Invasive Plant Science and Management 2017 10:313–321

WSSA WEED SCIENCE SOCIETY OF AMERICA

Mislabeling of an Invasive Vine (*Celastrus orbiculatus*) as a Native Congener (*C. scandens*) in Horticulture

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The horticultural industry is an important source of invasive ornamental plant species, which is part of the motivation for an increased emphasis on using native alternatives. We were interested in the possibility that plants marketed in the midwestern United States as the native *Celastrus scandens*, or American bittersweet, were actually the difficult-to-distinguish invasive *Celastrus orbiculatus* (oriental bittersweet) or hybrids of the two species. We used nuclear microsatellite DNA loci to compare the genetic identities of 34 plants from 11 vendors with reference plants from wild populations of known species identity. We found that 18 samples (53%) were mislabeled, and 7 of the 11 vendors sold mislabeled plants. Mislabeled plants were more likely to be purchased through Internet or phone order shipments and were significantly less expensive than accurately labeled plants. Vendors marketed mislabeled plants under five different cultivar names, as well as unnamed strains. Additionally, the most common native cultivar, 'Autumn Revolution,' displays reproductive characteristics that diverge from the typical *C. scandens*, which could be of some concern. The lower price and abundance of mislabeled invasive plants introduces incentives for consumers to unknowingly contribute to the spread of *C. orbiculatus*. Revealing the potential sources of *C. orbiculatus* is critical for controlling further spread of the invasive vine and limiting its impact on *C. scandens* populations.
Nomenclature: American bittersweet, *Celastrus scandens* L.; oriental bittersweet, *Celastrus orbiculatus* Thunb.
Key words: Horticultural industry, invasive species, microsatellite DNA, mislabeling, molecular testing.

Many introductions of invasive plants have been the direct result of human cultivation, from agriculture and horticulture. More than half of the naturalized (Mack and Erneberg 2002) and invasive plants (Lehan et al. 2013) in the United States were deliberately introduced, and 85% of invasive woody plants were first introduced as ornamentals (Reichard and Hamilton 1997). There has been an increasing emphasis on using native plants as ornamentals, in part because horticulturalists recognize the problem of invasive plants (Peters et al. 2006). Consumers are encouraged to use native plants in horticulture by government agencies, universities, environmental organizations, and for-profit vendors (Burghardt et al. 2009; Tallamy 2007). Additionally, some state and local governments have prohibited the sale and use of plants deemed to be invasive or noxious. Nonetheless, there has been some resistance from horticulturalists to remove invasive plants from their inventories. Peters et al. (2006) note that characteristics that make plants suitable for mass production in horticulture (rapid reproduction, hardiness) are also associated with their potential to become invasive. Additionally, consumer demand for familiar horticultural products and a lack of effective communication about what species are considered problematic can increase the likelihood that invasive species persist in horticultural catalogs.

Celastrus orbiculatus (oriental bittersweet, Celastraceae) is a highly invasive ornamental woody vine (or liana) introduced to the eastern United States (Leicht-Young and

DOI: 10.1017/inp.2017.37

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Management Implications

Native species alternatives are often touted as replacements for invasive species with long histories in horticulture. In the case of the native American bittersweet and introduced invasive oriental bittersweet in the eastern United States, the two species are difficult to distinguish when plants are immature. In a survey of plants sold by vendors across the Midwest, by using genetic markers, we found that most products marketed as American bittersweet or *Celastrus scandens* were actually mislabeled "oriental bittersweet." These mislabeled plants were less expensive than true American bittersweet. Parties intending to purchase and propagate American bittersweet may be contributing to the spread of the invasive. Special care should be taken to properly identify species when propagating bittersweet plants, especially when material is obtained from horticultural vendors. However, identification is not straightforward in the absence of flowers or fruit. As increased effort is put into preventing the spread of oriental bittersweet through statutory and other measures, the cryptic sale of oriental bittersweet through the horticultural industry should be considered an obstacle to attempts to curtail the invasive vine and to the conservation and restoration of American bittersweet populations.

Pavlovic 2015). The species is widely recognized as a threat to native ecosystems because of its rapid growth, which crowds out native vegetation, negatively affects forestry operations, and can alter natural successional trajectories (Fike and Niering 1999; Leicht-Young et al. 2007b). The species has been listed as a prohibited or restricted plant across much of its introduced range (e.g., Vermont, North Carolina, Minnesota). *Celastrus scandens* (American bittersweet, or American staff vine) is a congener native to the region that *C. orbiculatus* has invaded in North America. *Celastrus scandens* is also a woody vine and is widely marketed as an ornamental alternative to *C. orbiculatus*.

There is great potential for mislabeling the two species, with plants marketed as *C. scandens* and American bittersweet actually being *C. orbiculatus* or hybrids of the two species. Mislabeling may occur unintentionally, as it is difficult to distinguish the *Celastrus* species in the absence of reproductive structures (Leicht-Young et al. 2007a), and plants purchased from vendors are usually small individuals that have not begun to flower. Additionally, seeds collected from pistillate *C. scandens* may be sired by *C. orbiculatus*, and hybrids of the two species have been found in the wild (Zaya et al. 2015). There may also be an incentive for deliberate mislabeling, because *C. orbiculatus* grows more rapidly than *C. scandens* (Leicht-Young et al. 2007b), thus increasing yields while decreasing investment of time and resources, and *C. orbiculatus* has a long history in horticulture (Del Tredici 2014).

We used molecular markers to determine the species identity of commercially available plants marketed as *C. scandens* or American bittersweet. Our goal was to determine whether *C. orbiculatus* or hybrids were sold in place of *C. scandens*. If the ultimate source of marketed plants is seed collected from wild plants, it is possible that a large proportion of individuals are hybrids. Alternatively, *C. orbiculatus* may be substituted, intentionally or not, because the two species are difficult to distinguish morphologically in the absence of reproductive structures. Human commerce is among the most important dispersal agents of introduced species, and understanding commerce's role in the continuing spread of *C. orbiculatus* is essential in any large-scale attempt to control its invasion and negative effects on natural communities, and on *C. scandens* in particular.

Materials and Methods

Study Species. *Celastrus scandens* L. (Celastraceae) is the only member of the genus native to North America (Hou 1955). It is a woody vine, usually found in open habitat ranging from full sun to forest edges or gaps. Its range extends from southern Quebec to South Dakota, south to western Texas through Georgia (USDA–Natural Resources Conservation Service [USDA-NRCS] 2017). The native range of *C. orbiculatus* Thunb. is in Korea, Japan, and China (Hou 1955), where it is one of approximately 25 species in the genus (Leicht-Young and Pavlovic 2015). It is found in thickets and lowland slopes, but can thrive in shaded habitat (e.g., forest understory) that would likely exclude *C. scandens* (Pavlovic and Leicht-Young 2011). Both species are usually dioecious, although rare individuals and populations displaying other breeding systems are known.

Celastrus orbiculatus was introduced as an ornamental vine to the eastern United States in 1874 (Del Tredici 2014). By the middle of the twentieth century, it was widely recognized as a pest species rapidly spreading in the eastern United States (Patterson 1974; EDDMapS 2017; USDA-NRCS 2017). *Celastrus orbiculatus* is a strong competitor that crowds out other vegetation and can be economically costly to forestry and alter natural succession (Fike and Niering 1999; Leicht-Young et al. 2007b). There is strong evidence that *C. orbiculatus* interferes with successful reproduction in *C. scandens* through asymmetric pollen flow and hybridization (Zaya 2013), and declines in *C. scandens* have been observed in regions where invasion by *C. orbiculatus* is oldest and most extreme (Dreyer et al. 1987; Leicht 2005; RI Bertin, personal communication). As a result, *C. scandens* has been listed as a threatened, endangered, or extirpated species in multiple states.

Sampling. We purchased plants marketed as American bittersweet or *C. scandens* from 11 vendors in the midwestern United States (in Indiana, Illinois, Missouri, and Nebraska; Figure 1) in summer and fall of 2009. Purchases were made in person from six vendors, and the other five

https://doi.org/10.1017/inp.2017.37 Published online by Cambridge University Press

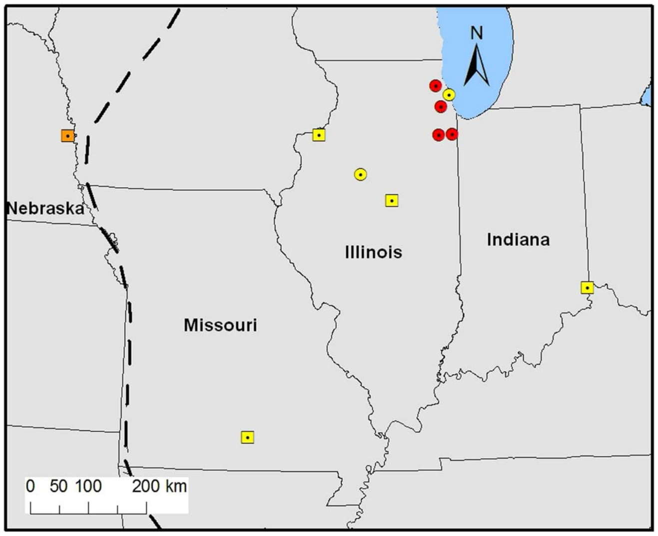

Figure 1. Distribution of *Celastrus* vendors in the midwestern United States. Circles represent vendors that were visited in person; squares represent vendors that shipped the product. Red points represent vendors that exclusively sold *C. scandens*; yellow points represent vendors that exclusively sold *C. orbiculatus*; and the single orange point represents a vendor that delivered both species. The dashed line represents the approximate western edge of the *C. orbiculatus* invasion front (from EDDMapS 2017).

Table 1. Sources and genetic identities for *Celastrus* samples.[a]

Vendor code	State	Cultivar	Count	Genetic identity
A	Indiana	None	2	*C. orbiculatus*
B	Illinois	None	5	*C. scandens*
C	Illinois	Autumn Revolution	3	*C. scandens*
D	Illinois	Autumn Revolution	3	*C. scandens*
E	Illinois	Indian Mix	4	*C. orbiculatus*
F	Illinois	Autumn Revolution	4	*C. scandens*
G	Illinois	None	3	*C. orbiculatus*
H	Illinois	None	2	*C. orbiculatus*
I	Illinois	Indian Brave	1	*C. orbiculatus*
		Indian Maiden	1	*C. orbiculatus*
J	Missouri	None	3	*C. orbiculatus*
K	Nebraska	Diana	1	*C. orbiculatus*
		Hercules	1	*C. orbiculatus*
		None	1	*C. scandens*

[a] Two vendors sold multiple cultivars, and one vendor sold both species.

purchases were made via the Internet or by telephone. We sought vendors that targeted a retail audience, though it is possible that some may have also served as wholesalers, growers, or at other levels in the horticultural industry supply chain (Drew et al. 2010). Telephone or Internet orders were shipped as bare-root samples that we later potted. In-person purchases were potted plants. Approximately half of the samples acquired through in-person purchases were larger than shipped samples, though some in-person purchases were similar in size to shipped plants. Sampling locations ranged across the invasion front of *C. orbiculatus* (EDDMapS 2017). In total, 34 individuals were genetically tested, representing six named cultivars and plants not labeled with a cultivar name (Table 1).

In addition to the purchased samples, we included three other types of control samples for genetic and statistical analysis. We used plants collected from the wild for which species identity was determined using reproductive morphology and verified genetically in a previous study as genetic benchmarks for *C. scandens* and *C. orbiculatus* (Zaya et al. 2015). In total, we used 182 *C. scandens* individuals from 15 populations in 9 states (Illinois, Indiana, Massachusetts, Michigan, Minnesota, North Carolina, Ohio, South Dakota, Wisconsin) and 180 *C. orbiculatus* individuals from 15 populations in 9 states (Connecticut, Illinois, Indiana, Massachusetts, Michigan, North Carolina, New Jersey, Tennessee, Virginia) as benchmarks. Data for these samples are not presented in detail here, but are summarized in Zaya et al. (2015) and available through this paper's dataset (see Acknowledgments). Additionally, we included 16 hybrids produced through hand cross-pollination conducted at the Indiana Dunes National Lakeshore, Porter County, IN (Zaya et al. 2015). Resulting seeds were collected, put through cold stratification, and germinated according to the protocol outlined by Young and Young (1992). We soaked seeds for 24 h, sowed them in an equal mix of potting soil and sand, watered the mixture, placed them in a bag, and kept them refrigerated at 4 C for 90 d. After 90 d, we germinated the seeds in a greenhouse.

Genetic Analysis. Genomic DNA was extracted using the DNeasy Plant Mini Kit (Qiagen, Germantown, MD). For 32 samples, DNA was extracted from 20 to 25 mg of ground leaf material following the manufacturer's protocol. Two samples from the same supplier (Vendor H in Table 1) were not viable upon delivery and did not have leaf material available. For those two samples, we used 50 to 70 mg of scraped wood shavings for DNA extraction. We used a modified protocol developed by Rachmayanti et al. (2009), which included addition of polyvinylpyrolidone to the lysis buffer to help with DNA extraction from wood tissue. We successfully extracted DNA from wood shavings that came from the thickest part of the dead stem, near the base of the plant. The five nuclear microsatellite loci described by Zaya et al. (2015) were used to genotype each individual. These five loci have been shown to distinguish the two species and

https://doi.org/10.1017/inp.2017.37 Published online by Cambridge University Press

their hybrids. Nuclear microsatellites are especially useful for the objectives of this study, because they are highly variable, making it possible to distinguish closely related species, and because they are codominantly inherited (one allele transmitted from each parent), which allows for accurate identification of hybrid individuals. Fragment sizes of PCR products were analyzed with the ABI 3730 DNA Analyzer, using a LIZ500 ladder (Applied Biosystems). All microsatellite genotypes were scored by analyzing the raw data using Applied Biosystems GeneMapper software v. 3.7.

Statistical Analysis. Species assignments were evaluated using the program Structure v. 2.3 (Falush et al. 2003). No a priori information on species identity was included in the analysis. Structure implements a Bayesian clustering approach and Markov chain Monte Carlo simulations to estimate the proportion of each individual's genome originating from each inferred population. We used the admixture model, assuming correlated allele frequencies, and set the number of clusters, K, equal to 2. These settings have been shown to successfully discriminate these two species and their hybrids (Zaya et al. 2015). Identical genotypes were collapsed into a single record for the analysis. We conducted three independent runs, each with 250,000 iterations after an initial burn-in of 50,000 iterations. Individuals were classified to one of the two species groups using the proportion of ancestry, q, from each run. We set the threshold for classifying an individual in one of the two species categories as 0.9 (Manel et al. 2002), so that if the maximum q was less than 0.9, a species was classified as a hybrid. All horticultural samples had a value of q greater than the threshold, and all individuals were assigned to the same group in each run. As each run gave the same result for every sample (test and control), we present the mean q values.

We used the nonparametric Mann-Whitney-Wilcoxon rank-sum test to compare prices of products identified as *C. orbiculatus* and *C. scandens*. The test was implemented in R v. 3.3.2 (R Core Team 2016).

Results and Discussion

All five primer pairs amplified polymorphic loci in all our test samples and the controls. Among the 34 horticultural samples tested, we identified 22 unique genotypes. For these unique genotypes, the mean number of alleles per locus was 10.2, and the mean observed heterozygosity was 0.72 (Table 2). Both the mean number of alleles and mean observed heterozygosity were greater in test samples that we identified as *C. orbiculatus* compared with those identified as *C. scandens* (Table 2). In control samples and other wild populations, large differences between species with respect to genetic diversity were only observed for one locus (CEOR7003; Zaya et al. 2015).

Genetic tests indicated that 18 of 34 (53%) of the purchased samples clustered with *C. orbiculatus*. The other 16 samples all clustered with *C. scandens* (Table 1). None of the samples clustered with hybrids. All of the Structure assignments were highly supported by the inferred proportion ancestry, q (Figure 2). Every sample had a maximum q greater than 0.96, and all but one maximum q value was greater than 0.99. Two of the samples we purchased showed signs of reproductive structures, both carrying fruits in terminal panicles typical of *C. scandens*. Structure correctly classified both samples as *C. scandens*.

Four of the 11 vendors sold only *C. scandens*. Six vendors sold only *C. orbiculatus*. The last vendor, located in Nebraska and at the *C. orbiculatus* invasion front, sold both species (Figure 1). The mislabeled samples came under five cultivar names, some of which are racially insensitive: 'Diana,' 'Hercules,' 'Indian Brave,' 'Indian Maiden,' and 'Indian Mix' (Table 1). We found multiple samples with the same genotype due to asexual propagation. The identical genotypes included samples from the westernmost vendor in Nebraska and the easternmost vendor in southeastern Indiana. The Indian Maiden, Indian Brave, and Hercules cultivars had identical genotypes, as did Diana and an unnamed sample (Table 2). The only named cultivar that was genetically determined to be *C. scandens* was 'Autumn Revolution,' also known as *C. scandens* 'Bailumn' (Bailey 2009). Autumn Revolution was purchased from three of the five vendors that sold *C. scandens*. Six vendors sold plants that were not labeled with a cultivar name, and in four of those cases, genetic tests classified the samples as *C. orbiculatus*. The multilocus genotypes of the horticultural samples are provided as a reference to parties interested in testing commercial products of unknown species identity (Table 2).

Four of the six vendors that were visited in person exclusively sold *C. scandens*. All of the online or phone order shipments included *C. orbiculatus*, a group that includes the vendor that sent both species (Figure 1). The price of true *C. scandens* was more than twice the price of *C. orbiculatus* (Figure 3), a significant difference (Mann-Whitney-Wilcoxon rank-sum test: $W = 31$, $P < 0.04$). Interestingly, the vendor that sold both species charged more for *C. scandens* (US$19.95) than mislabeled *C. orbiculatus* (US$13.95).

In testing the genetic identity of plants marketed as the native *C. scandens*, we found that the majority of vendors sampled in the midwestern United States were selling a mislabeled introduced species, *C. orbiculatus*. Mislabeled *C. orbiculatus* is available on both sides of the invasion front and can easily be shipped to any state in the contiguous United States. Some vendors also ship internationally, which could exacerbate the *C. orbiculatus* invasion in Canada and even in distant regions like New Zealand (Williams and Timmins 2003). None of the purchased samples were *C. scandens* × *C. orbiculatus* hybrids. We sampled near the invasion front, and it may be that the

Table 2. Microsatellite genotypes for horticultural *Celastrus* samples.[a]

Species	Mean A	Mean H_O	Cultivar	Vendors	CESC002	CESC003	CESC006	CEOR7004	CEOR7003
					Microsatellite loci				
C. scandens	4.4	0.65	Autumn Revolution	3	217/217	190/192	220/228	151/151	216/220
					217/217	190/192	228/228	151/151	216/220
			Unnamed	2	217/217	190/204	228/228	151/151	216/220
					233/237	192/204	228/228	151/157	212/214
					233/235	190/206	228/228	151/157	220/222
					235/237	190/204	224/228	151/157	227/235
					217/233	190/202	224/228	151/157	214/214
					225/225	202/202	228/228	151/151	214/216
C. orbiculatus	6.6	0.75	Indian Mix	1	235/239	214/222	201/219	159/173	243/243
					235/239	222/222	201/201	159/169	213/242
					235/235	220/222	201/201	169/173	242/248
			Diana/unnamed	1	231/235	220/222	219/226	169/169	227/232
			Hercules/Indian Brave/Indian Maiden	2	219/231	220/220	201/219	169/173	242/242
			Unnamed	4	229/231	220/220	201/219	169/171	218/232
					231/239	220/220	201/219	163/169	232/242
					227/231	220/224	219/226	161/163	217/232
					227/231	218/220	219/219	163/169	224/232
					219/225	218/220	201/219	159/161	NA
					233/235	220/222	219/226	163/173	NA
					231/235	220/222	201/201	163/169	218/232
					231/245	220/222	201/226	169/169	218/244
					219/219	222/222	201/226	169/169	232/244
Combined	10.2	0.72							

[a] Individuals are diploid, with two alleles per locus. The numbers under each locus heading represent the length of the allele in base pairs, and alleles are separated by a slash. Mean number of alleles (Mean A) and observed heterozygosity (Mean H_O) were calculated across all five loci and across all cultivars, after excluding repeated genotypes. Genotypes were determined for 18 *C. orbiculatus* individuals and 16 *C. scandens* individuals. Vendors refers to the number of vendors, and NA indicates missing data. Note that the allele sizes used here depend on the usage of the method described by Schuelke (2000), and the same fluorescent label for each locus. The following Applied Biosystems standard dyes were used: NED, CESC006; VIC, CEOR7004 and CEOR7003; PET, CESC002 and CESC003.

observed patterns would change farther east, where *C. scandens* has greatly declined, or farther west, where *C. orbiculatus* is not known to occur. Mislabeling of *Celastrus* is problematic, because the phenomenon promotes the spread of an invasive species inhibits the success of a native species, and consumers pay for a product that they did not choose—an aggressively growing plant that can be a nuisance.

A useful clue as to the accuracy of product labeling might be the mode of purchase. Four of six in-person purchases were accurately labeled. Every vendor that shipped a product provided us with *C. orbiculatus*, though one of those vendors sold both species. All of the shipped products were initially found through Internet searches, though some were ordered over the telephone. Shifts in distribution patterns and marketing strategies, prerequisites for widespread Internet purchasing, may accelerate the spread of incorrectly labeled *Celastrus* and invasive species in general (Drew et al. 2010). Additionally, mislabeled products can be shipped to areas where the sale and propagation of *C. orbiculatus* is illegal, such as the city of Chicago, IL—where all of the products included in this study were shipped. Although the municipal code restricting the sale of *C. orbiculatus* in Chicago may have influenced the accuracy of labels in the region where we made our in-person purchases, we do not believe this was the case, for three reasons. First, only two vendors were in the jurisdiction covered by the law at the time, and one of them sold the mislabeled product. Second, expertise is not available at the municipal level to discriminate the two *Celastrus* species, thus a mislabeled plant

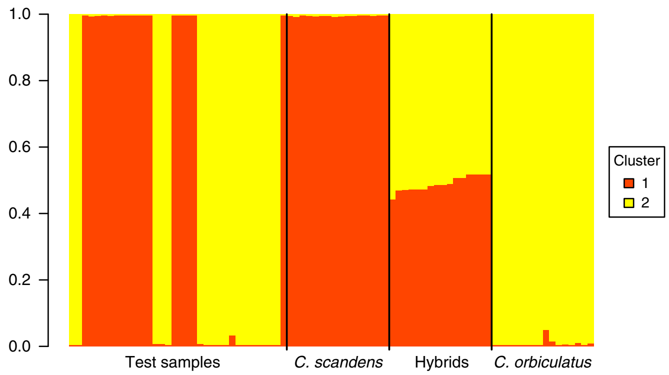

Figure 2. Bayesian clustering results from Structure with two inferred clusters ($K=2$) for *Celastrus* individuals. Results for each individual are represented in a single column. The colors in each column show the proportion of the individual's genome assigned to the two clusters. "Test samples" ($N=34$) are plants purchased for this study. The other three categories were control plants of known genetic identity ($N=378$). For clarity, only 16 randomly selected control samples in each category are shown.

is likely to go unnoticed. Finally, the city has limited resources for enforcement of the law and is slow or unable to respond to reports of illegal sales, even for *C. orbiculatus* plants that are not mislabeled as "American bittersweet" (DNZ, personal observation).

The significant difference in price between mislabeled and correctly labeled plants may suggest that *C. orbiculatus* is easier to obtain or it can be propagated more efficiently. *Celastrus orbiculatus* has a long history in North American horticulture and has become more common than *C. scandens* in many regions of the United States. Ecological and physiological studies have found *C. orbiculatus* to be a stronger competitor than *C. scandens*, exhibiting more rapid growth (Leicht-Young et al. 2011), tolerance of a larger range of conditions (Leicht-Young et al. 2007b) and herbivory (Ashton and Lerdau 2008), and greater reproductive output (Dreyer et al. 1987; Zaya 2013). However, at this point, we can only speculate about the connection between species biology and product price. Because most Internet purchases were *C. orbiculatus* and most in-person purchases were *C. scandens*, myriad confounding factors (e.g., plant size, economic advantages for different types of vendors) may be influencing the price difference. Anecdotally, the case of the vendor that sold both species is revealing, as mislabeled plants cost 30% less. Whatever the cause, the lower price creates an incentive to purchase mislabeled *C. orbiculatus*.

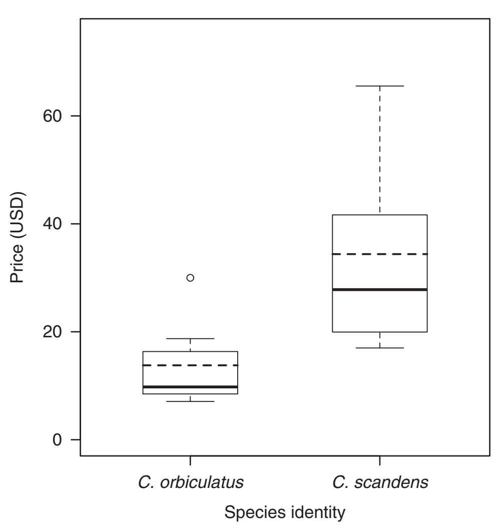

Figure 3. Prices of correctly labeled *C. scandens* ($n=5$) and mislabeled *C. orbiculatus* ($n=7$). Heavy solid lines represent the median, while dashed lines represent the mean.

Properly labeled *C. scandens* appears to be difficult to obtain, even when purchasing from vendors that claim to sell American bittersweet. Only one of the named cultivars turned out to be *C. scandens*, that one being Autumn Revolution, or *C. scandens* 'Bailumn,' patented by Bailey Nurseries Inc. (St Paul, MN; Bailey 2009). The availability of Autumn Revolution has increased recently, which means a properly labeled *C. scandens* can be more easily obtained. However, overreliance on this cultivar may be troublesome. Autumn Revolution has the potential to become naturalized, as individuals readily set germinable seed that can be widely dispersed by birds. Plants grow vigorously and set larger seeds at a greater rate than typical *C. scandens* (Bailey 2009; DNZ, personal observation). Also, the breeding system of Autumn Revolution is atypical in that all individuals have hermaphroditic flowers, while *C. scandens* is almost always dioecious (Bailey 2009). Eight of the nine Autumn Revolution samples that we tested, from three different vendors, were genetically identical (Table 2). The spread of the cultivar into the wild may threaten native *C. scandens* by decreasing genetic diversity of wild populations. Decreased genetic diversity may have several negative consequences, but in cultivated plants in particular, it may lead to increased susceptibility to disease (Zhu et al. 2000). The potential for intraspecific crossing, long-distance pollen dispersal, and introgression between horticultural plantings and wild conspecifics has been demonstrated and may threaten the genetic integrity of *C. scandens*. Johnson and Galloway (2008) provided evidence that individuals from natural *Lobelia cardinalis* L. (cardinalflower) populations were pollinated by horticultural *L. cardinalis* up to 1 km away, while Whelan et al. (2006) found the potential for introgression of unusual morphological characteristics from garden populations of *Grevillea macleayana* (McGill) Olde & Marriott (Jervis Bay grevillea) into wild populations. It is currently challenging for conscientious midwestern U.S. consumers to find an alternative to Autumn Revolution. Only one vendor sold

https://doi.org/10.1017/inp.2017.37 Published online by Cambridge University Press

only *C. scandens* plants that were not Autumn Revolution. That vendor, located in Monee, IL, sold unnamed plants.

The rate of mislabeling found in this study (64% of vendors, and 53% of samples tested) is large compared with previous studies that used molecular markers to survey commercial plant products (Zaya and Ashley 2012). For example, several studies have tested the accuracy of labels on herbal medication and have reported mislabeling of 8% to 60% of the products tested (Del Serrone et al. 2006; Fan et al. 2009; Feng et al. 2010; LeRoy et al. 2002; Lin et al. 2008; Manissorn et al. 2010; Mihalov et al. 2000; Srirama et al. 2010; Vongsak et al. 2008; Wang et al. 2007; Xue et al. 2006). Our study is unlike most examples reported in the scientific literature, in that we tested viable plants capable of spreading into the wild. Most reported studies test nonliving material, which is usually meant for human consumption. However, Honjo et al. (2008) tested the reported source of stocks of an endangered plant species, *Primula sieboldii* E. Morren. The authors found that at least 17% of the stocks studied were not derived from the reported source populations and argued that these stocks should not be used for restoration, because they might alter the gene pool of locally adapted populations.

For parties that purchase or propagate *Celastrus scandens*, including in gardens and native plant community restorations, reproductive structures are the best indication of the true species identity; differences between species include anther color of staminate flowers, inflorescence size and structure, and the color of fruit capsules. In the absence of reproductive structures, the best vegetative structure to differentiate the species is the shape of leaves unfolding from winter buds during spring leaf out (Leicht-Young et al. 2007a). Emerging *C. orbiculatus* leaves are conduplicately folded, while *C. scandens* leaves are involute. However, this characteristic is only visible for a brief period in spring. Other vegetative characteristics, such as mature leaf shape, can provide clues as to the true species identity, but those characteristics are not always conclusive and are not quantified for hybrids.

In the case of *Celastrus* in North America, what parties are responsible for the mislabeled samples? Can mislabeling be purely accidental? The two species are difficult to distinguish morphologically in the absence of flower or fruits (Leicht-Young et al. 2007a), and in most cases vendors are selling small plants that have not reached reproductive maturity. Thus, vendors that do not act as their own growers may not be responsible. It is implausible that producers and wholesale growers propagating *C. orbiculatus* at a large scale and over an extended period of time never observe the axillary inflorescences and yellow fruit capsules that readily distinguish the introduced vine from *C. scandens*, with its flowers in terminal panicles and orange fruit capsules. Indeed, we were surprised to find labels with our Diana and Hercules samples that included photos of mature plants that clearly had the yellow, axillary fruits of *C. orbiculatus*. Internet shopping searches for "American bittersweet" or "*Celastrus scandens*" yield results of products that are clearly *C. orbiculatus*. Mislabeling may still be unintentional, but it is avoidable.

Plant collectors and botanists interested in novel species started the invasion of *C. orbiculatus* in North America (Del Tredici 2014). The first introducers and propagators did not realize the potential for *C. orbiculatus* to spread in the wild, altering ecosystems and interfering with successful reproduction in a native congener. Nor did they likely espouse an understanding of biological invasions and the value of native planting that is increasingly the norm among scientists, horticulturalists, and the public at large. Parties responsible for the propagation of *C. orbiculatus* today are aiding in the invasion of a known problematic weed and exacerbating the decline of a native species that can be used as a horticultural substitute. Any attempt to halt mislabeling of *C. orbiculatus* must overcome the systematic issues that drive the practice, including intense market pressures, intensifying competition, and a lack of accurate information (Drew et al. 2010). One approach to curb the problem of mislabeled horticultural products is to attempt to institute penalties on suppliers through legal means. Another possible approach is to encourage self-policing. Both approaches have limitations, and a lack of proper enforcement may lead to virtually no improvement in the situation. Dissemination of useful information in a manner accessible to a wider public will help to create well-informed consumers and producers, which will in turn help the problem, although it may not eliminate it.

Acknowledgments

We would like to thank Ralph Grundel, Krystal Frohnapple, Boris Igic, Jeremie Fant, Henry F. Howe, John Wilk, Emi Kuroiwa, Janet Backs, Eun Sun Kim, Jason Palagi, Carrie Seltzer, Jenny Zambrano, Greg Spyreas, and two anonymous reviewers for providing helpful comments that improved the study and the article. Bob Streitmatter aided in sample collection. Kevin Feldheim helped with genetic analysis. Financial support was provided by the University of Illinois at Chicago, U.S. Geological Survey, Chicago Wilderness, and the Illinois State Academy of Science. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. This article was completed in partial fulfillment of the doctoral degree from the Graduate College at the University of Illinois at Chicago to DNZ. The data for the study were archived on the University of Illinois Data Bank archive at http://https://doi.org/10.13012/B2IDB-3661776_V2.

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Received June 12, 2017, and approved November 9, 2017.

Associate Editor for this paper: Marie Jasieniuk, University of California, Davis.