

Size, age and composition: characteristics of plant taxa as diversity predictors of gall-midges (Diptera: Cecidomyiidae)

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Received 25-X-2010. Corrected 27-II-2011. Accepted 30-III-2011.

Abstract: Many hypotheses have been proposed to explain the diversity of gall-midge insects (Diptera: Cecidomyiidae), some of them taking into account plant diversity. This study aims to test the importance of size, age and composition of host plant taxa in the diversity of Cecidomyiidae. For this we used inventories data on the diversity of galling and host plants in Brazil. We found that Asterales, Myrtales and Malpighiales, were the most important orders, with 34, 33 and 25, gall morphotypes, respectively. The most representative host families were Asteraceae (34 morphotypes), Myrtaceae (23) and Fabaceae (22). In general, the order size and the plant family were good predictors of the galling diversity, but not the taxon age. The most diverse host genera for gall-midges were *Mikania*, *Eugenia* and *Styrax*, with 15, 13 and nine galler species, respectively. The size of plant genera showed no significant relationship with the richness of Cecidomyiidae, contrary to the prediction of the plant taxon size hypothesis. The plant genera with the greatest diversity of galling insects are not necessarily those with the greatest number of species. These results indicate that some plant taxa have a high intrinsic richness of galling insects, suggesting that the plant species composition may be equally or more important for the diversity of gall-midges than the size or age of the host taxon. Rev. Biol. Trop. 59 (4): 1599-1607. Epub 2011 December 01.

Key words: Cecidomyiidae, floristic composition, galls, hypotheses, plant richness, superhosts.

Gall-midges of the family Cecidomyiidae (Diptera) are the most diverse group of galling insects (Gagné 1994, 2004, Carneiro *et al.* 2009). These insects are found in all zoogeographical regions and comprise about 5 400 species and 598 genera (Gagné 2004). In the Neotropical region about 170 genera are known, and just over 159 species and 75 genera are recorded in Brazil (Maia 2005).

Forecasts indicate that the number of species of Cecidomyiidae might be about 85 000, representing 64% of the total diversity of galling insects in the world (Espírito-Santo & Fernandes 2007). This can be attributed to adaptive radiation within the group to be largely opportunistic (Price 2005), species within an insect genus can be found in many genera

and families of host plants, as occurs in *Dasi-neura* Rondani, 1840 (Diptera: Cecidomyiidae) (Gagné 1989). Although gall-midge species are highly specific (Carneiro *et al.* 2009), the genera do not seem to be, thus promoting the high richness within the group.

Many hypotheses have been proposed to explain the diversity of gall-inducing insects, providing explanations at the intra-specific, interspecific and community levels (Fleck & Fonseca 2007). Some of these hypotheses take into account the possibility that plant diversity influences galling diversity both temporarily and spatially, for example, the plant taxon size hypothesis and plant taxon age hypothesis. The first hypothesis proposes that the most diverse host taxa have a greater galling richness, taking

into account that each host species is a potential niche for insects (Mendonça 2007). The second proposes that older host taxa should have more species of gallers, since greater evolutionary time leads to an increase in number of speciation events (Fernandes 1992). Thus, one would expect a positive correlation between the number of species of gall-midges and size and age of the host taxon.

In a pioneer study, Veldtman & McGeoch (2003) proposed that plant community composition is a determining factor in the diversity of gall-inducing insects. According to them, some taxa, known as super-hosts, increase the diversity of galling insects regardless of their size or age. This issue becomes more important at lower taxonomic levels (eg., genera and species), whereas in higher taxa, the composition effect is dissipated by the high number of species. Thus, if composition is an important factor, one would expect no correlation, or a negative correlation, between the size of the plant genera, and the richness of gall-midge, thus contradicting the hypothesis of taxon size, which should be important in explaining diversity at higher taxonomic levels such as family and order. The aim of this study is to answer the following questions: 1) Is the richness of gall-midges proportional to plant taxon size? 2) Do older host taxa have a greater richness of Cecidomyiidae? and 3) Is taxa composition an important factor for the diversity of gall-midges?

MATERIAL AND METHODS

The database of gall-midges and their host plants was obtained from Carneiro *et al.* (2009). In this paper, the author conducted a comprehensive review and listed all Brazilian species of gall-midges and their host plants registered in the literature. In addition, I used some data of Cecidomyiidae from a series of inventories of gall diversity in the state of Goiás (Araújo *et al.* 2007a, b, Santos *et al.* 2010, Araújo *et al.*, unpublished results), totaling six families and 14 genera of host plants added. Gall-midges were separated by species or, if undetermined,

by gall morphotype. Data on the size of plant order, families and genera were obtained from Judd *et al.* (2002) and Souza & Lorenzi (2008). The age of the taxa was obtained from Wikström *et al.* (2001). Multiple regression and linear regression analysis was used to correlate gall-midges richness to the size and age of botanical taxa in the software Statistica 7.0 (all data were submitted to normality tests and other assumptions). The analyses were done at the levels of order, family and genus of the host plants. Altogether 233 gall morphotypes were analyzed, belonging to 23 orders, 49 families and 102 genera of plants.

RESULTS

Asterales, Myrtales and Malpighiales were the most important orders of host plant of gall-midges in Brazil, with 34, 33 and 25 galls morphotypes, respectively. The most representative host families were Asteraceae (34 morphotypes), Myrtaceae (23) and Fabaceae (22) (Table 1). Gall-inducing insect richness was

TABLE 1
Gall-midge richness and plant family size (number of species and genera). Family size obtained from Judd *et al.* (2002) and Souza & Lorenzi (2008)

Plant family	Number of plant species	Number of plant genera	Gall-midge richness
Asteraceae	2000	250	34
Myrtaceae	1000	26	23
Fabaceae	1500	175	22
Nyctaginaceae	70	10	15
Euphorbiaceae	1000	70	12
Clusiaceae	150	18	9
Styracaceae	20	2	9
Sapindaceae	400	24	7
Verbenaceae	250	16	7
Boraginaceae	100	12	6
Burseraceae	60	7	6
Malpighiaceae	300	45	6
Melastomataceae	1000	70	6
Rubiaceae	2000	120	6
Loranthaceae	100	10	4
Moraceae	250	27	4

TABLE 1 (Continued)
Gall-midge richness and plant family size (number of species and genera). Family size obtained from Judd *et al.* (2002) and Souza & Lorenzi (2008)

Plant family	Number of plant species	Number of plant genera	Gall-midge richness
Piperaceae	500	3	4
Sapotaceae	200	14	4
Anacardiaceae	70	15	3
Bignoniaceae	350	32	3
Chrysobalanaceae	250	7	3
Erythroxylaceae	100	1	3
Lamiaceae	350	28	3
Meliaceae	100	6	3
Apocynaceae	850	95	2
Celastraceae	100	17	2
Olacaceae	60	12	2
Smilacaceae	32	1	2
Solanaceae	350	32	2
Malvaceae	400	80	2
Annonaceae	250	33	1
Araliaceae	50	6	1
Cactaceae	200	40	1
Caryocaraceae	13	2	1
Urticaceae	80	12	1
Combretaceae	60	6	1
Convolvulaceae	300	18	1
Dilleniaceae	80	6	1
Salicaceae	80	19	1
Lauraceae	400	22	1
Lythraceae	150	10	1
Menispermaceae	100	16	1
Myrsinaceae	70	8	1
Ochnaceae	120	13	1
Onagraceae	50	4	1
Passifloraceae	120	5	1
Poaceae	1500	70	1
Ulmaceae	5	2	1
Vochysiaceae	150	6	1

positively related with the size of the host plant order, in terms of number of species ($r^2=0.59$, $n=23$, $p<0.01$, Fig. 1A), but not with the age of the order ($p=0.59$). Size of the host plants accounted for 59% of gall-inducing insect richness variation. Gall-midge richness was also positively correlated with the size of the plant family ($r^2=0.48$, $n=49$, $p<0.001$, Fig. 1B).

However, the age of the plant families were not related to gall-midge richness ($p=0.32$, Fig. 2).

Unlike what was observed for the size of plant order and family, a positive and linear relationship between the size of plant genera and gall-midge richness was not found ($r^2=0.002$, $n=102$, $p=0.60$, Fig. 3). The size of plant genera ranged from four to 1 500 species (mean 218.9 ± 271.9). The most diverse host genera for gall-midges were *Mikania*, *Eugenia* and *Styrax*, with 15, 13 and nine galler species, respectively (Table 2). These genera occupy only the 15th, 16th and 77th positions in genus size ranking. The three plant genera with the most species of plants were *Psychotria*, *Solanum* and *Vernonia*, but, these genera had only one species of gall-midge each (Table 2).

DISCUSSION

The diversity patterns of gall-midges observed in this study are supported by previous investigation where the size of plant taxon was positively correlated with the richness of gall-inducing insects (Fernandes 1992, Gonçalves-Alvim & Fernandes 2001, Mendonça 2007). As expected, the most diverse plant taxa in terms of number of species had a greater diversity of gall-midges. At the family level, in addition to the number of species, the number of genera was also a predictor of diversity of Cecidomyiidae.

The plant taxon size hypothesis has been tested mainly for the taxonomic level of family (also known as the plant family size hypothesis) (Fernandes 1992), while at the order level, the hypothesis has rarely been tested (for example, Mendonça 2007). Gonçalves-Alvim & Fernandes (2001) found a positive relationship between family size and gall richness in the Cerrado of Southeast of Brazil, where Fabaceae was the most important family. Fabaceae is the most species rich family in the Brazilian Cerrado, peaking at 777 species (Mendonça *et al.* 1998), and is also registered as the host family with the greatest number of Neotropical cecidomyiid galls (Gagné 1994). Araújo *et al.* (unpublished results) also found Fabaceae to be

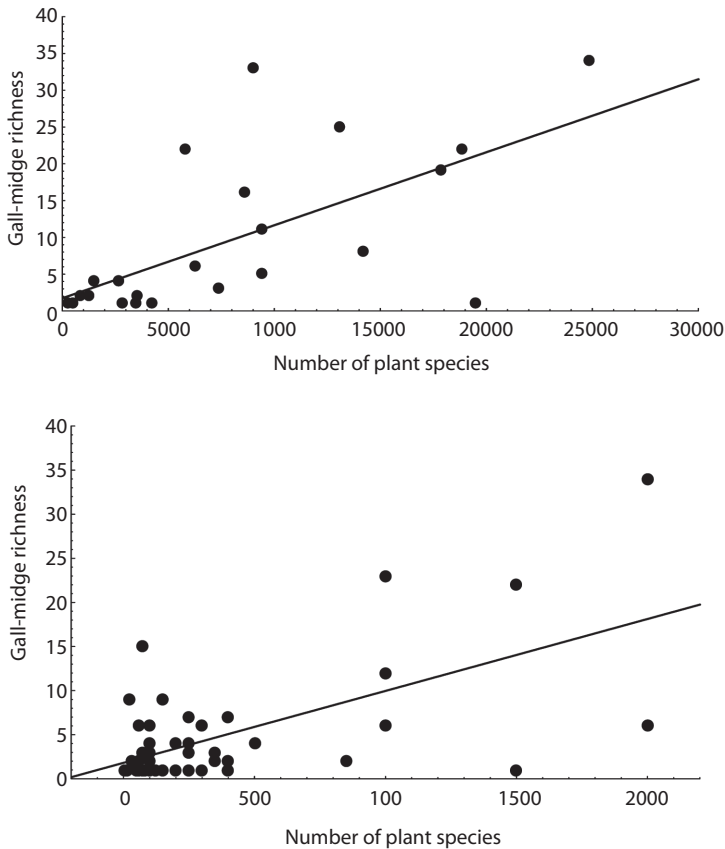


Fig. 1. Relationship between gall-midge richness and A) host plant order size in terms of number of species. ($y=1.725 + 0.001x$) and B) host plant family size in terms of number of species ($y=1.811 + 0.008x$). Order size obtained from Judd *et al.* (2002) and Souza & Lorenzi (2008) and family size obtained from Judd *et al.* (2002) and Souza & Lorenzi (2008).

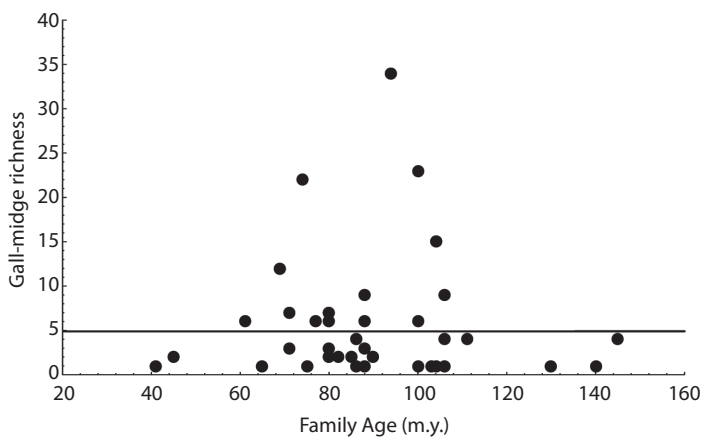


Fig. 2. Relationship between gall-midge richness and host plant family age in million years ($y=4.890 + 3.832x$). Family age obtained from Wikström *et al.* (2001).

TABLE 2
 Ranking of the plant genus size in terms of number of species and richness of gall-midges.
 Genus size obtained of Judd *et al.* 2002

Ranking	Plant genus	Gall-midge Richness	Number of plant species	Ranking	Plant genus	Gall-midge Richness	Number of plant species
1	<i>Psychotria</i>	1	1500	52	<i>Chromolaena</i>	6	126
2	<i>Solanum</i>	1	1400	53	<i>Jacquemontia</i>	1	120
3	<i>Vernonia</i>	1	1000	54	<i>Nectandra</i>	1	120
4	<i>Miconia</i>	2	1000	55	<i>Heteropteris</i>	2	120
5	<i>Piper</i>	4	1000	56	<i>Diodia</i>	2	119
6	<i>Ficus</i>	2	800	57	<i>Myrciaria</i>	3	116
7	<i>Croton</i>	3	750	58	<i>Waltheria</i>	1	107
8	<i>Didymopanax</i>	1	600	59	<i>Couepia</i>	2	103
9	<i>Eupatorium</i>	3	600	60	<i>Dalechampia</i>	1	100
10	<i>Mimosa</i>	1	500	61	<i>Physalis</i>	1	100
11	<i>Ouratea</i>	1	500	62	<i>Psidium</i>	1	100
12	<i>Hyptis</i>	1	400	63	<i>Tabebuia</i>	1	100
13	<i>Passiflora</i>	1	400	64	<i>Qualea</i>	1	98
14	<i>Baccharis</i>	7	400	65	<i>Duguetia</i>	1	93
15	<i>Eugenia</i>	13	400	66	<i>Tetrapterys</i>	1	90
16	<i>Mikania</i>	15	400	67	<i>Melissa</i>	1	83
17	<i>Paspalum</i>	1	330	68	<i>Heisteria</i>	1	81
18	<i>Pouteria</i>	3	325	69	<i>Fleischmannia</i>	1	80
19	<i>Cordia</i>	4	320	70	<i>Protium</i>	6	80
20	<i>Smilax</i>	2	310	71	<i>Neea</i>	7	80
21	<i>Licania</i>	1	309	72	<i>Trema</i>	1	76
22	<i>Myrcia</i>	2	300	73	<i>Parkia</i>	1	70
23	<i>Cuphea</i>	1	275	74	<i>Stachytarpheta</i>	1	70
24	<i>Combretum</i>	1	250	75	<i>Arrabidaea</i>	2	70
25	<i>Senna</i>	1	250	76	<i>Guapira</i>	8	70
26	<i>Sterculia</i>	1	250	77	<i>Styrax</i>	9	60
27	<i>Erythroxylum</i>	3	250	78	<i>Kielmeyera</i>	1	59
28	<i>Inga</i>	3	250	79	<i>Vanillosmopsis</i>	1	57
29	<i>Bauhinia</i>	4	250	80	<i>Marcetia</i>	1	52
30	<i>Tibouchina</i>	2	240	81	<i>Hymenaea</i>	1	50
31	<i>Serjania</i>	4	220	82	<i>Piptocarpha</i>	1	50
32	<i>Rubia</i>	1	211	83	<i>Sorocea</i>	1	50
33	<i>Myrsine</i>	1	200	84	<i>Psittacanthus</i>	2	50
34	<i>Dalbergia</i>	2	200	85	<i>Struthanthus</i>	2	50
35	<i>Maytenus</i>	2	200	86	<i>Coussapoa</i>	1	46
36	<i>Calophyllum</i>	4	200	87	<i>Selenicereus</i>	1	44
37	<i>Casearia</i>	1	180	88	<i>Ximena</i>	1	37
38	<i>Ossaea</i>	1	167	89	<i>Guarea</i>	3	35
39	<i>Clusia</i>	4	160	90	<i>Urvillea</i>	1	34
40	<i>Jussiaea</i>	1	157	91	<i>Andira</i>	4	31
41	<i>Sebastiania</i>	2	155	92	<i>Mangifera</i>	1	30
42	<i>Borreria</i>	2	150	93	<i>Schinus</i>	1	30
43	<i>Paullinia</i>	2	150	94	<i>Porophyllum</i>	2	30
44	<i>Tournefortia</i>	2	150	95	<i>Davilla</i>	1	25
45	<i>Byrsonima</i>	3	150	96	<i>Cissampelos</i>	1	20
46	<i>Lantana</i>	6	150	97	<i>Neomitranthes</i>	4	19
47	<i>Manihot</i>	6	150	98	<i>Acosmium</i>	1	18
48	<i>Manilkara</i>	1	146	99	<i>Caryocar</i>	1	16
49	<i>Aegiphila</i>	1	130	100	<i>Chlorophora</i>	1	12
50	<i>Machaerium</i>	3	130	101	<i>Anacardium</i>	1	10
51	<i>Piptadenia</i>	1	126	102	<i>Peplonia</i>	2	4

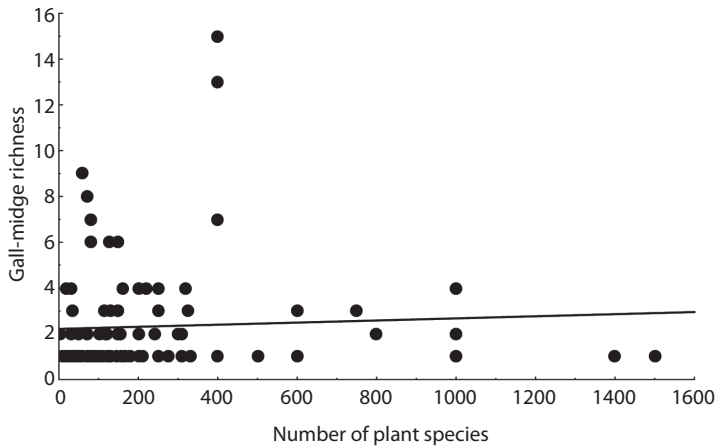


Fig. 3. Relationship between gall-midge richness and host plant genus size in terms of number of species ($y=2.213 + 0.0005x$). Genus size obtained of Judd *et al.* (2002).

important in areas of the Cerrado in Goiás State in Midwestern Brazil, so that when the family was excluded from the analysis the positive relationship between family size and richness gall-inducing insects disappeared.

In this study, Asteraceae was the host family with most species of Cecidomyiidae. This family is one of the most diverse not only in Brazil but also throughout the neotropics (Judd *et al.* 2002), being recorded in Southern Brazil as the most important host family for gall inducers (Mendonça 2007). According to Gagné (1994) this family is the second largest host family of gall-midges in the Neotropical region.

The plant taxon size hypothesis seems to be important in explaining the diversity of galls at the level of host order and family. According to Mendonça (2007), the process that leads to this pattern, is a result of plant taxa being natural groups with chemical, structural and ecological similarities. Gall-midges usually have univoltine cycles and are highly synchronized with their host plants (Araújo & Santos 2009), principally in temperate areas (Gagné 1989, Yukawa 2000). This synchrony could lead to speciation via host change being more common among plants within the same

family, at least more often than between plants of different families (Mendonça 2001). Thus, the greater the number of species within a taxon, the more likely they have synchronous development, involve the greater the chances of speciation and, consequently, the greater the diversity of gall-midges.

However, unlike taxon size, taxon age was not a good predictor of diversity of Cecidomyiidae. Older orders and families did not have a greater diversity of gall-midges. The age hypothesis suggests that geologically older taxa offer more opportunities for the host plant change of galling insects and thus accumulate a greater number of species over time (Fernandes 1992, Mendonça 2007). However, contrary to what the hypothesis predicts, some relatively young taxa, such as Asteraceae and Fabaceae, have a higher galling insect diversity than older host plant taxa (Fernandes 1992). In fact, the adaptive opportunism of Cecidomyiidae can explain this (Price 2005). There seems to be a remarkable capacity for host shifting across families and genera, resulting in a wide range of galled plants and adaptive radiation within some families/genera can then proceed (Price 2005). As previously mentioned, the most diverse taxa have higher rates of speciation

and synchrony (Price 2002). This makes measures of plant diversity, local richness of host plants (Cuevas-Reyes *et al.* 2004) or taxon size (Araújo *et al.* unpublished results), in terms of number of genera or species, better predictors of gall-midge diversity than taxon age.

Composition also seems to be a relevant factor in explaining gall-midge diversity. The main largest host genera are not necessarily the most diverse in galling species (Araújo *et al.* unpublished results). Results similar to those observed in this study were also obtained by Mendonça (2007) and Araújo *et al.* (unpublished results), where the size of the host plant genus did not explain the richness of gall-inducing insects. This repetition of patterns suggests that certain genera might be important hosts regardless of their species richness. Some plant genera and species have a high diversity of galls (Blanche & Westoby 1995, Veldtman & McGeoch 2003), for example, *Baccharis* (Fernandes *et al.* 1996), *Eucalyptus* (Blanche & Westoby 1995), *Quercus* (Oyama *et al.* 2006) and *Solidago* (Weis & Abrahamson 1986). I believe factors like the development synchrony and the sympatric occurrence of species may be responsible for the appearance of these taxa, although the reasons why a genus or species is a super-host is still not clear. As noted earlier, the size of the genera does not necessarily match its ranking in terms of gall-midge diversity. In some cases, the relationship may be inversely proportional, where the genera with fewer species harbor the largest number of gall-inducing insects, thus confirming the hypothesis that some taxa positively affect the galling diversity and that plant composition is a determining factor in the richness of gall-midges.

All of these patterns observed for the size of the plant orders and families and flora composition, indicate the importance of plant community to galling diversity (Veldtman & McGeoch 2003). However, there is a chance that these observations may be sampling artifacts, as argued by Fleck & Fonseca (2007). According to them, the most diverse taxa are probably sampled more and super-hosts may be the result of an over-sampling. On the other

hand, if this were true, major genera have a higher diversity of gall-midges and super-hosts taxa would also be the most diverse in species number. Further studies are necessary to address these issues at local and regional scales. Moreover, these questions should be examined in other groups of galling insects. Apparently, the plant taxon size hypothesis as well as the plant composition hypothesis, are good predictors of gall-midges diversity.

ACKNOWLEDGMENTS

I am very grateful to V.C. Maia, M.S. Mendonça Jr. and M.A.A. Carneiro for their important suggestions and criticisms of the manuscript; to N. Coelho for English revision and to Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the scholarship grant.

RESUMEN

Muchas hipótesis se han propuesto para explicar la diversidad de dípteros de la familia Cecidomyiidae, algunos de ellos teniendo en cuenta la diversidad de las plantas. Este estudio tiene como objetivo probar la importancia del tamaño, la edad y la composición de las plantas en la diversidad de Cecidomyiidae, a través de los inventarios de las agallas y las plantas hospedadoras, en Brasil. Asterales, Malpighiales y Myrtales fueron los órdenes más importantes, con 34, 33 y 25 tipos de agallas, respectivamente. Las familias más importantes fueron Asteraceae (34 morfotipos), Myrtaceae (23) y Fabaceae (22). En general, el tamaño de los órdenes y las familias de las plantas es un buen predictor de la diversidad de insectos de agallas, pero no de la edad de la taxon. Los géneros más diversos fueron *Mikania*, *Eugenia* y *Styrax*, con 15, 13 y nueve especies con agallas, respectivamente. El tamaño de los géneros no mostró relación significativa con la riqueza de Cecidomyiidae, lo que contradice la hipótesis del tamaño de los táxones de plantas. Los géneros de plantas más diversos en insectos inductores de agallas no son necesariamente los que tienen el mayor número de especies. Estos resultados indican que algunos táxones de plantas tienen una alta riqueza intrínseca de insectos agalleros, lo que sugiere que la composición de especies de plantas pueden ser igualmente o más importante para la diversidad de los cecidomyiideos agalleros que el tamaño o la edad del taxón.

Palabras clave: agallas, Cecidomyiidae, composición florística, hipótesis, riqueza de plantas, superhospedeiras.

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