Frankel (1989) had reported kudzu in 1989 (Supplemental Material, Table S1). The sites in this study include city parks and along roadways and parking lots. Nineteen of the populations were located in urban areas, while three populations were in rural areas. All but one of the sites (number 18) had suitable habitat for the current growth of kudzu. Site 18 was reported as an empty lot in 1989, but by 2011, a garage had been constructed at that location and no area around that site could have supported the growth of kudzu. Therefore, *P. montana* var. *lobata* persisted in 7 of the 21 (33%) sites that could have supported plant growth. All seven populations persisting in 2011 were in urban areas.

At the core of the range in the southeastern USA, 18 out of 19 (95%) sites had *P. montana* var. *lobata* growing when we resurveyed in 2012 (Supplemental Material, Table S2). Seven of these sites were in urban areas, while 12 were designated as rural. Suitable habitat remained in all 19 sites, and there was no evidence at any site for conditions that would prevent *P. montana* var. *lobata* from growing. The only population that went extinct in the southeastern US sites was in a rural area.

Overall, kudzu in the New York metropolitan area was significantly less persistent than in the southeastern USA (χ^2 test, df $= 1$, $P < 0.0001$). Likewise, for urban sites only, persistence was significantly higher in the core of the range (χ^2 test, df $= 1$, $P < 0.01$) than in the New York metropolitan area. For rural sites only, persistence was significantly higher at the core of the range (χ^2 test, df $= 1$, $P < 0.01$). Both overall and within regions, there were no statistically significant differences between persistence at urban and rural sites.

Discussion. All species have range limits, and much research has been done to understand the factors that limit a species' range, particularly for native species (Gaston 2009). Data such as those in Frankel (1989) are valuable to understand the range dynamics of abundant and widespread invasive species because they provide a specific date and location of known populations. Datasets documenting locations of an invasive species are more common for new and emerging invaders (Wallace and Bargeron 2014) than for well-established species like *P. montana* var. *lobata*. With Frankel's (1989) data, it is possible to study differences between sites where populations persisted and went extinct, which can reveal factors that constrain a species' range.

We found that populations persisted more often in the southeastern USA than in the New York metropolitan area, and this comparison held when comparing only urban sites within each region. Our estimate of persistence is likely a conservative underestimate of true persistence rates of all *P. montana* var. *lobata* populations because we have assumed that the probability of detecting kudzu, if it is present at a site, is 1, instead of the product of the population surviving and the research team detecting it (Doherty Boulinier, and Nichols 2003; Kery *et al*. 2006). At a landscape scale, species persistence is influenced by the distribution of suitable habitat (including the disturbance regime and availability of resources) and metapopulation dynamics of the species (Pergl *et al*. 2012).

Few studies have addressed the historical persistence of invasive species at a regional spatial scale. Pysek *et al*. (2001) studied how persistence rates vary by habitat type in *Reynoutria japonica* Houtt., *Reynoutria sachalinensis* Nakai, and *Rudbeckia laciniata* L. (invasive perennial clonal plant species, like kudzu), and found that persistence at urban sites was 75%, significantly below the average of 79% for all 458 sites, since the introduction of these species (1892, 1855, and early 1600s, respectively; Osawa 2015, Shaw 2015a, b). Wade *et al*. (1997) recorded persistence of populations of *Heracleum mantegazzianum* Sommier & Levier (giant hogweed), a sexually reproducing monocarpic perennial plant, that were previously recorded in distribution maps and species catalogues across Ireland and found a much lower persistence of 45% (43 of 96 populations) since the introduction of the species in the 19th Century. Pergl *et al*. (2012) expanded upon this work by investigating how persistence of *H. mantegazzianum* varies by habitat type in the Czech Republic. Pergl *et al*. (2012) show that only 124 of 521 (24%) historical sites remained occupied when resurveyed 2 to 131 yr after being recorded in herbaria records, and that *H. mantegazzianum* persisted less often in urban areas (13%) than outside of urban areas (34%). We found that persistence of *P. montana* var. *lobata* does not statistically differ between urban and rural habitats, although the number of rural sites available to sample in the New York metropolitan area is limited. Further, the US Census definition of urban and rural areas may not reflect the relevant scale necessary to understand the dynamics of kudzu populations.

As expected from theoretical (Hardie and Hutchings 2010) and empirical (Nantel and Gagnon 1999, Vucetich and Waite 2003) studies on peripheral populations of native species, we found that fewer peripheral populations persisted than core populations, and that *P. montana* var. *lobata* is capable of persisting for at least 42 yr, as it did at one of our census sites in the southeastern USA. In a study of a noninvasive, endangered, clonal, perennial plant (*Swertia perennis* L.), 63 sites from herbaria records were revisited 5 to 127 yr (mean: 69 yr) after they were recorded and 76% persisted, independent of time since the site was recorded (Lienert, Fischer, and Diemer 2002). Similar to our study, *S. perennis* persisted in 42% of the 19 peripheral sites and 91% of the 44 sites located in the range core (Lienert, Fischer, and Diemer 2002). The increased extinction rate we report could be due to either harsh environmental conditions or public or private management efforts. Despite an assessment of whether suitable habitat remained at each site, we did not investigate the cause of extinction at each site and found no evidence of human-mediated extinctions.

Although Frankel and other scientists were concerned about the northward movement of kudzu, our data are not consistent with this prediction because we show that kudzu does not persist often at the northern periphery of its range. Furthermore, reports of the northern range edge of *P. montana* var. *lobata* have been, and continue to be, anecdotal and conflicting (Snyder 1987, Sorrie and Perkins 1988, Frankel 1989, Waldron and Larson 2012). It is important to specifically record the northern range edge to carefully assess range expansion in kudzu and know when control efforts are prudent. More generally, it is important to consider the effects of climate change separately on invasive and native species because the two often have different characteristics, abundances, and relationships with people (Hellmann *et al.* 2008). Although climate change is causing a poleward shirt in the range of many species (Parmesan 2006), methods of species dispersal, biological interactions between species, and land use changes can also influence the range of a species (Pearson and Dawson 2003).

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