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A brief review of *Triadica sebifera* (Chinese tallowtree) in the southern United States, emphasizing pollinator impacts and classical biological control

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Running head: Chinese tallowtree, pollinators, and biocontrol

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Abstract

Throughout history a great many plant species have been purposefully transported to new areas around the globe. Horticulture, the promise of new sources of plant material for industry, forage, food, and stabilization of soil are only a few of the motives for the early transcontinental exchange of plants. Many introductions have been beneficial or benign, however, some plants introduced into new areas are now considered invasive and detrimentally impact the environment. Chinese tallowtree [*Triadica sebifera* (L.) Small] (Euphorbiaceae) is an excellent example of the best intentions leading to unanticipated negative effects many decades later. Native to eastern Asia and now naturalized and widespread in many tropical, subtropical, and temperate areas in the world, Chinese tallowtree has proven to be one of the worst woody invasive plants. It is known for shading out native vegetation, capable of dominating areas following disturbance or even invading previously diverse undisturbed habitats. It is prevalent in the southern United States, especially along the Gulf Coast. Investigations into classical biological control of Chinese tallowtree have yielded at least two promising candidates but have raised objections among beekeepers and beekeeping organizations who prize the quality honey produced from an abundant spring nectar flow. In this review we discuss Chinese tallowtree's invasive characteristics, detrimental effects, potential use as a biomass crop, and demonstrated or potential direct and indirect effects on native and non-native pollinators. We review the current state of identification and screening of biological control agents. Four research questions are presented which are designed to fill gaps in our knowledge of Chinese tallowtree and pollinators. Classical biological control has the potential to reduce Chinese tallowtree populations across the landscape, which would likely result in greater understory and tree diversity, benefitting native and exotic pollinators.

Keywords

beekeeping, European honey bee, invasive species, nectar flow, understory restoration

Introduction

Chinese tallowtree [*Triadica sebifera* (L.) Small] (Euphorbiaceae) (tallowtree, hereafter) is a small- to medium-size tree that is native to eastern Asia. It has become widely established and naturalized in many tropical, subtropical and temperate parts of the world and is considered invasive in the United States (U.S., hereafter), India, and Australia (CABI 2000). Tallowtree is especially widespread and problematic across the southern U.S. (Meyer 2011; USDA NRCS PLANTS Database 2019). Other common names include popcorn tree, due to its clusters of white seeds (Figure 1), Florida aspen, and chicken tree. Trees produce an abundance of seeds, which are rich in oils and covered with a thick layer of white, fatty material known as tallow. In China, where it has been cultivated for centuries, all parts of the tree are utilized in some manner, for food, traditional medicine, industrial applications, carvings, and furniture (Macgowan 1851). Soon after its introduction into the U.S. from China in 1776 by Benjamin Franklin (Randall and Marinelli 1996), it was noted that cultivated tallowtree around Charleston, SC and Savannah, GA was "…spreading spontaneously into the coastal forests" (Michaux 1803). Nonetheless, in the early 1900s, the U.S. Department of Agriculture encouraged planting of tallowtree in the U.S. Gulf States in hopes of establishing a soap industry (Flack and Furlow 1996). Over the last two and a half centuries, various organizations have touted the benefits of tallowtree and the species has been promoted as a crop for production of edible and industrial oil, and biomass for hydrocarbon fuels (Jamieson and McKinney 1938; Howes 1949; Scheld and Cowles 1981; Scheld et al. 1984). It has also been widely planted as a landscape tree for its colorful autumn foliage and by beekeepers as forage for honey production (Lieux 1975). For a comprehensive review of tallowtree biology and its introduction into the U.S., see Bruce et al. (1997).

Tallowtree has been present in the U.S. for nearly 250 years, but rapid expansion has occurred over the last few decades (Oswalt 2010) (Figure 2). Numerous studies have documented its impacts in a variety of habitats, and its facultative wetland status allows for new colonization in a majority of southern U.S. ecoregions (USDA NRCS PLANTS Database 2019, Legal Status). Considering its initial introduction in the late 18th century, followed by additional purposeful introductions, the more recent spread in the southern U.S. over the last 70 years may be due to a lag-phase or accumulation of adaptations and/or genetic diversity since its initial introduction period (Elton 1958; Crooks 2005; Aikio et al. 2010). Contributing factors to the lag-phase include, but are not solely attributed to, increases in genetic information via secondary contact contributing to an increase in genomic response and adaptability (Sakai et al. 2001), biotic and abiotic factors (Catford et al. 2009), density-dependence (such as an Allee effect) (Pachepsky and Levine 2011; Sullivan et al. 2017), and the propagule pressure during the period(s) of introduction (Lockwood et al. 2005; Catford et al. 2009; Blackburn et al. 2013; Cassey et al. 2018).

Non-native, invasive tree species generally have profound and lasting impacts on the communities they invade (Lamarque et al. 2011). Trophic and competitive interactions may be relatively straightforward and easily observed, while more subtle effects associated with longer term changes in flora and fauna may not be immediately apparent. Trees are particularly effective ecosystem engineers, a term coined by Jones et al. (1994, 1997) for "…organisms that directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials." In this review, we consider recent studies that have directly addressed tallowtree spread and impacts on the environment, likelihood of cultivation as a biomass / biofuel crop, potential for classical biological control, and potential impacts of tallowtree on introduced and native pollinators. We include a review of scientific and selected popular literature addressing tallowtree and *Apis mellifera*, the European or Western honey bee, as tallow is often promoted as an important nectar source for honey production. We present four research questions that could increase our understanding of interactions between tallowtree and pollinators. We conclude that classical biological control efforts to reduce tallowtree in the introduced range of the U.S. are justified.

Invasive characteristics of Chinese tallow

Life-history and evolutionary traits contribute to tallowtree's success as an invasive, perenniating tree. Successful invasive species tend to be r-selected species rather than K-selected species. R-selected species are generally tolerant of a wide range of biotic and abiotic pressures in the naïve invasive range, exhibit high fecundity, effective dispersal, and the ability to rapidly colonize disturbed habitats. Successful invasive plants are generally ruderal and may be superior resource competitors as compared to native plants (Davis et al. 2000; Tilman 2004). Though it has been proposed that forested systems are intrinsically more resistant to invasion (Martin et al. 2009), canopy gaps resulting from stochastic and/or anthropogenic disturbances create opportunities that can result in a breakdown of local biotic resistance (Elton 1958; Martin et al. 2009). Tallowtree's ability to invade both disturbed and undisturbed habitats in the southern U.S. as an r-selected species have been well-documented.

Disturbance-mediated spread has been shown for many invasive plant species (Lozon and MacIsaac 1997) and tallowtree is no exception. Several other environmental factors are predictors of successful tallowtree invasion, including proximity to bodies of water, private land ownership, low elevation and slope, and younger stands (Gan et al. 2009). Fire regimes can influence tallowtree invasion, with shorter fire intervals favoring seedlings and saplings, which may be killed or top-killed by subsequent fires, and longer intervals favoring large trees which can survive low-intensity burns (Meyer 2011, Fan et al. 2021). Proximity to edge habitats such as roads and fire breaks, which can harbor mature, seed-bearing trees, can favor tallowtree invasion (Fan et al. 2018, Yang et al. 2019). Once established, tallowtree can form a dense canopy (Figure 3). In certain ecosystems, community resistance to invasion can be overcome without disturbance (e.g. Bruce et al. 1995). Bruce et al. (1997) documented an invasion by tallowtree in a native Texas coastal prairie, with canopy closure within 20-25 years. Empirical data derived from the U.S Department of Agriculture, Forest Service, Forest Inventory and Analysis program demonstrated increased coverage and northward movement of tallowtree in east Texas, at a rate of just under 2 km/year (Suriyamongkol et al. 2016). By the mid-1990s, there were naturalized populations of tallowtree in over half of Florida's counties; at one study site, tallowtree had been present for only 20 years but had the greatest density of all woody species, with seedling cover exceeding that of all other woody species combined (Jubinsky and Anderson 1996). The first author has seen large areas (tens of hectares) in southern Louisiana where the only trees present a few years after cutting were tallowtree and a few large sentinel oaks. Riparian areas in California's Central Valley are also susceptible to invasion, especially downstream from areas where it has naturalized (Bower et al. 2009).

Tallowtree satisfies two of the classes of successional drivers proposed by Meiners et al. (2015); species availability, and species performance. Tallowtree produces an abundance of seeds, with local dispersal near the mother-plant and longer-distance dispersal due to bird-mediated dispersal, which increases species availability in locations near existing populations. Fecundity is a strong characteristic of tallowtree favoring invasiveness, with trees producing seed three years after germination (McCormick 2005). The species is vagile, with a tree producing up to 100,000 seeds which are readily dispersed by water and birds (Renne et al. 2002). Tallowtree produces a seed bank that remains viable for at least 2 years (Harper 1995, Renne and Spira 2001). Seeds that are placed in cold storage can germinate for as long as 7 years, although the percentage of viable seed drops substantially (Cameron et al. 2000). Furthermore, reproductive flexibility in non-native plants further contributes to nascent invasives' success in establishment and spread. In tallowtree, local vegetative sprouting from below-ground root tissue contributes to individual regeneration and persistence (Meyer 2011).

Several other characteristics of tallowtree favor establishment and spread. Tallowtree seedlings are shade-tolerant (Jones and McLeod 1989), exhibit growth equal to or exceeding native vegetation (Jones and Mcleod 1989, 1990; Bruce 1993; Hall 1993), and can withstand occasional flooding and saltwater intrusion (Conner and Askew 1983; Jones and Sharitz 1990). While some tolerance to saltwater intrusion has been observed, tallowtree is not adapted to high soil salinity (Barrilleaux and Grace 2000). Relatively low rates of herbivory have been observed on tallowtree in the U.S. (Jones and McLeod 1989; Jones and Sharitz 1990) as compared to China (Zhang and Lin 1994). Invasive ecotypes of tallowtree in the U.S. differ from their counterparts in China, in agreement with the evolution of the increased competitive ability hypothesis (EICA) (Blossey and Nötzold 1995), as demonstrated by Rogers and Siemann (2004). The invasive ecotypes allocate more resources to growth and/or reproduction and fewer resources to herbivore defense as compared to Chinese ecotypes, presumably as a result of decreased herbivory in the invaded range. A few generalist herbivores have been documented on tallowtree in the U.S. (Johnson and Allain 1998; Siemann and Rogers 2003; Lankau et al. 2004) and one specialized herbivore, a moth (Lepidoptera: Gracillariidae) occurs throughout much of the invaded range in the U.S (Wheeler et al. 2017b). Pile et al. (2017) provide a comprehensive review of invasion mechanisms for tallowtree.

Researchers have had ample opportunities to observe and quantify tallowtree invasions following hurricanes. Hurricanes and other catastrophic weather events are relatively common perturbations in southern U.S. forests (Vogt et al. 2020), altering stand dynamics and influencing succession at local to landscape scales. Following Hurricane Katrina in 2005, Chapman et al. (2008) noted that "The creation of large canopy gaps from wind disturbance has resulted in some areas being essentially carpeted with tallow seedlings and saplings." In a floodplain area that escaped major wind damage from the storm but was inundated by floodwater for an extended period of time, tallowtree increased in abundance and dominance due to mortality of other species (in spite of some tallowtree mortality from flooding) and rapid recruitment following the event. This strengthens the case for tallowtree's ability to withstand, and capitalize on, a wide range of biotic and abiotic conditions during stochastic events like hurricanes (Howard 2012). In a study approximately five years later, Henkel et al. (2016) documented prolific growth and recruitment of adult tallowtree in previously uninfested, highly damaged, low elevation areas. Following Hurricane Andrew, Conner et al. (2002) documented tallowtree invasion in previously uninfested areas with many of the trees at least 10-cm DBH by 1999, only seven years after the hurricane.

Biofuels

As recently as the 1980s through the 2000s some continued to advocate for tallowtree as a crop. Scheld et al. (1980, 1984) suggested commercial production of tallowtree as a cash and petroleum substitute crop. Scheld and Cowles (1981) and Glumac and Cowles (1989) demonstrated tallowtree's potential value as a woody biomass crop. Breitenbeck (2009a) reviews the potential of tallowtree as a biodiesel feedstock. Elsewhere, referring to southwestern Louisiana, Breitenbeck (2009b) argues that "Commercial production of tallow tree seed in this area poses little environmental threat as the tree is already widespread." Tallowtree continues to be considered and evaluated as a candidate for biofuels and other uses. For example, Zappi et al. (2020) list tallowtree among 12 energy/lipid crop plants evaluated for suitability as bioenergy crops to be grown in highway rights-of-way. Despite tying with tung oil tree (*Vernicia fordii* (Hemsl.) Airy Shaw) for second place in their assessment of growth, productivity, status as foodstock, and potential secondary co-products, tallowtree was ultimately not recommended based upon lack of processing infrastructure, toxic tree components, and its status as a "nuisance plant" throughout the area of consideration (southeastern U.S). There is no question that tallowtree is prized in its native range for many uses, and has tremendous potential as a source of biofuels, but this may be a moot point in the U.S. Though not yet a listed Federal Noxious Weed, several states have listed tallowtree as "noxious" (FL, MS, and TX; National Plant Board 2020). It is listed as invasive by state Invasive Plant Councils in Alabama, California, Florida, Georgia, South Carolina, and Tennessee. The Louisiana Department of Wildlife and Fisheries lists tallowtree as invasive (Holcomb et al. 2015). It is considered among the top 10 invasive plants in Mississippi, where the "Help Stop the Pop" program aims to assist municipalities with tree removal and educate the public (Mississippi Forest Commission 2020).

Effects on pollinators

Observations and studies have aptly demonstrated the invasiveness of tallowtree, and its persistence in the environment. Surprisingly, relatively few studies have documented pollination of tallowtree and its potential effects on native pollinators. Tallowtree can be expected to have both direct and indirect effects on flower-visiting insect communities. While the direct effects involve the provision of nectar and pollen, indirect effects are likely to include displacement of native plant species. These different effects are reviewed separately below followed by suggestions for future research.

Direct effects

Tallowtree produces drooping spike-like inflorescences up to 20 cm long with female flowers at the base and male flowers along the remainder of the spike (Miller et al. 2010) (Figure 4). Trees flower prolifically and the flowers produce an abundance of pollen and nectar during the spring and early summer months. Because the pollen grains exhibit limited potential for wind dispersal (Clark 2016), tallowtree largely depends on insects for pollination (Clark and Howard 2019).

Most information on the value of tallowtree to pollinators relates to honey bees. It is well established that tallowtree contributes greatly to honey production in both its native and introduced range. In subtropical China, for example, a related species of *Triadica*, *T. cochinchinensis* Lour. (formerly *Sapium discolor*), is the most important nectar resource for eastern honey bees (Liu et al. 2020). North American beekeepers have reported similar benefits of tallowtree to European honey bee (Hayes 1977, 1979). Indeed, tallowtree is so prized by beekeepers that professional organizations supporting beekeeping in the southern U.S. have argued against release of classical biological control agents targeting this invasive tree (e.g. Dittfurth 2018; Moore 2018; Payne 2018). In addition to citing the benefits of tallowtree to honey production, some have expressed concern that introduced species may have unintended consequences, such as attacking multiple plant species, or pointed out that not all biological control organisms are 100% effective (e.g. Meny 2018). Others have argued for cost-benefit analysis for removal of tallowtree across the landscape and replacement with suitable honey bee forage (Anonymous 2018). Tallowtree appears in extension publications aimed at beekeepers in Louisiana (Pollet and Cancienne 2006), Mississippi (Harris 2019), and Georgia (Delaplane 2010). Alabama Cooperative Extension Service and Clemson Cooperative Extension (South Carolina) both list tallowtree among non-native trees that are nectar sources but discourages planting or spreading them (Tew et al. 2018, Anonymous 2020, respectively).

Compared to the debate centered on the importance of tallowtree to honey bees, very little is known about the value of tallowtree flowers to native pollinators. This is unfortunate considering the many threats facing this fauna (Goulson et al. 2015) as well as the important role native bees play in pollinating crops. As a group, native bees can contribute more to crop pollination than honey bees (Winfree et al. 2007a; Breeze et al. 2011), for instance, and diverse pollinator communities provide a degree of redundancy, thus reducing our dependence on any single species (Calderone 2012). Various threats to honey bee populations and their pollination services such as climate warming (Rader et al. 2013) and colony collapse disorder (Ellis et al. 2010) underscore the importance of native bees to food security (Winfree et al. 2007b). To our knowledge, only one study specifically sought to survey native insects visiting tallowtree flowers. Clarke and Howard (2019) sampled insects from tallowtree flowers at four locations in Mississippi and Louisiana. They collected only six species of bees visiting flowers. Of these, the

European honey bee (*Apis mellifera*) was the most abundant and consistently present species. All five native bee species reported in that study are opportunistic generalists with broad host ranges and represent less than 3% of the bee species known from the region (Bartholomew et al. 2006). In a broader study of non-native plants, native plants, and pollinators, pollinators visiting non-native plants tended to be more generalized species (Memmott and Waser 2002). Moreover, unlike some non-native plant species (Salisbury et al. 2015), tallowtree blooms during the period of greatest flower availability (April-June) (Bruce et al. 1997) and therefore provides no benefit to bees later in the season when fewer floral resources are available. Landowner guidelines for enhancing pollinator abundance and reproduction stress the importance of having a variety of flowering plants that provide nectar throughout the season (e.g. Delaplane 2010).

Studies on other taxa warrant the conclusion that tallowtree supports a depauperate arthropod fauna within its introduced range. Hartley et al. (2004) found that Diptera, Acari and Araneida comprise the atypical arthropod fauna found in monocultures of tallowtree in Texas. Hymenoptera (ants and wasps) were not very abundant in their study (39 individuals, 16 species) and pollinators were not mentioned at all. Predators and detritivores comprised 70% of collections overall. Fewer herbivores were found on tallowtree than in nearby natural areas in other, previous studies. Taken together, the findings from these studies suggest tallowtree has little direct value to native insects.

Indirect effects

Tallowtree is capable of shading out competitors and rapidly forming a closed canopy, reducing understory diversity and thereby lowering pollen and nectar availability for much of the year (Bruce et al. 1997). It is generally accepted that more open forest conditions favor pollinators (Hanula et al. 2016) and previous work has documented the negative effects of thick growths of invasive shrubs on native plants (Hanula et al. 2017) as well as pollinators (Hudson et al. 2014). Open, natural areas, such as Texas coastal prairie where tallowtree can invade and form closed-canopy monocultures (Bruce et al. 1997) provide diversity of native plants and resources for pollinators. Coastal prairie habitats and longleaf pine savannahs are two sensitive communities which are limited in distribution and are susceptible to tallowtree invasion (Grace 1998, Varner and Kush 2004). Diverse pollinator communities have been documented in longleaf pine savannahs (Bartholomew et al. 2006) and those pollinator communities benefit from thinning (Breland et al. 2018, Odanka et al. 2020). Conversely, one would expect that loss of understory from tallowtree invasion would result in decreased pollinator diversity and abundance. Pollinator abundance and pollination services are closely linked to landscape change (Kremen et al. 2007, Ricketts et al. 2008). It therefore seems likely that invasion by tallowtree has strong indirect effects on pollinator communities.

A second potential indirect effect of tallowtree on pollinators involves the facilitation of honey bees. Honey bees are known to compete strongly with native bees for nectar and pollen, although the long-term consequences of this for native bee diversity and population sizes remain largely unresolved (Goulson 2003). The existing literature indicates that tallowtree flowers strongly benefit honey bees but are visited by few native bee species and only provide a source of nectar and pollen for a few months each year. By favoring honey bees over native bees, tallowtree may promote honey bee dominance within invaded landscapes. If so, this is likely to increase the competition native bees face when visiting other nectar and pollen sources, especially later in the year when tallowtree is not in bloom.

Finally, mutualisms between non-native plants and pollinators may facilitate the spread of invasive plants or otherwise impact pollinator and plant communities. In North America, at least two invasive weeds rely heavily on European honey bees for pollination: purple loosestrife (*Lythrum salicaria* L.) (Mai et al. 1992) and wild populations of radish (*Raphanus sativus* L.) (Stanton 1987). Several studies outside of the United States have documented preferences of introduced bees for non-native plants over native flora (Donovan 1980; Pearson and Braiden 1990; Woodward 1996; Stimec et al. 1997; Morales and Aizen 2006). There is evidence that non-native plants in cultivation receive fewer flower visits than naturalized non-native and native plants, suggesting that successful naturalization may be linked to flower visitation (Razanajatovo et al. 2015). The extent to which tallowtree invasion may benefit from European honey bees is not known, but it is not unreasonable to suspect that such a relationship exists given the affinity honey bees show for tallowtree flowers.

Biological Control

Classical biological control of weeds can provide a cost-effective, sustainable reduction in populations of invasive species (Coulson et al. 2000, Clewley et al. 2012). Some potentially promising classical biological control agents for tallowtree have been identified. Three fungal pathogens and 115 species of arthropods have been reported to damage tallowtree and related *Triadica* species in China (Zheng et al. 2006). A flea beetle [*Bikasha collaris* (Baly)] (Coleoptera: Chrysomelidae) whose larvae feed on tallowtree roots and adults feed on foliage was unable to complete its life cycle on 77 non-target plant taxa (Wheeler et al. 2017a, c). A lepidopteran, *Gadirtha fusca* Pogue (Lepidoptera: Nolidae) showed high host specificity for tallowtree in choice and no-choice tests with 78 non-target taxa (Wheeler et al. 2018b). Both *G. fusca* and *B. collaris* have been recommended for release (8/10/2016 and 10/19/2018, respectively) by the Technical Advisory Group for Biological Control Agents of Weeds (TAG), whose mission is “To facilitate biological control of weeds in North America by providing guidance to researchers and recommendations to regulating agencies for or against the release of nonindigenous biological control agents, based on considerations of potential non-target impacts and conflicts of interest” (USDA APHIS 2020). As of this writing, neither has been released.

Other herbivorous insects have also been studied as potential biological control agents. Wang et al. (2011) conducted feeding studies with two specialist herbivores: a weevil, *Heterapoderopsis bicallosicollis* (Voss) (Attelabidae) and a moth, *Gadirtha inexacta* Walker (Noctuidae) (but see below). Insects were provided seedlings of native (Chinese) and invasive (southeastern U.S.) tallowtree. More insects fed and developed on foliage from invasive populations but impacts on growth of seedlings were lower. In host suitability experiments, *H. bicallosicollis* was able to complete development on several plants native to the U.S. and is not considered a viable candidate for biological control (Steininger et al. 2013). In another study, *G. inexacta* was shown to have a narrow host range and significantly damaged tallowtree (Wang et al. 2012b). However, subsequent morphological (Pogue 2014) and molecular studies (Wheeler et al. 2018a) indicated that Wang et al. (2011, 2012b) had misidentified *G. inexacta* and were actually working with *G. fusca*. Another tested moth, *Sauris* nr. *purpurotincta* (Lepidoptera: Geometridae) was found to feed on some native southeastern plants including *Hippomane mancinella* L., which is listed as endangered in Florida, thus the moth is not being considered for importation and release (Fung et al. 2017). A newly described gall midge, *Schizomyia triadicae* Elsayed & Tokuda (Diptera: Cecidomyiidae) forms flower bud galls on young branches of tallowtree (Elsayed et al. 2019). Efforts to collect, identify, and screen additional insects have been hampered by recent events (COVID-19 pandemic) but there are many other herbivorous insects on tallowtree in its native range that could be considered as candidate biological control agents (G.S. Wheeler, personal communication).

A few other potentially damaging organisms have been documented on tallowtree. *Meloidogyne javanica* (Treub), the root-knot nematode has been reported to cause damage to the tree, while root rots caused by *Armillaria mellea* (Vahl) P.Kumm. (1871), *Armillaria tabescens* (Scop.) Emel (1921), *Pythium* spp., and *Phymatotrichopsis omnivora* (Duggar) Hennebert, (1973); leaf spots caused by *Alternaria* spp., *Pseudocercospora stillingiae* (Ellis & Everh.) J.M.Yen, A.K.Kar & B.K.Das, and *Phyllosticta stillingiae* (Ellis & Everh.); and dieback caused by *Diploidia* spp. have been associated with tallowtree (Bogler 2000; McCormick 2005). The potential of these organisms to contribute to integrated pest management programs for tallowtree has not been investigated.

Biological control is not without its risks. *Cactoblastis cactorum* Berg (Lepidoptera: Pyralidae) was introduced in 1957 to Nevis in the Lesser Antilles in an effort to reduce populations of *Opuntia* (prickly pear) species (Simmonds and Bennett 1966), then to nearby islands (Tudurí et al. 1971). Initial introductions into Australia in the 1920s (Dodd 1940) were considered successful in reducing undesirable *Opuntia* species. It has since arrived in the U.S., and has been found in Alabama, Florida, Georgia, Louisiana, Mississippi, and South Carolina (Anonymous 2009) where it threatens native *Opuntia* species. The other well-known example of non-target effects related to classical biological control of weeds can be found in efforts to control invasive musk thistle in the U.S. The flower head weevil *Rhinocyllus conicus* Froel. attacks many non-target thistle species, some of which are uncommon (Louda 2000).

Future research directions on tallow and pollinators

Beyond the well-documented value of tallowtree to honey bees and honey production (Lieux 1975; Hayes 1977, 1979), there appear to be few benefits of tallowtree invasion to pollinators. Few studies have investigated the direct and indirect effects of tallowtree on pollinators, however. Priorities for future research include:

1) Additional surveys of native pollinators on tallowtree flowers.
2) Effects of tallowtree invasion on native plants and non-tallowtree floral availability.
3) Potential mutualism between European honey bees and tallowtree.
4) Recovery of pollinator communities following the restoration of tallowtree-invaded sites.

Question 4 above is of particular interest to the beekeeping industry. While a strong case can be made that tallowtree invasion is generally detrimental to pollinators, and can render monoculture areas useless for honey production during the majority of the season, it will be important to document changes in understory composition as well as pollinator diversity and abundance following restoration efforts.

Conclusions

Invasive plants can generate a broad suite of effects, altering fire regimes, nutrient cycling, hydrology, and energy budgets, and they can greatly reduce native vegetation in invaded areas (Mack et al. 2000). Tallowtree suppresses fire regimes by changing fuel loads and via rapid decomposition of its leaves (Cameron and Spencer 1989, Grace 1998), and tallowtree itself appears to be somewhat fire-adapted (Grace 1998). Rapid decay of leaves may increase nutrient input to the soil, altering nutrient cycling (Cameron and Spencer 1989) and tallowtree leaf litter may reduce reproductive success of anurans such as southern leopard frog (Adams and Saenz 2012). There are numerous examples of tallowtree displacing native plant species. These detrimental aspects of tallowtree invasion are well documented, although there is a need to further address ecosystem costs associated with conversion to tallowtree monoculture (see Funk et al. 2014) and to answer the specific research questions listed above. Wetland ecosystems, which are favorable for tallowtree invasion, were estimated some 23 years ago to contribute at least \$14,785 ha^{-1} yr^{-1} in ecosystem services (Costanza et al. 1997). Costs to agricultural systems such as timber are more straightforward and easier to estimate. In a study modeling economic costs of tallowtree invasion to the forest industry under a 20-year expansion model, Wang et al.

(2012a) predicted costs ranging from $200 million to $400 million depending on the level of tallowtree control, with higher costs associated with lower control.

The potential benefits of tallowtree as a biofuel or source of specific products derived from its seeds are not likely to materialize on an operational basis due to its status as invasive or noxious in the states where it occurs. The benefits of tallowtree's early-season nectar flow to European honey bees must be weighed against its impacts on native flora and fauna as it continues to convert both disturbed and unique, undisturbed ecosystems to tallowtree monoculture. Given the highly invasive nature of tallowtree, its broad distribution, and lack of long-term control using traditional control measures (e.g., cultural/mechanical controls and/or herbicides) classical biological control may offer more cost-effective and long-term control (Wheeler and Ding 2014). Many have presented arguments for biological control of tallowtree, including detrimental effects associated with crowding out of native pollen and nectar sources and creation of "nectar deserts" for ten months out of the year (e.g. Bammer 2018). Investigations into biological control of tallowtree were recommended by the Florida Exotic Pest Plant Council's Chinese Tallow Task Force in 2005 (McCormick 2005). While host specificity appears to be well-established for *G. fusca* and *B. collaris*, their success as biological control agents would depend on a wide range of factors, including potential interactions with native predators and parasitoids (Schultz et al. 2019) and the degree to which they limit growth and reproduction of tallowtree.

While there is inherent risk in any attempt to manage or control invasive plants, including use of conventional means, biological control of weeds rarely results in non-target effects (Simberloff and Stiling 1996, Delfosse 2005, Suckling and Sforza 2014). Relatedness of native plant species has been taken into account when considering importation of classical biological control agents for tallowtree (Wheeler and Ding 2014). As discussed in this review, tallowtree is widely regarded as one of the worst woody invasive species in southern U.S. ecosystems, is capable of invading some ecosystems without disturbance, frequently invades and dominates areas following disturbance, and interferes with regeneration and forest management. Tallowtree is predicted to continue spreading northward in the U.S. (Pattison and Mack 2008). The inherent costs of doing nothing to reduce tallowtree populations on a landscape scale are demonstrably high. Efforts to reduce tallowtree population density, including classical biological control, could potentially result in increased tree and understory diversity to the ultimate benefit of native and exotic pollinator communities.

Disclaimer

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Figures

Figure 1. Ripened Chinese tallow tree fruit. Nancy Loewenstein, Alabama Cooperative Extension System.

Figure 2. Chinese tallow tree distribution in the southern United States. United States Department of Agriculture, Forest Service, Forest Inventory and Analysis estimates of trees per acre, by county in 2000, 2010, and 2020. These estimates do not capture all infested counties but demonstrate increasing coverage and density over a 20-year span.

Figure 3. A dense stand of Chinese tallow trees in southern Louisiana. The only other trees present in the stand are a couple of surviving sweet gums (*Liquidambar styraciflua* L.). Dense stands of tallow are a common sight in the U.S. gulf coast states. Stephen Oglesby, USDA Forest Service.

Figure 4. Chinese tallow tree flowers. Nancy Loewenstein, Alabama Cooperative Extension System.

Figure 1

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Figure 2.

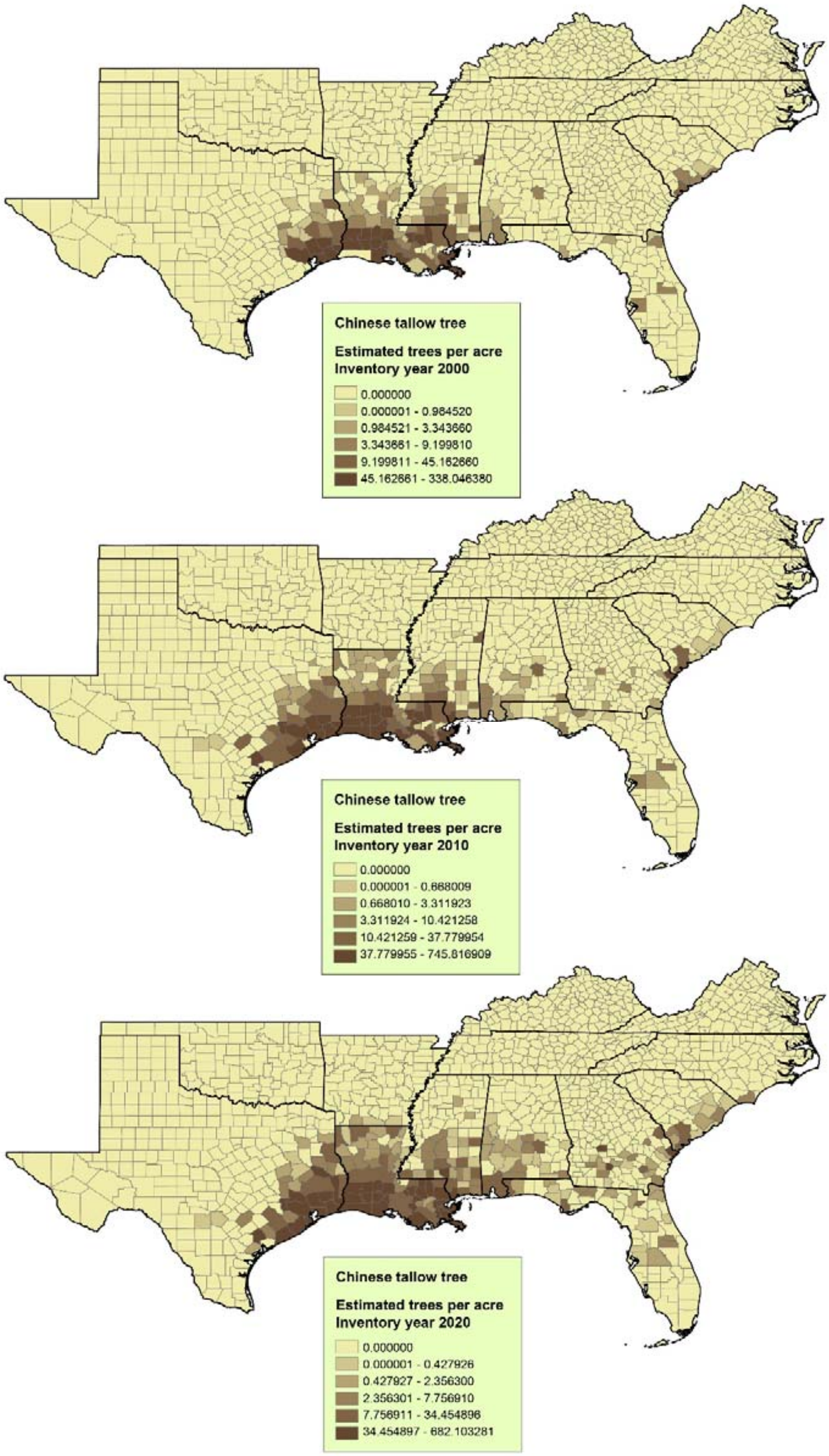

Figure 3.

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