To everyone who supports my love of plants
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Humans have a long history of introducing and domesticating non-native plants for food, aesthetics, and biomass production and, throughout this history, species have been domesticated to meet changing needs and desires. While most domesticated plants provide benefits without escaping into natural areas, others have become prominent invaders in introduced ranges. Trait changes during domestication can enhance or reduce invasion risk, so I reviewed the literature to more thoroughly explore this connection. Broadly, food crops that are intensively managed tend to have low invasion risk while plants used for aesthetic purposes generally have high invasion risk across variable management intensities. Biomass species bred for high productivity are minimally managed and tend to have high risk. Then, in a case study with wild *Lespedeza cuneata*, I explored differences in performance and foliar chemistry among wild genotypes and domesticated cultivars that could influence invasion risk. First, I conducted a bioassay and found that herbivores performed better on domesticated cultivars, suggesting lower invasion risk, relative to wild genotypes, in the presence of herbivores. Secondly, I used a greenhouse experiment with factorial treatments of
herbivory and competition native species and showed that the performance of *L. cuneata* cultivars was similar to the wild genotype, indicating a similar invasion risk potential. Overall, invasion risk assessment should be expanded to examine how trait changes through domestication and environmental contexts might alter invasion risk of cultivated non-native species.
CHAPTER 1
POTENTIAL EFFECTS OF DOMESTICATION ON INVASION RISK OF NON-NATIVE PLANTS

Introduction

Humans have intentionally moved plants to non-native regions for food, fiber, fuel, and aesthetic uses (Mack et al. 2000, Mack and Lonsdale 2001, Richardson and Pyšek 2012). The movement of non-native species across the globe is increasing as new technology allows for more species to be intentionally and unintentionally transported more rapidly, in larger quantities, and to more distant places (Seebens et al. 2017). Most of these non-native species do not cause harm when introduced, but a small proportion of introduced plant species establish, survive, and reproduce beyond cultivation (Richardson et al. 2000, van Kleunen et al. 2015, 2018, Pyšek et al. 2017). Some of these non-native species have then become invasive, impacting native species, ecosystem services, and public health (Pyšek et al. 2002, Pimentel et al. 2005, Vilà et al. 2011). The introduction, cultivation, and domestication of non-native plants differs from natural dispersal because more propagules are being transported (van Kleunen et al. 2018), planting pressure is higher (Buddenhagen et al. 2009), there is selection of particular traits for human uses (Doebley 2006), and there is the addition of cultural amendments (Mack et al. 2000). All of these difference in the invasion pathway could increase the likelihood of establishment and potentially invasion (Williamson and Fitter 1996, Pyšek and Richardson 2008, Richardson and Pyšek 2012). Thus, the practice of cultivating and domesticating non-native plants potentially aids non-native species in the invasion process.

Domestication, the process of genetically altering wild species by selecting traits to make them more useful to humans (Diamond 2002, Kareiva et al. 2007), can
enhance non-native plant invasion risk by altering the probability a non-native species can escape, establish, and spread. Selection of traits commonly occurs over multiple generations during domestication (Price 1984), and often more than one trait is altered within a species (Hammer 1984, Meyer et al. 2012). Trait changes through domestication commonly include altered growth (van Kleunen et al. 2018), reproduction (Meyer et al. 2012), phenotypic appearance (Maurel et al. 2016), or traits related to fitness and propagule pressure (Martínez-Ghersa and Ghersa 2006, Lockwood et al. 2013). Domestication encompasses many different trait changes that could provide non-native species with varying abilities to overcome the barriers to invasion in the introduced range.

Domestication may enhance invasion risk because traits that are desired for domesticated plants, such as high productivity and environmental matching (Donald 1968, Parrish and Fike 2005, Drew et al. 2010), also are traits linked to greater invasion risk (Blumenthal and Hufbauer 2007, Pyšek and Richardson 2008, van Kleunen et al. 2018). There has been relatively little direct effort to breed non-invasive plant cultivars (van Kleunen et al. 2018), other than breeding sterile cultivars (Lewandowski et al. 2000, Freyre et al. 2018). Reduced invasion risk from lower propagule pressure through sterility could be offset in certain cases, particularly with respect to bioenergy crops, by colonization through vegetative growth (Parrish and Fike 2005) or through reversion of sterility outside of cultivation (Lambertini 2019). Breeding and introducing non-native domesticated plants that possess traits that enhance their use for food, aesthetics, or biomass production, while ensuring the species are not at high risk of escape from cultivation and invasion, is a critical need.
Trait-based ecology can be used to predict the causes and consequences of biotic or abiotic species interactions, as a function of the physiological, morphological, chemical, or phenological characteristics of organisms (McGill et al. 2006, Westoby and Wright 2006, Martin and Isaac 2015). Consideration of multiple traits in combination with specific environmental and social contexts is a reliable indicator of invasion risk (Richardson 2006, Hulme et al. 2011, Richardson and Pyšek 2012), but see (Thompson et al. 1995, Thompson and Davis 2011). These trait-based evaluations can be beneficial for predicting and managing invasions, and they are the premise for tools to predict invasions, including weed risk assessments (WRA) (Pheloung et al. 1999, Simberloff et al. 2010, Koop et al. 2012). While invasion ecologists have had success identifying and limiting the spread of naturally dispersing potentially invasive species (Gordon et al. 2008), screening measures to prevent introductions for domesticated non-native plants has been less successful (Bradley et al. 2012). The Australian Weed Risk Assessment (AWRA) assumes species that have undergone multiple generations of human selection are of lower invasion risk than those that have not (Pheloung et al. 1999). Yet, positively answering the AWRA question concerning domestication requires evidence that one or more traits have been modified to reduce invasiveness (Gordon et al. 2010). Often there is insufficient evidence to positively answer this question (Gordon et al. 2010), which could mean that cases where domestication has reduced invasion risk may not be accounted for when assessing some species or related cultivars. Trait-based approaches can be beneficial for identifying potential invaders and determining the invasion risk of domesticated non-native species, but more empirical evidence is needed improve species invasion risk assessments.
In this review, I compare trait changes that may occur during domestication of plants for different purposes to improve understanding of how to limit future breeding of non-native plants with invasive traits. I focus on the domestication of terrestrial plants, although some aquatic plants also have been domesticated (e.g., seaweed; Loureiro et al. 2015). First, I describe how the invasion process framework varies for cultivated plants compared to naturally dispersing non-native species. Then, I reflect on specific considerations of invasion risk depending on if plants are bred to be intensively, variably, or minimally managed. Finally, I synthesize the findings of my review to draw general conclusions about domestication and invasion risk.

**Framework for the Invasion Process of Domesticated Plants**

Non-native species must pass through a series of stages to become invasive in the introduced range, including transport, introduction, establishment (i.e., survive and reproduce), and spread (i.e., overcome dispersal and environmental barriers) (Blackburn et al. 2011). I propose that domesticated non-native plants face these stages under slightly different circumstances than naturally dispersing plants, including an additional preliminary step where wild plants are domesticated. Differences in the invasion process for domesticated individuals, relative to non-cultivated non-native species, arise because of different traits prior to being introduced, trait selection by breeders as opposed to natural selection, and differences in the level of human intervention (Meyer et al. 2012, van Kleunen et al. 2018). Humans play a key role in the early stages of invasion (transport and introduction), while context dependent factors, such as environmental conditions and biotic interactions, are commonly more meaningful in later stages (establishment and spread) (Williamson 2006, Blackburn et al. 2011). Here, I provide an overview of each stage of the invasion process and how
the process differs for cultivated non-native plants compared to naturally dispersing species (Figure 1-1).

**Domestication**

Domestication can occur in the native or introduced range but, historically, domestication has been more common in the native range (Stage 1 in Figure 1-1). The majority of domestication has occurred in one of eight major centers of origin around the world, such as the Chinese Center, Indian Center, and Indo-Malayan Center (Hawkes 1998, Meyer et al. 2012). Previously, it was thought that geographic barriers between plants introduced into cultivation and plants in natural areas led to reproductive isolation and ultimately to trait differences between wild and domesticated populations (i.e., the marginality model; (Verhoeven 2004, Meyer et al. 2012, Dempewolf et al. 2012)). However, early farmers in these centers of origin relied on interbreeding between domesticated species and wild native species to create more productive and ecologically tolerant crops (Hawkes 1998). While domestication of plants for agriculture is the longest practiced form of domestication (Khush 2001), plant species for aesthetics and environmental solutions have been domesticated under similar conditions of isolation from native wild populations with intermediate cases of outcrossing with native species or other domesticated species (McNeely 2001, Low et al. 2011). The centralized histories of domesticated plants have led to similar selection of plants and traits under cultivation.

Within a given purpose for domestication, such as for agriculture, aesthetics, or biomass production, certain traits are commonly selected for, including changes to seed morphology and size or number of fruits (Meyer et al. 2012). However, selection of other traits, including phenology and annual or perennial life cycle, varies depending on the
conditions in the region where the plant is domesticated (Meyer et al. 2012). Origins of the native range of certain cultivated plant species remains unclear today (e.g., multiple proposed origins for 38 major crops are unknown; (Meyer et al. 2012)), or the wild type might have disappeared altogether through introgression of wild and domesticated populations (e.g., *Cannabis sativa*; (Pollio 2016)). Historical knowledge of trait selection and place of origin also provide insights into how species could survive and evolve outside of cultivation (Doebley 2006, Turcotte et al. 2017). Information on the location of domestication, species chosen for cultivation, and trait changes under domestication are needed to understand the invasion risk of each domesticated non-native plant.

**Transport**

Humans intentionally transport domesticated non-native plants, which can occur more rapidly than naturally dispersing non-native species and ensures a higher likelihood of introduction (Stage 2 in Figure 1-1) (Pyšek et al. 2011, Richardson and Pyšek 2012). Species transported by humans also are more likely to be kept in healthy physical condition to ensure they are desirable and profitable, which leads to greater likelihood that escaped individuals will be vigorous (Lockwood et al. 2013). Transportation of species can occur before or after domestication, which could influence the types of traits under selection and the suitability of plants to the introduced environment. Domestication events in the introduced ranges are becoming more common, and often occur in agricultural research programs (Meyer et al. 2012), which could potentially lead to crops that are better suited to particular areas or require less management to survive in the introduced range. Transportation of domesticated plants facilitates successful movement of adapted, healthy plants, which potentially increases
the ability of cultivated non-native species to survive without human intervention and advances the species in the invasion process.

**Introduction**

By nature, domesticated plants are introduced into fields and gardens in a non-native range (Stage 3 in Figure 1-1). Cultivated plants often benefit from cultural amendments, including irrigation, fertilization, and the introduction of beneficial mutualists (Mack et al. 2000, Ricciardi et al. 2017), which are associated with greater invasion risk (Mack et al. 2000, Pyšek et al. 2011, Richardson and Pyšek 2012). Similarly, high propagule pressure under cultivation, due to planting intensity or repeated introductions (Martínez-G horsa and Ghersa 2006, Buddenhagen et al. 2009, Cruzan 2019), is generally related to greater invasion risk (Alpert et al. 2000, Rouget and Richardson 2003, Richardson and Pyšek 2012). The growing conditions designed by humans for domesticated non-native plants during introduction lead to greater likelihood of success at this stage and raise the invasion risk of the species.

Cultivation ensures direct planting into a suitable area and assistance in adapting to the introduced range, potentially for an extended length of time. The longer a species is in a systems, the more likely the species will adjust to that new range and become an invader (Richardson and Pyšek 2012). Quantifying the residence time for cultivated plants presents a challenge because domestication for different uses has occurred for different amounts of time (Khush 2001, Diamond 2002, Bouton 2007) and a single species can be introduced and domesticated repeatedly (Parrish and Fike 2005, Ball and Mosjidis 2007, Cruzan 2019). Non-native species also may gain in public popularity over time and be planted more often, confounding residence time with propagule pressure (Pemberton and Liu 2009). Conversely, longer periods of domestication and
cultivation could lead to a greater likelihood of breeding out of noxious characteristics, as is considered in the AWRA (Pheloung et al. 1999, Gordon et al. 2010). Thus, the length of time a non-native species is introduced and maintained under cultivation could have a variable influence on overall invasion risk.

**Establishment**

Establishment requires that a non-native species can survive and reproduce outside of the areas where human cultivation occurs, such as along a corridor, in disturbed areas, or in natural areas (Stage 4 in Figure 1-1). Success in overcoming barriers to survival and reproduction is difficult to predict, even in cases of naturally dispersing species (Richardson and Pyšek 2012), since human influence is indirect and could provide either advantages or disadvantages for cultivated species. Domesticated species are selected and bred to grow in fields or gardens where human disturbance is high (Martínez-Ghersa and Ghersa 2006, Buddenhagen et al. 2009, van Kleunen et al. 2018), and the survival of naturally dispersing non-native plants is positively related to disturbance (Cadotte and Lovett-Doust 2001, Lake and Leishman 2004, Cadotte et al. 2006). Survival of non-native species also is dependent on access to nutrients (Davis et al. 2000, Davis and Pelsor 2001, Richardson and Pyšek 2012). The ability of a cultivated non-native species to uptake nutrients is variable based on selection for competitive ability (Denison et al. 2003, Kitajima et al. 2006, Eckberg et al. 2018), resource requirements (Low et al. 2011), ecological tolerance (Khush 2001), and other abiotic factors in the new environment (Khush 2001, Sanchez-Hernandez 2019). The survival of domesticated non-native species outside of cultivation, and subsequent establishment, varies but may be enhanced by selection for high productivity in disturbed sites.
The influence of domestication on the reproduction of escaped populations also is highly variable because both sexual and asexual reproduction can be manipulated directly (e.g., more flowering parts, faster growth of ramets; (Parrish and Fike 2005, van Kleunen et al. 2018)) or indirectly (e.g., greater growth results in less allocation to reproduction; (Sahramaa 2003)). Wild plants often have multiple reproductive strategies (Meyer et al. 2012), but one reproductive system is generally selected as the main strategy of propagation for that species under cultivation (Meyer et al. 2012). Sexually reproductive breeding systems are found in around 77% of domesticated plants worldwide (Meyer et al. 2012), allowing for outcrossing with wild congeners or other domesticated species (Martin and Isaac 2015). Conversely, cultivars may be bred to be sterile (Lewandowski et al. 2000, Perez-Prat and Lookeren Campagne 2002, Freyre et al. 2018), potentially reducing the invasion risk of the species by limiting the genetic diversity in the introduced population (Anderson et al. 2006). Thus, domestication both enhances and limits reproduction making the likelihood of establishment dependent on the specific species.

**Spread**

In the last stage of invasion, non-native species must spread within the introduced range, without the assistance of humans, by overcoming dispersal and environmental barriers (Stage 5 in Figure 1-1). Because the intention of domestication is for plants to remain in a single location (e.g., field, garden), there is a lack of evidence on how domestication influences dispersal ability and tolerance to environmental conditions outside of cultivation (Denison et al. 2003, Gross and Olsen 2010, Turcotte et al. 2017). Humans may limit the ability of domesticated species to spread, such as when cultivars are bred for sterility (Freyre et al. 2018), where there is selection for seed
retention (Meyer et al. 2012), or when there is an economic incentive to preventing future generations of viable propagules (e.g., genetic patenting; (Hayenga 1998)). Conversely, domestication could enhance the ability of a plant to spread if the reproductive strategies have been altered to contribute to greater dispersal. For instance, prolific seed production or attractiveness of fruits to frugivores could enhance non-native species spread (Anderson 1995, Greenberg et al. 2001, Parrish and Fike 2005). Lastly, some of the traits related to dispersal of cultivated non-native species may be different than those of naturally dispersing species, since long range dispersal ability is not necessary when humans are intentionally transporting species (Price 1999, Lockwood et al. 2013). The trait changes directly related to dispersal ability in cultivated non-native plants, as opposed to wild species, could lead to potentially novel advantages, or disadvantages, in the ability to spread.

The success of cultivated non-native species in spreading also is related to their ability to tolerate environmental conditions in natural areas. Traits altered during domestication that could aid species in overcoming adverse abiotic and biotic conditions in the introduced range, such as broad climatic tolerance (van der Veken et al. 2008, Hui et al. 2014) and changes in tolerance or resistance to herbivory (Byers and Sherwood 1979, Magnussen and Hauser 2007, Barney and DiTomaso 2008). Additionally, phylogeny is a strong predictor of successful spread (Dawson et al. 2009) and many cultivated plants belong to ‘weedy’ taxa (Lonsdale 1994, Buddenhagen et al. 2009), indicating that species selected for cultivation potentially have an inherent capability to spread (Pyšek 1998, Cadotte et al. 2006). Altogether, enhanced or innate
environmental tolerance of cultivated non-native plants could lead to a greater likelihood of successful invasive plant spread.

**Invasion Risk by Management Intensity of Cultivated Species**

Non-native plants have been domesticated for a wide range of purposes, including for food, aesthetics, and biomass production. While I’ve discussed how the process of cultivation for any non-native species can influence invasion risk, here I focus on how invasion risk differs for cultivated species associated with different management strategies. Focusing on management accounts for the fact that some plant species, such as corn produced for food and ethanol, are grown under the same management intensities but have multiple purposes. I designated three broad categories of domestication based on management intensity: intensively managed (e.g., food crops), variably managed (e.g., ornamental species), and minimally managed (e.g., biomass producing species). Consideration of these three types of domestication can provide further insight into how traits influence invasion risk. For each type of domestication management intensity, I provide a brief overview, identify commonly selected for traits, specify cases of concern for invasion risk, and synthesize overall invasion risk (Table 1-1).

**Domestication for Food Crops Under Intensive Management**

Globally, more than 95% of intensively managed plants, animals, and microbes used in agriculture have been intentionally introduced from a non-native range (Pimentel 2002). Around 88% of crop species are domesticated within their native range and then transported elsewhere for cultivation (Meyer et al. 2012). Intentional transportation to non-native ranges with different environmental conditions often results in the need for intensive management for crop production. Recently, an interest in
breeding food crops with resistance to changing climates has led to more local
domestication efforts in the introduced range (Meyer et al. 2012). In short, intensive
management of crops occurs on a select group of species, which are crucial for
agricultural stability.

Common trait changes for intensively managed food plants include greater
productivity (e.g., growth rate, height, seed production) and ease of harvest (e.g., seed
retention). Broadly speaking, maximizing the productivity of a plant is achieved by
regulating the competitive ability of each individual plant such that plants grow as large
as possible without hindering the growth of their neighbors (Donald 1968). Highly
focused efforts to domesticate a few traits in a limited range of the world has resulted in
a “domestication syndrome”, or a set of traits that are commonly linked and altered
during domestication (Doebley 2006). These linkages are commonly referred to as
phenotypic integration and can be both an advantage and disadvantage to crop
breeding. The benefit of phenotypic integration is that by intentionally altering a single
trait, multiple changes can occur in the plant through a cascade effect, resulting in a
rapid adjustment to novel conditions or environments (e.g., cultivated fields) (Doebley
2006, Milla et al. 2014). However, severing this integration can allow for the targeting of
a particular trait without a potential trade-off with another desirable trait, maximizing the
utility of the plant (Denison et al. 2003). In these cases, more frequent cultural
amendments may be needed to compensate for an inability of plants to adjust to
environmental changes. Thus, intensively managed crops have a collection of
alterations to enhance production of certain traits across an entire field, but trait
selection involves a balance between environmental tolerance and maximum plant performance.

De-domestication and hybridization complicate predictions of invasion risk for crops under intensive agricultural domestication. De-domestication is the process by which domesticated individuals revert back to phenotypes resembling feral, wild type species (Guo et al. 2018). However, it is unlikely that these de-domesticated individuals possess all the same traits as the wild type genotypes that were originally domesticated or lose all traits gained under domestication (Guo et al. 2018). Often de-domesticated genotypes are better suited to the introduced range than the original wild type and may experience fewer barriers to outcrossing with native species, such as through a reversion from seed retention back to shattering seed heads allowing for more effective dispersal (Ellstrand et al. 2010). Agricultural hybridization events are most often outcrosses between domesticated crops and native agricultural weeds (Campbell et al. 2006). These outcrosses can result in rapid evolutionary adaptation and greater invasion risk (Ellstrand and Schierenbeck 2000). Hybridization may be enhanced by high propagule pressure (e.g., high crop density, multiple introductions), and through greater similarity between crops and agricultural weeds, such as when weeds respond to selective pressures by evolving traits similar to crops (i.e., Vavilovian mimicry) (Pasteur 1982). Intensively managed crops capable of outcrossing with other species, or that revert to a wilder phenotype, can lead to invasion events.

In short, domestication of intensely managed food crops in the native range limits the ability of crops to survive without human intervention. As a result, crops may be less successful in adapting to natural environmental changes without cultural amendments,
and thus less likely to invade due to a lack of environmental suitability (Wiens and Graham 2005, Pyšek et al. 2009). However, the high propagule pressure associated with agricultural plants and abundant opportunities for hybridization with native species or other invaders, could promote invasion in certain cases. Therefore, overall invasion risk of intensively managed food crops tends to be low relative to non-domesticated non-native species (Table 1-1).

**Domestication for Aesthetic Species Under Variable Management**

Variable management intensities are used when cultivating plants for aesthetics. There is a long history of humans introducing aesthetically pleasing plants for a sense of nostalgia, beautification, and wonder that has led to extensive domestication of ornamental species (McNeely 2001, van Kleunen et al. 2018). Today, marketable plants are selected for their hardiness and ease of propagation (Mack 2005, van Kleunen et al. 2018), and promoted by nursery marketing campaigns that often create interest in a new species or cultivar (Dehnen-Schmutz and Touza 2008, Pemberton and Liu 2009). Overall, ornamental plants must be visually attractive, but they possess a range of robustness and are selected for many different traits.

Domestication of plants for aesthetic uses involves selection for larger flowers, more fruiting parts, fuller foliage, various growth forms, and for flowers that are retained on the plant for extended periods of time or at a particular time in the growing season (Mack and Lonsdale 2001, Novoa et al. 2015, van Kleunen et al. 2018). The altered reproductive traits and extended or altered flowering periods of domesticated plants can enhance pollination and fecundity, which is correlated with greater invasion risk (Crawley et al. 1996, Hamilton et al. 2005, Pyšek and Richardson 2008). Fast growth rate to promote visibility in a garden or landscape often is a desired trait in ornamental
species (Maurel et al. 2016, van Kleunen et al. 2018). However, in some cases, slower growth rate might be selected, such as to ensure high allocation to reproduction (Kitajima et al. 2006) or low required maintenance (e.g., cactus; (Novoa et al. 2015)). Non-native species cultivated for ornamental purposes are selected and bred to be high quality plants, often this process comes at the cost of other beneficial traits or the intensity of cultural amendments.

Specific cases for concern about invasion risk of variably managed, ornamental plants include focus on high-quality, abundant reproductive parts and possible hybridization events. While all cultivated plants must be maintained in healthy condition (Lockwood et al. 2013), plants sold for their aesthetic value also must be attractive to consumers throughout their entire life (Mack and Lonsdale 2001). It is especially important to maintain the long-term attractiveness of enhanced reproductive parts, which could directly increase propagule pressure (van Kleunen et al. 2018). Hybridization among ornamental plants, native congeneres, and invasive congeneres, may occur often since ornamental plants are usually grown around other species post-sale, rather than in a monoculture like other cultivated non-native plants (Gaskin and Kazmer 2009, Klonner et al. 2017). Hybridization also may offset the intent to reduce invasion risk of cultivars, as was the case with callery pears (Pyrus calleryana) that were bred to be sterile but regained the ability to outcross through hybridization with other cultivars (Culley and Hardiman 2009). There may be a greater occurrence of hybridization events of ornamental plants under climate change scenarios, if climate change promotes range overlap of reproductively compatible species that have previously been isolated plantings (van der Veken et al. 2008, Klonner et al. 2017). Both
the desired quality of cultivated ornamental plants, and the species with whom they interact in the introduced range, may contribute to greater invasion risk.

Domestication for ornamental plants emphasizes enhancement of reproduction, growth, or both, leading to a range of management requirements. Historically, consumers have sought plants with numerous flowers or fruits, full foliage, and limited cultural amendments (Kitajima et al. 2006, van Kleunen et al. 2018). Some programs have identified and bred for traits that could reduce invasiveness without lowering commercial value, such as a lack of pollinator rewards, lack of edible fruit, lack of seed germination, and sterility or programmed death prior to seed production (Anderson et al. 2006). But these attempts are not widely used in the ornamental plant industry (van Kleunen et al. 2018), or changes may be insufficient to prevent invasions (Culley and Hardiman 2009). Most new species and cultivars in the ornamental trade are derived from existing accessions rather than wild collections (Turbelin et al. 2017, van Kleunen et al. 2018), leading to an emphasis on marketing cultivars from breeding programs. Increased marketing has been shown to correlate with higher naturalization of non-native species, presumably via higher propagule pressure (Dehnen-Schmutz and Touza 2008, Pemberton and Liu 2009). However, marketing could be used to reduce invasions if there was a shift to promoting plants with fewer invasive traits. Breeding and marketing plants with only a single high invasion risk trait (e.g., fast growth rate, high seed production) but multiple other traits that lower invasion risk (e.g., lack of viable seeds, lack of pollinator rewards), could result in a cultivar that meets public demands without threatening natural communities. The overall invasion risk of variably managed
ornamental plants is high but breeding and marketing efforts could reduce risk by breeding plants with low invasion risk traits (Table 1-1).

**Domestication for Biomass Production Under Minimal Management**

Biomass-producing species are those grown for maximum yield, including bioenergy, forage, and forestry species (Wilkins and Humphreys 2003, Ennos et al. 2019, Lambertini 2019), or for particular biomass functions, such as erosion control or phytoremediation (Salt et al. 1998, Cook and Dias 2006). Biomass-producing species are bred to be self-sustaining and usually require minimal or initial cultural amendments (Salt et al. 1998, Sanchez-Hernandez 2019). There has been a relatively long history of using plants for erosion control or slope stabilization (Cook and Dias 2006), forage (Miller 1984), and forestry products (Wenger 1984). More recently, focus has shifted to the production of plants for bioenergy (Ragauskas et al. 2006, Lambertini 2019) and phytoremediation, a method of using plants to remove harmful chemicals from polluted environments (Salt et al. 1998, Sanchez-Hernandez 2019). Some of these biomass-producing species have multiple uses, for example, *Lespedeza cuneata* is cultivated for both erosion control and forage (Allred et al. 2010), and *Phalaris arundinacea* for both forage and bioenergy (Sahramaa 2003, Jakubowski et al. 2011). Despite their wide range of purposes, the same types of species, selection of traits, and minimal management strategies are used for biomass-producing species.

Domestication of plants that are minimally managed generally involves selection for high productivity and broad ecological tolerance. Biomass-producing species are often grown in areas with poor soils that are unsuitable for other crops, requiring low human inputs to facilitate growth, and reducing production costs (Salt et al. 1998, Barney and DiTomaso 2008). To overcome adverse growing conditions, these species
often are selected from ‘weedy’ phylogenetic families (Buddenhagen et al. 2009) or are capable of accessing unique nutrient deposits, such as through symbiotic relationships with nitrogen fixating bacteria (Dear and Ewing 2008). Additionally, to maximize allocation to growth, some biomass-producing species are bred to be sterile (e.g., Miscanthus x giganteus; (Lewandowski et al. 2000)). Thus, biomass-producing species are hardy plants requiring limited management to thrive in harsh environments.

Factors associated with greater invasion risk of non-native plants used for biomass production include the timing of crop harvests, hybridization events, and shorter domestication times than other types of cultivation. Unlike selection for greater productivity of agricultural and ornamental plants, plants used for biomass production are often harvested after the plants senesce and seeds have dispersed, which may promote naturalization (Lambertini 2019). In addition, there are reported cases of hybridization events among biomass-producing species and native species (Lavergne and Molofsky 2007, Cruzan 2019). Bioenergy species are often self-incompatible and thus are likely to retain the ability to outcross, raising concerns about hybridization with closely related species and other cultivars (Sutherland 2004, Lambertini 2019). Additionally, biomass-producing species often are not domesticated for many generations (Bouton 2007), relative to agriculture and ornamental plants, suggesting their invasion risk may be relatively high, as there have not been as many generations to select against noxious traits. As such, limited barriers to outcrossing outside of cultivation contributes to a potentially high invasion risk of minimally managed biomass-producing species.
Overall, biomass-producing species are selected for fast growth and high environmental tolerance with limited human involvement (Lewandowski et al. 2003, Küster et al. 2008, West et al. 2014). The cultivation of these biomass-producing species is likely to expand in the future as there are large societal benefits to using plants to solve environmental issues (Knowler and Barbier 2005). However, to minimize risk, more empirical studies are needed to determine the invasion risk of these domesticated non-native species (Richardson and Blanchard 2011, Flory et al. 2012, Richardson et al. 2014) along with the development and implementation of best management practices (Barney 2014). Overall, minimally managed biomass-producing species have a high associated invasion risk, and their continued use should be accompanied by more research and regulation to prevent future invasions (Table 1-1).

Conclusions

Despite the long history of plant cultivation by humans, new species continue to be domesticated and introduced for food, aesthetics, and biomass production. Across all cultivation management intensities, a better understanding of how variation in species and trait selection influences invasion risk is needed. Knowledge of why a plant was domesticated can provide insights into invasion risk predictions, regardless of the species. Earlier stages of the invasion process for cultivated non-native species (domestication, transport, and introduction) are directly facilitated by humans, which may increase the likelihood of a domesticated species progressing through these stages. The likelihood of domesticated plants completing later stages of the invasion process (establishment and spread) is indirectly related to domestication, as trait changes could lead to advantages or disadvantages under different abiotic and biotic conditions outside of cultivation. The desire to breed plants with particular traits and
without natural trade-offs (e.g., growth and reproduction) can lead to the breeding of high invasion risk species. Additionally, even under intensive management conditions, breeding plants that require less cultural amendments is desirable, leading to the selection of traits that make species more likely to survive outside of cultivation. The length of time that a species has been domesticated may influence invasion risk by altering how readily the plant can outcross with other species, the propagule pressure in the introduced range, and the degree of reliance on human cultural amendments. Altogether, invasion of cultivated non-native species appears to be related to the level of human involvement and, as such, direct human involvement will be needed to limit the future introduction and spread of non-native species.

Currently, breeding programs commonly are designed to work separately for different management levels because of particular requirements and resources to produce a specific set of desired traits (e.g., agricultural research stations are separate from ornamental nursery breeding programs). But, efforts to reduce invasion risk must transcend these programs in order to reduce overall invasion risk of cultivated non-native species. For instance, selecting only one high invasion risk trait to retain in a domesticated species is an applicable approach to lowering invasion risk, even if the selected trait that is remains varies by breeding program. Thus, the likelihood of invasion varies based on domestication purpose, but solutions to limiting the total number of invasive species requires effort from all areas of plant domestication.

Efforts that could be taken to breed non-native plants with lower invasion risk include selection of wild plants with lower invasion risk, or breeding for specific traits changes, greater reliance on cultural amendments, or retention of traits over
consecutive generations. Greater investment in research to select wild species that have less noxious traits, such as those requiring high management intensities, or breeding domesticated plants for traits that lower invasion risk, such as sterility and slow growth rate, is needed. While cultural amendments can contribute to higher survival during introduction, future domestication efforts could select for plants that rely on resources not found in neighboring natural areas, such as certain water quality, fertilizer, or sun protection, to ensure closer reliance on humans. The inclusion of durable traits that lower invasion risk should reduce the likelihood that these traits will revert back to the wild phenotype. Overall, evaluation of domesticated plant invasion risk must be expanded, to consider both differences between domesticated and wild non-native plant introductions and specific trait changes or management considerations for cultivated non-native plant species.
Figure 1-1. A framework for the role of domestication in biological invasions of non-native plants. This framework follows the stages of the invasion process and outlines how domestication might alter the process, including the direct effect early in the invasion process and the residual effect of domestication in later stages. I describe commonly altered traits and how they might influence invasion risk (elaborated on in Table 1-1) and list possible outcomes of domestication at each stage in the process. Lastly, I identify gaps in knowledge about the interaction of domestication and the invasion process at each stage. The darker shading in the top half of the figure emphasizes the direct role of humans in the early stages.
Table 1-1. A comparison of traits altered under domestication that can contribute to invasion risk. Arrows indicate if a trait is known to enhance (up arrow), sometime enhance (slanted up arrow), decrease (down arrow), sometimes decrease (slanted down arrow), or have a variable impact (arrows in both directions) on invasion risk. The same arrow ranking system is used to indicate how commonly the trait is altered under the three types of plant domestication (intensely managed, variably managed, and minimally managed). Blanks indicate a lack of information, or potential lack of alteration, for a given trait. Key references are indicated with superscripts in the table and full references are provided below the table.

<table>
<thead>
<tr>
<th>Traits</th>
<th>Contribution to Invasion Risk</th>
<th>Intensively Managed (Food Plants)</th>
<th>Variably Managed (Aesthetic Plants)</th>
<th>Minimally Managed (Biomass Plants)</th>
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<tbody>
<tr>
<td>General</td>
<td></td>
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<tr>
<td>Attractiveness to Humans</td>
<td>↑1,2</td>
<td>↑3</td>
<td>↑4</td>
<td>↑5</td>
</tr>
<tr>
<td>Ease of Propagation</td>
<td>↑6</td>
<td></td>
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<tr>
<td>Propagule Pressure</td>
<td>↗8–10</td>
<td>↑11</td>
<td>↑12</td>
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<td>Residence Time</td>
<td>↑2,9,14</td>
<td>↑15</td>
<td>↑16</td>
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<tr>
<td>Reproduction</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Abiotic Dispersal</td>
<td>↗14,18</td>
<td>↓15,19</td>
<td></td>
<td></td>
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<tr>
<td>Altered Flowering Season Compared to Natives</td>
<td>↑1,20,21</td>
<td>↑22</td>
<td>↑12</td>
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<tr>
<td>Fecundity</td>
<td>↑6,24,25</td>
<td>↑↓15</td>
<td>↑↓12,26</td>
<td>↓7,28</td>
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<tr>
<td>Hybridization</td>
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<td>↑↓30,31</td>
<td>32,33</td>
<td>↑34,35</td>
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<tr>
<td>Self-Incompatible</td>
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<td>↓15,37</td>
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<td>↓34</td>
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<tr>
<td>Transient Seed Bank</td>
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<td>↑39</td>
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<tr>
<td>Vegetative Reproduction</td>
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<td>↑15</td>
<td>↑40</td>
<td>↑27</td>
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<td>Growth</td>
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<tr>
<td>Competitive Ability in Non-Monoculture</td>
<td>↗20,41</td>
<td>↑42</td>
<td>↑43</td>
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<tr>
<td>Consistent Growth</td>
<td>↑45</td>
<td></td>
<td>↑19</td>
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<tr>
<td>Erect, Leafy Stems</td>
<td>↑38</td>
<td></td>
<td>↑↓22</td>
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<tr>
<td>Faster Growth Rate</td>
<td>↑1</td>
<td>↑22</td>
<td>↓↓12,43</td>
<td>↑46</td>
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<tr>
<td>Greater Height</td>
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<td>↓22</td>
<td>↑47</td>
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<tr>
<td>Productivity</td>
<td>↑41</td>
<td>↑22</td>
<td>↑43</td>
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Table 1-1. Continued

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<th>Traits</th>
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<th>Variably Managed (Aesthetic Plants)</th>
<th>Minimally Managed (Biomass Plants)</th>
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<td>Drought Tolerance</td>
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<td>$55$</td>
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<td></td>
<td>Ecological Tolerance</td>
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<td>$57$</td>
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<td></td>
<td>Grow in Disturbed Habitats</td>
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<td>$11$</td>
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<td>Greater Herbivore Resistance/Tolerance</td>
<td>$20,59$</td>
<td>$60$</td>
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<td>Life History</td>
<td>Belonging to Weedy Taxa</td>
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<td>$64$</td>
<td>$47$</td>
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<td></td>
<td>Herbaceous</td>
<td>$20,36$</td>
<td>$36,58,65$</td>
<td>$19$</td>
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<td></td>
<td>Perennial</td>
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CHAPTER 2
DOMESTICATION DOES NOT CONSISTENTLY ALTER INVASION RISK UNDER HERBIVORY AND COMPETITION

Domestication of non-native plant species selects for traits that improves their usefulness to humans (Diamond 2002, Kareiva et al. 2007), but such changes also may increase invasion risk (Reichard and Hamilton 1997, Pyšek and Richardson 2008). Non-native plants are domesticated for many reasons, including agriculture (e.g., row crops for food, forestry, or forage; (Meyer et al. 2012)), horticulture (e.g., landscaping plants to improve aesthetics; (Mack and Lonsdale 2001)), and as environmental solutions (e.g., erosion control or phytoremediation; (Salt et al. 1998, Cook and Dias 2006)). The process of domestication may alter multiple traits related to invasion risk (Mack and Lonsdale 2001, Blumenthal and Hufbauer 2007, Küster et al. 2008), including productivity, reproduction, and phenotype (Hammer 1984, Meyer et al. 2012, van Kleunen et al. 2018). The invasion risk of non-native species is determined by the likelihood of a species completing a series of stages, including transportation from the native range, introduction to the new range, establishment (e.g., survival and reproduction), and spread (e.g., overcome dispersal and environmental barriers) (Blackburn et al. 2011). The introduction of domesticated plants differs from dispersal of non-cultivated non-native species because traits are selected based on human preferences (Doebley 2006), more propagules are introduced (Buddenhagen et al. 2009, van Kleunen et al. 2018), and plants are cultivated to promote establishment (Mack et al. 2000). Thus, non-native domesticated species overcome the first two stages of the invasion process, transport and introduction. Furthermore, in some cases, the trait changes made during domestication can enhance the ability of cultivars to establish and spread.
Traits commonly selected for during domestication, such as altered flowering time, allocation to reproductive organs, and faster growth (Donald 1968, Palik et al. 2016, van Kleunen et al. 2018), are also traits associated with greater invasion risk (Reichard and Hamilton 1997, Lake and Leishman 2004, Pyšek and Richardson 2008). Invasion risk assessment tools, such as the Australian Week Risk Assessment (AWRA) (Pheloung et al. 1999) and the USDA Animal Plant and Health Inspection (APHIS) PPQ-WRA (Koop et al. 2012), incorporate information about traits related to the establishment and spread of a non-native species and the impacts of the species where it has become invasive (Gordon et al. 2008). Risk assessment tools accurately determine invasion risk at the species level (Gordon et al. 2008), but improved screening tools are needed to identify invasion risk of domesticated plant species (e.g., cultivars) (Bradley et al. 2012). Guidance for answering the AWRA indicates that a positive answer is rarely given for the question concerning domestication because there is often insufficient evidence showing that one or more traits have been modified through domestication to reduce invasiveness (Gordon et al. 2010). More information on how cultivars vary in traits related to invasion risk may improve risk assessment tools for evaluation of domesticated species.

Determining how invasion risk is altered through domestication requires an understanding of the traits altered by breeding and the environmental context where the non-native species is introduced (Buddenhagen et al. 2009, Richardson and Pyšek 2012, van Kleunen et al. 2018). Two traits that are commonly altered during agricultural domestication are productivity (Donald 1968, Fuller 2007, Meyer et al. 2012) and defense against natural enemies (Magnussen and Hauser 2007, Milla et al. 2014).
Growth and defense can exhibit a trade-off in some plants because both are metabolically costly (Herms and Mattson 1992). Breeding often seeks to avoid tradeoffs and maximize both traits, because highly productive plants are more profitable and well defended plants require fewer pesticide applications (Denison et al. 2003, Milla et al. 2014). Growth is an important trait for predicting invasion risk because highly productive plants may outcompete native species (Siemann and Rogers 2001, Denison et al. 2003, Lake and Leishman 2004). Similarly, for defense, plants that are resistant or tolerant to biotic pressures may have greater success in invading natural habitats through deterrence of native herbivores (Herms and Mattson 1992, Lake and Leishman 2004, Sanders et al. 2007) or a competitive advantage over native species that undergo pressure from native herbivores (Cappuccino and Carpenter 2005, Zou et al. 2008).

Determining how cultivars vary in response to environmental contexts, such as competition and herbivory, can improve invasion risk assessments of domesticated non-native species.

To explore these concepts, I evaluated how trait variation among cultivars of an invasive species might influence invasion risk under different environmental contexts. I used the legume Lespedeza cuneata (Dum. Cours.) G. Don (Chinese bush clover, Fabaceae) as a case study because the wild genotype is a well-documented invasive species in the United States and multiple cultivars have been bred for forage production and ruminant health (Brandon et al. 2004, Allred et al. 2010, Houseman and Mahoney 2015). First, I conducted a no-choice feeding bioassay to determine if wild L. cuneata genotypes and L. cuneata cultivars (hereafter cumulatively referred to as L. cuneata types) and native congener altered the performance of a generalist herbivore,
*Spodoptera frugiperda* (fall armyworm, Noctuidae). I analyzed foliar chemistry (tannins, phenolics, carbon-nitrogen) of the *L. cuneata* types and native congeners to examine their potential effects on herbivore performance. I hypothesized that *S. frugiperda* would develop better (i.e., greater survival, weight more, develop faster) on *L. cuneata* types and native congeners with lower plant defense compounds because they would provide a more palatable or higher quality food source. If generalist herbivores performed better on the *L. cuneata* that were domesticated to have lower plant defense compounds than the wild genotypes, then biotic resistance could potentially limit the spread of *L. cuneata* should cultivars escape from cultivation into natural areas.

Second, to test for variation in performance among *L. cuneata* types under different environmental contexts, I conducted a factorial greenhouse experiment, combining treatments that included herbivory by *S. frugiperda* and competition with native plant species. I hypothesized that cultivars with greater plant defense compounds, relative to the wild genotype, would show lower impacts of herbivory, and that cultivars with greater productivity (e.g., biomass, relative growth rate) would be better competitors against native plant species. Greater tolerance to herbivory and higher competitive ability could contribute to greater invasion risk should the cultivars escape cultivation. Conversely, cultivars with less resistance or tolerance to herbivory and lower competitive ability could offer agricultural alternatives with a lower risk of invading surrounding natural areas.

**Methods**

**Study Species**

*Lespedeza cuneata* is a perennial legume native to Southern and East Asia that was introduced to the United States in the late 1800s for erosion control (Allred et al.)
The species has now spread throughout the U.S. southeast and southern Great Plains (Brandon et al. 2004, Cummings et al. 2007). *Lespedeza cuneata* is commonly found in old fields and tall grass prairies and can survive in oligotrophic soils by fixing its own nitrogen (Brandon et al. 2004). In North America, *L. cuneata* suffers less than 2% arthropod herbivory and is thought to be protected by high tannin levels and other plant defense compounds (Beaton et al. 2011). *Lespedeza cuneata* suppresses the growth of native plants, possibly through high productivity that allows it to shade out surrounding species (Brandon et al. 2004).

*Lespedeza cuneata* was adapted for forage in the 1920s and by the 1950s the first cultivar was developed by the Soil Conservation Service (SCS). Today, there are 11 cultivars including Serala, AU Donnelly, and AU Grazer (Eddy and Moore 1998, Ball and Mosjidis 2007). Serala, released in 1962, was bred to have finer stems for greater palatability to livestock, a change that resulted in slightly lower tannin levels relative to wild *L. cuneata* genotypes (Mosjidis 1986, Broderick and Albrecht 1997, Ball and Mosjidis 2007). The cultivar AU Donnelly, released 1987, was bred for even lower tannins, but it has lower productivity relative to the wild genotype (Broderick and Albrecht 1997, Ball and Mosjidis 2007). The discovery that feed with high tannins improved intestinal health in small ruminants (e.g., goats, sheep) in the early 1990s, resulted in further cultivar development. In 1997, the cultivar AU Grazer was released, which had both higher tannin levels and greater productivity (Mosjidis 2001). The United States wild *L. cuneata* genotype is likely a genetic hybrid of the three earliest *L. cuneata* cultivars but, all of these cultivars were direct descendants of the original Asiatic plants and the hybridization occurred outside of cultivation (Beaton et al. 2011). The
domesticated cultivars were compared against both this U.S. wild genotype and the true wild genotype from the native range.

The generalist herbivore *S. frugiperda* has a widespread distribution in the Americas and feeds on over 350 plant species (CABI 2019). *Spodoptera frugiperda* is particularly common in agricultural systems and likely co-occurs with *L. cuneata* in North America (van Huis 1981, Hruska and Gould 1997, CABI 2019). I selected two congeners, *Lespedeza virginica* (Slender Lespedeza) and *Lespedeza capitata* (Roundhead Lespedeza), that are both native to the United States for comparison to the *L. cuneata* types in the bioassay experiment (USDA, NRCS 2018).

I used four common midwestern prairie plant species as the native competitors in the greenhouse experiment, all of which likely co-occur with *L. cuneata* in the invaded range (USDA, NRCS 2018). Two of the competitors were grasses, *Schizachyrium scoparium* (Little Bluestem, Poaceae) and *Sporobolus asper* (Rough Dropseed, Poaceae), and two were forbs, *Aster ericoides* (White Health Aster, Asteraceae) and *Kuhnia eupatorioides* (False Boneset, Asteraceae).

**Sources and Preparation of Plants and Herbivores**

I obtained AU Donnelly seeds from the Germplasm Resources Information Network (GRIN, USA), Serala from Hancock Seed Company (Dade City, FL, USA), and AU Grazer from Seed World (Odessa, FL, USA). Seeds from six wild populations of *L. cuneata* in Kansas (Greenwood and Elk Country, Kansas, USA) were collected in fall 2016 by Dr. Gregory Houseman (Wichita State University, Kansas, USA) and pooled for use as the U.S. wild genotype in the invaded range. Seeds from native populations in China, Japan, and South Korea were collected by the GRIN (USA), pooled, and designated the wild genotype from the native range. Seeds of the two native congeners
and the four native competitor species were purchased from Prairie Moon Nursery (Winona, MN, USA).

In April 2018, seeds were germinated in petri dishes in a growth chamber set to average southeastern summer temperatures with a photoperiod of 13:11 (L:D) and then transferred to trays in a greenhouse in Gainesville (FL, USA). The greenhouse was set to temperatures between 21°C to 32°C with 70% to 75% relative humidity. To ensure uniform nutrient levels, presence of soil biota, and efficient drainage, I used a blend of even parts sand (Alachua County, FL, USA), Sungro horticulture professional growing mix soil (Agawam, MA, USA), and Alachua County topsoil (Alachua County, FL, USA).

*Spodoptera frugiperda* eggs were obtain from the USDA, ARS (Gainesville, FL, USA), hatched and reared on artificial diet (Benzon Research, Carlisle, PA, USA). They were kept in an incubator with temperatures ranging from 15.1°C to 27.7°C and a photoperiod of 12:12 prior to initiation of the experiments.

**Bioassay Experimental Design**

To determine how a generalist herbivore performed when fed wild *L. cuneata* genotypes, domesticated *L. cuneata* cultivars, and native congers, I conducted a no-choice feeding bioassay. The experiment included a wild type from the native range (WTN), a wild type from the invaded range (WTI), three cultivars (AU Donnelly (AUD), Serala (SER), and AU Grazer (AUG)), and two native *Lespedeza* congeners (LVIG, LCAP) with 20 replicates per type (total n=140). To prepare the *L. cuneata* types and native congeners used in the bioassay, ten seedlings of each of the *L. cuneata* types and native congeners were transplanted into seventy 9 L pots (Elite Nursery Containers, Greenhouse Megastore, USA) after one month in the greenhouse as described above. All seedlings were approximately 10 cm tall when transplanted and were fertilized with 5
g of Osmocote 14-14-14 slow release fertilizer (Everris, Netherlands). Plants were then fertilized weekly with Miracle-Gro water soluble all-purpose plant food (Marysville, OH, USA). Throughout the experiment, the leaves were treated with a solution of diluted soapy water as needed to control for aphids, at low levels as to not deter the *S. frugiperda* from feeding. Once the plants had sufficient biomass, 140 similarly sized (ANOVA, F=2.17, p=0.488, df=6,133) *S. frugiperda* were transferred to individual 100 mm x 15 mm petri dishes and placed in the growth chamber where they were reared on artificial diet for six days, at which time they were large enough to be handled. *Spodoptera frugiperda* larva then were fed leaves of each *L. cuneata* type and native congener for the duration of the experiment, with leaves being replenished from the greenhouse plants as needed.

Each *S. frugiperda* larva was weighed every two to three days to track their survival and growth. Once surviving larva reached pupation, the pupae were weighed and then placed back into the growth chamber to monitor emergence. I recorded days to pupation and days to emergence for those that reached those stages. The experiment reached its conclusions when all *S. frugiperda* had either died, pupated, or emerged, and no adults had emerged from pupae for a week.

**Bioassay foliar chemistry**

To determine if *L. cuneata* types and native congeners in the bioassay experiment varied in plant defense compounds, which might alter herbivore performance, I measured total condensed tannins, total phenolics, and carbon-nitrogen for each type. First, 100 mg of fresh leaf biomass (around 10 leaves) was collected from 35 plants, consisting of five plants from each of the seven *L. cuneata* types or native congeners. Half of all the samples (50 mg for each plant) were used in the carbon-
nitrogen analysis and the other half were used for total phenolics and condensed tannins. All leaves were stored on ice when collected, transported to a -80°C freezer, then freeze dried within a week of collection. Samples were ground in their entirety using a Wiley Mill with a 20-mesh screen. For extraction, 25 mg ± 5 mg of each sample was weighed into an individual 2.0 mL microcentrifuge tube. Samples were extracted exhaustively by addition of 0.5 ml of 70% acetone with 1 mM ascorbate, sonication for 30 min at 0°C, centrifugation at 3,900g RCF, and 4°C for 15 min, decanting the supernatant into a separate microcentrifuge tube, and for a total of four cycles (Adams et al. 2009). After extraction, the acetone was removed by rotary evaporation and samples were made up to a constant volume of 1.0 ml.

Foliar phenolics, reported as tannic acid equivalent (%TAE), and condensed tannins, reported as white oak tannin equivalent (%WOTE), were measured using the Folin-Ciocalteu assay (Schultz and Baldwin 1982) and the acid-butanol assay (Rossiter et al. 1988, Rehill et al. 2006), respectively. Tannic acid was used as a standard for the Folin-Ciocalteu assay. In repeated trials, the slope of standard curves produced by this method differed by less than 1% from the slope of standard curves using purified pentagalloyl glucose, a common hydrolysable tannin. These results are reported as percent tannic acid equivalents per dry weight, giving sample reactivity relative to the purified standard. In essence, the results express the reactivity of the sample as if it consisted of the given percentage of the standard, permitting quantitative comparisons among samples (Schultz and Baldwin 1982). Following a modification of the method of Hagerman & Butler (1980) as discussed in Rehill et al. (2006), for the acid-butanol assay I used a previously prepared standard created from equal amounts of lyophilized,
ground leaf powder from lower-level canopy *Quercus alba* leaves collected along a latitudinal gradient from Georgia to Maine in late May – late July (Hagerman and Butler 1980, Rehill et al. 2006, Adams et al. 2009). The results of these assays are quantified as percentage tannin equivalents, indicating reactivity relative to the purified standard (Adams et al. 2009). For the acid-butanol assay of condensed tannins, a standard of Quebracho tannin was used. This method permitted expressing tannin concentrations as percent Quebracho tannin equivalents (i.e., giving the reactivity of the sample relative to the purified standard). Carbon-nitrogen ratios were analyzed against a standard of atropine according to standard protocols by Dr. Jason Curtis (University of Florida, Gainesville, USA).

**Bioassay statistical analysis**

I tested for differences in *S. frugiperda* survival among *L. cuneata* types and native congeners with a non-parametric Kruskal-Wallis test. Insufficient *L. virginica* biomass remained to feed the *S. frugiperda* past Day 20, so only relative growth rate could be calculated for this treatment. One-way Analysis of Variance (ANOVA), and Tukey post hoc tests, were used to determine if *S. frugiperda* performance traits (pupal mass, days to pupation, and days to emergence) or foliar chemistry traits (total condensed tannins, total phenolics, and carbon-nitrogen ratios) varied among the *L. cuneata* types and native congeners. Performance and chemistry variables were compared among the *L. cuneata* types and native congeners given that domestication has resulted in known, dissimilar changes from the wild genotype. General differences among combined groups of wild genotypes, cultivars, and native congeners also were explored with comparison of post-hoc tests. Relative growth rates (RGR) were calculated per *S. frugiperda*, if they survived past the fourth check point (Day 7, n=122).
using the maximum of the first derivative of a smoothing spline with log-transformed y-values (Kahm et al. 2010). The RGR for each *S. frugiperda* was averaged by treatment group. All statistical analyses were conducted in R (version 3.5.1, package *stats, growthrates*) (R Core Team 2013, Petzoldt 2018).

**Greenhouse Experimental Design**

To assess how *L. cuneata* types varied in performance among different environmental contexts, I conducted a blocked factorial greenhouse experiment with competition and herbivory treatments. Each of the *L. cuneata* types (invaded range wild genotype, Serala, AU Donnelly, or AU Grazer) were planted individually into the center of separate pots and the native plant species were added to half the pots as the competition treatment. *Spodoptera frugiperda* individuals were added to half the pots as the herbivory treatment. In total, there were two levels of herbivory by two levels of competition by four *L. cuneata* types by 10 replicates for a total of 160 pots. Each pot was assigned to a block and re-randomized within the block once per month.

Seedlings were grown for two months in the greenhouse and then transplanted into 9 L pots (Elite Nursery Containers, Greenhouse Megastore, USA). For the competition treatment, four native seedlings were randomly planted around the *L. cuneata* individual. All *L. cuneata* seedlings were between 10 cm to 20 cm when transplanted and the competitors were all the same size or larger than the *L. cuneata* when transplanted. The smallest of the native species, *Kuhnia eupatorioides*, was at least 5 cm taller than the *L. cuneata*, and the largest native species, *Schizachyrium scoparium*, was a maximum of 35 cm taller, thus simulating *L. cuneata* encroachment into established native stands. Seedlings were fertilized with 5 g of Osmocote 14-14-14 slow release fertilizer when planted (Everris, Netherlands) and fertilized weekly with
Miracle-Gro water soluble all-purpose plant food throughout the experiment (Marysville, OH, USA). Plants were treated once, two weeks prior to the addition of *S. frugiperda*, with Bushdoctor Force of Nature Miticide to protect against spider mites and treated with a solution of diluted soapy water as needed against aphids (FoxFarm Soil and Fertilizer Company, Pendleton, SC, USA).

Two months after transplanting the seedlings, tomato cages covered in clear 2mm$^2$ mesh (Enviromesh Netting, Greenhouse Megastore, USA) where placed over all pots, and four one-week old *S. frugiperda* were added to each cage receiving the herbivory treatment. The herbivory treatment was maintained throughout the experiment by adding five *S. frugiperda* after three weeks and three *S. frugiperda* after six weeks. The variation in the number of *S. frugiperda* reflected the amount of biomass remaining on plants (to avoid *L. cuneata* mortality), the availability of *S. frugiperda*, and the maximum number of *S. frugiperda* that could be added to a single pot given larvae are prone to cannibalism (Chapman et al. 1999).

I measured the height and diameter at base of each *L. cuneata*, the number of branches, and evaluated the reproductive stage (no reproduction, buds, flowering) at planting, the day the herbivory treatment was implemented, and then one and two months after *S. frugiperda* were added. For the native species, I measured the height and evaluated flowering. After two months, foliar herbivory (percent damage) was estimated and aboveground and belowground biomass was harvested, dried to constant mass, and weighed. Aboveground biomass was separated by leaves and stems, and the number of root nodules, number of seeds, and seed maturity were recorded for each *L. cuneata* individual.
Greenhouse foliar chemistry

I collected one sample from each *L. cuneata* individual in the greenhouse experiment prior to the addition of the *S. frugiperda* (n=160). Plants with sufficient remaining biomass at the end of the experiment were resampled (n=157). The same methods used to test for total condensed tannins and total phenolics in the bioassay experiment were used to evaluate these aspects of foliar chemistry in the greenhouse experiment.

Greenhouse statistical analysis

To visually examine all the variables and potential treatment combinations of competition and herbivory impacting the *L. cuneata* types, I used principal components analysis (PCA), which allowed for the ordination of each sample pot in non-dimensional space. The PCA of a data matrix can reveal dominant patterns through a complementary set of score and loading plots (Wold et al. 1987). After examining the data, the final PCA was simplified to include 9 loading factors: Biomass (biomass of *L. cuneata* stems, leaves, and roots), Seeds (total *L. cuneata* seed production), Diameter (RGR), Height (RGR), Branches (RGR), WOTE (initial total condensed tannins), TAE (initial total phenolics), Natives (total above and below biomass for native plants), Root_Shoot (Root to shoot ratio for *L. cuneata*). Factors that were not normally distributed, did not vary by treatment, or were highly correlated with another factor were removed or combined into the categories above. The number of seeds per *L. cuneata* individual was calculated by weighing 100 seeds from 10 samples of each *L. cuneata* type (at least two samples from each treatment), to determine a conversion rate of weight to number of seeds. Relative growth rate for the height, diameter at base, and number of branches of each *L. cuneata* individual was calculated as the natural log of
the size at the end of the experiment (Month 2) minus the natural log of the size at the start of the herbivory treatment (Month 0) over the difference in time (2), then averaged by treatment. I combined above and belowground biomass measures for each native plant and then averaged the biomass of native plants within the same pot (as each competition pot has 4 native plants) to get a measure of total native competitor biomass. These ordinations were conducted in R (version 3.5.1, package vegan) (Oksanen et al. 2008, 2015).

Subsequently, ANOVAs and t-tests were conducted to further explore connections suggested by the PCA amongst the treatment groups. Total seed production and total biomass were compared by two-way Analysis of Variance (ANOVA), where L. cuneata type and treatment group were the independent variables. One-way Analysis of Variance, and Tukey post hoc tests, were used to determine if important L. cuneata performance traits (total seed production and total biomass in control treatment, percent damage from S. frugiperda in the herbivory treatments, and RGR of height) or foliar chemistry traits (total condensed tannins and total phenolics prior and post addition of S. frugiperda) varied among the L. cuneata types. The herbivory treatments and the non-herbivory treatments were compared for both total foliar herbivory and total biomass with a t-test. The percent damage from herbivory was also compared between the combined L. cuneata types and the native species with a t-test. Tannin levels were compared prior and post addition of S. frugiperda independently for each L. cuneata type for both the control (no competition, no herbivory) and combined pressure (competition and herbivory) treatments (R, version 3.5.1, package stats and ggplot) (R Core Team 2013).
Results

Bioassay Experiment Results

The survivorship of *S. frugiperda* larvae did not vary based on *L. cuneata* type or native congeners (Kruskal-Wallis test, p=0.5655, H=3.89, df=5). Pupal weight (ANOVA, p=0.014, F=3.041, df=5,95), days to pupation (ANOVA, p<0.001, F=17.34, df=5,95), days to emergence (ANOVA, p<0.001, F=13.38, df=5,78), and relative growth rate (ANOVA, p<0.001, F=27.75, df=6,114) revealed a general trend for *S. frugiperda* fed AU Donnelly and AU Grazer to develop the fastest, with development at an intermediate rate on Serala and both wild genotypes, and slowest development on both native congeners (Figure 2-1).

*Lespedeza capitata* had higher total condensed tannins than *L. virginica* and all other *L. cuneata* types, except for AU Grazer; AU Donnelly had significantly lower tannins than AU Grazer (ANOVA, p<0.001, F=6.803, df=6,28) (Figure 2-2). A similar pattern was found upon comparing total phenolics across *L. cuneata* type and native congeners (ANOVA, p=0.002, F=4.857, df=6,28). Serala had a significantly lower carbon-nitrogen ratio than *L. virginica*, but *L. capitata* and the other *L. cuneata* types had similar, intermediate levels (ANOVA, p=0.023, F=2.945, df=6,28) (Figure 2-3).

Greenhouse Experiment Results

In the PCA analysis, the first two axes explained 39.68% and 18.74% of the total variation, respectively (Figure 2-4A). The first axis (PC1) represented a trade-off between total seed production and biomass of the *L. cuneata* types (Seeds, Biomass) and the biomass of the native competitors (Natives), and thus was represented as a composite measure of competition (Figure 2-4B). The second axis (PC2) was positively
related to total condensed tannins (WOTE) and total phenolics (TAE), which varied according to *L. cuneata* type (Figure 2-4C). Higher values on the first and second axes indicate smaller *L. cuneata* individuals (PC1) with higher total condensed tannins and phenolics (PC2).

Total seed production did not vary by *L. cuneata* type for herbivory or competition (ANOVA, p=0.544, F=0.716, df=3,148; p=0.106, F=2.077, df=3,148; respectively), but herbivory and competition reduced seed production across all treatments (ANOVA, p<0.001, F=8.5, df=1,148; p<0.001, F=137.6, df=1,148; respectively) (Figure 2-5). Even in the control treatment, seed production and total biomass did not vary by *L. cuneata* type (ANOVA, p=0.26, F=1.395, df 3,36; p=0.248, F=1.436, df 3,36; respectively). Relative growth rate (by height) shows that the wild genotype *L. cuneata* grew significantly faster than any other *L. cuneata* type (ANOVA, p<0.001, F=6.659, df=3,15).

All *L. cuneata* in the herbivory treatments had more damage from herbivory than those in the non-herbivory treatments (t-test, p<0.01, t=10.31, df=93.81) and there was more herbivory on *L. cuneata* than native species (t-test, p<0.001, t=6.91, df=79.87). The comparison between herbivory damage to a single *L. cuneata* and the combined four native species per pot is meaningful as 278 native plants (87%) had no damage compared to only 30 undamaged *L. cuneata* (19%). However, there was no significant difference in damage by *S. frugiperda* in the herbivory treatments by *L. cuneata* type (ANOVA, p=0.288, F=1.277, df=3,76). Additionally, the final biomass of the *L. cuneata* types did not differ between herbivory and non-herbivory treatments, as the average total biomass was almost identical between the treatments (t-test, p=0.052, t=-1.96, df=157.36).
There was no difference in foliar chemistry among the wild genotype, Serala, and AU Grazer, but AU Donnelly had lower total condensed tannins and total phenolics than any other L. cuneata type both prior to the addition of S. frugiperda (ANOVA, p<0.001, F=16.35, df=3,156, p<0.001, F=38.28, df=3,156; respectively) and at the end of the experiment (ANOVA, p<0.001, F=16.35, df=3,156, p<0.001, F=26.03, df=3,156; respectively). The wild genotype showed an inducible defense to herbivory, as tannin levels increased after the addition of S. frugiperda under competition and herbivory (paired t-test, p=0.022, t=2.839, df=8), but tannin levels did not change in the control (paired t-test, p=0.512, t=-0.683, df=9). The reverse was found for Serala, which gained tannins with age in the control (paired t-test, p=0.017, t=2.488, df=9), but had no change in tannins after the addition of S. frugiperda under competition and herbivory (paired t-test, p=0.174, t=1.475, df=9). Tannins consistently increased with plant age in AU Donnelly in both treatments (paired t-test, p=0.002, t=4.018, df=9, p=0.008, t=3.053, df=8). AU Grazer showed no change in tannins in either treatment (paired t-test, p=0.146, t=1.593, df=9, p=0.592, t=0.559, df=8).

Discussion

Here, I experimentally evaluated how trait changes from domestication potentially altered in invasion risk of a known invasive species. While wild plants are selected for cultivation due to a common set of desirable traits, domestication involves adapting plants to agricultural fields, making it difficult to predict the performance of plant species that might escape into natural areas (Denison et al. 2003, Doebley 2006). This case study with L. cuneata demonstrates that, even within a single species, shifts in invasion risk for natural areas can be variable depending on the cultivars and environmental context.
The bioassay indicated that generalist herbivore performance was generally enhanced (e.g., higher RGR, faster pupation and emergence, greater weight) on domesticated *L. cuneata* cultivars relative to wild *L. cuneata* genotypes or native congeners, regardless of tannin, phenolic, or carbon-nitrogen levels. This greater herbivore productivity could indicate that biotic resistance might deter the spread of domesticated *L. cuneata*, as opposed to wild genotypes, as cultivars offer a higher quality or more palatable food source for generalist herbivores. However, all *L. cuneata* in the greenhouse experiment responded in similar ways to the combined pressures of competition and herbivory, suggesting that domestication might not alter invasion risk under multiple ecological stressors. Thus, based on the performance of traits related to resistance or tolerance to herbivory and competitive ability, I found that domestication did not consistently alter the invasion risk of *L. cuneata*.

Domestication of wild *L. cuneata* genotypes decreased tannins in both Serala and AU Donnelly, while increasing tannins in AU Grazer (Broderick and Albrecht 1997, Mosjidis 2001, Ball and Mosjidis 2007). However, for the plants in my bioassay, difference in tannin levels were only found between AU Donnelly and AU Grazer. Another study comparing tannin levels among a wider selection of *L. cuneata* cultivars harvested from an agricultural research field found that tannin levels only varied in stems, not leaves (Sidhu 2010). The lack of difference in herbivore performance on low tannin AU Donnelly and high tannin AU Grazer could be related to the fact that *S. frugiperda* almost exclusively eat leaves. Additionally, Buntin and Wiseman (1990) performed feeding trials with *S. frugiperda* and cultivars of *L. cuneata*, including Serala and three others not tested here. When fed flesh foliage of *L. cuneata*, no differences in
*S. frugiperda* performance was found between low and high tannin *L. cuneata* genotypes (Buntin and Wiseman 1990). Here, the reason for the decline in *S. frugiperda* performance when fed Serala or wild genotypes is still unclear, since the lack of both variation in tannin level between *L. cuneata* types and *S. frugiperda* response to tannins, would be predicted to resulted in no difference between any of the *L. cuneata* types. Total phenolics were highly correlated with total condensed tannins, and thus do not provide additional insight. The performance of *S. frugiperda* in the bioassay is likely not related to tannins or phenolics, but some other factor did contribute to greater herbivore performance, and potentially lower invasion risk, on domesticated *L. cuneata* types.

Carbon-nitrogen ratio varied little among the *L. cuneata* types and native congeners in the bioassay and is unlikely to be related to differences in *S. frugiperda* performance. Similarly, a previous study comparing *L. cuneata* cultivars found low variation in carbon-nitrogen ratio (Sidhu 2010). The lack of variation in carbon-nitrogen ratio in the *L. cuneata* types and native congeners could be mean that all of the plants had optimal nutrient levels to achieve peak performance. To this point, *L. cuneata* is a similar crop to young Alfalfa (*Medicago sativa*) (Terrill 2014), which is used as a cover crop due to its common carbon-nitrogen ratio of 13:1 (USDA, NRCS 2011), and here the carbon-nitrogen ratio of the *L. cuneata* types and native congeners was in that same range. Thus, carbon-nitrogen ratio for all *L. cuneata* types and native congeners was fairly similar, and therefore is unlikely to explain the observed variation in the bioassay or alter overall invasion risk.
The lack of difference in *L. cuneata* type performance under the herbivory treatment in the greenhouse experiment could be because all *L. cuneata* types had an equal ability to tolerate that level of herbivory without exhibiting a tradeoff with performance. The average amount of damage inflicted on an individual *L. cuneata* in the herbivory treatment was a 30% to 50% loss of leaf biomass, while the invaded range, wild *L. cuneata* genotype can lose up to 80% of leaf biomass without a tradeoff in seed production or growth (Schutzenhofer and Knight 2007). However, the stress from herbivory was strong enough to induce compensatory growth, as there was significant leaf damage observed in the herbivory treatment but no difference in final biomass or seed production. This pattern indicates that all *L. cuneata* types were able to withstand large losses of biomass through herbivory, regardless of domestication, and thus have a similar invasion risk potential in terms of tolerance or resistance to a native generalist herbivore.

Competition had a strong, negative influence on all *L. cuneata* types in the greenhouse experiment, regardless of domestication. The invasive wild *L. cuneata* genotype has a wide native distribution across 15 countries in Asian and Australia (EPPO 2019) and, once established, *L. cuneata* can suppress native species (Eddy and Moore 1998). However, this wild genotype may be slow to establish, is a poor competitor against more aggressive species, and is less prevalent on nutrient enriched soils (Wright et al. 1978, Brandon et al. 2004). Since this experimental design involved transplanting *L. cuneata* seedlings into pots with mature native species in soils with high nutrients, all *L. cuneata* types may have been at a competitive disadvantage or compensated in the same ways. Overall, all *L. cuneata* were smaller under competition
treatments, indicating to a similar invasion risk of domesticated and wild *L. cuneata* in areas with high species richness or soils with high fertility.

The conclusion from the bioassay, indicating that tannin and phenolic levels were not strongly influencing the performance of *S. frugiperda*, is likely true for the performance of *L. cuneata* as well. In the greenhouse experiment, AU Donnelly had significantly lower tannins than any other *L. cuneata* type. But the amount of foliar herbivory still did not vary by *L. cuneata* type. Changes in tannin levels at the start and end of the experiment revealed a similar lack of correlation with *L. cuneata* performance. Tannin levels in *L. cuneata* can be highly variable over time, but they generally increase over a season (Donnelly 1959, Mosjidis 1986). The variability in growth rates between *L. cuneata* types could be driving these differences in tannin levels over time because plants sampled on the same day would be of different sizes. As in the bioassay, total phenolics co-varied with total tannins and do not offer new conclusions. Additionally, the wild genotype displayed an inducible defense by raising tannin levels only in the presence of herbivores, which is in line with previous documentation of this strategy in wild *L. cuneata* (Beaton et al. 2011). But it would appear that this trait is not present in domesticated *L. cuneata*, as none of the cultivars had that same response. This defense mechanism in the wild genotype could indicate a potentially greater invasion risk of non-domesticated *L. cuneata* than cultivars and could also explain the reduction in *S. frugiperda* performance on wild *L. cuneata* genotypes compared to two of the cultivars. In short, domestication of *L. cuneata* did not strongly alter tannin and phenolic levels or deter herbivory, but cultivars may lack an inducible defense to herbivores which could decrease their invasion risk potential.
Ultimately, both experiments suggest that domestication may only influence *L. cuneata* invasion risk in certain cases, such as in the presence of a generalist herbivore. The greenhouse experiment results indicate that under multiple stressors (i.e., competition and herbivory), simulating a realistic encroachment of the *L. cuneata* types into natural areas, domestication influenced neither performance nor invasion risk. However, in the bioassay, *S. frugiperda* performance was enhanced when fed two cultivars as opposed to wild genotypes or native congeners of *L. cuneata*, indicating that domestication potentially lowers invasion risk potential. Yet, the results of the bioassay are limited because I cannot say from this experiment if *S. frugiperda* performance was due to greater consumption of *L. cuneata* cultivars or from the cultivars being a higher quality food source. Also, the mechanism driving the greater performance of *S. frugiperda* when fed cultivars is unclear as it does not appear to be related to total tannins, phenolics, or carbon-nitrogen since there were few differences in these measures across the *L. cuneata* types.

A number of other chemicals related to plant defense have been isolated in the leaves of *L. cuneata* which could be influencing *S. frugiperda* performance, including isoflavanone, isoflavone, sterol, triterpenoid, flavonol, flavonol glycosides, flavone C-glycosides, and volatile organic compounds (Beaton et al. 2011, de Oliveira et al. 2017). Future studies could examine the potential roles of these chemicals on herbivore performance to expand on the strength of the potential decrease in invasion risk from domestication of *L. cuneata*, due to lower herbivore resistance or tolerance in cultivars.

There is a growing need for studies that test how domesticated traits can influence the success or failure of non-native plant species in overcoming the barriers to
invasion. Evaluating the invasion risk of domesticated plants in natural environments is critical because domesticated plants generally receive less regulatory scrutiny than the introduction or identification of known wild genotype invasive species (Bradley et al. 2012, USDA, NRCS 2019). Yet, at the species level, there often is a lack of evidence demonstrating that domestication has lowered invasion risk (Gordon et al. 2010). In this case, spread of *L. cuneata* in natural areas is unlikely to subside even with regulation limiting the sale of wild genotype seeds to certain states because cultivars of *L. cuneata* are readily available and will potentially perform similarly to the wild genotype in natural settings. This lack of regulation is particularly concerning since cultivars of *L. cuneata* cannot be easily distinguished from the wild genotype by appearance, which could cause a lag time in detecting the spread of a cultivar.

For some species, cultivation has clearly been demonstrated to alter invasion risk. For example, there is a subspecies and variety of *Sorghum bicolor* that are both considered low invasion risk and two subspecies that are considered high invasion risk according to the Australian Weed Risk Assessment adapted for Florida (UF, IFAS 2018). This high level of variation in invasion risk within a species could be challenging for regulations because it is not feasible to individually test every cultivar of every non-native species. However, knowing that domestication can alter invasion risk suggests it could be beneficial to adopt a white list policy for domesticated plants where it becomes the breeder’s responsibility to prove that cultivars have low invasion risk prior to introduction. Thus, a greater understanding of variation in trait changes occurring within a species under domestication and how that influences invasion risk potential can
facilitate the development of cultivars that have less invasion risk for natural areas and are still beneficial for human use.

This method for experimentally evaluating the invasion risk of multiple cultivars of a non-native species provides a new way to generate evidence that can aid in cultivar invasion risk assessments. The procedure includes three steps: First, identify the traits that were intentionally selected for under domestication. Second, consider what physical or environmental barrier that trait change might help the domesticated species to overcome. Finally, identify traits that are commonly a tradeoff in allocation with the intentionally selected for trait, then repeat the second step to evaluate if that unintended change alters invasion risk as well. Using these steps will help streamline invasion risk evaluation of domesticated species across variable environments. Where there is a lack of evidence demonstrating that domestication lowered invasion risk, risk assessment tools for species that have been domesticated could be improved by raising the overall determination of invasion potential of the species, when traits related to higher invasion risk are present in the domesticated type. For instance, when evaluating a species that has a cultivar with enhanced seed production, the AWRA question about prolific seed production could be given positive answer, or point addition, even if the wild genotype does not have prolific seed production. This weight would account for the fact that designation of lower invasion risk for the wild genotype could lead to distribution of the cultivar as well, either intentionally from lack of separate regulation or unintentionally from an inability to visually differentiate the wild and domesticated plants. Overall, invasion risk assessment must be expanded to focus on what trait changes and under what context domestication alters invasion risk of cultivated non-native species.
Figure 2-1. Average relative growth rate (RGR) of the *S. frugiperda* fed different *L. cuneata* types and native congener (n=122). For broader implications on invasion risk, labels are also given for the multispecies groups of wild *L. cuneata* genotypes, *L. cuneata* cultivars, and the native congeners.

Figure 2-2. Differences in the average total condensed tannins, reported as white oak tannin equivalent (%WOTE), amongst *L. cuneata* types and native congeners from the bioassay (n=35).
Figure 2-3. Differences in the average carbon-nitrogen ratios amongst different types of *L. cuneata* types and native congeners from the bioassay (n=35).

Figure 2-4. Principal component analysis (PCA) for all *L. cuneata* individuals in the greenhouse experiment (n=160) A) General distribution of samples with simplified loading values B) Color coded by the competition or no competition treatment, showing the correlation to PC1 C) Color coded by *L. cuneata* type, showing that total phenolics (TAE) and total condensed tannins (WOTE) are main drivers of PC2 separating out cultivar AUD from the other two cultivars and the wild genotype.
Figure 2-5. Average total number of seeds for each *L. cuneata* type in the greenhouse experiment (n=160). All sixteen treatment groups are represented by showing the four stress combinations of herbivory (*S. frugiperda*) and competition for each of the four *L. cuneata* types.
CHAPTER 3
CONCLUSIONS ON DOMESTICATION AND INVASION RISK OF NON-NATIVE PLANTS

In summary, more focused attention in invasion ecology should be given to how trait changes from domestication unintentionally alter the invasion risk of the species. Domesticated plants approach the barriers to invasion in a different way and with different traits than wild plants, often leading to greater success at overcoming earlier barriers due to enhanced human involvement. In later stages, the traits that influence invasion success are challenging to predict, for both domesticated and wild plants, as invasion success is often dependent on the environment. Additionally, plants are bred to be managed under a range of intensities and these conditions can provide insights into specific concerns and overall invasion risk associated with a given purpose of domestication. Intensively managed plants tend to have lower invasion risk due to closer reliance on humans. Future breeding efforts could seek to intentionally breed non-native species for a closer reliance on cultural amendments in order to ensure that species do not establish outside of cultivated areas. Case studies examining a single domesticated plant with notable invasion concerns can be beneficial for framing an understanding of the context dependency of invasions. These studies also provide evidence to fill in the knowledge gap between trait changes from domestication and implications in invasion risk. Increased efforts to advance our understanding this knowledge gap could include greater restrictions on the distribution of wild species with cultivars of unknown invasion risk potential. Although more reviews and case studies are needed, trait changes from domestication have clear means of altering invasion risk and must be addressed to ensure continued human use of plants does not have widespread negative impacts on natural areas.
LIST OF REFERENCES


BIOGRAPHICAL SKETCH

Tabitha Petri is broadly interested in how plant community dynamics influence the resistance of native populations to disturbance regimes. She received her Master of Science in interdisciplinary ecology from the University of Florida in December 2019, and dual bachelor's degrees in biology and environmental science from Stetson University in 2016. Her undergraduate research focused on the implications of plant-soil interactions on restoration of a sandhill ecosystem. Before starting graduate school, she worked at Archbold Biological Station, researching the role of soil crust in deterring invasive plants in a scrub ecosystem, and at The Jones Center at Ichauway, studying management implications on the success of woody and herbaceous plants in a longleaf pine understory. She hopes to continue researching plant community ecology throughout her career.