The ecological effects of Chinese privet (*Ligustrum sinense*) invasion: a synthesis

James S. Cash[1] ⓘ, Christopher J. Anderson[2] and William D. Gulsby[3]

[1]Graduate Research Assistant, Auburn University, School of Forestry and Wildlife Sciences, Auburn, AL, USA; [2]Associate Professor, Auburn University, School of Forestry and Wildlife Sciences, Auburn, AL, USA and [3]Assistant Professor, Auburn University, School of Forestry and Wildlife Sciences, Auburn, AL, USA

Abstract

Chinese privet (*Ligustrum sinense* Lour.) is a deciduous to evergreen shrub with an expansive nonnative global range. Control costs are often high, so land managers must carefully consider whether the plant's potential negative effects warrant active management. To help facilitate this decision-making process, we reviewed and synthesized the literature on the potential ecological effects of *L. sinense* invasion. We also identified research gaps in need of further study. We found ample evidence of negative relationships between *L. sinense* invasion and native plant communities. While observational studies are not able to confirm whether *L. sinense* is driving these relationships, experimental evidence suggests that there is a cause–effect relationship. Of particular concern is the possibility that *L. sinense* could suppress forest regeneration and cause areas to transition from forest to *L. sinense*–dominated shrublands. Although this outcome would obviously impact a wide variety of wildlife species, empirical evidence of negative effects of *L. sinense* on wildlife are limited, and some species may actually benefit from the additional cover and foraging opportunities that *L. sinense* can provide. Further research on the potential effects of *L. sinense* invasion on large-scale forest structure and wildlife populations is needed. In areas where *L. sinense* invasion is a concern, evidence suggests early detection and management can mitigate control costs.

Introduction

Chinese privet (*Ligustrum sinense* Lour.), which is native to southeast Asia, has been introduced to every continent except Antarctica (Figure 1) and is considered invasive in at least 20 U.S. states, 6 Pacific islands, Australia, Italy, Argentina, and Puerto Rico (CABI 2018). *Ligustrum sinense* is particularly problematic in the southeastern United States, where it is often listed as one of the most threatening invasive species in the region (Miller et al. 2004). Introduced for landscaping in 1852, *L. sinense* (along with the very similar European privet [*Ligustrum vulgare* L.]) was estimated in 2008 to cover more than 1 million hectares in the southeastern United States alone (Maddox et al. 2010; Miller and Chambliss 2008). In Mississippi and Alabama, *L. sinense* and *L. vulgare* were estimated to have occupied 0.12 million hectares (<2%) of forests in 2003, but are projected to reach 2.83 million hectares (31%) by 2023 (Wang et al. 2016). *Ligustrum sinense* control is typically labor-intensive and expensive (US\$216 to US\$1,820 ha^{-1}; Benez-Secancho et al. 2018; Klepac et al. 2007), due to its propensity to form dense stands and resprout following cutting. Understanding the potential ecological impacts of *L. sinense* invasions can help land managers determine whether control measures are warranted. Accordingly, we reviewed known and potential relationships between *L. sinense* and native vegetation and wildlife communities. We also provide recommendations for future research priorities based on important research gaps identified in our review.

Ligustrum sinense is an evergreen to deciduous (depending on local climate) single or multi-stemmed shrub/small tree that reaches a maximum height of 10 m (Maddox et al. 2010; Miller and Miller 2005). *Ligustrum sinense* seeds are encased in ovoid drupes and are spread via endozoochory and hydrochory (Foard 2014; Miller and Miller 2005). An Australian study found that *L. sinense* can produce 1,300 fruits m^{-2} of canopy, with fruit production positively related to light availability and stem diameter (Westoby et. al. 1983). Flowering occurs during spring and early summer, and ripe fruit is available during fall and winter (McCall and Walck 2014; Miller and Miller 2005). Local dispersal can also occur via root-sprouting (i.e., new shoots can grow from belowground roots; Miller and Miller 2005). *Ligustrum sinense* has broad environmental tolerances and can survive in areas with full sun or heavy shade (Brown and Pezeshki 2000; Dirr 1998; Grove and Clarkson 2005), although research has shown that seedling survival is higher in areas with high afternoon and low morning light (Kuebbing et al. 2015). It is found in a variety of sites, including bottomland hardwood forests, upland forests, forest edges (including stream and roadsides; Figure 2), swamps, cedar glades, and disturbed sites such as old fields (Cofer et al. 2008; Grove and Clarkson 2005; Hagan et al. 2014; Kuhman et al. 2010; Merriam 2003; Miller and
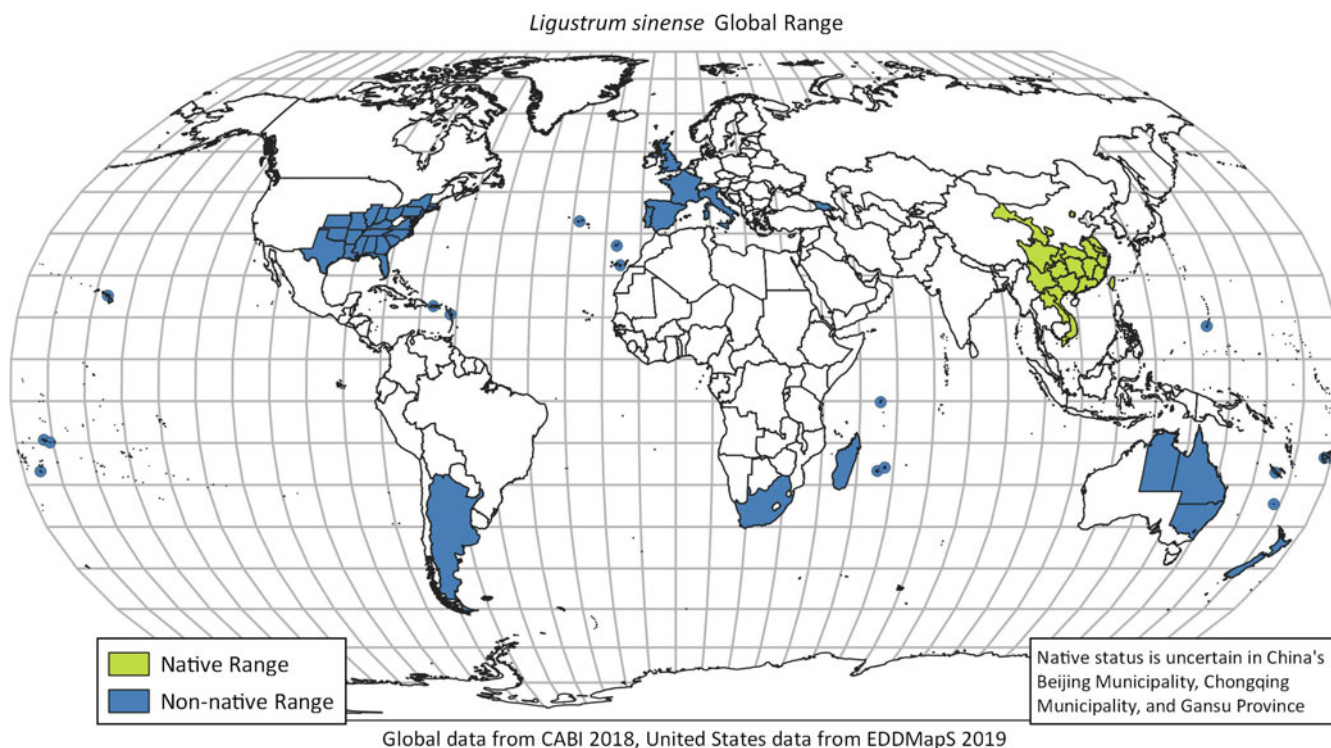
Figure 1. Global range of *Ligustrum sinense*. Data for the United States, Australia, and China are displayed at the state/province level. All other data are at the country level. Invaded islands have a circular buffer to aid in visibility. *Ligustrum sinense* is considered "invasive" in only a portion of its nonnative range. Records retrieved from CABI (2018) and EDDMapS (2019).

Figure 2. Example of a *Ligustrum sinense* invasion along a mixed pine–hardwood forest edge in Alabama. Photo taken in March 2018.

Miller 2005; Pokswinski 2009). Transplant experiments and field surveys have shown that *L. sinense* can regenerate under a canopy of conspecifics, indicating that invasions can likely sustain themselves over long periods of time (Greene and Blossey 2012; Grove and Clarkson 2005; McAlpine et al. 2018)—although for how long is unknown.

Methods

To evaluate the current understanding of relationships between *L. sinense* and ecosystems outside its native range, we searched the Web of Science database using the search terms "Chinese privet" and "*Ligustrum sinense*" (last accessed March 21, 2019). All articles pertaining to relationships among *L. sinense* and flora and fauna outside its native range were reviewed, and their reference lists were searched for additional relevant articles. This search yielded 48 peer-reviewed papers that contained information on the relationship between *L. sinense* invasions and native flora and fauna. We also cite additional peer-reviewed sources that contain general background information on *L. sinense* or invasive species, plus sources such as books, government and environmental organization documents, web pages, and dissertations/theses when important information was unavailable in the peer-reviewed literature. We have focused this review on *L. sinense*, but occasionally reference research on other *Ligustrum* species and similar exotic shrubs where relevant *L. sinense* research did not exist for specific subjects. The vast majority of the studies we found were conducted in the eastern United States, so we only identified the location of the study in our discussion if it occurred outside this area. We generally catalogued papers as pertaining to either vegetation or wildlife, although there were several instances in which papers covered both topics. Further, we reviewed and included papers that may have been less directly focused on vegetation or wildlife (e.g., impact of *L. sinense* on soil properties) that still contributed to our understanding of the potential impact of *L. sinense* on native plant and animal communities.

We begin our results and discussion section with a review of relevant invasion frameworks and their implications for interpreting trends and relationships between *L. sinense* and native species. We then present summaries of documented relationships between *L. sinense* and native vegetation, split into sections on herbaceous and woody species. Following those summaries we explore the possible mechanisms through which *L. sinense* could drive these relationships. Next we cover relationships between *L. sinense* and wildlife, split into discussions on invertebrates, mammals,

birds, and herpetofauna. Finally, the potential for native community recovery following *L. sinense* removal is discussed.

Results and Discussion

Invasion Frameworks

Before we present the results of our literature review, it is important to discuss how observed relationships between *L. sinense* and native species could be interpreted. In cases where *L. sinense* is found to be correlated with changes in vegetation communities, there may be uncertainty regarding whether *L. sinense* is a driver, passenger, or backseat driver of these changes. In other words, did *L. sinense* cause changes in the plant community (driver), take advantage of changes from other sources (passenger), or take advantage of initial changes and then drive further changes (backseat driver; Bauer 2012; Foard 2014; MacDougall and Turkington 2005)? For instance, Wilcox and Beck (2007) observed that native plant species richness was lower in areas with high *L. sinense* cover, but was this because *L. sinense* excluded native species or because areas with lower species diversity may be easier to invade (i.e., the "diversity resistance hypothesis"; Kennedy et al. 2002)? In another example, Hagan et al. (2014) found that *L. sinense* was more prevalent in areas with lower overstory basal area, but again is this because *L. sinense* was more likely to invade sites with those conditions or because *L. sinense* caused those conditions to develop? Sites with low overstory basal area (possibly due to natural or anthropogenic disturbance) may have more available resources (e.g., sunlight) for *L. sinense* to take advantage of, increasing the likelihood of it successfully invading (Hagan et al. 2014). On the other hand, if *L. sinense* outcompetes tree species and leads to the reduction of overstory basal area through reduced regeneration or growth, then *L. sinense* is acting as a driver. There is empirical evidence that, once established, *L. sinense* can decrease survival of herbaceous and woody plants. Greene and Blossey (2012) carried out a transplant experiment that involved planting boxelder (*Acer negundo* L.), false nettle [*Boehmeria cylindrica* (L.) Sw.], blunt broom sedge (*Carex tribuloides* Wahlenb.), and Indian woodoats [*Chasmanthium latifolium* (Michx.) Yates] seedlings in an area dominated by *L. sinense* (95% ± 4.2 cover, little herbaceous understory) and an adjacent area with no *L. sinense* and a herbaceous understory community. At the conclusion of the 63-wk trial, each species, except for *B. cylindrica*, had significantly lower survival rates in the *L. sinense*–dominated area. This suggests that *L. sinense* can drive declines in native plant species (Greene and Blossey 2012). However, because *L. sinense* often takes advantage of vegetational or hydrological disturbance during initial invasions, it may be best classified as a backseat driver (Foard 2014). It is important to keep the driver–passenger–backseat driver models in mind when interpreting results from observational studies. Although evidence shows that *L. sinense* can act as a driver/backseat driver, that may not always be the case and the possibility that *L. sinense* is a passenger in a given example of ecological change should be considered by managers planning restoration actions.

Vegetation

Herbaceous Species

It is common to see very sparse native ground cover under a dense *L. sinense* midstory (Figure 3). Studies have confirmed that herbaceous species diversity and stem density tend to be lower in areas with high (~100%) monospecific cover of *L. sinense* compared with those with little or no *L. sinense* cover (Kittel 2001; Merriam and Feil 2002). Further, studies that surveyed a range of *L. sinense* cover

Figure 3. Example of the understory of a bottomland hardwood forest in Alabama invaded by *Ligustrum sinense*. The midstory of this site is dominated by *L. sinense*, and the understory is comprised primarily of leaf litter and coarse woody debris, with very few native herbaceous or woody plants present. Photo courtesy of Jimmy Stiles (Auburn University), taken June 14, 2019.

classes have documented negative correlations between *L. sinense* cover and herbaceous species richness, cover, and stem density (Greene and Blossey 2012; Wilcox and Beck 2007). For example, Greene and Blossey (2012) found that as *L. sinense* cover increased along a gradient from 0% to 60%, herbaceous cover decreased from 58% to 25%, herbaceous species richness decreased from 10 to 5 species m^{-2}, and herbaceous species stem density decreased from 225 to 100 stems m^{-2}. Additionally, *L. sinense* has been noted as a potential contributor to the decline of several plant species of conservation concern, including the green pitcherplant [*Sarracenia oreophila* (Kearney) Wherry; Schnell et al. 2000], fringed campion [*Silene polypetala* (Walter) Fernald & B.G. Schub.; Allison 1996], and Schweinitz's sunflower (*Helianthus schweinitzii* Torr. & A. Gray; Urbatsch 2000; Weakley and Houk 1994).

Woody Species

Similar to herbaceous species, the density of understory and midstory woody plants, including shrubs, saplings, and seedlings, is often lower in invaded areas compared with uninvaded areas and has been shown to be negatively correlated with measures of *L. sinense* prevalence (Barksdale and Anderson 2015; Hanula et al. 2009; Hart and Holmes 2013; Kittel 2001; Loewenstein and Loewenstein 2005; Merriam and Feil 2002). Specifically, Wilcox and Beck (2007) found that native shrub density in plots with high (90.6 ± 4.6%) *L. sinense* cover was about one-third that of plots with low (0.4 ± 0.6%) or medium (13.6 ± 1.5%) *L. sinense* cover. Negative relationships have also been observed between *L. sinense* and woody species diversity (Burton et al. 2005; Foard et al. 2016; Hanula et al. 2009; Hart and Holmes 2013; Kittel 2001; Loewenstein and Loewenstein 2005; Merriam and Feil 2002; Wilcox and Beck 2007).

Given the relationship between *L. sinense* and relatively low density, diversity, and richness of woody seedlings and saplings, and the potential for *L. sinense* to be a causative factor in this relationship, multiple authors have expressed concern that invaded forests could convert to *L. sinense*–dominated shrublands over time due to inadequate woody species regeneration (e.g., Greene and Blossey 2012; Hart and Holmes 2013; Loewenstein and

Loewenstein 2005; Merriam and Feil 2002). Several studies have detected a negative relationship between *L. sinense* cover and tree density, possibly supporting this hypothesis (Barksdale and Anderson 2015; Hagan et al. 2014; Hanula et al. 2009; Wilcox and Beck 2007). Additionally, Hagan et al. (2014) reported that tree basal area was lower in invaded plots (but recall the earlier discussion on invasion frameworks). However, Hanula et al. (2009) and Greene and Blossey (2014) found no significant relationship between tree basal area and *L. sinense* cover, and others have found no significant relationship between *L. sinense* and overstory and subcanopy tree diversity (Kittel 2001; Wilcox and Beck 2007). Examples of large-scale forest-to-*L. sinense* shrubland conversion are lacking in the literature, perhaps because not enough time has elapsed since the introduction of *L. sinense* or the length of studies has been insufficient to observe such a change. Nonetheless, Hart and Holmes (2013) reported that *L. sinense* can occasionally occupy canopy-dominant positions, which may represent localized areas of tree-to-shrub conversion in their study area.

In addition to potential effects on woody regeneration, *L. sinense* invasion may also impact forest stands by influencing the growth and survival of mature trees. For example, Foard et al. (2016) observed that mature *Quercus* spp. in an invaded stand had higher rates of self-thinning and slower growth compared with an uninvaded stand (although their sample size was small). In contrast, Brantley (2008) found no detectible relationship between *L. sinense* and overstory tree growth, and Hudson et al. (2014) observed no response in tree growth 5 yr after *L. sinense* removal. The mixed reports regarding the relationship between tree basal area and *L. sinense* presence (Greene and Blossey 2014; Hagan et al. 2014; Hanula et al. 2009) further complicate our understanding of how *L. sinense* may or may not affect mature trees. More research is needed to determine the potential effect of *L. sinense* on overstory tree health, stand regeneration, and woody community composition. Specifically, replicating Foard et al. 2016—which looked at tree growth before and after *L. sinense* invasion based on dendrochronology—with a larger and more spatially diverse data set would improve our understanding of how the presence of *L. sinense* could affect mature tree species, with implications for both natural area and plantation management. Additional transplant experiments, similar to Greene and Blossey (2012), with more tested species and a greater number of replicates would also help clarify the extent to which *L. sinense* is driving reduced woody regeneration.

Mechanisms of Impact

As previously discussed, it may not always be the case that *L. sinense* is driving observed relationships between its presence and diminished or altered native plant communities. However, evidence suggests that *L. sinense* can function as a driver/backseat driver (Foard 2014; Greene and Blossey 2012), and so it is worth considering the mechanisms through which it may do so. Better understanding these mechanisms may help guide efforts to mitigate them.

Competition for light is an important mechanism through which nonnative plants influence native species (Gioria and Osborne 2014) and seems the most obvious mechanism by which *L. sinense* would affect native plants (Greene and Blossey 2012). Decreased light availability tends to promote shade-tolerant species over shade-intolerant species (e.g., Lin et al. 2002), potentially restructuring plant communities. For example, Osland et al. (2009) documented roughly four times greater light availability in areas where privet had been removed compared with areas where it

was still present. However, Brantley (2008) and Pokswinski (2009) did not detect a significant relationship between *L. sinense* cover and light intensity. These conflicting results could be due to differences in methodology or the overstory structure of the study sites. An *L. sinense* midstory may not have a significant effect on understory light availability in closed canopy forests; however, competition for light may play a role when *L. sinense* is competing against native species in canopy gaps and along forest edges. Further research into the role that light availability plays in *L. sinense* invasions could help guide management and restoration actions.

In addition to light competition, *L. sinense* may affect native plant communities by altering soil nutrient dynamics and fungal communities. *Ligustrum sinense* could affect soil nutrient cycles by altering litter decomposition rates, litter chemical composition, and leaf abscission timing (Mitchell et al. 2011). Mitchell et al. (2011) found that litter turnover decreased from 7.1 to 2.6 yr as the percent of *L. sinense* in the leaf litter increased from 0% to 50% (with the remaining litter composed of an equal mix of sweetgum [*Liquidambar styraciflua* L.], yellow poplar [*Liriodendron tulipifera* L.], water oak [*Quercus nigra* L.], and elm [*Ulmus* spp.] litter). The greater decomposition rate was likely due to the greater nitrogen and lower lignin content, lower C:N ratios, and lower lignin:N ratios of *L. sinense* litter (Mitchell et al. 2011). Alteration of soil nutrient cycles and nutrient availability can change competitive interactions among plant species (e.g., Aerts and Berendse 1988), but this has not been directly studied in relation to *L. sinense*. Changes in soil microbial and fungal communities have been suggested as another mechanism through which *L. sinense* influences native and nonnative plant communities (Greipsson and DiTommaso 2006; Kuebbing et al. 2014, 2015, 2016), and some of these changes are likely associated and interact with changes in soil nutrient dynamics (Deyn et al. 2004; Ehrenfeld 2003), which in turn are likely related to changes in litter decomposition. The complexity of the biogeochemical process as it relates to these changes makes it difficult to parse out simple cause–effect relationships. Research by Greipsson and DiTommaso (2006) found that *L. sinense* can alter arbuscular mycorrhizal fungi (AMF) communities in the soil. Specifically, the mycorrhizal infectivity potential of the soil, as measured by AMF root colonization on a bait plant, was higher in soil from invaded sites compared with noninvaded sites (Greipsson and DiTommaso 2006). Changes in AMF communities could affect competitive interactions among native and nonnative species, but was not directly studied (Greipsson and DiTommaso 2006). Other research has shown that native species tend to perform better (as measured by shoot and root mass) in soils without a history of invasion by *L. sinense*, and altered AMF or other soil properties were suggested as a cause but not directly tested (Kuebbing et al. 2016). Research by Kuebbing et al. (2014, 2015, 2016) also points to nonadditive effects on soils when *L. sinense* and other nonnative plants are present simultaneously, which suggests that studies on *L. sinense* in isolation may not grasp its full potential impact in mixed native/nonnative plant communities. Additionally, soils conditioned by *L. sinense* alone or in combination with Amur honeysuckle [*Lonicera maackii* (Rupr.) Herder] may promote continued or further invasion by those species or other nonnative species (Kuebbing et al. 2014, 2015, 2016), which possibly indicates some form of "invasion meltdown" (Simberloff and Von Holle 1999). The role played by altered soil nutrients, fungal communities, or other properties in *L. sinense* invasion deserves further research, particularly as it relates restoration actions. Identifying the specific soil alterations involved, how they may affect native plants

and nonnative plants, and how long they last following *L. sinense* removal may help guide restoration actions or at least guide expectations of the short-term results of restoration actions (Greipsson and DiTommaso 2006; Kuebbing et al. 2015, 2016).

A related way that invasive plants may gain a competitive advantage over native plants is through the deployment of "novel weapons," allelopathic or antimicrobial biochemicals that native species have no evolved resistance to (Callaway and Ridenour 2004). There is limited evidence to suggest *L. sinense* may affect native plant communities via allelopathy. Several have evaluated the allelopathic potential of *L. sinense* by watering the seeds of multiple plant species with diluted *L. sinense* extracts. These extracts had negative effects on the germination and growth of radish (*Raphanus sativus* L.) and tomato (*Solanum lycopersicum* L.) seedlings (Grove and Clarkson 2005; Pokswinski 2009). Barnett et al. (2016) conducted a similar experiment with species native to the southeastern United States, including common persimmon (*Diospyros virginiana* L.), red mulberry (*Morus rubra* L.), soapberry (*Sapindus saponaria* L.), and American beautyberry (*Callicarpa americana* L.). They found negative effects of *L. sinense* extract on *S. saponaria* and *C. americana* germination rates and *C. americana* root growth. These experiments demonstrate the potential for *L. sinense* allelopathy, but without identification of the specific chemical(s) involved and evidence that such chemical(s) have a significant effect under field conditions, it is not possible to definitively say that *L. sinense* exhibits allelopathy (Pokswinski 2009).

Another mechanism through which *L. sinense* could impact native plant communities is by altering fuel loads and types in fire-dependent ecosystems. Specifically, *L. sinense* may reduce fine fuels at ground level by outcompeting herbaceous species and reducing litter accumulation (Faulkner et al. 1989; Mitchell et al. 2011; Stocker and Hupp 2008), although Hagan et al. (2014) found increased litter accumulation in invaded sites—which may have been due to the prevalence of *L. sinense* in flatter microsites in their study area, where litter accumulation was more likely. Dense midstory vegetation also tends to increase fine fuel moisture, further reducing fire frequency and intensity (Nowacki and Abrams 2008). Additionally, *L. sinense* has low ignitability (Tiller 2015). The potential for reduced understory fuel loads and increased fuel moisture under an *L. sinense* canopy may suppress fires under some conditions. Fire suppression by *L. sinense* could alter disturbance regimes and successional processes, but this possibility has not been studied. However, the affinity that *L. sinense* shows for moist bottomland areas may conflate observations of the ignitability of *L. sinense*–invaded areas (Batcher 2000; Faulkner et al. 1989). Some land managers have experienced success using prescribed fire to control *L. sinense*, particularly under dry conditions (Batcher 2000), which indicates that the risk of *L. sinense* suppressing fires in drier fire-dependent uplands may not be significant. There is even some concern that as the climate becomes warmer and drier, *L. sinense* could become more ignitable and function as a ladder fuel, resulting in increased incidence of crown fires (Wang et al. 2016), although this is a highly speculative prediction.

Finally, invasion by nonnative plants can also affect native plant communities by altering wildlife–plant interactions (Traveset and Richardson 2006). For instance, nonnative plants can compete with native plants for pollinators or seed dispersers (Traveset and Richardson 2006). An example of such an interaction occurs between the nonnative Himalayan balsam (*Impatiens glandulifera* Royle) and the native marsh woundwort (*Stachys palustris* L.), which experiences reduced pollinator visits and seed set when

I. glandulifera is present (Chittka and Schürkens 2001). This mechanism has not been directly studied for *L. sinense*; however, it is a possibility. There is research that suggests *L. sinense* negatively affects pollinators due, in part, to reductions in the herbaceous understory (Hanula and Horn 2011a, 2011b; Hudson et al. 2013), and it is possible that a reinforcing loop exists whereby reductions in pollinator communities further limit pollination potential for remaining flowering species.

Wildlife

Wildlife conservation is a priority for many public and private landowners, so understanding how *L. sinense* may affect wildlife is important for informing land management decisions. Wildlife diversity is often positively correlated with vegetation structural diversity, likely because structural diversity opens up more ecological niches (Tews et al. 2004). Based on this relationship, it is possible that *L. sinense* at low to moderate densities could benefit some wildlife communities by providing additional cover and food without effecting native plant communities to a great extent. Some species may also benefit from the conditions created by high-density invasions. Indeed, some landowners may perceive *L. sinense* as beneficial for wildlife and thus may be reluctant to initiate control measures (Howle et al. 2010). However, our literature review found that *L. sinense* tends to be correlated with, and is likely a driver of, reduced native plant diversity and density (e.g., Greene and Blossey 2012). Given the common relationship between wildlife diversity and vegetation structural diversity (Tews et al. 2004), we predict that wildlife communities could be negatively affected by *L. sinense* invasion (especially high-density invasions), although the effect at the species level would be dependent on the species' ecological niche. Unfortunately data on relationships between wildlife and *L. sinense* are sparse, and most of what is available is observational. We present the findings of these studies organized into subsections on invertebrates, mammals, birds, and herpetofauna.

Throughout these sections, we use somewhat arbitrary distinctions between the terms "low density" and "high density" in order to standardize our discussion of potential impacts, even though these terms may not be specifically used by the papers we cite. When we discuss specific studies, we note the *L. sinense* cover/density of the study plots when applicable. We use the term "low density" to describe situations in which scattered *L. sinense* individuals are present, with assumed minor appreciable effect on native vegetation. "High density" refers to situations where *L. sinense* is the dominant understory or midstory species and cover of native species may be limited. *Ligustrum sinense* individuals in high-density stands tend to have limited foliage at ground level and thus provide limited cover at ground level (Figure 3). It is important to take into consideration that every high-density invasion started off at a lower density, so even if a given invasion does not have obvious impacts now, it may develop into a problem down the road.

Invertebrates

An incredibly diverse group, invertebrates represent the majority of animal life on Earth and play important ecosystem roles as herbivores, predators, prey, decomposers, and so on (New and Yen 1995). Given this diversity, it is impossible to make broad generalizations regarding how *L. sinense* invasion may affect these taxa. Even so, there have been a few studies that have directly examined the impact of *L. sinense* on invertebrate groups.

Kuebbing et al. (2014), for example, did not detect significant differences in ground-dwelling arthropod communities between plots invaded by *L. sinense* (>75% *L. sinense* cover) and control plots. However, researchers found that plots with little to no *L. sinense* present (either naturally or following *L. sinense* control operations) generally had greater species richness and abundance of native bees and butterflies than invaded plots, and most of these parameters were negatively correlated with *L. sinense* cover (Hanula and Horn 2011a, 2011b; Hudson et al. 2013). In a related study, beetle communities near ground level had greater species richness in plots where *L. sinense* had been removed compared with invaded plots; however, beetle species richness 5 and 15 m from the ground did not differ significantly between treatments (Ulyshen et al. 2010). There was also a high proportion of an exotic beetle (*Xylosandrus crassiusculus* Motschulsky) at 5 m in plots that still had *L. sinense* (Ulyshen et al. 2010). In the same study area, overall earthworm abundance tended to be lower in plots that were naturally free (or nearly so) of *L. sinense*, but the proportion of native earthworm species was greater in plots where *L. sinense* was absent (naturally or following control) than in invaded plots (Lobe et al. 2014).

There are various mechanisms through which *Ligustrum sinense* invasion could elicit changes in invertebrate communities. For example, a reduction in native herbaceous species under an *L. sinense* canopy could limit the availability of native nectar-producing plants and those suitable for hosting pollinator larvae (Hanula and Horn 2011a). Changes to vegetation structure likely also have an impact. For instance, deer ticks (*Ixodes scapularis* Say) frequently use young *L. sinense* stems when questing for hosts (Goddard 1992). However, it seems likely that at high *L. sinense* densities, where herbaceous ground cover is reduced and the *L. sinense* canopy may be ≥5 m, platforms for questing may be limited. Either way, these findings could have implications for disease transmission among vertebrate species.

The chemical makeup of *L. sinense* may also affect invertebrate communities. For example, both the invasive gypsy moth (*Lymantria dispar* L.) and native lace bug (*Leptoypha mutica* Say) had relatively low performance when feeding on *L. sinense* compared with plants native to the southeastern United States (Kalina et al. 2017; McEwan et al. 2009). A similar species, border privet (*Ligustrum obtusifolium* Siebold & Zucc.), produces a chemical (oleuropein) in its leaves that inhibits absorption of nutrients by invertebrate herbivores (Konno et al. 2009), and it is conceivable that *L. sinense* has similar traits. This could explain why some have observed decreased invertebrate herbivory on *L. sinense* compared with native plants and may contribute to its competitive advantage (Greene and Blossey 2012; Morris et al. 2002). Similarly, *L. sinense* leaves shed into water sources could negatively impact aquatic invertebrates by changing the water chemistry (Llewellyn 2005). Experimental evidence has shown that leaf extracts from *L. sinense* can reduce survival of at least one aquatic invertebrate (*Anisops* sp.) in a laboratory setting; however, more research is necessary to determine whether such effects occur in the wild (Llewellyn 2005). *Ligustrum sinense* may also alter the chemical properties of the soil that it grows in, such as increasing pH (Lobe et al. 2014). An increase in pH was considered a likely reason for the differences in earthworm communities observed by Lobe et al. (2014), because one of the nonnative earthworm species in their study prefers the relatively higher pH soils found under *L. sinense* (Lobe et al. 2014). Hagan et al. (2014) also found higher soil pH in invaded plots (1.5% to 85% cover, mean 30.4%), but Kuebbing et al. (2014)

did not detect a significant difference. Hagan et al. (2014) acknowledged that their study could not determine whether *L. sinense* caused the difference in pH, preferred areas with higher pH, or if the difference was due to *L. sinense* preferring flatter microsites with different soil nutrient dynamics. The finding by Lobe et al. (2014) that pH was lower in plots where *L. sinense* was removed via hand felling suggests that *L. sinense* was a driver of the pH differences, rather than a passenger (although pre-removal pH measurements were not conducted, and there were some differences in soil type across sites).

Mammals

Low- to moderate-density *L. sinense* invasions are probably beneficial for some mammalian species. For example, white-tailed deer (*Odocoileus virginianus* Zimmermann) and American beaver (*Castor canadensis* Kuhl) show moderate selective preference for *L. sinense* browse (Rossell et al. 2014; Stromayer et al. 1998), and studies in the United States and New Zealand show that small mammals, such as the white-footed mouse (*Peromyscus leucopus* Raf ; O'Malley et al. 2003) and common brushtail possum (*Trichosurus vulpecula* Kerr; Williams et al. 2000), will eat the fruits. Overall, *L. sinense* is a suitable forage species for *O. virginianus*, as its browse contains >12% crude protein during winter (Stromayer et al. 1998), which meets the requirements of all age classes during this season (NRC 2007). Browsing on *L. sinense* is particularly heavy when acorns are limited (Stromayer et al. 1998). However, at high densities, *L. sinense* may compete with native plants and reduce food availability for *O. virginianus* during spring and summer (Stromayer et al. 1998).The potential for competition with herbaceous vegetation is particularly concerning, given that forbs are the most nutritious and preferred plants of *O. virginianus* (Warren and Hurst 1981). An interesting potential avenue for future research is the possibility that *L. sinense* provides significant levels of available browse in areas that might not typically have such resources available for *O. virginianus*, particularly during winter, allowing *O. virginianus* to maintain high population levels that in turn put too much browsing pressure on more palatable native understory species that may be present (Stromayer et al. 1998). Over the longer term, the potential reduction of oak (*Quercus* spp.) regeneration by *L. sinense* is concerning given the dependence of not only *O. virginianus* but a wide array of wildlife species on acorns, even if *L. sinense* berries and browse are available as alternatives.

In terms of providing cover, the literature on this is very sparse, but the effect of *L. sinense* invasion is likely variable depending on the density and spatial extent of the invasion and the habitat requirements of different mammalian species. Christopher and Barrett (2006) found that two similar rodent species (*P. leucopus* and golden mouse [*Ochrotomys nuttalli* Harlan]) coexisted in areas dominated by *L. sinense* in the understory shrub layer, and it is possible that the increased vertical structure provided by *L. sinense* helped facilitate this coexistence despite the relative lack of cover at ground level. High rodent capture rates in *L. sinense* patches were also reported by Kittell (2001). When *L. sinense* forms hedges along forest edges (Figure 2) or is present in forest interiors at moderate densities, it may provide thermal and escape cover for *O. virginianus* and other mammalian species, but this has not been studied. Despite the handful of documented or potential ways in which *L. sinense* may be used as cover by mammals, it also has the potential to reduce habitat structure and cover. As *L. sinense* forms dense, mature stands, the amount of cover at ground level tends to be lower. Further, others have expressed concern regarding the potential loss of bat roosting habitat from reduced

tree regeneration caused by *L. sinense* (Pallin 2000). The potential for significant vegetation structural changes in areas invaded by *L. sinense* may thus alter the mammal communities that are able to take cover in those areas; however, further research is needed to clarify what these changes may look like in different regions.

Birds

Invasion by *L. sinense* has variable effects on bird species, depending on their life history and habitat requirements. For example, the small ovoid drupes of *L. sinense* are persistent throughout winter and early spring (Greenberg and Walter 2010) and may serve as a food source for frugivorous birds during this period of relative scarcity (Lochmiller 1978 [*L. vulgare*]; McCall and Walck 2014; Miller and Miller 2005; Wilcox and Beck 2007). Specifically, researchers have documented significant winter use of *Ligustrum* spp. fruit by northern bobwhite (*Colinus virginianus* L.; McRae 1980), the dusky-legged guan in Argentina (*Penelope obscura* Temminck; Merler et al. 2001), and hermit thrush (*Catharus guttatus* Pallas; Strong et al. 2005). Preference for *L. sinense* is species specific: *P. obscura* appeared to select for *L. sinense* disproportionate to its availability at some sites (Merler et al. 2001), whereas *C. guttatus* consume *L. sinense* slightly less often than expected given availability (Strong et al. 2005). *Ligustrum sinense* fruit was reported to contain 63.66% (±1.10) moisture, 1.91% (±0.06) crude protein, and 7.02% (±3.41) crude fat (McCall and Walck 2014).

Despite the documented use of *L. sinense* as a winter food source, potential population- and community-level effects on bird species are relatively unknown. It is possible that species reliant on herbaceous groundcover or overstory trees for foraging, nesting, or cover could be negatively impacted by high-density invasions of *L. sinense* because of its possible effects on those vegetation strata. The potential effects on species that utilize understory and mid-story woody plants are likely variable, depending on the needs of the species. For example, differences in the height and branching structure of invasive plants versus the natives they replace can impact bird-nesting success (e.g., Schmidt and Whelan 1999). However, the relative quality of *L. sinense* as a nesting substrate has not been studied.

We identified only one study that used an observational design with multiple replicates to compare bird use of sites with a range of *L. sinense* cover. Wilcox and Beck (2007) found significant positive correlations between *L. sinense* cover and bird species richness and abundance during winter, further supporting the hypothesis that birds will use *L. sinense* for cover and/or food. The majority of birds observed in high-density *L. sinense* areas (90.6 ± 4.6% cover) were primarily insectivorous, not frugivorous, possibly indicating that they were using the *L. sinense* stands for cover or foraging for insects that preferred that habitat or were more easily hunted in that habitat. Wilcox and Beck (2007) also documented differential use patterns of *L. sinense*–invaded areas that were related to their ecological niches, suggesting that *L. sinense* invasion could alter local bird community composition. Additionally, Wilcox and Beck (2007) observed that singing (total of all species) during summer tended to be less common in plots with high-density *L. sinense*, suggesting that mate attraction is more difficult in high-density areas or that high-density areas are not preferred for breeding. McCall and Walck (2014) reported that birds commonly used *L. sinense* for cover or perching platforms; however, *L. sinense* was "nearly ubiquitous" in their study area, so whether individuals select for or against *L. sinense* requires further study. McCall and Walck (2014) did not detect nesting or roosting in *L. sinense*. Woodcock (*Scolopax rusticola* L.) are known to use areas

invaded by *L. sinense* during fall migration and as winter habitat (Miller and Miller 2005; Myatt and Krementz 2007), although whether this is a preferred vegetation type is unclear.

The additional food that *L. sinense* provides in winter could have complex effects on global ecological patterns by enticing migrating birds to overwinter in areas that they would not otherwise, although such effects are speculative to date. Researchers have suggested that *Ligustrum* spp. may provide such an incentive for species in southern Argentina that would normally overwinter farther north (Merler et al. 2001; Montaldo 1993). In North America it is possible that supplementary feeding stations (i.e., bird feeders) could affect the timing of migrations (Robb et al. 2008), and if this is the case, *L. sinense* may have complementary or additive effects. However, *L. sinense* fruits might ripen too late to be much of an enticement for most fall migrants (McCall and Walck 2014). Species such as American robin (*Turdus migratorius* L.) are known to feed on *L. sinense* fruits on their northbound trip in spring (Miller and Miller 2005), but it seems unlikely that this would alter spring migration patterns. The effects of additional winter food may also interact with or be swamped out by the effects of climate change on migrations (e.g., Jenni and Kéry 2003; Zaifman et al. 2017).

Herpetofauna

The effects of invasive plants on herpetofauna (i.e., reptiles and amphibians) are generally understudied, and there have been no studies, to our knowledge, on the effects of *L. sinense* specifically. Martin and Murray (2011) reviewed the limited available literature on invasive plant effects on herpetofauna and developed a general predictive framework of possible changes to herpetofaunal habitat quality, food availability, and reproductive success. They predicted that invasive plants that are structurally different from the native plant assemblage will have the greatest effects and that small-bodied herpetofauna with small home ranges will be most affected (either positively or negatively), because they will have greater difficulty moving to uninvaded areas. The general structure of *L. sinense* is not necessarily unique to the systems it commonly invades, such as bottomland hardwood forests; however, it seems to reach much greater densities across larger areas than native understory and midstory species.

Many herpetofaunal species are "heliothermic," meaning they bask in sunlight to aid in thermoregulation (Bogert 1959). Some species, such as freshwater turtles, also choose nest sites with the necessary sun exposure to maintain proper nest temperatures (Bodie et al. 1996). The published data are not clear on the degree to which *L. sinense* invasion reduces light levels at ground level (e.g., Brantley 2008; Osland et al. 2009; Pokswinski 2009), but it seems likely that basking and nest-site availability would be affected by *L. sinense* cover. The first step in exploring how *L. sinense* could affect herpetofaunal thermoregulation is to better quantify light-level differences among sites with varying levels of *L. sinense* and native vegetation cover.

In addition to thermoregulation, herpetofauna need cover to aid in moisture retention and predator avoidance. Common cover types include leaf litter, coarse woody debris (CWD), burrows, and herbaceous vegetation. Leaf litter, a particularly important cover type for salamanders, may be reduced by *L. sinense* invasion due to its ability to intercept leaves from the canopy layer (Faulkner et al. 1989), increase decomposition rates (Mitchell et al. 2011), and possibly suppress overstory regeneration (e.g., Hart and Holmes 2013). However, Hagan et al. (2014) found that litter depth was positively correlated with *L. sinense* invasion, possibly because leaf litter tends to accumulate in the flatter microsites that

L. sinense occupied in their study area. Limited evidence also shows that CWD cover may be greater in areas with *L. sinense*, possibly due to increased self-thinning by resource-constrained trees (Foard et al. 2016). However, this increase in CWD cover may be temporary if overstory tree regeneration is impeded. Potential herbaceous ground cover reductions associated with *L. sinense* (e.g., Wilcox and Beck 2007) could also limit thermal and escape cover for herpetofauna.

Potential for Restoration

Assuming that *L. sinense* plays a role as a driver/backseat driver of vegetation community change, it is important to determine whether removing *L. sinense* stands leads to the recovery of plant communities (and thus wildlife habitat). Merriam and Feil (2002) took an early pass at this question by removing *L. sinense* from an invaded area and found that herbaceous species richness, herbaceous stem density, and woody stem density increased the first year following *L. sinense* control. Hanula et al. (2009) studied the effects of *L. sinense* removal more extensively in a study that involved removing *L. sinense* in 2-ha plots using mulching and hand felling in combination with cut-stump herbicide treatments (2005) and a follow-up foliar herbicide treatment (2006). They then compared the plant communities among control plots (*L. sinense* present, no treatment), treatment plots (mulching or hand felling), and "desired future condition" (DFC) plots that had little to no *L. sinense* cover. In 2007, they found that herbaceous cover and diversity in treated plots was higher than in control plots and similar to DFC plots (except for cover in hand-felled plots, which were intermediate between controls and mulched/DFC). The treated, control, and DFC plots developed distinct community compositions by 2007 due to the proliferation of early successional species in the treatment plots. Hudson et al. (2014) returned to those same plots in 2012 and found that herbaceous cover and diversity were still greater in treatment plots than in control plots and similar to DFC plots. Community composition was still distinct among the control, treatment, and DFC plots, with treatment plots having more early successional species such as pokeweed (*Phytolacca americana* L.). For woody species, Hudson et al. (2014) found that *L. sinense*–removal plots did not have statistically significant differences in shrub/sapling cover or species richness or diversity compared with control plots, although there was a nearly significant difference in cover. Woody seedlings and small saplings appear to have been included in their "herbaceous" plant category, so it is difficult to interpret differences in woody regeneration from their results—although they did state that "woody saplings covered more of the removal plots in 2012 than 2007" (Hudson et al. 2014).

How a site responds to *L. sinense* control efforts likely depends on site-specific factors such as soil type, climate, overstory canopy closure, disturbance regime, and proximity to native plant propagule sources. More research is needed across a range of site conditions and across longer time periods to better understand how natural systems respond to *L. sinense* control. Even so, based on the limited research to date and a general understanding of vegetation successional dynamics, it is reasonable to predict that when dense *L. sinense* midstory thickets are controlled, more resources (e.g., sunlight, water, nutrients) will become available for other species. The species that take advantage of these newly available resources will vary depending on site conditions, particularly in terms of light availability at ground level. In situations where removal of *L. sinense* substantially increases light availability, it is likely that early successional herbaceous species will

initially dominate. In closed canopy forests, light availability may not increase substantially following *L. sinense* removal, and the species that take its place will likely be relatively shade-tolerant species more characteristic of later successional stages. It is also important to remember that *L. sinense* may be a backseat driver in many situations, meaning that some underlying disturbance to the natural system allowed *L. sinense* to invade (Foard 2014). Addressing this disturbance may be necessary for long-term control of *L. sinense* and other invasive species and/or to promote recovery of native species (Bauer 2012; Foard 2014; MacDougall and Turkington 2005).

Conclusions and Recommendations

Our literature review revealed many negative correlations between native plant communities and *L. sinense* invasion, although more research is needed to confirm the degree to which *L. sinense* is driving declines and the mechanisms involved. Reduced understory cover and diversity are perhaps the most visible today, but long-term reductions in overstory regeneration could dramatically alter future landscapes. Research on the effects on wildlife are limited, but changes to vegetation species composition and structure could affect wildlife in a variety of ways (some positive, but many negative). Low-density *L. sinense* invasions likely have limited negative consequences for plant species and may have positive effects on some wildlife species (due to increased structural complexity and food resources). However, low-density invasions may develop into high-density invasions, and the negative impacts of *L. sinense* invasion (i.e., suppression of native plants and the predicted reductions in wildlife habitat quality) tend to be most apparent at higher *L. sinense* densities.

Low-density *L. sinense* invasions may be more cost-effective to control than high-density invasions, depending on the method used (Benez-Secancho et al. 2018). For this reason, we recommend taking early action to control *L. sinense* when possible to prevent further invasion and increasing control costs. Whenever *L. sinense* control operations are implemented, particularly in high-density invasions, the response of native vegetation should be monitored and reported (when possible) to improve our understanding of the best practices for restoring invaded areas. Additionally, managers whose objectives include increasing coverage of shade-intolerant woody or herbaceous species should be aware that *L. sinense* control alone may not be sufficient if sunlight is also limited by the overstory canopy or if there are underlying environmental changes that led to the invasion. Maddox et al. (2010) and Urbatsch (2000) provide recommendations on control options, and many state Extension agencies also provide guidance (e.g., Enloe and Loewenstein 2018).

A substantial amount of evidence regarding the ecological relationships between *L. sinense* and native species has accumulated over the past several decades, but we identified several critical knowledge gaps worthy of future study. There is a particular need for additional research on the effects of *L. sinense* invasion on wildlife species. With the exception of a few studies on invertebrates, most research has simply documented use patterns of invaded areas. Instead, we recommend future research focus on how *L. sinense* invasion affects population dynamics and community composition. The effects of *L. sinense* on wildlife are likely dependent on the scale of the *L. sinense* invasion, which interacts with various wildlife species in different ways depending on their daily movements and home-range sizes. As such, we recommend future studies consider the appropriate scale for the wildlife taxon in question. There is

also a need for additional research on the effects of *L. sinense* on overstory trees. Although many studies provide evidence that *L. sinense* may negatively impact the woody regeneration layer, more research is needed to determine the spatial and temporal scales at which conversions from forest to shrubland may occur. Direct negative effects of *L. sinense* on mature trees are also important to understand, as they could speed forest conversion and have implications for landowners managing for timber production or wildlife habitat.

Future research into the mechanisms by which *L. sinense* may affect native plants could help managers mitigate those effects, particularly for legacy effects that may persist after *L. sinense* is removed from a site. More generally, further research into restoration options is needed so that land managers have the best tools at their disposal for managing *L. sinense* and have realistic expectations for how forest plant communities will respond. Due to the dynamic response of vegetation communities to various management actions, researchers and managers should also report on covariates such as canopy coverage, site type, past management history, and so on to better inform managers concerning the expected response of vegetation communities to *L. sinense* control across a variety of sites.

References

Aerts R, Berendse F (1988) The effect of increased nutrient availability on vegetation dynamics in wet heathlands. Vegetatio 76:63–69

Allison JR (1996) Technical/Agency Draft Recovery Plan for Fringed Campion, *Silene polypetala* (Walt.) Fern. & Schub. Atlanta, GA: Southeast Region, US Fish and Wildlife Service. P 8

Barksdale WF, Anderson CJ (2015) The influence of land use on forest structure, species composition, and soil conditions in headwater-slope wetlands of coastal Alabama, USA. International Journal of Biodiversity Science, Ecosystem Services & Management 11:61–70

Barnett JM, Hudack PF, Dick GO (2016) Removing Chinese privet (*Ligustrum sinense* Lour.) and establishing native plants in a flooded riparian corridor in north-central Texas, USA. Environ Qual Manage 26:121–129

Batcher MS (2000) Element Stewardship Abstract for *Ligustrum* spp. Privet. Arlington, VA: Nature Conservancy. 10 p

Bauer J (2012) Invasive species: "back-seat drivers" of ecosystem change? Biol Invasions 14:1295–1304

Benez-Secanho FJ, Grebner DL, Ezell AW, Grala RK (2018) Financial trade-offs associated with controlling Chinese privet (*Ligustrum sinense* Lour.) in forestlands in the southern USA. J Forest 116:236–244

Bodie JR, Smith KR, Burke VJ (1996) A comparison of diel nest temperature and nest site selection for two sympatric species of freshwater turtles. Am Midl Nat 136:181–186

Bogert CM (1959) How reptiles regulate their body temperature. Sci Am 200:105–120

Brantley EF (2008) Influence of Chinese Privet (*Ligustrum sinense* Lour.) on Riparian Forests of the Southern Piedmont: Net Primary Productivity, Carbon Sequestration, and Native Plant Regeneration. PhD dissertation. Auburn, AL: Auburn University. 239 p

Brown CE, Pezeshki SR (2000) A study on waterlogging as a potential tool to control *Ligustrum sinense* populations in western Tennessee. Wetlands 20:429–437

Burton ML, Samuelson LJ, Pan S (2005) Riparian woody plant diversity and forest structure along an urban-rural gradient. Urban Ecosyst 8:93–106

CABI (2018) *Ligustrum sinense* [original text by D Shaw]. *In* Invasive Species Compendium. Wallingford, UK: CAB International. https://www.cabi.org/isc/datasheet/30763. Accessed: March 1, 2019

Callaway RM, Ridenour WM (2004) Novel weapons: invasive success and the evolution of increased competitive ability. Front Ecol Environ 2:436–443

Chittka L, Schürkens S (2001) Successful invasion of a floral market. Nature 411:653

Christopher CC, Barrett GW (2006) Coexistence of white-footed mice (*Peromyscus leucopus*) and golden mice (*Ochrotomys nutalli*) in a southeastern forest. J Mammal 87:102–107

Cofer MS, Walck JL, Hidayati SN (2008) Species richness and exotic species invasion in middle Tennessee cedar glades in relation to abiotic and biotic factors. J Torrey Bot Soc 135:540–553

Deyn GBD, Raaijmakers CE, Van der Putten WH (2004) Plant community development is affected by nutrients and soil biota. J Ecol 92:824–834

Dirr MA (1998) Manual of woody landscape plants: their identification, ornamental characteristics, culture, propagation and uses. 5th ed. Champaign, IL: Stipes Publishing. P 563

EDDMapS (2019) Early Detection and Distribution Mapping System. University of Georgia–Center for Invasive Species and Ecosystem Health. https://www.eddmaps.org/distribution/usstate.cfm?sub=3035. Accessed: June 24, 2019

Ehrenfeld JG (2003) Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems 6:503–523

Enloe S, Loewenstein N (2018) Control Options for Chinese Privet. Alabama Cooperative Extension System. 4 p. https://www.aces.edu/blog/topics/control-invasive-plants/control-options-for-chinese-privet. Accessed: March 1, 2019

Faulkner JL, Clebsch EEC, Sanders WL (1989) Use of prescribed burning for managing natural and historic resources in the Chickamauga and Chattanooga National Military Park, USA. Environ Manage 13:603–612

Foard M (2014) Causes and Consequences of Chinese privet (*Ligustrum sinense* Lour.) Invasion in Hydrologically Altered Forested Wetlands. Master's thesis. Jonesboro, AR: Arkansas State University. 172 p

Foard M, Burnette DJ, Burge DRL, Marsico TD (2016) Influence of river channelization and the invasive shrub, *Ligustrum sinense*, on oak (*Quercus* spp.) growth rates in bottomland hardwood forests. Appl Veg Sci 19:401–412

Gioria M, Osborne BA (2014) Resource competition in plant invasions: emerging patterns and research needs. Front Plant Sci 5:article 501, 10.3389/fpls.2014.00501

Goddard J (1992) Ecological studies of adult *Ixodes scapularis* in central Mississippi: questing activity in relation to time of year, vegetation type, and meteorological conditions. J Med Entomol 29:501–506

Greenberg CH, Walter ST (2010) Fleshy fruit removal and nutritional composition of winter-fruiting plants: a comparison of non-native invasive and native species. Nat Area J 30:312–321

Greene BT, Blossey B (2012) Lost in the weeds: *Ligustrum sinense* reduces native plant growth and survival. Biol Invasions 14:139–150

Greene BT, Blossey B (2014) Patterns of privet: urbanizing watersheds, invasive *Ligustrum sinense*, and performance of native plant species in Piedmont floodplain forests. Ecosystems 17:990–1001

Greipsson S, DiTommaso A (2006) Invasive non-native plants alter the occurrence of arbuscular mycorrhizal fungi and benefit from this association. Ecol Restor 24:236–241

Grove E, Clarkson BD (2005) An Ecological Study of Chinese Privet (*Ligustrum sinense* Lour.) in the Waikato Region. Hamilton, New Zealand: Centre for Biodiversity and Ecology Research Contract Report No. 41. 17 p

Hagan DL, Mikhailova EA, Shearman TM, Ma PT, Nankaya JS, Hart SK, Valdetero HE, Bridges WC, Yun H (2014) The role of soil and landscape factors in Chinese privet (*Ligustrum sinense*) invasion in the Appalachian Piedmont. Invasive Plant Sci Manag 7:483–490

Hanula JL, Horn S (2011a) Removing an exotic shrub from riparian forests increases butterfly abundance and diversity. Forest Ecol Manag 262:674–680

Hanula JL, Horn S (2011b) Removing an invasive shrub (Chinese privet) increases bee diversity and abundance in riparian forests of the southeastern United States. Insect Conserv Diver 4:275–283

Hanula JL, Horn S, Taylor JW (2009) Chinese privet (*Ligustrum sinense*) removal and its effect on native plant communities of riparian forests. Invasive Plant Sci Manag 2:292–300

Hart JL, Holmes BN (2013) Relationships between *Ligustrum sinense* invasion, biodiversity, and development in a mixed bottomland forest. Invasive Plant Sci Manag 6:175–186

Howle MB, Straka TJ, Nespeca MC (2010) Family forest owners' perceptions on chemical methods for invasive species control. Invasive Plant Sci Manag 3:253–261

Hudson JR, Hanula JL, Horn S (2013) Removing Chinese privet from riparian forests still benefits pollinators five years later. Biol Conserv 167:355–362

Hudson JR, Hanula JL, Horn S (2014) Impacts of removing Chinese privet from riparian forests on plant communities and tree growth five years later. For Ecol Manag 324:101–108

Jenni L, Kéry M (2003) Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. Proc R Soc Lond B Biol Sci 270:1467–1471

Kalina J, Braman SK, Hanula JL (2017) Host utilization of Chinese privet (Lamiales: Oleaceae) and host choice by *Leptoypha mutica* (Hemiptera: Tingidae). J Entomol Sci 52:141–153

Kennedy TA, Naeem S, Howe KM, Knops JMH, Tilman D, Reich P (2002) Biodiversity as a barrier to ecological invasion. Nature 417:636–638

Kittel MM (2001) Relationship among Invasive Chinese Privet, Plant Diversity, and Small Mammal Captures in Southeastern Deciduous Forests. Master's thesis. Clemson, SC: Clemson University. 35 p

Klepac J, Rummer RB, Hanula JL, Horn S (2007) Mechanical Removal of Chinese Privet. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station SRS-43. 5 p

Konno K, Hirayama C, Shinbo H, Nakamura M (2009) Glycine addition improves feeding performance of non-specialist herbivores on the privet, *Ligustrum obtusifolium*: in vivo evidence for the physiological impacts of anti-nutritive plant defense with iridoid and insect adaptation with glycine. Appl Entomol Zool 44:595–601

Kuebbing SE, Classen AT, Call JJ, Henning JA, Simberloff D (2015) Plant-soil interactions promote co-occurrence of three nonnative woody shrubs. Ecology 96:2289–2299

Kuebbing SE, Classen AT, Simberloff D (2014) Two co-occurring invasive woody shrubs alter soil properties and promote subdominant invasive species. J Appl Ecol 51:124–133

Kuebbing SE, Patterson CM, Classen AT, Simberloff D (2016) Co-occurring nonnative woody shrubs have additive and non-additive soil legacies. Ecol Appl 26:1896–1906

Kuhman TR, Pearson SM, Turner MG (2010) Effects of land-use history and contemporary landscape on non-native plant invasion at local and regional scales in the forest-dominated southern Appalachians. Landscape Ecol 25:1433–1445

Lin J, Harcombe PA, Fulton MR, Hall RW (2002) Sapling growth and survivorship as a function of light in a mesic forest of southeast Texas, USA. Oecologia 132:428–435

Llewellyn DC (2005) Effect of toxic riparian weeds on the survival of aquatic invertebrates. Aust Zool 33:194–209

Lobe JW, Callaham MA Jr., Hendrix PF, Hanula JL (2014) Removal of an invasive shrub (Chinese privet: *Ligustrum sinense* Lour) reduces exotic earthworm abundance and promotes recovery of native North American earthworms. Appl Soil Ecol 83:133–139

Lochmiller RL (1978) Privet as a potential winter food supplement for songbirds. Bird-Banding 49:279–280

Loewenstein NJ, Loewenstein EF (2005) Non-native plants in the understory of riparian forests across a land use gradient in the Southeast. Urban Ecosyst 8:79–91

MacDougall AS, Turkington R (2005) Are invasive species the drivers or passengers of change in degraded ecosystems? Ecology 86:42–55

Maddox V, Byrd J Jr., Serviss B (2010) Identification and control of invasive privets (*Ligustrum* spp.) in the middle southern United States. Invasive Plant Sci Manag 3:482–488

Martin LJ, Murray BR (2011) A predictive framework and review of the ecological impacts of exotic plant invasions on reptiles and amphibians. Biol Rev 86:407–419

McAlpine KG, Timmins SM, Jackman SD, Lamoureaux SL (2018) Composition of the understory in 132 woody weed populations and implications for succession. New Zeal J Ecol 42:277–283

McCall LJ, Walck JL (2014) Dispersal characteristics of two native and two nonnative fleshy-fruited sympatric shrubs. Castanea 79:88–99

McEwan RW, Rieske LK, Arthur MA (2009) Potential interactions between invasive woody shrubs and the gypsy moth (*Lymantria dispar*), an invasive insect herbivore. Biol Invasions 11:1053–1058

McRae WA (1980) Unusual bobwhite foods on abandoned Piedmont farmlands. Georgia Journal of Science 38:49–54

Merler JA, Diuk-Wasser MA, Quintana RD (2001) Winter diet of dusky-legged guan (*Penelope obscura*) at the Paraná River Delta region. Stud Neotrop Fauna E 36:33–38

Merriam RW (2003) The abundance, distribution and edge associations of six non-indigenous, harmful plants across North Carolina. J Torrey Bot Soc 130:283–291

Merriam RW, Feil E (2002) The potential impact of an introduced shrub on native plant diversity and forest regeneration. Biol Invasions 4:369–373

Miller JH, Chambliss EB (2008) Estimates of Acres Covered of Nonnative Invasive Plants in Southern Forests. Auburn, AL: U.S. Department of Agriculture, Forest Service, Southern Research Station. 1 p. https://www. invasive.org/fiamaps/summary.pdf. Accessed: March 1, 2019

Miller JH, Chambliss EB, Bargeron CT (2004) Invasive Plants of the Thirteen Southern States. https://www.invasive.org/south/seweeds.cfm?sort=3. Accessed: March 1, 2019

Miller JH, Miller KA (2005) Forest Plants of the Southeast and Their Wildlife Uses. Rev. ed. Athens, GA: University of Georgia Press. P 360

Mitchell JD, Lockaby BG, Brantley EF (2011) Influence of Chinese privet (*Ligustrum sinense*) on decomposition and nutrient availability in riparian forests. Invasive Plant Sci Manag 4:437–447

Montaldo NH (1993) Dispersión por aves y éxito reproductive de dos especies de *Ligustrum* (Oleaceae) en un relicto de selva subtropical en la Argentina. Rev Chil Hist Nat 66:75–85

Morris LL, Walck JL, Hidayati SN (2002) Growth and reproduction of the invasive *Ligustrum sinense* and native *Forestiera ligustrina* (Oleaceae): implications for the invasion and persistence of a nonnative shrub. Int J Plant Sci 163:1001–1010

Myatt NA, Krementz DG (2007) Fall migration and habitat use of American woodcock in the central United States. J Wildl Manag 71:1197–1205

[NRC] National Research Council (2007) Nutrient Requirements of Small Ruminants: Sheep, Goats, Cervids, and New World Camelids. Washington, DC: National Academies Press. 384 p

New TR, Yen AL (1995) Ecological important and invertebrate conservation. Oryx 29:187–191

Nowacki GJ, Abrams MD (2008) The demise of fire and "mesophication" of forests in the eastern United States. BioScience 58:123–138

O'Malley M, Blesh J, Williams M, Barrett GW (2003) Food preferences and bio-energetics of the white-footed mouse (*Peromyscus leucopus*) and the golden mouse (*Ochrotomys nuttalli*). Georgia Journal of Science 61:233–237

Osland MJ, Pahl JW, Richardson CJ (2009) Native bamboo [*Arundinaria gigantea* (Walter) Muhl., Poaceae] establishment and growth after the removal of an invasive non-native shrub (*Ligustrum sinense* Lour., Oleaceae): implications for restoration. Castanea 74:247–258

Pallin N (2000) Ku-ring-gai flying-fox reserve. Ecol Manag Restor 1:10–20

Pokswinski SM (2009) Invasive Characteristics of Chinese privet (*Ligustrum sinense* Lour.) in a Bay Swamp in the Fall Line Hills of East-Central Alabama. Master's thesis. Auburn, AL: Auburn University. 69 p

Robb GN, McDonald RA, Chamberlain DE, Bearhop S (2008) Food for thought: supplementary feeding as a driver of ecological change in avian populations. Front Ecol Environ 6:476–484

Rossell CR Jr., Arico S, Clarke HD, Horton JL, Ward JR, Patch SC (2014) Forage selection of native and nonnative woody plants by beaver in a rare-shrub community in the Appalachian Mountains of North Carolina. Southeast Nat 13:649–662

Schmidt KA, Whelan CJ (1999) Effects of exotic *Lonicera* and *Rhamnus* on songbird nest predation. Conserv Biol 13:1502–1506

Schnell D, Catling P, Folkerts G, Frost C, Gardner R, *et al.* (2000) *Sarracenia oreophila*. *In* The IUCN Red List of Threatened Species. http://dx.doi.org/10.2305/IUCN.UK.2000.RLTS.T39718A10260069.en. Accessed: March 1, 2019

Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: invasional meltdown? Biol Invasions 1:21–32

Stocker R, Hupp KVS (2008) Fire and nonnative invasive plants in the Southeastern Bioregion. Pages 91–112 *in* Zouhar K, Smith JK, Sutherland S, Brooks M, eds. Wildland Fire in Ecosystems: Fire and Nonnative Invasive Plants. Vol. 6. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station Gen. Tech. Rep. RMRS-GTR-42. 355 p

Stromayer KAK, Warren RJ, Johnson AS, Hale PE, Rogers CL, Tucker CL (1998) Chinese privet and the feeding ecology of white-tailed deer: the role of an exotic plant. J Wildlife Manage 62:1321–1329

Strong CM, Brown DR, Stouffer PC (2005) Frugivory by wintering hermit thrush in Louisiana. Southeast Nat 4:627–638

Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J Biogeogr 31:79–92

Tiller MB (2015) Effects of Yaupon, Chinese Privet, and Chinese Tallow on Understory Fuel Flammability in East Texas Hardwood and Pine Ecosystems. Master's thesis. Nacogdoches, TX: Stephen F. Austin State University. 171 p

Traveset A, Richardson DM (2006) Biological invasions as disruptors of plant reproductive mutualisms. Trends Ecol Evol 21:208–216

Ulyshen MD, Horn S, Hanula JL (2010) Response of beetles (Coleoptera) at three heights to the experimental removal of an invasive shrub, Chinese privet (*Ligustrum sinense*), from floodplain forests. Biol Invasions 12:1573–1579

Urbatsch L (2000) Chinese Privet *Ligustrum sinense* Lour. Baton Rouge, LA: U.S. Department of Agriculture, Natural Resources Conservation Service Plant Guide. 5 p

Wang H-H, Wonkka CL, Grant WE, Rogers WE (2016) Range expansion of invasive shrubs: implication for crown fire risk in forestlands of the southern USA. AoB Plants 8:plw012, 10.1093/aobpla/plw012

Warren RC, Hurst GA (1981) Rating of Plants in Pine Plantations as White-Tailed Deer Food. Mississippi Agricultural and Forestry Experiment Station, Information Bulletin 18. Mississippi State, MS: Mississippi State University. 18 p

Weakley AS, Houk RD (1994) Recovery Plan for Scweinitz's Sunflower (*Helianthus schweinitzii*). Atlanta, GA: Southeast Region, U.S. Fish and Wildlife Service. P 11

Westoby M, Dalby J, Adams-Acton L (1983) Fruit production by two species of privet, *Ligustrum sinense* Lour. and *L. lucidum* W.T. Ait. in Sydney. Aust Weeds 2:127–129

Wilcox J, Beck CW (2007) Effects of *Ligustrum sinense* Lour. (Chinese privet) on abundance and diversity of songbirds and native plants in a southeastern nature preserve. Southeast Nat 6:535–550

Williams PA, Karl BJ, Bannister P, Lee WG (2000) Small mammals as potential seed dispersers in New Zealand. Austral Ecol 25:523–532

Zaifman J, Shan D, Ay A, Jimenez AG (2017) Shifts in bird migration timing in North American long-distance and short-distance migrants are associated with climate change. Int J Zool 2017, 10.1155/2017/602564