Article

Analysis of Plant Trait Data of Host Plants of *Lycorma delicatula* in the US Suggests Evidence for Ecological Fitting

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Abstract: Plant traits, used by the invasive insect herbivores to find and select suitable hosts, can play an important role in insect host range expansion. With regard to invasive *Lycorma delicatula*, it is not well explored, however, how the plant origin affects insect host selection, and whether native and introduced host plants differ in their morphology, lifespan, as well as environmental requirements for growth. We addressed this issue in our study through the comprehensive assessment of 25 relevant plant traits (a total of 27,601 records retrieved from the TRY database), as well as the origin and phylogenetic relationships of 37 host plants of *L. delicatula* in the U.S. Our results showed that only leaf area, leaf chlorophyll content, and canopy size were significantly greater in the introduced hosts than that in native plants. We did not detect a significant effect of the plant origin on other characteristics. Additionally, no significant differences between native and introduced hosts of *L. delicatula* in genetic distances from introduced *Ailanthus altissima* (the most preferred host) were detected. These results, for the first time, suggest strong evidence for ecological fitting which might drive the host plant selection of *L. delicatula* and its rapid spread in the U.S.

Keywords: forest pests; invasive species; novel associations; plant defenses; plant-insect interactions; spotted lanternfly; trophic interactions

1. Introduction

The globalization of human activities, especially in agriculture, has facilitated the range expansion of insect pests, promoting species invasions in new territories [1,2], and affecting native communities [3] and human health [4]. Species introduction in novel environments results in mixing native and non-native biota across the regions [2–8], as well as in communities that are composed largely of introduced species [9]. In a new range, the host plant choice of an introduced insect can be driven by many mechanisms; of these, ecological fitting is considered to be especially important in exploitation of novel host plants [10].

The term "ecological fitting" was initially proposed by Janzen [11] to describe a novel interaction of an organism with its novel environment, either when an organism uses novel resources and forms novel associations with other species, or when an organism persists in a changing environment. Later, ecological fitting became the central focus of a number of reviews, especially to describe the host plant switch by insect herbivores [10,12]. Specifically, Agosta and Klemens [10] defined ecological fitting as "the process whereby organisms colonize and persist in novel environments, use novel resources or form novel associations with other species as a result of the suites of traits that they carry at the time they encounter the novel condition". Ecological fitting can represent a situation when species interactions with abiotic or biotic environment suggests coevolutionary history, but in fact a long history of coevolution is not necessarily involved as species continue to exploit the same resources they used to exploit [9,10,13]. As a result, diverse communities with complex species composition can be formed exclusively through ecological interactions among species, i.e.,

ecological "fitting" and "sorting" [9]. In this regard, resource tracking, and not tracking of a certain species, underlies ecological fitting and shapes species interactions [14]. Our study focuses on the phenomenon of ecological fitting in relation to plant traits of the hosts of the invasive spotted lanternfly, *Lycorma delicatula* (White, 1845) (Hemiptera: Fulgoridae), a highly polyphagous insect pest in the eastern US which utilizes a wide range (more than 100 species) of forest trees, fruit trees, and ornamental plants for feeding.

A broad variety of morphological, biochemical, physiological, and other plant traits play an important role in plant responses to biotic and abiotic factors [15]. Consequently, plant trait data are an important source for plant ecology and conservation studies, restoration, as well as landscape management and pest control. Particularly, patterns in plant defensive traits and plant environmental requirements may offer important insights into host plant selection by insect pests, and especially by invasive insect pests in their introduced range. Thus, plant traits used by *L. delicatula* and other insect herbivores to find and select suitable host plants can play an important role in insect host range expansion. Cipollini and Peterson [16] showed that host plants that share visual appearance and chemical traits, such as volatiles and phloem chemistry, with ancestral hosts (i.e., co-evolved host plants) are especially important. Following Janzen [11], the authors indicated that utilization and host range expansion to novel hosts can happen via ecological fitting using the following mechanisms: (1) phenotypic plasticity which allows an invasive insect to colonize and utilize a novel host resource; (2) preadaptation to novel environment; and (3) phylogenetic mechanisms, such as phylogenetic conservatism of traits which are related to efficient host use [16]. For novel plant-insect associations, Agosta [12] acknowledged that even though many examples of host shifts by insect herbivores can be explained by ecological fitting, such host shifts occur among taxonomically related plants, apparently due to similarity in chemical responses and physical defenses.

Phylogenetic constraints, in addition to being an important part of ecological fitting, can also be a standalone factor facilitating novel plant-insect interactions by providing opportunities for rapid spread of insect pests among closely related host plants, and changing host plant breadth [17]. Biogeography can have a strong effect on plant-insect interactions: coevolutionary history between insect herbivores and their native host plants can result in strong coevolved resistance of host plants to their insect herbivores. As a result, insect pests can have different impact on host plants in their native range and introduced range. The emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), is one of such examples: while it is an aggressive insect pest on *Fraxinus* species in North America, it is only a nuisance in its native range of Asia [17].

Given that the tree-of-heaven, *Ailanthus altissima* (Mill.) Swingle (Simaroubaceae), has been shown to be the preferred host plant of *L. delicatula* in its native and introduced ranges, little is known about the plant traits of other hosts, and how other host plants are being selected by *L. delicatula* in the introduced range in the US. Are host plants of *L. delicatula* (both native and introduced to the US) closely related to *A. altissima*? Do native and introduced host plants differ in their leaf and canopy morphology, plant architecture, as well as moisture and temperature requirements? Are there differences in other plant traits and/or environmental conditions for plant growth? These are the primary questions that are addressed in our study through the comprehensive assessment of plant traits related to defense against herbivory and habitat, as well as the origin, life form, and phylogenetic relationships of the host plants of *L. delicatula* in the U.S. We specifically focused on determining whether plant origin of host plants of *L. delicatula* (i.e., plants native to the U.S. and plants introduced to the U.S.) drives the differences (if any) in host plant traits which, in turn, might affect *L. delicatula* preferences for host plants. We hypothesized that similarity in plant traits among native and introduced host plants might provide evidence for ecological fitting which *L. delicatula* might demonstrate in the introduced range. This information is critically important for future studies on predicting potential host plant and, consequently, mitigating spread of *L. delicatula* in native plant communities. For the purpose of this study, we will use the definitions for the terms presented in Table 1.

Table 1. Terminology in the context of the study.

Term	Definition
Native species	"a species that, other than as a result of an introduction, historically occurred or currently occurs in that ecosystem" [18].
Invasive species	A non-native species in relation to a particular ecosystem, "whose introduction causes or is likely to cause economic or environmental harm or harm to human health" [18].
Novel species association	The association between resident (e.g., native plant) and non-resident (e.g., introduced insect) species, "in which at least one species has little or no experience with relevant ecological traits of its interaction counterpart" [19].
Host plants	Following our previous research on host plant usage by *L. delicatula* [20,21], we will use the term "host plants" to refer to insect food plants—i.e., the plants which an insect pest utilizes as a food source and not for resting, molting, egg-laying, etc.
Host plant range	For the purpose of this proposed study, we will use the term "host plant range" to indicate the range of plants on which an insect pest feeds. Insect pests with a wide host plant range are *polyphagous*.
Host plant shift	A process "by which one or more formerly used host plant species are abandoned in favor of one or more new host plant species" [22].
Host plant range expansion	A process of "the addition of one or more host plant species to the total number used by the herbivore species" [22].
Ecological fitting	"the process whereby organisms colonize and persist in novel environments, use novel resources or form novel associations with other species as a result of the suites of traits that they carry at the time they encounter the novel condition" [10].
Coevolution	"an evolutionary change in a trait of the individuals in one population in response to a trait of the individuals of a second population, followed by an evolutionary response by the second population to the change in the first" [23]. For the purpose of this proposed study, we consider such evolutionary change in a trait of a certain native plant species in response to herbivory by a certain native insect species, and vice versa (i.e., adaptations of certain native insects to feeding on certain native plants).

2. Materials and Methods

2.1. Plant Trait Data Collection and Processing

The plant trait data were retrieved from the TRY database which contains a wide range of plant trait records submitted by researchers and available upon request [15]. We requested data for both, plant traits which presumably mediate insect herbivory and essential environmental covariates which accompanied the primary plant trait data—all of them are publicly available at the TRY database. For the purpose of this study, the plant trait data were retrieved only for species (37 total) included in a host plant list of *L. delicatula*, compiled and published in the most recent review by Barringer and Ciafré [24] (Table 2).

The datasets for each trait obtained from the TRY database were accessed through the command line, and standard UNIX tools (e.g., grep, cut, etc.) were used to extract the plant trait data for the study species. Standardized values, available for standardized traits, were extracted and used for data analysis. In the output files, each plant trait was presented with the following default information: (a) author and dataset information ("LastName", "FirstName", "DatasetID", "Dataset"; (b) plant species information ("SpeciesName", "AccSpeciesID", "AccSpeciesName"; (c) trait and observation information ("ObservationID", "ObsDataID", "TraitID", "TraitName", "DataID", "DataName", "OriglName"; (d) data values and measurement units ("OrigValueStr", "OrigUnitStr", "ValueKindName", "OrigUncertaintyStr", "UncertaintyName", "Replicates", "StdValue", "UnitName"); and (e) additional information and comments ("RelUncertaintyPercent", "OrigObsDataID", "ErrorRisk", "Reference", "Comment"). The output information was then reduced to include only the data used in the data analysis, such as: trait and species names ("TraitName", "AccSpeciesName"), trait values and units ("OrigValueStr", "StdValue", "UnitName") (Supplementary Material).

Table 2. Host plants of *Lycorma delicatula* in the introduced range in the US, and their plant origin.

# [1]	Family [2]	Genus [2]	Species [2]	Common Name	Plant Origin [3]	Life Form [3]	Perenniality [3]
1	Aceraceae	*Acer*	*buergerianum*	Trident maple	Introduced	Tree	Perennial
2	Aceraceae	*Acer*	*negundo*	Boxelder	Native	Tree	Perennial
3	Aceraceae	*Acer*	*palmatum*	Japanese maple	Introduced	Shrub/tree	Perennial
4	Aceraceae	*Acer*	*pictum*	Yellow-paint maple	Introduced	Tree	Perennial
5	Aceraceae	*Acer*	*platanoides*	Norway maple	Introduced	Tree	Perennial
6	Aceraceae	*Acer*	*pseudoplatanus*	Sycamore maple	Introduced	Tree	Perennial
7	Aceraceae	*Acer*	*rubrum*	Red maple	Native	Tree	Perennial
8	Aceraceae	*Acer*	*saccharinum*	Silver maple	Native	Tree	Perennial
9	Simaroubaceae	*Ailanthus*	*altissima*	Tree of heaven	Introduced	Tree	Perennial
10	Asteraceae	*Arctium*	*lappa*	Greater burdock	Introduced	Forb/Herb	Biennial
11	Brassicaceae	*Armoracia*	*rusticana*	Horseradish	Introduced	Forb/Herb	Perennial
12	Betulaceae	*Betula*	*pendula*	European white birch	Introduced	Tree	Perennial
13	Betulaceae	*Betula*	*alleghaniensis*	Yellow birch	Native	Tree	Perennial
14	Betulaceae	*Betula*	*lenta*	Sweet birch	Native	Tree	Perennial
15	Celastraceae	*Celastrus*	*orbiculatus*	Oriental bittersweet	Introduced	Woody vine	Perennial
16	Fagaceae	*Fagus*	*grandifolia*	American beech	Native	Tree	Perennial
17	Cannabaceae	*Humulus*	*lupulus*	Common hop	Both	Forb/Herb/Vine	Perennial
18	Juglandaceae	*Juglans*	*cinerea*	Butternut	Native	Tree	Perennial
19	Juglandaceae	*Juglans*	*nigra*	Black walnut	Native	Tree	Perennial
20	Magnoliaceae	*Liriodendron*	*tulipfera*	Tulip tree	Native	Tree	Perennial
21	Fabaceae	*Maackia*	*amurensis*	Amur maackia	Introduced	Tree	Perennial
22	Meliaceae	*Melia*	*azedarach*	Chinaberrytree	Native	Shrub/Tree	Perennial
23	Cornaceae	*Nyssa*	*sylvatica*	blackgum	Native	Tree	Perennial
24	Vitaceae	*Parthenocissus*	*quinquefolia*	Virginia creeper	Native	Woody vine	Perennial
25	Rosaceae	*Prunus*	*serotina*	Black cherry	Native	Shrub/Tree	Perennial
26	Fagaceae	*Quercus*	*acutissima*	Sawtooth oak	Introduced	Tree	Perennial
27	Fagaceae	*Quercus*	*rubra*	Northern red oak	Native	Tree	Perennial
28	Anacardiaceae	*Rhus*	*typhina*	Staghorn sumac	Native	Shrub/Tree	Perennial
29	Fabaceae	*Robinia*	*pseudoacacia*	Black locust	Native	Tree	Perennial
30	Salicaceae	*Salix*	*udensis*	Japanese fantail willow	Introduced	Tree	Perennial
31	Salicaceae	*Salix*	*babylonica*	Weeping willow	Introduced	Tree	Perennial
32	Styracaceae	*Styrax*	*japonicus*	Japanese snowbell	Introduced	Shrub/Tree	Perennial
33	Cupressaceae	*Thuja*	*occidentalis*	Arborvitae	Native	Tree	Perennial
34	Anacardiaceae	*Toxicodendron*	*radicans*	Eastern poison ivy	Native	Forb/Herb/Shrub/Subshrub/Vine	Perennial
35	Ericaceae	*Vaccinium*	*angustifolium*	Lowbush blueberry	Native	Shrub/Subshrub	Perennial
36	Vitaceae	*Vitis*	*vinifera*	Wine grape	Introduced	Shrub/Vine	Perennial
37	Rutaceae	*Zanthoxylum*	*simulans*	Chinese-pepper	Introduced	Shrub/Tree	Perennial

[1] Currently known host plants in the US. [2] Retrieved from Barringer and Ciafré [24]. [3] Determined according to the USDA Plants Database.

For this study, we compiled a total of 25 datasets each containing plant trait data or data on environmental covariates relevant to *L. delicatula* consumption and feeding behavior on 37 host plants. A total of 27,601 plant trait records were extracted from the TRY database and prepared for data analysis (Supplementary Material). The origin and life form of host plants, as well as plant taxonomy, were then determined using the USDA PLANTS Database. The datasets which included at least one introduced and at least one native plant species were included in the data analysis. Among 37 host plant species, we identified 19 native and 17 introduced to the U.S.; status "both" was determined for one plant species (*Humulus lupulus* L. (Cannabinaceae)) (Table 2). The native origin for all introduced plants except two species (*Arctium lappa* L. (Asteraceae), and *Vitis vinifera* L. (Vitaceae) originated in Eurasia) overlapped with the native origin of *L. delicatula*. Since we were interested in comparing the plant trait data between species native and introduced to the U.S., data for *H. lupulus* were excluded from these comparisons and were used for phylogenetic reconstructions only.

2.2. Plant Trait Data Synthesis and Statistical Analysis

For the purpose of this study, i.e., to target the plant traits which affect insect food choice and plant consumption, all the retrieved data were combine into the following categories: (1) data related to leaf characteristics, (2) data related to plant architecture

and plant lifespan, and (3) plant species habitat characterization and/or environmental requirements for plant growth.

For continuous data (leaf trait data, plant architecture and lifespan data), separate linear mixed models (LMMs) were fitted by REML to determine the differences in the plant trait data among native and introduced plants. For count data (such as species environmental indicator values according to Ellenberg), generalized linear mixed models (GLMMs) using Poisson distribution were fit by maximum likelihood (Laplace Approximation). In both LMMs and GLMMs, plant origin was treated as fixed effect, and plant species were included in the model as a random effect, to account for variation among plant species within each plant group (native and introduced). For the purpose of this study, we were interested in difference between native and introduced plants only. Both LMMs and GLMMs were performed using *lme4* package in R (version 4.2.0) [25]. For each plant trait, density plots were built using *ggplot2* package and were used to determine the type of the data distribution. For each significant term from LMMs and GLMMs, multiple means comparisons were performed by computing Estimated Marginal Means (aka Least-Squares Means) using *emmeans* package in R. Package *sjPlot* was used to record the output from LMMs and GLMMs in a table format (Supplementary Material); and dplyr package was used to rearrange, filter, and summarize data for data analysis.

2.3. Phylogenetic Reconstruction and Genetic Distance Analysis

Plant phylogenetic metrics were calculated using sequence data for the *rbc*L gene (ribulose-1,5-biphosphate carboxylase-oxygenase), one of the universal plant DNA barcodes, available in NCBI GenBank. Overall, we retrieved 165 sequences for the rbcL gene available for 37 host plant species used in the plant trait data analysis (~5 sequences per plant species). Each sequence was retrieved and downloaded as a FASTA file during the period between 13 October 2021 and 4 November 2021. Multiple sequence alignment, for each plant species, was then performed in the Unipro UGENE platform using the ClustalW algorithm. Once aligned, 37 consensus sequence files were generated (Supplementary Material). Molecular Evolutionary Genetics Analysis (MEGA) software (v. 10.0.5) was then used to generate a maximum likelihood tree from the aligned consensus files. The bootstrap method was run with a total of 150 replications. "Neighbor-Join and BioNJ algorithms were applied to a matrix of pairwise distances estimated using the Tamura-Nei model. The topology with superior log likelihood value was selected to obtain initial trees for the heuristic search. There were a total of 1084 positions in the final dataset. For each plant species, from the matrix with pairwise genetic distances, a genetic distance from introduced *Ailanthus altissima*, tree-of-heaven (most preferred host plant of *L. delicatula* in its native range), was retrieved and used in the subsequent comparisons between native and introduced plants (Supplementary Material). Differences in genetic distances from *A. altissima* between native and introduced host plants were analyzed using one-way ANOVA in R (version 4.2.0) [25].

3. Results

3.1. Plant Trait Data and Environmental Requirements

Data for a total of 25 plant traits and their environmental covariates containing a total of 27,601 records were compared among 37 documented host plants of *L. delicatula* reported as its food plants in the US, based on Barringer and Ciafré [24]. We compiled nine datasets for leaf trait data, each contained from a minimum of 21 (for Leaf nitrogen (N) content per leaf) to a maximum of 5037 (Leaf area (in case of compound leaves: leaf, petiole excluded)) retrieved records available in the TRY database. The number of introduced and native plant species in each dataset varied from one to 19. Data for a total of nine leaf traits were compared between native and introduced host plants of *L. delicatula* (Table 3, Figure 1). Leaf area measurements (when the petiole was excluded) and leaf chlorophyll content only were significantly higher in introduced plants that those in native plants (LMM, fixed effects: $p_{adj} < 0.0001$ and $p_{adj} = 0.0009$, respectively). These datasets, however, contained data for

one introduced species only, Ailanthus altissima. No significant differences in other leaf traits, such as leaf area with the petiole included, leaf length, leaf dry and fresh mass, as well as leaf nitrogen and water content, were observed (Table 3).

Table 3. Mean values and standard errors (Mean $\pm$ SE) for each plant trait of native and introduced host plants of *Lycorma delicatula*.

Plant Trait Group	Full Plant Trait Name [1]	Total Number of Records per Dataset	Plant Origin [2]	Number of Plant Species per Dataset	Mean $\pm$ SE	Units
Leaf characteristics	Leaf area (in case of compound leaves: leaf, petiole excluded)	2537	I *	1	778.56 $\pm$ 161.45	cm^2
			N	12	52.63 $\pm$ 0.51	cm^2
	Leaf area (in case of compound leaves: leaf, petiole included)	2740	I	5	155.73 $\pm$ 21.11	cm^2
			N	20	53.63 $\pm$ 0.63	cm^2
	Leaf dry mass (single leaf)	5035	I	6	1.03 $\pm$ 0.21	g
			N	18	0.16 $\pm$ 0	g
	Leaf fresh mass	4716	I	3	3.07 $\pm$ 0.59	g
			N	12	0.45 $\pm$ 0.01	g
	Leaf chlorophyll content per leaf area	313	I *	1	26.32 $\pm$ 1.09	CCM
			N	5	13.88 $\pm$ 0.14	CCM
	Leaf length	160	I	2	0.92 $\pm$ 0.22	cm
			N	7	1.05 $\pm$ 0.04	cm
	Leaf nitrogen (N) content per leaf	21	I	4	8.35 $\pm$ 2.43	g m^{-2}
			N	8	11.95 $\pm$ 3.06	g m^{-2}
	Leaf nitrogen (N) content per leaf dry mass	3320	I	17	0.03 $\pm$ 0	g/g
			N	19	0.02 $\pm$ 0	g/g
	Leaf water content per leaf dry mass (not saturated)	3320	I	12	25.48 $\pm$ 0.32	g/g
			N	11	22.6 $\pm$ 0.12	g/g
Plant architecture and lifespan	Crown (canopy) length: diameter along the longest axis	146	I *	1	0.98 $\pm$ 0.05	m
			N	4	0.07 $\pm$ 0	m
	Crown (canopy) height	117	I	4	3.5 $\pm$ 0.51	m
			N	1	0.33 $\pm$ 0	m
	Crown (canopy) width	146	I *	1	0.98 $\pm$ 0.06	m
			N	4	0.05 $\pm$ 0	m
	Plant lifespan (longevity) max	21	I	4	185.83 $\pm$ 51.31	years
			N	7	324.56 $\pm$ 96.3	years
	Plant lifespan (longevity) mean	36	I	3	310 $\pm$ 55.54	years
			N	11	240.65 $\pm$ 36.76	years
	Plant lifespan (longevity) min	16	I	4	174 $\pm$ 50.69	years
			N	4	157.5 $\pm$ 47.08	years
	Plant height vegetative max	442	I	17	22.85 $\pm$ 0.74	m
			N	19	25.46 $\pm$ 0.65	m
	Stem diameter	2609	I	9	0.25 $\pm$ 0.02	m
			N	16	0.21 $\pm$ 0	m
Species habitat characterization/Plant requirements	Precipitation max	25	I	6	54.17 $\pm$ 2.01	in/ft
			N	19	57.5 $\pm$ 2.5	
	Precipitation min	25	I	6	31.33 $\pm$ 0.42	in/ft
			N	19	28.5 $\pm$ 2.03	
	Temperature: species environmental indicator value according to Ellenberg	20	I	8	5.5 $\pm$ 0.54	EV [3]
			N	3	5.8 $\pm$ 0.49	EV
	soil pH max	25	I	6	7.28 $\pm$ 0.1	pH value
			N	19	6.98 $\pm$ 0.25	
	soil pH" min	25	I	6	5.13 $\pm$ 0.14	pH value
			N	19	4.98 $\pm$ 0.17	
	Light: species environmental indicator value according to Ellenberg	23	I	8	5 $\pm$ 0.53	EV
			N	4	4.29 $\pm$ 0.71	EV
	Atmospheric CO_2 concentration	193	I	3	435.28 $\pm$ 32.28	ppm
			N	10	379.18 $\pm$ 6.54	ppm
	Elevation, m	627	I	8	238.32 $\pm$ 9.77	m
			N	14	271.64 $\pm$ 8.82	m

[1] As retrieved from TRY database. [2] The plant origin was determined according to the USDA Plants Database: I, introduced; N, native. The plant origin with an asterisk represents a significantly greater plant trait measurement at α = 0.05. [3] EV, Ellenberg Value.
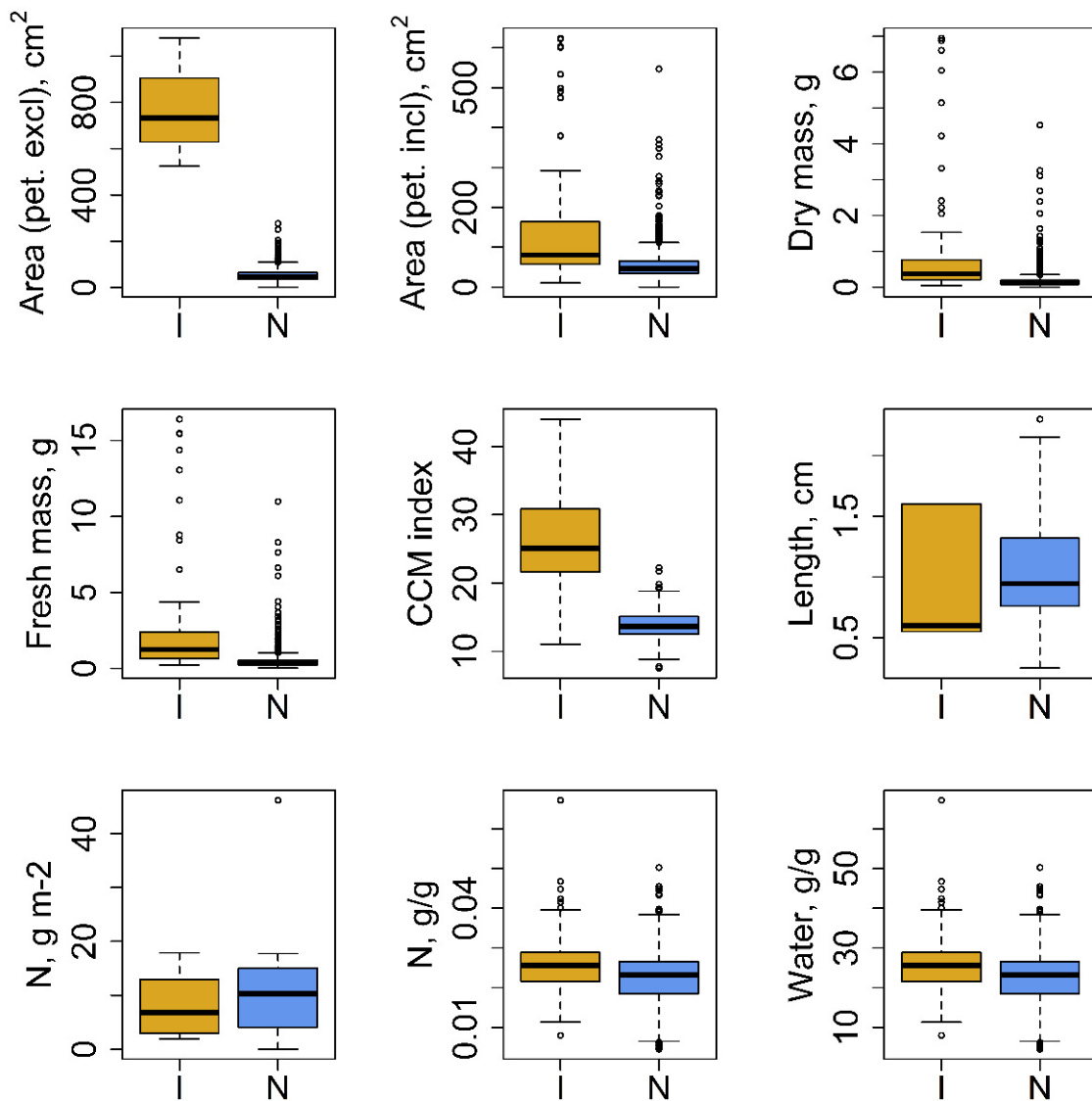
Figure 1. Leaf trait data compared between native (N) and introduced (I) host plants of Lycorma delicatula. The trait names are as follows (from left to right, and from top to bottom): Leaf area (in case of compound leaves: leaf, petiole excluded); Leaf area (in case of compound leaves: leaf, petiole included); Leaf dry mass (single leaf); Leaf fresh mass; Leaf chlorophyll content per leaf area (CCM index); Leaf length; Leaf nitrogen (N) content per leaf (g m^{-2}); Leaf nitrogen (N) content per leaf dry mass (g/g); and Leaf water content per leaf dry mass (not saturated). Boxplots represent the median (thick horizontal line), the 25th and 75th percentiles (the box), the 5th and 95th percentiles (the whiskers). Leaf area (petiole excluded) and leaf chlorophyll content per leaf area (CCM index) only were significantly higher in introduced plants that those in native plants (LMM, fixed effects: $p_{adj} < 0.0001$ and $p_{adj} = 0.0009$, respectively). All other pairwise comparisons were not significant different at $\alpha = 0.05$.

Eight datasets were compiled for data relevant to plant architecture and plant lifespan. The results of comparisons of these data among the spotted lanternfly host plants showed a significantly longer and wider canopy recorded in the introduced host plants than that in native plants (LMM, fixed effects: $p_{adj} = 0.0007$ and $p_{adj} = 0.0003$, respectively); whereas no difference were observed in plant lifespan, height, and stem diameter (Table 3, Figure 2). Similar to leaf trait data, in both canopy length and canopy width datasets, only one introduced plant species, *Arctium lappa*, was present in each dataset.
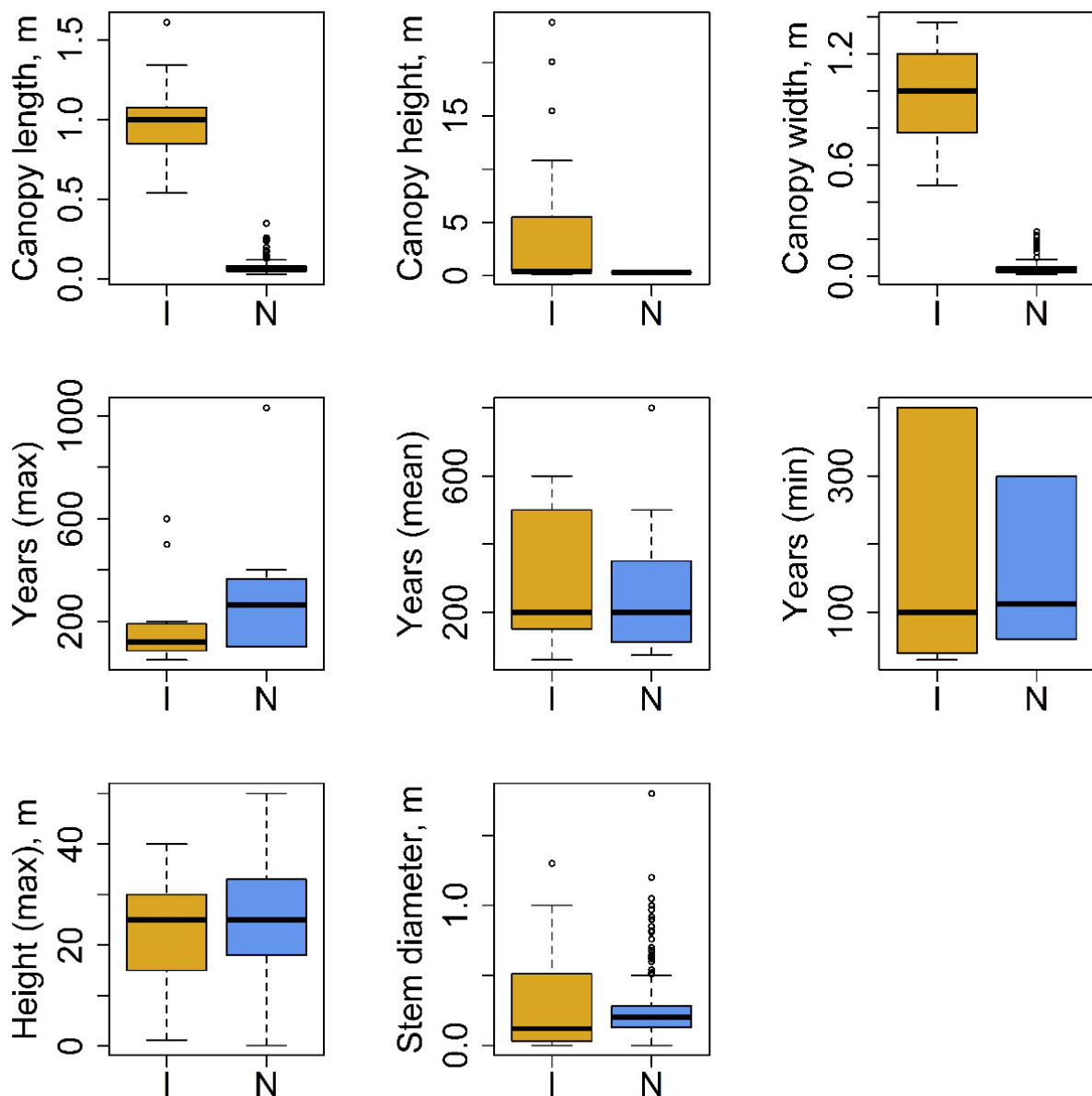
Figure 2. Plant architecture and plant lifespan data compared between native (N) and introduced (I) host plants of *Lycorma delicatula*. The trait names are as follows (from left to right, and from top to bottom): Crown (canopy) length: diameter along the longest axis; Crown (canopy) height; Crown (canopy) width; Plant lifespan (longevity) max; Plant lifespan (longevity) mean; Plant lifespan (longevity) min; Plant height vegetative max; and Stem diameter. Boxplots represent the median (thick horizontal line), the 25th and 75th percentiles (the box), the 5th and 95th percentiles (the whiskers). Crown (canopy) length and Crown (canopy) width only were significantly higher in introduced plants that those in native plants (LMM, fixed effects: p_{adj} = 0.0007 and p_{adj} = 0.0003, respectively). All other pairwise comparisons were not significant different at α = 0.05.

Finally, no significant differences were observed in the environmental requirements for plant growth, such as light, soil pH, precipitation, temperature, atmospheric CO_2 concentration, and elevation (Table 3, Figure 3).
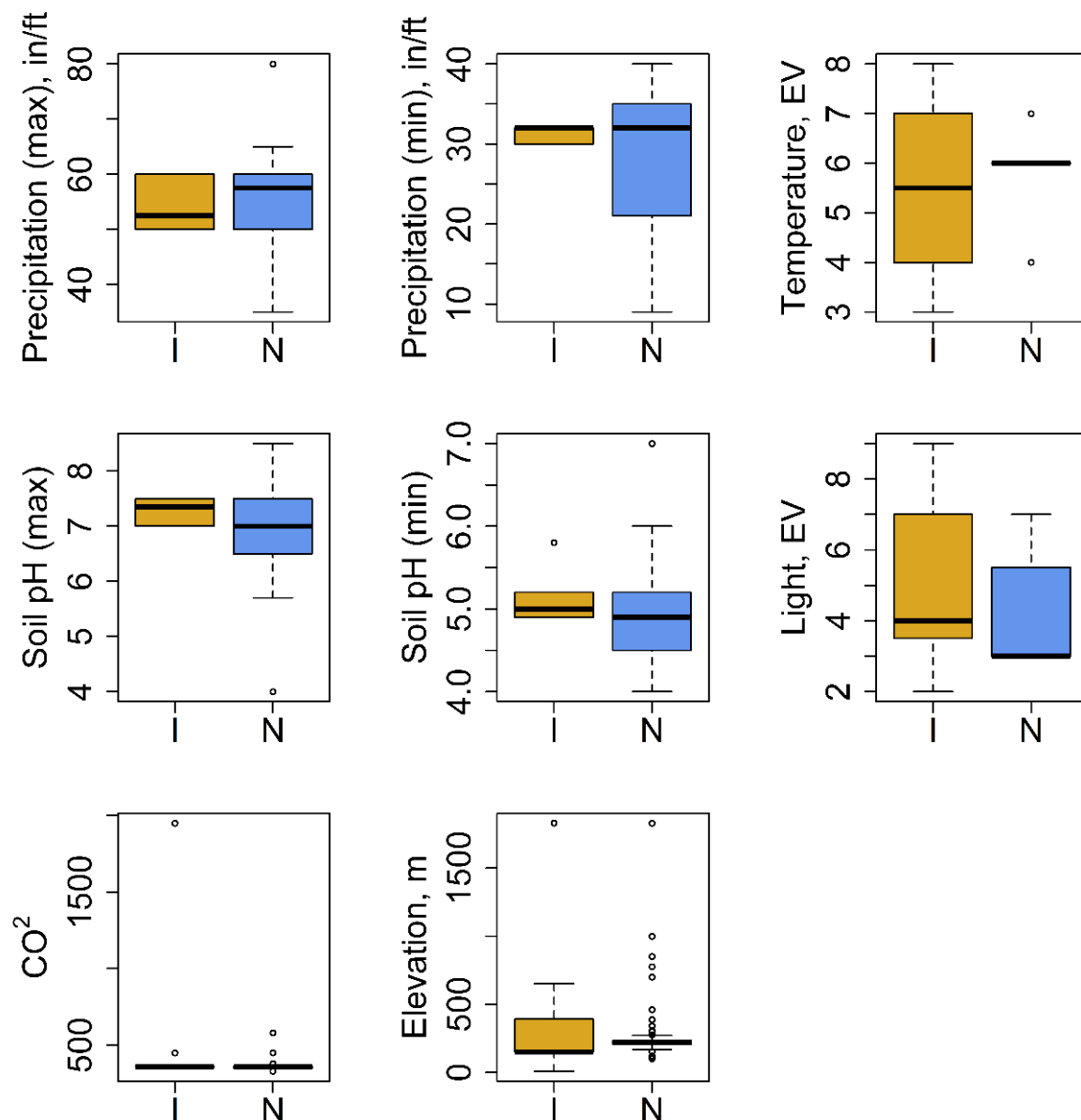
Figure 3. Plant species habitat characterization and plant environmental requirements compared between native (N) and introduced (I) host plants of *Lycorma delicatula*. The trait names are as follows (from left to right, and from top to bottom): Precipitation (max); Precipitation (min), Temperature: species environmental indicator value according to Ellenberg (EV, Ellenberg Value); Soil pH (max); Soil pH (min); Light: species environmental indicator value according to Ellenberg (EV, Ellenberg Value); Atmospheric CO_2 concentration (ppm); Elevation. Boxplots represent the median (thick horizontal line), the 25th and 75th percentiles (the box), the 5th and 95th percentiles (the whiskers). No significant differences between native and introduced host plants were detected at $\alpha = 0.05$.

3.2. Phylogenetic Reconstruction and Genetic Distance from Ailanthus altissima

A total of 37 host plant species were included in reconstruction of their phylogenetic relationships based on the rbcL gene (Figure 4). Pairwise genetic distances among the plant species from of *A. altissima* varied (Supplementary Material). Not surprisingly, the shortest distance of 0.0275 from *A. altissima* was recorded for introduced Zanthoxylum simulans Hance (Rutaceae), while the maximal genetic distance (0.1465) was recorded for native Thuja occidentalis L. (Cupressaceae) (Supplementary Material). However, when plant origin was considered as a factor, the analysis of genetic distances from introduced

Ailanthus altissima showed no significant difference between native and introduced host plants of *L. delicatula* ($F_{1,32}$ = 0.985, *p* = 0.328; Figure 5).
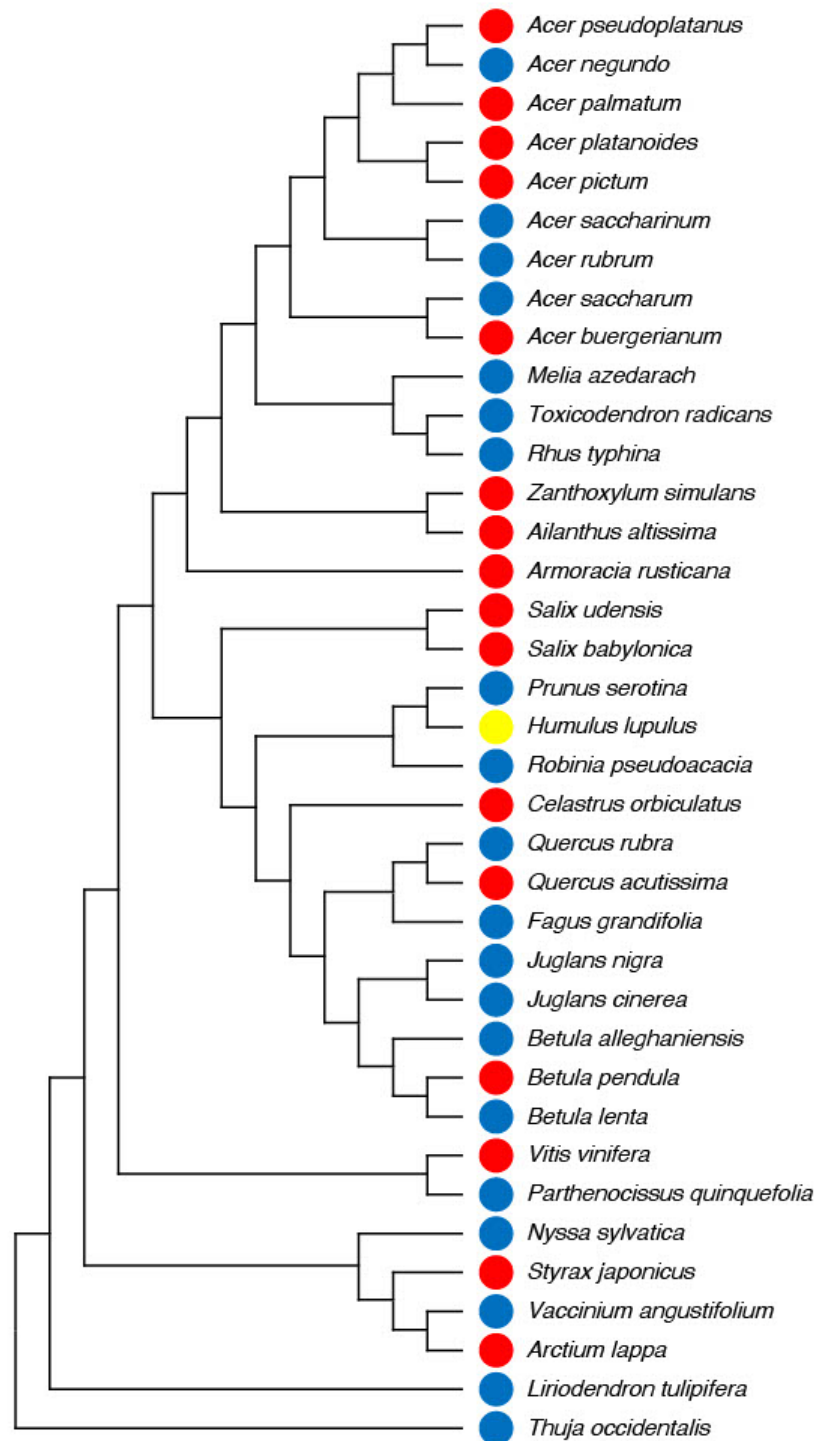

Figure 4. Phylogenetic relationships constructed based on sequence data for the *rbc*L gene (ribulose-1,5-biphosphate carboxylase-oxygenase) for native (blue circles) and introduced (red circles) host plants of *Lycorma delicatula*. The status for *Humulus lupulus* (yellow circle) was determined as "both" according to the USDA Plant Database. Sequences were retrieved from the NCBI GenBank Database. Maximum likelihood tree with bootstrap replicates of 150 was generated using Molecular Evolutionary Genetics Analysis (MEGA) software (v. 10.0.5).
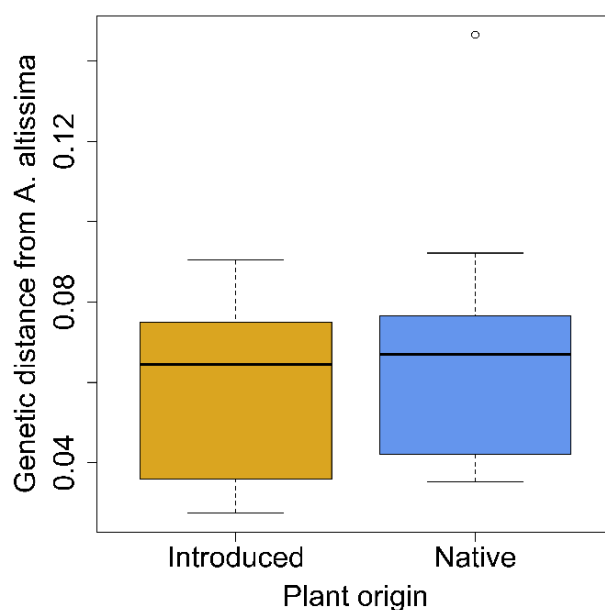
Figure 5. Genetic distances from *Ailanthus altissima* of native and introduced host plants of *Lycorma delicatula* based on the sequence data for the *rbc*L gene (ribulose-1,5-biphosphate carboxylase-oxygenase) retrieved from the NCBI GenBank Database. Boxplots represent the median (thick horizontal line), the 25th and 75th percentiles (the box), the 5th and 95th percentiles (the whiskers). No significant differences between native and introduced host plants were detected at $\alpha = 0.05$.

4. Discussion

In this one-year study, we focused on determining whether the plant origin of host plants of *L. delicatula* drives the differences (if any) in host plant traits which, in turn, might affect *L. delicatula* preferences for host plant selection in the U.S. Overall, our hypothesis of similarity in plant traits among native and introduced host plants of *L. delicatula* in the U.S. was supported in the majority of plant trait comparisons. Our results provide evidence for ecological fitting which *L. delicatula* could potentially demonstrate in any introduced range. Below, we discuss possible factors which might explain the results from our study, as well as potential future directions for studies on host plant selection by *L. delicatula*.

4.1. Plant Trait Data and Environmental Requirements

In our study, we focused on plant traits which play an especially important role in mediating the interactions between insect herbivores and their host plants. It has been shown that plant mechanical and chemical traits can affect the amount of plant damage [26,27]. Given the preference of *L. delicatula* for trees, and its cyclic behavior on a host tree [28], we focused on leaf traits and canopy characteristics which could potentially facilitate feeding and attachment of *L. delicatula*.

Our results suggest that most of the visual leaf features and leaf nutritional content can be shared between native and introduced host plants of *L. delicatula*. Such similarity in plant traits utilized by herbivorous insects can explain rapid host range expansions by insect pests [16,29]. Cipollini and Peterson [16] in the experiments with the invasive emerald ash borer, *Agrilus planipennis*, showed that secondary metabolites, and phenolics, in particular, can mediate the insect preferences for leaves which can explain the utilization of the white fringetree by *A. planipennis*. The authors pointed out that identification of key plant traits shared by co-evolved and novel host plants may be critical for predicting potential host plants attacked by insect pests [16]. The introduced tree-of-heaven, *Ailanthus altissima*, one of the most preferred host plants of *L. delicatula*, contains cytotoxic alkaloids [30,31], which might play an important role in insect host selection and oviposition. A recent study by Nixon et al. [32] showed that especially young potted *A. altissima* trees were successfully

utilized by *L. delicatula* as a food source and positively affected the insect development the first instar nymph through the adult stage, and their survivorship. It would be helpful for future studies to investigate the presence of cytotoxic alkaloids, and leaf chemical content in general, in other suitable host plants of *L. delicatula*.

Plant architecture plays an important role not only in visual stimulation, but also in providing an insect with habitat, oviposition substrate, and various food sources [27]. Diverse branching architecture, plant age, and different amount of shade also add to the complexity of plant canopy used as habitat for many insects [33]. *Ailanthus altissima*, the preferred host tree of *L. delicatula*, has a very dense canopy provided by its compound leaflets [34]. In our study we focused on the overall plant height, stem diameter, and canopy size only, but it would be interesting for future studies to explore deeper various aspects of plant morphology and their effect on the lanternfly feeding. Price et al. [35] in their study with several insect pests showed that patterns of modular gradients of shoot were similar among the attacked host plants even when various life forms (trees, shrubs, grasses) were compared. Our findings of the maximum plant height of 22–25 m support the previous studies on the flight and moving abilities of *L. delicatula*. Ascending and descending a host tree are important parts of *L. delicatula* behavior [28,34,36]. It has been recorded that the adults can move up to 4–16 m in tree canopy, and then cover up to 50–100 m in the air being carried away by the wind before landing on another host plant [36,37].

An interesting study by Grevstad and Klepetka [38] on predatory coccinellid beetles showed that plant morphology affected the predator foraging success as well. The authors found that the foraging behavior of lady beetles (Coccinellidae) searching for aphids, specifically, their falling rates, movement, time and location of foraging, were mediated directly by plant architecture. The knowledge of *L. delicatula* preferred host plant architecture and evaluation of the host plant accessibility for predators has also important implications for biological control of this pest.

Environmental requirements needed for host plant growth are also critical for the dispersal of *L. delicatula* populations. Nixon et al. [32] found that the reduction of the daylength to 12L:12:D increases the oviposition of *L. delicatula*. Interestingly, both native and introduced host plants in our study demonstrated a preference for semi-shade light conditions, based on the mean Ellenberg's indicator value of 5 ± 0.53. A few models have been proposed to predict the potential distribution of *L. delicatula* based on climatic conditions [39] and spatial distribution of economically valuable commodities [40], with temperature being shown as one of the most important factors mediating the lanternfly development which positively affects egg developmental rates [41]. However, there are data showing that incubating eggs at low temperatures can prolong egg viability and hatching later in the season as it might be expected in the regions with cold climate [32]. We did not record any difference in temperature requirements with 8 being the mean Ellenberg's indicator corresponding to a range from submontane-temperate to Mediterranean climate zones.

4.2. Plant Phylogenetic Relatedness and Ecological Fitting

Previous studies showed a strong phylogenetic signal in host plant range of some insect herbivores [42,43]. Plant phylogeny has also been shown to have a significant effect on the magnitude of plant defenses and associated herbivory [29]. Rasmann and Agrawal [42], in particular, found that larval survivorship of the red milkweed beetle, *Tetraopes tetraophthalmus* Forster, 1771 (Cerambycidae), decreased with increasing phylogenetic distance from its true host, the common milkweed, *Asclepias syriaca* L. (Apocynaceae); the authors suggested that adaptation to host plant traits drives specialization of the red milkweed beetle. In contrast to some of the previous studies [44,45], however, we did not detect a preference of *L. delicatula* for closely related hosts—the genetic distances from *A. altissima* did not differ between native and introduced plants. This can be partially explained by the fact that even though *A. altissima* is a preferred host and support the development of *L. delicatula*, other plants can be similarly suitable. Nixon et al. [32] pointed out that

L. delicatula can develop on other hosts, such as *Salix babylonica* L. (Salicaceae), *Betula nigra* L. (Betulaceae), and *Vitis vinifera*, without the presence of *A. altissima*.

Species invasions can represent a "natural experiment" on species interactions in novel environments and species "fitting" into a novel community without adaptation, that can provide important evidence for ecological fitting [9]. The concept of ecological fitting also drives many research studies on invasive insects and their novel host plants, explaining how new species fit in a community. Thus, there is evidence from studies on the emerald ash borer, *Agrilus planipennis*, an invasive woodborer, that this pest uses its novel hosts via ecological fitting: the novel hosts often show similar phloem chemistry and other traits with the ancestral hosts (i.e., co-evolved hosts) of the emerald ash borer. Though this degree of similarity in plant traits is important, apparently the emerald ash borer has enough plasticity to utilize various host plants [16]. The overall results of a comprehensive analysis of plant traits we conducted in this study suggest that *L. delicatula* might select the host plants via ecological fitting at this time, and the co-evolutionary history with its hosts may not be critical for successful host plant selection. Our results demonstrated the role of plant traits, for both native and introduced host plants, in driving host selection by *L. delicatula*; as part of this, we identified a set of plant trait mean ($\pm$SE) measurements which can be used to predict potential host plants for *L. delicatula*.

It is possible that the factors other than plant phylogenetic relatedness might drive *L. delicatula* host plant selection at a certain site, such as plant abundance, plant cover, plant diversity and species richness. In our previous research on chewing insect herbivores we showed the importance of plant composition and availability at a field site in insect food selection [46]. In our experiments with *Melanoplus* grasshoppers we demonstrated that the proportion of native and introduced host plants at a certain field site was similar to the proportion of ingested plant species. However, we accounted for the number of unique plant species only. It would be interesting for future studies to focus on vegetation cover in relation to native and introduced plants and determine its effect on *L. delicatula* food choice.

4.3. Potential Limitations

This study focused on known host plants of *L. delicatula* in the U.S., for both adults and nymphs. This could be a potential limitation of our study since the host plant range of *L. delicatula* decreases as the insect develops through several life stages [20,28,32]. Future studies might explore the patterns in plant traits specifically for each developmental stage. Additionally, given that *L. delicatula* is an important invasive pest, we focused on delivering the results of this study as quickly as possible; as a result, the study was conducted within one year only.

Additionally, five out of 25 datasets (leaf area with petiole excluded, leaf chlorophyll content, canopy length, canopy height, and canopy width) contained either only one native host plant, or one introduced host plant. Even though each dataset contained 117–2537 records, such a small sample size for plant origin group certainly affected the interpretation of the results of the comparisons between native and introduced host plants. Interestingly enough, the only differences between native and introduced plants we detected were found in four of these plant traits (in all but canopy height). In this regard, our conclusions of the lack of differences in plant trait measurements among native and introduced hosts (based on other 20 traits) are fully supported by a large sample size.

Another potential limitation is data availability in TRY database for specific plant species and/or specific plant traits. In this study, we used readily available data with short retrieval time, for plant species known as *L. delicatula* hosts in the U.S. only. Future studies might expand the biogeographical host plant range of *L. delicatula* and focus specifically on the comparisons between co-evolved host plants and absolutely novel hosts. Such targeted comparisons will provide more information to better understand the mechanisms underlying the potential ecological fitting.

Finally, determining the climatic factors affecting the behavior of *L. delicatula* was outside of the focus of this study, and it could be an interesting future research direction [47–50].

For example, Rahmathulla et al. [47] showed negative correlation between the infestation by the insect pest, *Diaphania pulverulentalis* Hampson (Lepidoptera: Pyralidae) in mulberry, and the increase of the temperature. It would be helpful to investigate a combined effect of climatic factors on the host plant choice by *L. delicatula* in the introduced range.

5. Conclusions

With continuing insect introductions to new areas, it is of great importance to address the questions, such as: Do the same mechanisms drive a host plant choice in various invasive insect species? What can we learn from the host plant usage of recent invaders? Using a case study of a recent invader in North America, the invasive spotted lanternfly, *L. delicatula*, we conducted a comprehensive analysis of 25 plant traits of native and introduced host plants and their environmental covariates. The results of our study may advance our knowledge on mechanisms of insect invasions, and particularly on ecological fitting and host plant utilization of *L. delicatula* in the introduced range. Future studies might focus on a deeper exploration of the phenomenon of ecological fitting which will allow us to obtain new information on host plant selection and utilization by the spotted lanternfly at each of its five developmental stages (1st–4th instars and adults).

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