Biological Control 108 (2017) 22–29

Contents lists available at ScienceDirect

Biological Control

journal homepage: www.elsevier.com/locate/ybcon

Phylogeny within the Anacardiaceae predicts host range of potential biological control agents of Brazilian peppertree

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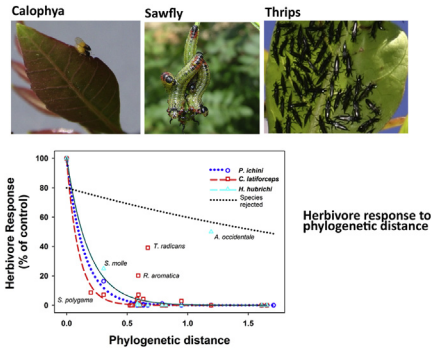
HIGHLIGHTS

- Phylogenetic signal of plant species may predict host range of biocontrol agents.
- We calculated phylogenetic distances between species with combined *ITS1* and *trnL-F*.
- Host range of recommended agents decreased steeply with phylogenetic distance.
- Phylogenetic distance had greater influence on recommended than rejected species.
- Phylogenetic distance can predict of host range and can assist in test plant lists.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 30 November 2016
Revised 23 January 2017
Accepted 31 January 2017
Available online 2 February 2017

Keywords:
Phylogenetic distance
Schinus terebinthifolia
Anacardiaceae
Molecular phylogeny
Host specificity
Diet breadth
Dietary specialization
Host specialists
Host range specialization

ABSTRACT

Predicting the host range of a biological control agent prior to release is one of the most important steps in the development of new agents. Knowing which species are most at risk of this non-target damage improves the predictability of these tests. To predict safety, the potential agent is exposed to a subset of the entire flora that represents valued native, agricultural and ornamental plant species. The list of plants includes those species that are the closest relatives to the target weed. To identify these species, molecular phylogenies can be useful tools that potentially identify the most vulnerable plant species. While conducting biological control research of the invasive weed Brazilian peppertree, *Schinus terebinthifolia*, we conducted nuclear *ITS1* and chloroplast *trnL-F* analysis of agricultural, commercial and native plants that are related to the weed. The results of this analysis support recent phylogenetic studies that have established two subfamily clades of the Anacardiaceae, the Anacardioideae and the Spondioideae. Moreover, our results indicate that species of concern from the genera *Cotinus*, *Lithrea, Pistacia*, *Rhus*, *Toxicodendron*, and *Schinus*, group together in the Anacardioideae, whereas the *Spondias* species, group in the Spondioideae subfamily clade. Further, the closest relatives to the target weed, those species most at risk of non-target damage by biological control agents include members of the *Schinus* and *Lithrea* genera. A review of the host testing results of 17 potential biological control candidates indicated that three of these species show a significant phylogenetic signal in their host range. These three species, the sawfly, *Heteroperreyia hubrichi*, the foliar gall inducing psyllid *Calophya latiforceps*, and the thrips *Pseudophilothrips ichini* have been recommended for release by USDA/APHIS/TAG. The remaining herbivore species do not sufficiently restrict their host range to the closest relatives but feed generally throughout the Anacardiaceae family. For members of this plant family our results indicate that a significant phylogenetic signal with host range was found for herbivore species identified for biological control of Brazilian peppertree. These results indicate that the testing of species with high phylogenetic

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http://dx.doi.org/10.1016/j.biocontrol.2017.01.017
1049-9644/Published by Elsevier Inc.

distances, such as safeguard species, could be minimized without loss of host range predictability of potential biological control agents.

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1. Introduction

Dietary specialization, where herbivores are restricted to plant species within a single taxon, is a common condition in tropical insects (Novotny and Basset, 2005; Novotny et al., 2002). This narrow host specificity is exploited in classical biological control by developing specialist herbivores to control invasive weeds. A major goal in the development of a biological control program is predicting the plant species that might serve as hosts to a new agent. Due to concerns for safety to valued native and economic plants, rigorous host specificity testing is conducted prior to consideration for release (McEvoy, 1996; Schaffner, 2001). As the testing of the entire flora of an invaded area is not possible, a subset is tested where the most vulnerable species are given priority. Determining this high priority list of species to include in the testing protocol is a critical step in this process.

Host range test plant lists have been traditionally compiled with the centrifugal phylogenetic approach which was based on morphological similarity among taxa (Wapshere, 1974). This morphological-based approach has been challenged and modified by advances in molecular phylogeny (Kelch and McClay, 2004). The species most closely related phylogenetically to the weed share similar traits and thus deserve close scrutiny as they are thought to be most at risk from the non-target effects of biological control (Agrawal, 2007; Futuyma and Agrawal, 2009; Pearse and Hipp, 2009). With this molecular approach, the testing of safeguard species, those that have important economic or environmental significance but are from distant phylogenetic relationships, become irrelevant as their analysis does not assist in predictions of host range (Briese, 2005; Briese and Walker, 2002). To prioritize testing of the close relatives, modern molecular phylogenies are needed that include the relevant species co-occurring in the weed's invaded range (Hinz et al., 2008).

For insect herbivores developed for biological control of weeds, molecular phylogenies assist in the prioritization and selection of plant species for testing (Briese, 1996; Briese and Walker, 2008). Knowing which valued plant species might be most vulnerable to non-target damage has obvious advantages when allocating resources during the host testing phase of a project. The strength of this phylogenetic signal can accurately predict host range of both plant pathogens and herbivores (Gilbert et al., 2015; Gilbert and Webb, 2007). To examine host range in terms of phylogeny, phylogenetic distances have been calculated among members of different potential host plants (Forister et al., 2015; Hinz et al., 2008; Novotny et al., 2006). Calculating the phylogenetic distance is a valuable method during pre-release screening, especially for plants below the family taxon, when evaluating the host range of potential agents for the biological control of weeds.

Brazilian peppertree, *Schinus terebinthifolia* Raddi, is a weed of agricultural and environmental concern of Florida and Hawaii, USA. This species is assigned to the Anacardiaceae family in the order Sapindales. Recent molecular analysis indicated that the Anacardiaceae family consists of two subfamilies, the Anacardioideae and the Spondioideae (Pell et al., 2011). Members of the Anacardioideae subfamily include the agricultural mango (*Mangifera indica* L.), pistachio (*Pistacia* spp.), and cashew (*Anacardium occidentale* L.) species (Mitchell and Mori, 1987; Pell et al., 2011). Additionally, this subfamily includes several native North American species, the smoketrees (*Cotinus* spp), poisonwood (*Metopium*), the sumacs (e.g., *Rhus* spp.) and poison ivy (*Toxicodendron* spp.). The only species in our range to be assigned to the Spondioideae subfamily include the species of the Caribbean mombin (*Spondias* spp.). Modern phylogenies have been compiled for several genera of the Anacardiaceae, including *Pistacia* (Al Saghir, 2010), *Rhus* (Yi et al., 2007), *Spondias* (Miller and Schaal, 2005), and *Toxicodendron* (Nie et al., 2009). However, the relationship among the genera of the family, e.g., which are most closely aligned with *Schinus*, remains uncertain (Pell, 2004). Knowledge of the relative phylogenetic proximity of these genera to *Schinus* could assist in the prioritization of test plants during the pre-release testing process.

The host range of several potential biological control agents of *S. terebinthifolia* examined during the past 50 years was recently summarized (Wheeler et al., 2016). The results of host range testing indicated that the majority of potential agents collected on *S. terebinthifolia* in its native range, showed relatively broad specificity within the Anacardiaceae family when examined in quarantine (Wheeler et al., 2016). However, three species, the defoliating sawfly, *Heteroperreyia hubrichi* Malaise (Hymenoptera: Pergidae), the foliar gall inducing psyllid *Calophya latiforceps* Burckhardt (Hemiptera: Calophyidae) and the thrips *Pseudophilothrips ichini* (Hood) (Thysanoptera: Phlaeothripidae) have demonstrated narrow host ranges and have been recommended for release by USDA/APHIS/TAG (Diaz et al., 2015; Medal et al., 1999; USDA/APHIS, 2016; Wheeler et al., 2017). Here, we examine the phylogenetic distance of members of the Anacardiaceae in the native and invaded ranges of *S. terebinthifolia* generated in this study and relate these retrospectively to host range determinations of previously studied potential agents.

2. Materials and methods

2.1. Source populations of plant material

Plant species were obtained from plant nurseries or wild populations (Supplementary Table 1). For species not available commercially, seeds were collected from wild populations in Florida, Hawaii, and Texas, USA. The South American species (e.g., *Lithrea* and *Schinus* spp.) were collected by the authors in the Brazilian states of Minas Gerais and Rio Grande do Sul. The Brazilian peppertree control plants were grown from locally collected seeds. In all cases, fresh leaf tips (~100 mg) were collected and preserved on silica gel until analysis. Two outgroup species were included, *Dodonaea viscosa* Jacquin and *D. elaeagnoides* Rudolphi ex Ledeb. & Alderst., (Sapindaceae) as a small amount of herbivory was found during previous testing of *D. viscosa* (Wheeler et al., 2017) (Supplementary Table 1).

2.2. Molecular extraction and analysis

DNA was extracted using the DNeasy Plant Mini kit (Qiagen Inc., Valencia, CA, USA). The nuclear *ITS1* sequences (*ITS1*, *5.8S*, and partial *ITS2* sequences) were amplified and sequenced using the *ITS*-A, *ITS*-B, *ITS*-C and *ITS*-D primers) (Blattner, 1999). The PCR reaction contained 10 mM Tris-HCl (pH 9.0), 50 mM KCl, 1.5 mM $MgCl_2$, 0.1% Triton X-100, 10% DMSO, 0.2 mM dNTPs, 0.5 μM each primer, and 0.04 U/μl EconoTaq polymerase (Lucigen Corp., Middleton, WI, USA). The *trnL-F* (chloroplast *trnL intron* and *trnL-F* intergenic spacer) were amplified and sequenced using the *trnL*-C, *trnL*-D,

trnL-E and *trnL*-F primers of Taberlet et al. (1991). Plastid reaction mixtures contained 10 mM Tris–HCl (pH 9.0), 50 mM KCl, 1.5 mM $MgCl_2$, 0.1% Triton X-100, 0.5 mM Betaine, 0.001% BSA, 0.2 mM dNTPs, 0.5 μM each primer, and 0.06 U/μl EconoTaq polymerase. The amplifications were carried out on a PTC-100 thermocycler (MJ Research, Inc. Waltham, MA, USA). PCR annealing temperatures were 56 °C for *trnL-F* and 58 °C for *ITS1*. PCR products were visualized using 1.5% agarose gels stained with ethidium bromide then were cleaned using DNA Clean & Concentrator (Zymo Research, Orange, CA, USA). Cycle sequencing was performed by Eurofins MWG Operon (Louisville, KY, USA) using BigDye terminator technology (Life Technologies, Carlsbad, CA, USA).

Trace files were compiled and viewed using SEQUENCER 4.1.4 (Gene Codes Corporation, Ann Arbor, MI, USA). Reference sequences were downloaded from the NCBI "Taxonomy" window or using BLASTn to find similar sequences. Sequences were aligned at one of the several MCoffee Web servers [http://tcoffee.crg.cat/]. MCoffee (Moretti et al., 2007; Wallace et al., 2006) uses an algorithm which aligns DNA by combining the output of multiple popular aligners (e.g., Clustal, Mafft, Probcons, Muscle) and produced a 761 b.p. alignment for the *ITS1* sequences and an 1181 b.p. alignment for *trnL-F*. The *ITS1* sequence contained gap coding (−) in 13.6% of individual sequence positions while *trnL-F* contained them in 22.9% of positions. Following MCoffee, a Transitive Consistency Score (TCS) was generated at the same server. TCS (Chang et al., 2014) is an alignment evaluation score which identifies the alignment positions most likely to be correct (homologous) and therefore also the most informative for estimating phylogenetic trees. This alignment allows systematic incorporation of some informative data from the regions of an alignment with gaps which otherwise might be excluded by "complete deletion". TCS produced a 643 bp alignment for the *ITS1* sequences and a 924 bp alignment for *trnL-F* with 0.8% and 3.8% individual position gaps respectively. Wiens and Morrill (2011) indicate that, in general, including characters with missing data either increases or has minimal effect on the mean accuracy of Bayesian phylogenetics. Similarly, Dwivedi and Gadagkar (2009) show that, when the indel events (without alignment error) represent ⩽20 percent of the sequence length, most methods, but especially Maximum Likelihood and Bayesian methods perform well. As gaps increase, Bayesian methods outperform other methods when the gaps are treated as missing data. Clearly, following TCS, the remaining sites contain low levels of gaps and should provide information with minimal phylogenetic distortion for Bayesian analysis.

To identify the phylogenetic relatedness to the target weed, Brazilian peppertree, a single distance metric was sought to aid the analysis. The search for an optimum model of nucleotide substitution led us to Kakusan4 (Tanabe, 2011), a program which facilitates model selection for multigene phylogenetic analysis by allowing for different nucleotide substitution models at different loci. The data was subdivided into five components: *ITS1* (251 b.p. alignment), 5.8S rRNA (162 b.p.), *ITS2* (213 b.p.), *TrnL* intron (450 b.p.), *TrnL-TrnF* intergenic spacer (370.b.p.), and then run through Kakusan4. A $\chi 2$ test showed nucleotide homogeneity among all taxa. After deciding to use MrBayes for analysis, the BIC4 criterion was used to compare Nonpartitioned, Proportional, Partitioned_Equal_Mean_Rate, and Separate models. The Proportional model, which assumes that branch lengths are proportional among arbitrarily specified partitions, proved optimal. Model configuration files for MrBayes (Ronquist and Huelsenbeck, 2003) generated in Kakusan4 were: 5.8SrRNA = K80_GammaInvariant, *ITS1* = GTR Gamma, *ITS2* = HKY85 Gamma, *TrnL* intron = GTR Gamma, *TrnL-TrnF* spacer = GTR Gamma. Bayesian analysis utilized MrBayes5D, an extended version of MrBayes [https://www.fifthdimension.jp/products/mrbayes5d/]. Because of model complexity and the relatively short sequence lengths, long burnin (1,000,000) and ngen (10,000,000) were chosen (also nchains = 6) to produce higher Effective Sample Sizes (ESS). ESS values were above 200 for all parameters, including model parameters.

2.3. Retrospective analysis of host range data

To examine the relationship between phylogenetic distance and host range, we retrospectively analyzed testing results from previous studies. To date, at least 17 insect herbivores have been tested to determine their suitability for biological control of *S. terebinthifolia* (Table 1). These include species of Hemiptera, Thysanoptera, Coleoptera, Lepidoptera, and Hymenoptera. Of these species, three have been recommended for release as biological control agents of *S. terebinthifolia* due to their narrow host range (Wheeler et al., 2016). Research showed that the sawfly, *H. hubrichi* had a narrow host range but was not released possibly due to concern for its potential mammalian toxicity (Dittrich et al., 2004; Hight et al., 2003; Medal et al., 1999). The leaf gall former, *C. latiforceps* was considered highly specific, only surviving on the target weed *S. terebinthifolia* (Diaz et al., 2015). The thrips, *P. ichini*, completed development and produced offspring only on two weedy *Schinus* species, *S. terebinthifolia* and *S. molle* L. (Wheeler et al., 2017). Other species released for biological control of *S. terebinthifolia* in Hawaii,

Table 1
Herbivore species that were evaluated for the biological control of *Schinus terebinthifolia*.

Genus	Species	Order	Family	Source
Calophya	*latiforceps*	Hemiptera	Calophyidae	Diaz et al. (2015)
Pseudophilothrips	*ichini*	Thysanoptera	Phlaeothripidae	Wheeler et al. (2017)
Apocnemidophorus	*pipitzi*	Coleoptera	Curculionidae	TAG decision[1]
Omolabus	*piceus*	Coleoptera	Curculionidae	Wheeler and Schaffner (2013)
Plectrophoroides	*lutra*	Coleoptera	Curculionidae	Wheeler et al. (2011)
Paectes	*longiformis*	Lepidoptera	Euteliidae	Manrique et al. (2014)
Hymenomima	*memor*	Lepidoptera	Geometridae	Broggi et al. (2016)
Oospila	*pallidaria*	Lepidoptera	Geometridae	Chawner and Wheeler (unpublished)
Oxydia	*vesulia*	Lepidoptera	Geometridae	Fung and Wheeler (2016)
Prochoerodes	*onustaria*	Lepidoptera	Geometridae	Jones and Wheeler (unpublished)
Eucosmophora	*schinusivora*	Lepidoptera	Gracillariidae	Rendon et al. (2012)
Leurocephala	*schinusae*	Lepidoptera	Gracillariidae	Mc Kay et al. (2012)
Tolype	*medialis*	Lepidoptera	Lasiocampidae	Wheeler (unpublished)
Nystalea	*ebalea*	Lepidoptera	Notodontidae	Wheeler et al. (2014)
Tecmessa	*elegans*	Lepidoptera	Notodontidae	Oleiro et al. (2011)
Episimus	*unguiculus*	Lepidoptera	Tortricidae	TAG decision[1]
Heteroperreyia	*hubrichi*	Hymenoptera	Pergidae	Hight et al. (2003) and Medal et al. (1999)

[1] Technical Advisory Group web site (http://www.aphis.usda.gov/).

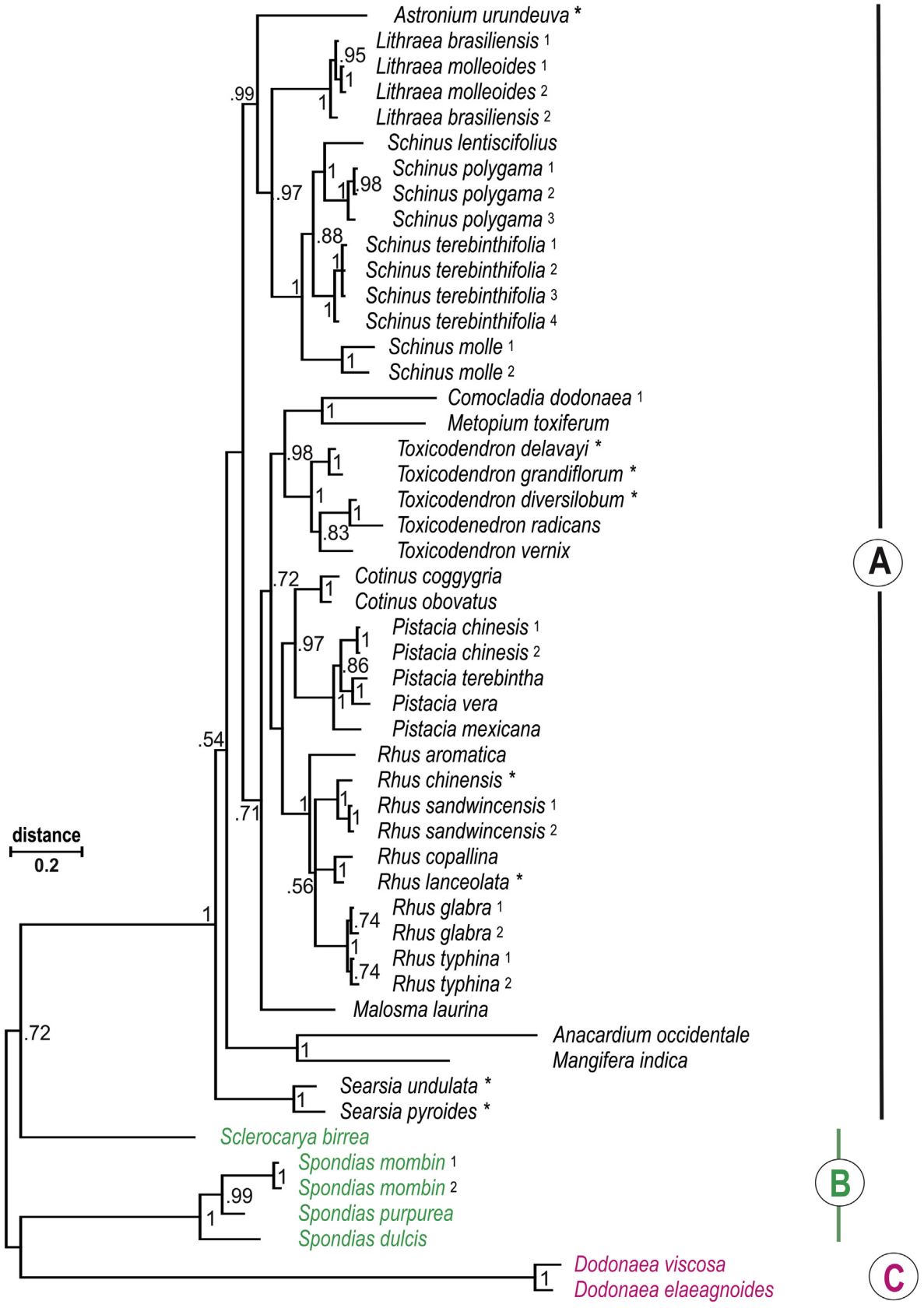

Fig. 1. Majority rule tree from Bayesian analysis (MrBayes) of combined nuclear and chloroplast sequence data from species of the Anacardiaceae and Sapindaceae. Branch lengths are proportional to Bayesian distances. Group A consists of genera of the subfamily clade Anacardioideae, B the subfamily Spondioideae and C the (outgroup) family Sapindaceae. The numbers at each node represent posterior probabilities. Species were collected by the authors unless names are followed by an asterisk. In these species, nuclear or chloroplast sequences were obtained from GenBank (www.nbci.nlm.nih.gov). Names followed by a number represent different accessions.

Crasimorpha infuscata Hodges (Lepidoptera: Gelechiidae) and *Lithraeus atronotatus* (Pic) (Coleoptera: Chrysomelidae) were not included here due the shortage of published host range data (Davis, 1961; Davis and Krauss, 1962; Krauss, 1962, 1963). A third species released in Hawaii, *Episimus unguiculus* Clarke (Lepidoptera: Tortricidae) was later tested and these host range data are included in the analysis here.

To examine the relationship between host range and phylogenetic distance, previous published and unpublished host testing results were compiled. These data were collected while determining the host range of potential biological control agents of *S. terebinthifolia* in quarantine. To standardize responses of each herbivore species we divided the results when fed a non-target (e.g., percent survival, growth rates, pupal weight) by that of those fed the target weed. We used both physiological (e.g., survival) and behavioral (e.g., oviposition) relative response values, each relative to the respective *S. terebinthifolia* – fed controls. We fit these results to an exponential decay equation $y = b_o * \exp(-b_1\ x)$ using PROC NLIN in SAS where y was the relative response (% of control), b_o was the y-intercept, b_1 was the slope coefficient and x was $\log_{10}$(distance + 1). To compare the relationship for species recommended for release (*H. hubrichi, C. latiforceps, P. ichini*) with those rejected due to broad host range, and to compare physiological and behavioral responses, we compared confidence limits (95%) for the non-linear regression coefficients and graphically visualized their relationships.

3. Results

3.1. Results of molecular analysis

The results of analysis of the combined nuclear and chlorophyll DNA data indicated that two subfamily clades were discernable and separately group species to the Anacardioideae and the Spondioideae (Fig. 1). Note that species within each genus *Cotinus*, *Lithrea Pistacia*, *Rhus*, *Schinus*, *Searsia*, *Spondias* and *Toxicodendron* all group together in their respective assigned genera. As expected, this analysis indicated that the species most closely related to *S. terebinthifolia* include members of the *Schinus* and *Lithrea* genera. Moreover, species least related phylogenetically to the weed are members of the subfamily Spondioideae (e.g., *Spondias* spp.) and the outgroup family Sapindaceae (Fig. 1). Calculated phylogenetic distances between taxa and the weed, *S. terebinthifolia* indicated that the species of the genus *Schinus* had an average range of 0.219–0.306 (Table 2). These results also demonstrated that the closest relatives of *Schinus* are assigned to the genera, *Cotinus, Lithrea, Pistacia, Rhus,* and *Toxicodendron* with average ranges 0.381 to 0.633. Within the family, the greatest distance was found between *S. terebinthifolia* and *A. occidentale, M. indica* (0.948–1.193) and the species of *Spondias* (1.61–1.708) (Table 2). Phylogenetic distances for the outgroup species of *Dodonaea* averaged from 2.474 to 2.496 (Table 2).

Table 2
Estimates of phylogenetic distances between sequences of *Schinus terebinthifolia* and each listed species. The average (SE) Bayesian phylogenetic distance per site compared with four *S. terebinthifolia* sequences are shown. Phylogenetic distance values ranged from 0.0009 to 3.038.

Family	Subfamily	Genus	Species	Mean	SE
Anacardiaceae	Anacardioideae				
		Schinus	*lentiscifolia*	0.219	0.0048
			molle	0.306	0.0033
			polygama	0.200	0.0033
		Lithrea	*brasiliensis*	0.381	0.0033
			molleoides	0.401	0.0035
		Cotinus	*coggygria*	0.546	0.0048
			obovatus	0.523	0.0048
		Astronium	*urundeuva*	0.543	0.0049
		Malosma	*laurina*	0.535	0.0048
		Rhus	*aromatica*	0.591	0.0047
			chinensis	0.582	0.0049
			copallina	0.582	0.0049
			glabra	0.593	0.0034
			lanceolata	0.558	0.0048
			sandwicensis	0.584	0.0034
			typhina	0.594	0.0035
		Toxicodendron	*delavayi*	0.538	0.0049
			diversilobum	0.596	0.0048
			grandiflorum	0.557	0.0048
			radicans	0.670	0.0048
			vernix	0.586	0.0049
		Pistacia	*chinensis*	0.604	0.0034
			terebintha	0.625	0.0048
			mexicana	0.607	0.0048
			vera	0.633	0.0049
		Searsia	*undulata*	0.636	0.0047
		Searsia	*pyroides*	0.659	0.0049
		Metopium	*toxiferum*	0.788	0.0049
		Comocladia	*dodonaea*	0.820	0.0047
		Mangifera	*indica*	0.948	0.0047
		Anacardium	*occidentale*	1.193	0.0047
	Spondioideae				
		Sclerocarya	*birrea*	1.389	0.0047
		Spondias	*dulcis*	1.653	0.0048
			mombin	1.708	0.0033
			purpurea	1.610	0.0047
Sapindaceae					
		Dodonaea	*elaeagnoides*	2.474	0.0047
			viscosa	2.496	0.0048

3.2. Analysis of retrospective host range results

The relative response of biological control agents recommended for field release initially declined steeply with slight increases in phylogenetic distance from the target weed, *S. terebinthifolia* (Fig. 2). In contrast to these results, those species that had unacceptable host ranges and were rejected for biological control had gradually decreasing responses to increased phylogenetic distance (Fig. 2). This steep decline in the approved agents was a function of the great reduction in relative performance in insects fed plants with greater phylogenetic distance. The slope coefficients for species recommended and rejected for field release differed significantly as indicated by the lack of overlap between their confidence intervals (95%) (Table 3). The shape and steepness of the phylogenetic signal of the three recommended agent responses were similar. Similarly, the coefficients for behavioral data were similar to physiological results (Table 3). Moreover, the behavioral results showed herbivore responses deviated slightly from the prediction. For example, the leaf gall former *C. latiforceps* only survived (physiological data) on *S. terebinthifolia*, however a few eggs were laid (behavioral data) on the non-target species such as *S. molle, Rhus aromatica* Aiton, and *Toxicodendron radicans* (L.) Kuntze (Fig. 2) (Diaz et al., 2015). Physiological data varied less than behavioral data for all species. For example, although relatively specific, the sawfly, *H. hubrichi*, fed and oviposited on several species like *Rhus copallina* L. and *Toxicodendron vernix* (L.) Kuntze but in quarantine host range testing they completed development only on the target weed, *Rhus sandwicensis* A. Gray and *A. occidentale* (Hight et al., 2003; Medal et al., 1999).

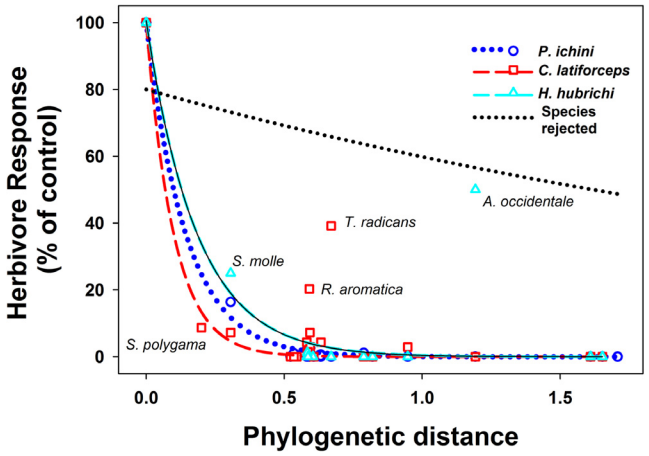

Fig. 2. Response (% of control) of different herbivore species when fed plants with a range of phylogenetic distances from the target weed *Schinus terebinthifolia.* The relative responses for recommended biological control agents (*C. latiforceps, H. hubrichi, P. ichini*) dropped precipitously when fed more distantly related plant species. Herbivores that were rejected for biological control because of broad host ranges, showed a gradual decrease in herbivore response with greater phylogenetic distance. Regression coefficients and confidence intervals are included (Table 3).

4. Discussion

Risks of damage to non-target species by biological control agents may include several factors among them, phylogenetic proximity to the target weed. One of the first steps to minimize this risk is the selection of target weeds for biological control that have few or no native or economically important relatives (Pemberton, 1996). Herbivores typically feed and develop on plant species that are closely related phylogenetically (Jaenike, 1990; Pearse and Altermatt, 2013) and so, risk of non-target damage is greatest toward species that are closely related to the target weed (Pemberton, 2000; Suckling and Sforza, 2014). However, when working on weeds from families with many genera and species in the invaded range, the testing protocol must prioritize those plants that are most vulnerable to non-target damage. This prioritization is facilitated by estimation of the phylogenetic distance to the target weed.

The results of analysis of the combined nuclear *ITS* and chloroplast *trnL-F* DNA data confirm recent phylogenetic studies that have established two subfamily clades of the Anacardiaceae (Pell et al., 2011). Our results group North and South American species into the Anacardioideae and the Spondioideae. Moreover, our results indicate that species of the genera *Cotinus*, *Lithrea Pistacia*, *Rhus*, *Toxicodendron*, and *Schinus* are distinctly separated by phylogenetic distance from species of *Spondias* (Pell et al., 2011). The results indicate that the species most closely related to the target, and so, most at risk of non-target damage by biological control agents include members of the *Schinus* and *Lithrea* genera. With the exception of the ornamental *S. molle* that was imported from South America, the species of these genera do not occur in North America. *Schinus molle* occurs in California, USA where it has also naturalized in wild habitats and is considered invasive (Howard and Minnich, 1989; Nilsen and Muller, 1980).

A retrospective analysis of previous host testing results of potential biological control agents of *S. terebinthifolia* indicate a strong phylogenetic signal that influenced the host range of insects recommended for field release. In previous host testing of the sawfly *H. hubrichi,* the psyllid *C. latiforceps* and the thrips *P. ichini* were shown to have narrow host ranges. The results presented here indicate that there was a strong phylogenetic signal predicting host ranges restricted to the target weed and its closest relatives. Where responses occurred in these specialists, they were directed at the non-target species most closely related to the weed, *S. terebinthifolia.* The remaining herbivore species of potential agents that were not petitioned or not recommended for release had host ranges that were too broad for biological control. The phylogenetic signal of these rejected species was significantly different from the approved biological control agents.

Table 3
Non-linear regression for herbivore relative responses that were either rejected or approved for biological control of *Schinus terebinthifolia*.

Herbivore species	B_o	B_1	F	P	B_0		B_1	
					LCI 95%	UCI 95%	LCI 95%	UCI 95%
Behavioral data								
Rejected	81.2	1.2	48.29	<0.0001	53.2	109.3	0.5	1.8
Approved	99.6	10	46.95	<0.0001	77.9	121.4	2.9	17.16
Physiological data								
Rejected	84.6	0.2	119.48	<0.0001	63.3	106	−0.1	0.6
Approved	99.8	10.3	283.79	<0.0001	91.4	108.2	6.4	14.3

Non-linear coefficients were obtained with the model: Response (% of control) = $bo * \exp(-b1\,x)$; b_o was the y-intercept, b_1 was the slope coefficient and x was log10(distance + 1).

Other factors, such as secondary plant chemistry, may influence host range (Agrawal, 2007; Gershenzon and Dudareva, 2007). Possibly the secondary chemistry of the taxa of Anacardiaceae accurately predict the host range of the apparent *Schinus* specialists (Becerra, 1997; Wahlberg, 2001; Wheeler and Schaffner, 2013). In one example, the host range of *Nystalea ebalea* Stoll (Lepidoptera: Notodontidae) was explained by the urushiol secondary chemistry of the members of the Anacardiaceae tested (Wheeler et al., 2014). However, neither terpenoids nor urushiol chemistry seemed to predict host range for the remaining potential agents tested. The results reported here show that, for biological control of *S. terebinthifolia*, phylogenetic distance accurately predicted host range in the potential agents tested. These results question the allocation of resources to test unrelated plant species with high phylogenetic distances. Although, the testing of safeguard species that are unrelated to the target weed is still required in the U.S. A. (Littlefield and Buckingham, 2004; USDA/APHIS, 2016), possibly results similar to those presented here on additional weed-agent systems will facilitate the modification of these requirements.

Acknowledgments

We thank K. Dyer for technical assistance, P. Conant (retired Hawaii Dept. of Agriculture, Hilo, HI), C. Kallsen (UC, Davis, CA), L. Miller (S & J Ranch, Pinedale, CA), T. Pernas (formerly National Park Service, Homestead, FL), J. Skiles (Langtry, TX), A. Vacek (USDA/ARS, Weslaco, TX) and R. Weaver (retired botanist DPI, Gainesville, FL) provided seeds of hard to find plant species. William Overholt (retired University of Florida, Ft Pierce FL) provided useful comments on a previous draft of this manuscript. This project was partially funded by the Florida Fish and Wildlife Conservation Commission (#08250, TA:088), the South Florida Water Management District (#4600001427), the USDA, ARS.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocontrol.2017.01.017.

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