

Exotic species and the structure of a plant-galling network

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Abstract

Gall-inducing insects are highly specialized herbivores and is expected that networks composed by gall-inducing insects and their host plants are also very specialized. However, presence of exotic species might reduce the interaction number for native species, which would lead to changes in the specialization of plant-galling networks. In this study, we use network metrics to describe, for the first time, the structure of a network of gall-inducing insects associated to ornamental host plants. We found that the plant-galling network has a low-connected structure and is more modular than expected by chance. Native insect herbivores were significantly more frequent on native host plant species, while exotic herbivores occurred mostly on exotic host plant species. On the other hand, the number of interactions between insect herbivores and native or exotic plant species did not vary. Our findings show that plant-galling networks are very specialized and structured independently of exotic species presence.

Keywords alien hosts; exotic herbivores; herbivory; network ecology.

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1 Introduction

Gall-inducing insects are known as the most specialized insect herbivores of nature (Shorthouse et al., 2005). These are the only arthropod herbivores (together with mites) able to modify the host plant structures at histological and cellular level to induce galls (Stone and Schönrogge, 2003). To induce galls, the insects must deal with the mechanical and chemical defenses of plants, besides being able to control the physiological apparatus of the host (Shorthouse et al., 2005). This high degree of intimacy between galling and plant leads to phylogenetic constraints in the gall induction (Stone and Schönrogge, 2003). Because of this, even the most generalist galling insects are only able to induce galls on host plant species with some degree of phylogenetic relatedness (Price, 2005).

The structure of interactions in plant-galling networks has been largely neglected until very recently in the ecological literature (Barbour et al., 2016). Due to the high specialization degree of insect galls, it is expected that networks composed by gall-inducing insects and their host plants establish very specialized, and often

species-specific, interactions. For this reason, is expected for plant-galling networks low connectivity and high compartmentalization in these interactions. The expected high degree of specialization of plant-galling networks, should affect the dynamics of these networks, because each plant species extinction may represent the extinction of a galling species.

A very interesting factor about the structure of plant-galling networks is the occurrence of exotic plant species. For example, Kollár (2011) recorded a network composed by galling insects that feed on ornamental trees and shrubs in the city of Nitra, Slovakia. Since it is located in an urban garden, the flora of this network is composed both by native species from the region as well as exotic plant species. Due their allochthonous origin, exotic plant species have not shared evolutionary history with the native species of galling insects. Many of the species able to induce galls in the exotic plants are also non-indigenous species that were introduced from the same place of origin as these plants (Kollár, 2011). Because of the different evolutionary histories, however, it is expected that native and exotic species both of plants and insects have distinctive ecological interactions in the network.

In the present work, we describe the structure of a network composed by native and exotic gall-inducing insects and ornamental host plants in the city of Nitra, Slovakia. To explore the network structure we calculate connectance, and also modularity and robustness of the interactions in contrast with null models. We also evaluated the structure of a network subset composed exclusively by native species of plants and insects. Additionally, we compare if native and exotic species of plants and insects in the network have differences in their number of interactions. As consequence of the phylogenetic restrictions of plant-galling interactions, we expected that exotic plant and insect species overall interact with a lower number of species than native ones. Finally, we tested whether exotic plant species have more interactions with exotic galling species than with native herbivores.

2 Material and Methods

2.1 Study area

The study was performed from 2004 to 2008 in the Nitra city park, Nitra, Slovakia (48° 19' 7" N, 18° 4' 55" E, 144 m a.s.l.). Nitra city is situated in southwestern Slovakia and its climate is characterized as semi-arid and humid (Kollár, 2011). The average annual total precipitation is about 600 mm and the average annual temperature is about 9.5 °C. The park, which covers 20 ha, has three parts: Sihot', New Park, and Connecting Park. Samples were collected from all parts. The park is bordered by Nitra River and comprises woody plants in various age stages.

2.2 Sampling of plant-galling interactions

Gall-inducing insects were examined across active search on all native and introduced host woody plants in the park. All galls encountered were recorded and placed individually in labeled plastic bags for transportation to the laboratory. Fragments of each host plant were collected for botanical identification. Insect species were determined in field whenever possible according to the gall morphological characteristics. Some galls were collected to be reared in the laboratory for better determination of the gall-inducers. In these cases the publications of Csóka (1997), Schnaider (1976), Skuhrový and Skuhrová (1998), Blackman and Eastop (1994), Redfern and Shirley (2002) were used for determination. These studies were also used to determine if the insect species status were native or exotic.

We use the Fauna Europaea database (www.faunaeur.org) for taxonomic classification and correct terminology of gall-inducing insects. Plant species were identified using flora catalogs. Host plant status was determined from a checklist of alien plants to Slovakia (Medvecká et al., 2012). We checked plant species nomenclature and synonymy using The Plant List database (www.theplantlist.org). After the species

determination, we build the network from the interactions between gall-inducing insect species and their host plant species.

2.3 Data analyses

Network structure analyses were done using the network descriptors connectance, modularity, and robustness. In order to compare changes in network structure caused by the introduction of exotic species, all three indices were computed for the entire network and for a network comprising only native insects and plants. The connectance (C) was calculated as the number of realized interactions (L) divided by number of possible interactions ($S_1 * S_2$, where S_1 is the number of plant species and S_2 is the number of insect species) (Dormann et al., 2009; Zhang, 2011, 2012). Connectance is an inverse measure of overall interaction specialization because, in networks with higher connectance, species tend to have more connections (i.e., to be less specialized); thus, the higher the connectance, the lower the specialization of plant-herbivore networks (Araújo et al., 2015).

In addition to the connectance, we also used modularity to describe the structure of the plant-galling network. The modularity is characterized by presence of species subsets densely connected within the network, also called of modules or compartments (Dormann, 2011; Dormann et al., 2009), indicating the degree of specialization of the interaction arrangement within the network. We computed the bipartite modularity index Q (Barber, 2007) using the DIRTLPAwb+ algorithm to detect network modules (Beckett, 2016). In order to compare modularity values between different networks, we normalized the obtained value by comparing it to the maximum possible value given the network size and marginal totals (Beckett, 2016). The normalized modularity index reaches one when the network has the maximum possible modularity and approaches 0 as the modularity decreases. We then compared the observed normalized value with normalized values computed for 500 null networks generated using the quasiswap algorithm (Dormann, 2009).

Robustness is a measure of the resistance degree of the network to coextinctions (Dormann et al., 2009; Zhang, 2016). To characterize network robustness we used the exponent of the curve generated by the proportion of remaining galling species in function of the proportion of primary extinctions of plant species (Dormann et al., 2009). Robustness values also were compared to null values obtained from the same 500 null networks mentioned above. We performed all network analyses using adaptations of function from the R-package Bipartite (Dormann et al., 2008) and code provided in Beckett (2016).

We also compared if native and exotic species in the network have different average degree (AvD) than is expected from the overall mean number of plant and insect interactions. In this sense we differentiated the AvD between host plants (natives vs. exotics) and galling insects (natives vs. exotics) using t-tests. Additionally we tested whether native insect species interacted more with native plant species than with exotics by using a chi-squared test.

3 Results

The plant-herbivore network contained 90 gall-inducing species belonging to five orders and nine families of insects (Table 1). The orders with most species were Hymenoptera with 32 and Hemiptera with 31 species. The families Cynipidae (Hymenoptera), Aphididae (Hemiptera) and Cecidomyiidae (Diptera) were the most diverse with 27, 25 and 24 species, respectively. Most galling insect species were natives (81) and only nine species were of exotic origin. Seventy-three galling species were monophagous (induced galls on only one plant species) and 16 were oligophagous (10 induced galls on two host species and six on three hosts). Only the species *Rhyacionia buoliana* (Tortricidae: Lepidoptera) can be considered polyphagous, since it induced galls on five host species.

Gall-inducing insects were found on 54 species and 32 genera of host plants. The higher numbers of

gall-inducing species were recorded on the host genera *Quercus* (28), *Populus* (8) and *Salix* (7). The native plant *Quercus robur* was the species that hosted the highest diversity with 27 galling species. Seventy-nine species of gall-inducing insects occurred on native plant species and 20 species on exotic host plants. Among all the species, only nine gall-inducing species occurred on both exotic and native host plants. Native insect herbivores were significantly more frequently observed on native host plant species, while exotic herbivores occurred mostly on exotic host plant species ($\chi^2 = 20.956$; p-value < 0.001).

Table 1 Checklist of host plants and gall-inducing insects recorded in Nitra City Park (Nitra, SW, Slovakia). Species marked with * are of exotic origin. Modification of Kollár (2011).

Host plants			Gall-inducing insects		
Family	Species	Order	Family	Species	Occurrence
Adoxaceae	<i>Viburnum lantana</i>	Hemiptera	Aphididae	<i>Aphis viburni</i>	Leaf
Adoxaceae	<i>Viburnum opulus</i>	Hemiptera	Aphididae	<i>Aphis viburni</i>	Leaf
Adoxaceae	<i>Viburnum rhytidophyllum*</i>	Hemiptera	Aphididae	<i>Aphis viburni</i>	Leaf
Betulaceae	<i>Betula pendula</i>	Diptera	Cecidomyiidae	<i>Anisostephus betulinus</i>	Leaf
Betulaceae	<i>Carpinus betulus</i>	Diptera	Cecidomyiidae	<i>Zygiobia carpini</i>	Leaf
Buxaceae	<i>Buxus sempervirens*</i>	Diptera	Cecidomyiidae	<i>Monarthropalpus flavus*</i>	Leaf
		Hemiptera	Psyllidae	<i>Psylla buxi*</i>	Leaf
Caprifoliaceae	<i>Lonicera ligustrina*</i>	Hemiptera	Aphididae	<i>Hyadaphis tataricae*</i>	Leaf
Caprifoliaceae	<i>Lonicera xylosteum</i>	Hemiptera	Aphididae	<i>Hyadaphis tataricae*</i>	Leaf
		Hemiptera	Aphididae	<i>Rhopalomyzus loniceriae</i>	Leaf
Celastraceae	<i>Euonymus europaeus</i>	Hemiptera	Aphididae	<i>Aphis fabae</i>	Leaf
Cornaceae	<i>Cornus sanguinea</i>	Diptera	Cecidomyiidae	<i>Craneiobia corni</i>	Leaf
Cupressaceae	<i>Juniperus communis</i>	Diptera	Cecidomyiidae	<i>Oligotrophus juniperinus</i>	Needle
Fabaceae	<i>Gleditsia triacanthos*</i>	Diptera	Cecidomyiidae	<i>Dasineura gleditchiae*</i>	Leaf
Fabaceae	<i>Robinia pseudoacacia*</i>	Diptera	Cecidomyiidae	<i>Obolodiplosis robiniae*</i>	Leaf
		Hemiptera	Aphididae	<i>Aphis craccivora*</i>	Leaf
		Hemiptera	Aphididae	<i>Aphis fabae</i>	Leaf
Fagaceae	<i>Fagus sylvatica</i>	Diptera	Cecidomyiidae	<i>Mikiola fagi</i>	Leaf
Fagaceae	<i>Quercus cerris</i>	Hymenoptera	Cynipidae	<i>Andricus cydoniae</i>	Leaf
Fagaceae	<i>Quercus hispanica</i>	Hymenoptera	Cynipidae	<i>Andricus anthracina</i>	Leaf
Fagaceae	<i>Quercus robur</i>	Diptera	Cecidomyiidae	<i>Macrodiplosis pustularis</i>	Leaf
		Diptera	Cecidomyiidae	<i>Macrodiplosis roboris</i>	Leaf
		Hymenoptera	Cynipidae	<i>Andricus anthracina</i>	Leaf
		Hymenoptera	Cynipidae	<i>Andricus conglomeratus</i>	Bud
		Hymenoptera	Cynipidae	<i>Andricus coriarius</i>	Bud
		Hymenoptera	Cynipidae	<i>Andricus curator</i>	Leaf/Bud
		Hymenoptera	Cynipidae	<i>Andricus fecundator</i>	Bud
		Hymenoptera	Cynipidae	<i>Andricus glutinosus</i>	Bud
		Hymenoptera	Cynipidae	<i>Andricus grossulariae</i>	Flower
		Hymenoptera	Cynipidae	<i>Andricus hungaricus</i>	Bud

		Hymenoptera	Cynipidae	<i>Andricus inflator</i>	Bud
		Hymenoptera	Cynipidae	<i>Andricus kollari</i>	Bud
		Hymenoptera	Cynipidae	<i>Andricus lucidus</i>	Fruit
		Hymenoptera	Cynipidae	<i>Andricus mayri</i>	Fruit
		Hymenoptera	Cynipidae	<i>Andricus solitarius</i>	Bud
		Hymenoptera	Cynipidae	<i>Andricus testaceipes</i>	Shoot
		Hymenoptera	Cynipidae	<i>Biorrhiza pallida</i>	Root/Bud
		Hymenoptera	Cynipidae	<i>Cynips caputmedusae</i>	Fruit
		Hymenoptera	Cynipidae	<i>Cynips disticha</i>	Leaf
		Hymenoptera	Cynipidae	<i>Cynips divisa</i>	Leaf
		Hymenoptera	Cynipidae	<i>Cynips longiventris</i>	Leaf
		Hymenoptera	Cynipidae	<i>Cynips quercuscalicis</i>	Fruit
		Hymenoptera	Cynipidae	<i>Cynips quercusfolii</i>	Leaf
		Hymenoptera	Cynipidae	<i>Neuroterus laevisculus</i>	Leaf
		Hymenoptera	Cynipidae	<i>Neuroterus numismalis</i>	Leaf
		Hymenoptera	Cynipidae	<i>Neuroterus quercus-baccarum</i>	Leaf/Flower
		Hymenoptera	Cynipidae	<i>Trigonaspis megaptera</i>	Bud/Shoot
Grossulariaceae	<i>Ribes aureum*</i>	Hemiptera	Aphididae	<i>Aphis idaei</i>	Leaf
		Hemiptera	Aphididae	<i>Aphis schneideri</i>	Leaf
Hydrangeaceae	<i>Philadelphus coronarius*</i>	Hemiptera	Aphididae	<i>Aphis fabae</i>	Leaf
Malvaceae	<i>Hibiscus syriacus*</i>	Hemiptera	Aphididae	<i>Myzus persicae*</i>	Leaf
Malvaceae	<i>Tilia cordata</i>	Diptera	Cecidomyiidae	<i>Contarinia tiliarum</i>	Petiole/flower/leaf and shoot
		Diptera	Cecidomyiidae	<i>Dasineura tiliae</i>	Leaf
Malvaceae	<i>Tilia platyphyllos</i>	Diptera	Cecidomyiidae	<i>Contarinia tiliarum</i>	Petiole/flower/leaf and shoot
		Diptera	Cecidomyiidae	<i>Dasineura tiliae</i>	Leaf
		Diptera	Cecidomyiidae	<i>Didymomyia tiliacea</i>	Leaf
Oleaceae	<i>Fraxinus excelsior</i>	Diptera	Cecidomyiidae	<i>Dasineura acrophila</i>	Leaf
		Diptera	Cecidomyiidae	<i>Dasineura fraxini</i>	Leaf
		Hemiptera	Aphididae	<i>Prociphilus bumeliae</i>	Leaf
		Hemiptera	Psyllidae	<i>Psyllopsis fraxini</i>	Leaf
Oleaceae	<i>Fraxinus ornus</i>	Diptera	Cecidomyiidae	<i>Dasineura fraxini</i>	Leaf
Oleaceae	<i>Ligustrum vulgare</i>	Hemiptera	Aphididae	<i>Myzus ligustri</i>	Leaf
Pinaceae	<i>Abies alba</i>	Hemiptera	Adelgidae	<i>Dreyfusia nordmanniana*</i>	Shoot
Pinaceae	<i>Abies concolor*</i>	Hemiptera	Adelgidae	<i>Dreyfusia piceae</i>	Shoot
Pinaceae	<i>Larix decidua</i>	Diptera	Cecidomyiidae	<i>Dasineura kellneri</i>	Shoot
		Hemiptera	Aphididae	<i>Adelges laricis</i>	Shoot
Pinaceae	<i>Picea abies</i>	Hemiptera	Adelgidae	<i>Sacchiphantes viridis</i>	Shoot
		Hemiptera	Aphididae	<i>Adelges laricis</i>	Shoot

Pinaceae	<i>Picea glauca*</i>	Hemiptera	Adelgidae	<i>Sacchiphantes viridis</i>	Shoot
Pinaceae	<i>Picea pungens*</i>	Hemiptera	Adelgidae	<i>Sacchiphantes viridis</i>	Shoot
Pinaceae	<i>Pinus contorta*</i>	Lepidoptera	Tortricidae	<i>Rhyacionia buoliana</i>	Bud
Pinaceae	<i>Pinus mugo</i>	Lepidoptera	Tortricidae	<i>Rhyacionia buoliana</i>	Bud
Pinaceae	<i>Pinus nigra*</i>	Lepidoptera	Tortricidae	<i>Rhyacionia buoliana</i>	Bud
Pinaceae	<i>Pinus ponderosa*</i>	Lepidoptera	Tortricidae	<i>Rhyacionia buoliana</i>	Bud
Pinaceae	<i>Pinus sylvestris</i>	Diptera	Cecidomyiidae	<i>Thecodiplosis brachyntera</i>	Needle
		Lepidoptera	Tortricidae	<i>Retinia resinella</i>	Bud
		Lepidoptera	Tortricidae	<i>Rhyacionia buoliana</i>	Bud
Pinaceae	<i>Pseudotsuga menziesii*</i>	Hemiptera	Aphididae	<i>Gilletteella cooleyi*</i>	Shoot
Rhamnaceae	<i>Rhamnus cathartica</i>	Hemiptera	Triozidae	<i>Trichoermes walkeri</i>	Leaf
Rosaceae	<i>Crataegus monogyna</i>	Hemiptera	Aphididae	<i>Dysaphis crataegi</i>	Leaf
Rosaceae	<i>Prunus avium</i>	Hemiptera	Aphididae	<i>Myzus cerasi</i>	Leaf
Rosaceae	<i>Rosa canina</i>	Diptera	Cecidomyiidae	<i>Dasineura rosae</i>	Leaf
		Hymenoptera	Cynipidae	<i>Diplolepis rosae</i>	Leaf bud
		Hymenoptera	Tenthredinidae	<i>Blennocampa pusilla</i>	Leaf
Rosaceae	<i>Rosa multiflora*</i>	Diptera	Cecidomyiidae	<i>Dasineura rosae</i>	Leaf
		Hymenoptera	Cynipidae	<i>Diplolepis rosae</i>	Leaf bud
Salicaceae	<i>Populus x canescens</i>	Coleoptera	Cerambycidae	<i>Saperda populnea</i>	Shoot
Salicaceae	<i>Populus nigra</i>	Hemiptera	Aphididae	<i>Chaitophorus populicola</i>	Leaf
		Hemiptera	Aphididae	<i>Pemphigus borealis</i>	Bud
		Hemiptera	Aphididae	<i>Pemphigus bursarius</i>	Petiole
		Hemiptera	Aphididae	<i>Pemphigus populi</i>	Leaf
		Hemiptera	Aphididae	<i>Pemphigus populinigrae</i>	Leaf
		Hemiptera	Aphididae	<i>Pemphigus spirothecae</i>	Petiole
		Hemiptera	Aphididae	<i>Thecabius affinis</i>	Leaf
Salicaceae	<i>Populus simonii*</i>	Hemiptera	Aphididae	<i>Pemphigus spirothecae</i>	Petiole
Salicaceae	<i>Salix alba</i>	Diptera	Cecidomyiidae	<i>Rabdophaga salicis</i>	Leaf
		Diptera	Cecidomyiidae	<i>Rabdophaga rosaria</i>	Leaf
		Hemiptera	Aphididae	<i>Aphis farinosa</i>	Leaf
		Hymenoptera	Tenthredinidae	<i>Euura amerinae</i>	Leaf
		Hymenoptera	Tenthredinidae	<i>Pontania proxima</i>	Leaf
		Hymenoptera	Tenthredinidae	<i>Pontania vesicator</i>	Leaf
Salicaceae	<i>Salix purpurea</i>	Hymenoptera	Tenthredinidae	<i>Pontania viminalis</i>	Leaf
Sapindaceae	<i>Acer campestre</i>	Diptera	Cecidomyiidae	<i>Dasineura rubella</i>	Leaf
		Diptera	Cecidomyiidae	<i>Driscina glutinosa</i>	Leaf
Sapindaceae	<i>Acer platanoides</i>	Diptera	Cecidomyiidae	<i>Acericecis vitrina</i>	Leaf
		Diptera	Cecidomyiidae	<i>Driscina glutinosa</i>	Leaf
Sapindaceae	<i>Acer pseudoplatanus</i>	Diptera	Cecidomyiidae	<i>Acericecis vitrina</i>	Leaf
		Diptera	Cecidomyiidae	<i>Driscina glutinosa</i>	Leaf
Taxaceae	<i>Taxus baccata</i>	Diptera	Cecidomyiidae	<i>Taxomyia taxi</i>	Bud
Ulmaceae	<i>Ulmus glabra</i>	Hemiptera	Aphididae	<i>Eriosoma ulmi</i>	Leaf

		Hemiptera	Aphididae	<i>Tetraneura ulmi</i>	Leaf
Ulmaceae	<i>Ulmus laevis</i>	Hemiptera	Aphididae	<i>Eriosoma ulmi</i>	Leaf
		Hemiptera	Aphididae	<i>Kaltenbachiella pallida</i>	Leaf
		Hemiptera	Aphididae	<i>Tetraneura ulmi</i>	Leaf
Ulmaceae	<i>Ulmus minor</i>	Hemiptera	Aphididae	<i>Eriosoma ulmi</i>	Leaf
		Hemiptera	Aphididae	<i>Tetraneura ulmi</i>	Leaf

Altogether the plant-galling network comprised 116 interactions (Fig. 1), corresponding to only 2.38% of the 4,860 possible interactions (Table 2). Considering only the network of native herbivores and native plants the connectance was 2.72%. The observed modularity to the entire plant-galling network was very high and significantly higher than expected by chance (Table 2). The native-only insect and plant network subset showed a very high and significant modularity. In turn, network robustness considering all herbivores and native-only subset did not differ from the null model values (Table 2).

Native and exotic host plant species showed similar average degrees ($t = -1.56$, $df = 39.05$, $p\text{-value} = 0.125$), with most species interacting with only one species. Similarly, the average degree did not differ between native and exotic insects ($t = -1.44$, $df = 17.91$, $p\text{-value} = 0.166$), with both groups showing a high prevalence of monophagous insects.

Table 2 Network structure analysis results for plant-galling network recorded in Nitra City Park (Nitra, SW, Slovakia).

Analysis	Value observed	Null expectation	ICI null	ICS null	Z value	p
Connectance: all herbivores	0.0238	–	–	–	–	–
Connectance: only natives	0.0272	–	–	–	–	–
Modularity: all herbivores	0.9716	0.7996	0.7726	0.8308	11.3291	0.0020
Modularity: only natives	0.9874	0.8558	0.8420	0.8789	10.9983	0.0020
Robustness: all herbivores	0.5271	0.5393	0.5252	0.5532	-1.6752	0.0539
Robustness: only natives	0.5366	0.5252	0.5095	0.5423	1.3351	0.9022

4 Discussion

Most taxonomic groups of gall-inducing insects have a highly specific and intimate parasitic life-form on plant hosts, and each insect species generally presents an unique gall morphology (Price, 2005). Our results corroborate this high galling specialization since 81% of insect species were recorded on a single host plant species (i.e., monophagous insects). Oligophagous (17.7%) and polyphagous (1.3%) gall-inducing species were recorded on related host plant species, usually in the same plant genus (as is the case for *Rhyacionia buoliana* that induced galls on five species of *Pinus*). Furthermore, most of the recorded galling species induced unique gall morphotypes, even those that induced galls on more than one host species.

The high specificity of plant-galling interactions has led to a highly specialized network structure. The plant-galling network studied here has very little connected (2.38% of potential interactions) and has a low connectance compared to other plant-herbivore networks (Araújo et al., 2015; Cagnolo et al., 2011). Because of high network specialization, the structure of plant-galling network is more modular than expected by chance, but not more robust to random extinctions than randomly structured networks. This means that the removal of

plant species causes few changes in the network structure, since each plant species is connected to one or a few species of galling insects. On the other hand, these results also mean that the loss of a plant species will, in most cases, inevitably lead to the extinction of an associated galling species in the network. Because the great dependence of gall-inducing insects on their host plants, the maintenance of galling insect populations necessarily depends on plant species conservation (Araújo, 2013).

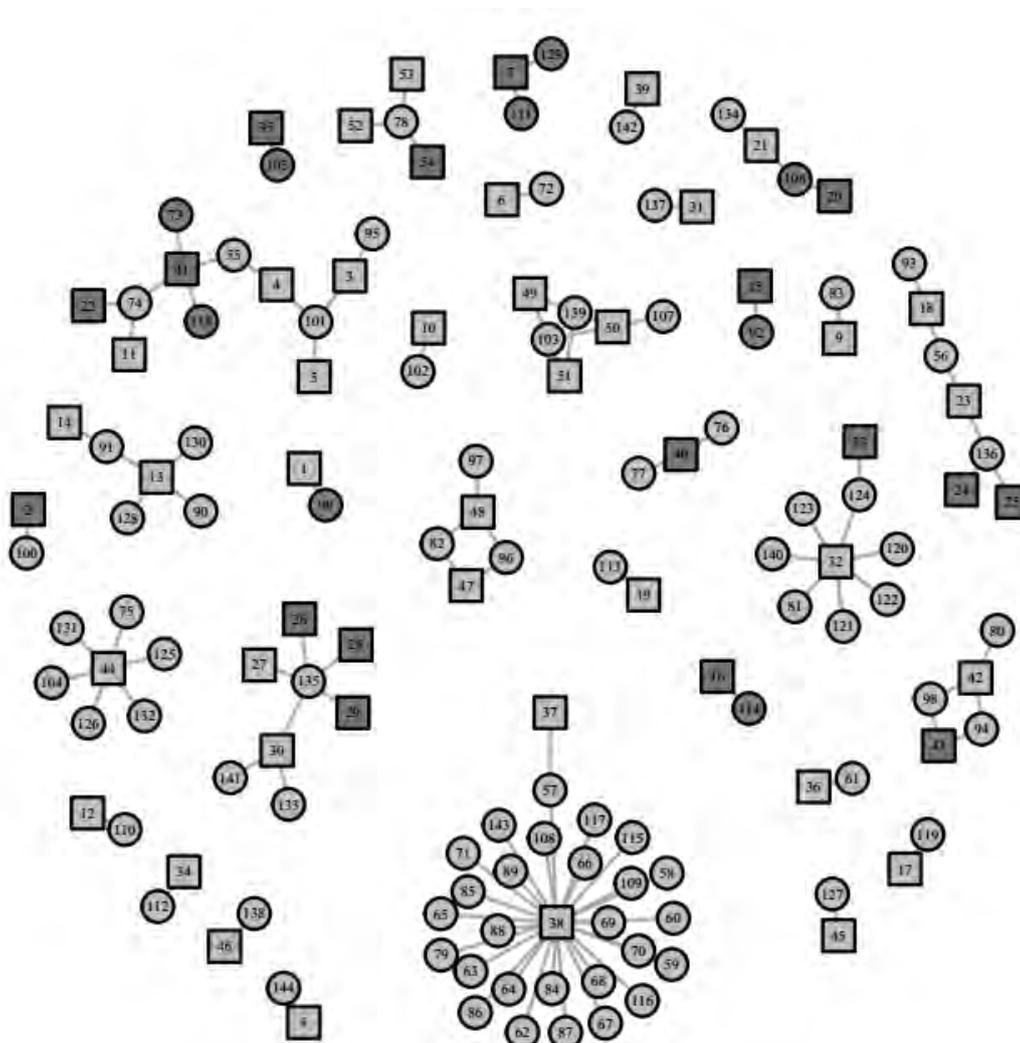


Fig. 1 Representation of the plant-galling network recorded in Nitra City Park (Nitra, SW, Slovakia). Host plant species are represented by squares and gall-inducing insect species are represented by circles. Dark gray indicates exotic species and light gray indicates native species of plants and insects. Codes of plant and insect species names are specified in the Table 3.

Contrary to expectations, native and exotic host plant species did not differ in the number of insect species they interact with. These findings indicate that the galling life-form presents very severe biological restrictions in that only a low number of insect species can induce galls, either on native or exotic plants. We also found that native and exotic insect species had a similar average degree (i.e., number of plant species that interact), counteracting our expectation of lower number of plant species being used by exotic insects than by natives. This absence of difference was observed because most of the insect species are monophagous, which results in average degrees ranging close to one for both native and exotic galling insects. Our findings are in

agreement with previous studies that report that most of gall-inducing species are monophagous (e.g., Carneiro et al., 2009; Stone and Schönrogge, 2003).

Our study is the first, to our knowledge, that systematically evaluated the effect of exotic species occurrence on the structure of a plant-galling network. As we expected, native insect herbivores were significantly more frequent on native host plant species, while exotic herbivores occurred mostly on exotic host plant species. This result indicates very specific interactions even for exotic plants and insects, which results in plant-galling networks very specialized and similarly structured independently of exotic species presence. Future studies may investigate whether this pattern is the same for other groups of galling arthropods less specialized than insects (e.g., galling mites) or higher trophic levels (e.g., predators and parasitoids).

Table 3 List of codes for plant and insect species occurring in the plant-galling network recorded in Nitra City Park (Nitra, SW, Slovakia).

Code	Taxon	Species	Code	Taxon	Species
1	Plant	<i>Abies alba</i>	73	Insect	<i>Aphis craccivora</i>
2	Plant	<i>Abies concolor</i>	74	Insect	<i>Aphis fabae</i>
3	Plant	<i>Acer campestre</i>	75	Insect	<i>Aphis farinosa</i>
4	Plant	<i>Acer platanoides</i>	76	Insect	<i>Aphis idaei</i>
5	Plant	<i>Acer pseudoplatanus</i>	77	Insect	<i>Aphis schneideri</i>
6	Plant	<i>Betula pendula</i>	78	Insect	<i>Aphis viburni</i>
7	Plant	<i>Buxus sempervirens</i>	79	Insect	<i>Biorrhiza pallida</i>
8	Plant	<i>Carpinus betulus</i>	80	Insect	<i>Blennocampa pusilla</i>
9	Plant	<i>Cornus sanguinea</i>	81	Insect	<i>Chaitophorus populicola</i>
10	Plant	<i>Crataegus monogyna</i>	82	Insect	<i>Contarinia tiliarum</i>
11	Plant	<i>Euonymus europaeus</i>	83	Insect	<i>Craneiobia corni</i>
12	Plant	<i>Fagus sylvatica</i>	84	Insect	<i>Cynips caputmedusae</i>
13	Plant	<i>Fraxinus excelsior</i>	85	Insect	<i>Cynips disticha</i>
14	Plant	<i>Fraxinus ornus</i>	86	Insect	<i>Cynips divisa</i>
15	Plant	<i>Gleditsia triacanthos</i>	87	Insect	<i>Cynips longiventris</i>
16	Plant	<i>Hibiscus syriacus</i>	88	Insect	<i>Cynips quercuscalicis</i>
17	Plant	<i>Juniperus communis</i>	89	Insect	<i>Cynips quercusfolii</i>
18	Plant	<i>Larix decidua</i>	90	Insect	<i>Dasineura acrophila</i>
19	Plant	<i>Ligustrum vulgare</i>	91	Insect	<i>Dasineura fraxini</i>
20	Plant	<i>Lonicera ligustrina</i>	92	Insect	<i>Dasineura gleditchiae</i>
21	Plant	<i>Lonicera xylosteum</i>	93	Insect	<i>Dasineura kellneri</i>
22	Plant	<i>Philadelphus coronarius</i>	94	Insect	<i>Dasineura rosae</i>
23	Plant	<i>Picea abies</i>	95	Insect	<i>Dasineura rubella</i>
24	Plant	<i>Picea glauca</i>	96	Insect	<i>Dasineura tiliae</i>
25	Plant	<i>Picea pungens</i>	97	Insect	<i>Didymomyia tiliaceae</i>
26	Plant	<i>Pinus contorta</i>	98	Insect	<i>Diplolepis rosae</i>
27	Plant	<i>Pinus mugo</i>	99	Insect	<i>Dreyfusia nordmanniana</i>
28	Plant	<i>Pinus nigra</i>	100	Insect	<i>Dreyfusia piceae</i>
29	Plant	<i>Pinus ponderosa</i>	101	Insect	<i>Drisina glutinosa</i>
30	Plant	<i>Pinus sylvestris</i>	102	Insect	<i>Dysaphis crataegi</i>

31	Plant	<i>Populus canescens</i>	103	Insect	<i>Eriosoma ulmi</i>
32	Plant	<i>Populus nigra</i>	104	Insect	<i>Euura amerinae</i>
33	Plant	<i>Populus simonii</i>	105	Insect	<i>Gilleteella cooleyi</i>
34	Plant	<i>Prunus avium</i>	106	Insect	<i>Hyadaphis tataricae</i>
35	Plant	<i>Pseudotsuga menziesii</i>	107	Insect	<i>Kaltenbachella pallida</i>
36	Plant	<i>Quercus cerris</i>	108	Insect	<i>Macrodiplosis pustularis</i>
37	Plant	<i>Quercus hispanica</i>	109	Insect	<i>Macrodiplosis roboris</i>
38	Plant	<i>Quercus robur</i>	110	Insect	<i>Mikiola fagi</i>
39	Plant	<i>Rhamnus cathartica</i>	111	Insect	<i>Monarthropalpus flavus</i>
40	Plant	<i>Ribes aureum</i>	112	Insect	<i>Myzus cerasi</i>
41	Plant	<i>Robinia pseudoacacia</i>	113	Insect	<i>Myzus ligustri</i>
42	Plant	<i>Rosa canina</i>	114	Insect	<i>Myzus persicae</i>
43	Plant	<i>Rosa multiflora</i>	115	Insect	<i>Neuroterus laevisculus</i>
44	Plant	<i>Salix alba</i>	116	Insect	<i>Neuroterus numismalis</i>
45	Plant	<i>Salix purpurea</i>	117	Insect	<i>Neuroterus quercus-baccarum</i>
46	Plant	<i>Taxus baccata</i>	118	Insect	<i>Obolodiplosis robiniae</i>
47	Plant	<i>Tilia cordata</i>	119	Insect	<i>Oligotrophus juniperinus</i>
48	Plant	<i>Tilia platyphyllos</i>	120	Insect	<i>Pemphigus borealis</i>
49	Plant	<i>Ulmus glabra</i>	121	Insect	<i>Pemphigus bursarius</i>
50	Plant	<i>Ulmus laevis</i>	122	Insect	<i>Pemphigus populi</i>
51	Plant	<i>Ulmus minor</i>	123	Insect	<i>Pemphigus populinigrae</i>
52	Plant	<i>Viburnum lantana</i>	124	Insect	<i>Pemphigus spirothecae</i>
53	Plant	<i>Viburnum opulus</i>	125	Insect	<i>Pontania proxima</i>
54	Plant	<i>Viburnum rhytidophyllum</i>	126	Insect	<i>Pontania vesicator</i>
55	Insect	<i>Acericecis vitrina</i>	127	Insect	<i>Pontania viminalis</i>
56	Insect	<i>Adelges laricis</i>	128	Insect	<i>Prociphilus bumeliae</i>
57	Insect	<i>Andricus anthracina</i>	129	Insect	<i>Psylla buxi</i>
58	Insect	<i>Andricus conglomeratus</i>	130	Insect	<i>Psyllopsis fraxini</i>
59	Insect	<i>Andricus coriarius</i>	131	Insect	<i>Rabdophaga rosaria</i>
60	Insect	<i>Andricus curvator</i>	132	Insect	<i>Rabdophaga salicis</i>
61	Insect	<i>Andricus cydoniae</i>	133	Insect	<i>Retinia resinella</i>
62	Insect	<i>Andricus fecundator</i>	134	Insect	<i>Rhopalomyzus lonicerae</i>
63	Insect	<i>Andricus glutinosus</i>	135	Insect	<i>Rhyacionia buoliana</i>
64	Insect	<i>Andricus grossulariae</i>	136	Insect	<i>Sacchiphantes viridis</i>
65	Insect	<i>Andricus hungaricus</i>	137	Insect	<i>Saperda populnea</i>
66	Insect	<i>Andricus inflator</i>	138	Insect	<i>Taxomyia taxi</i>
67	Insect	<i>Andricus kollari</i>	139	Insect	<i>Tetraneura ulmi</i>
68	Insect	<i>Andricus lucidus</i>	140	Insect	<i>Thecabius affinis</i>
69	Insect	<i>Andricus mayri</i>	141	Insect	<i>Thecodiplosis brachyntera</i>
70	Insect	<i>Andricus solitarius</i>	142	Insect	<i>Trichoermes walkeri</i>
71	Insect	<i>Andricus testaceipes</i>	143	Insect	<i>Trigonaspis megaptera</i>
72	Insect	<i>Anisostephus betulinus</i>	144	Insect	<i>Zygiobia carpini</i>

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