



Legume (Fabaceae) and seed beetle (Coleoptera, Chrysomelidae, Bruchinae) species of Europe: distribution and host specialization

Árpád Szentesi¹

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Abstract

The paper investigates the distributions of legumes (Fabaceae) and their associated seed beetle species (Bruchinae) across vegetation zones and regions of Europe and evaluates the host range and specialization of seed beetles. 1584 legume species/subspecies/varieties were included in the study and ca. 16% of these serve as known hosts by the 175 seed beetle species found in Europe. Both plant and seed beetle species richness increased from the Boreal to Mediterranean zones/regions. 717 legume species occurred only in single zones/regions and only 4.7% of these (34 species) were hosts for 38 bruchine species specific to a zone/region. Europe has 664 native legume species and 381 of these are Eu-endemics. There were 52 alien legume species found. Similarities in plant species composition by the Sørensen index were pronounced between the Central-European and the Mediterranean, between the Transcaucasian and Mediterranean, and between the Colchis-Caucasian and the Pontic-Caspian areas. The most species-rich genus is *Astragalus* L. with 334 species and 16 subspecies. Of the two major pre-dispersal seed predator genera, *Bruchidius* Schilsky species are sensu lato oligophagous, using a wide range of leguminous tribes as hosts, but restricted to few host species within a tribe. In contrast, members of the *Bruchus* L. genus are sensu stricto oligophagous species and, despite being constrained to the Fabeae tribe, most of them feed on several *Lathyrus* L. and *Vicia* L. species. The ways annual and perennial life cycles as well as chemical constituents of legumes might affect the colonization success of the seed beetles are discussed.

Keywords Bruchines · Distribution · Host plants · Seed predation · Specialization · Vegetation zones and regions

Introduction

Endophagous pre-dispersal seed predation is an ecological event with important population dynamic and community-level effects (Janzen 1971; Crawley 2000; Szentesi 2006; Jeffs et al. 2018). It impacts plant distribution, recruitment, and species diversity, and it can cause considerable economic losses. The major insect taxa of pre-dispersal seed-consuming species belong to the Bruchinae subfamily, representing ca. 1,700 species worldwide (Johnson et al. 2004), and are mostly associated with species of the Fabaceae (Leguminosae) family (Johnson 1981a).

Seed beetles of European legumes discussed in this paper belong to the so-called “green pod oviposition guild” (Szentesi and Jermy 1998) differing from the guilds described by Johnson (1981b). The females of the “green pod oviposition guilds” likely synchronize their reproduction with host development and lay eggs only on immature green pods containing hardly differentiated embryos (Boivin et al. 2015). Eggs are stuck to the pod’s surface and the hatching first instars bore on-site through the pod wall into nearby embryos. The larva grows together with the seed, consuming the cotyledon, and then it pupates in it unless due to larval and seed mass differences, it must devour more than one seed, as in the case of some species in the Loteae DC. (Jermy and Szentesi 2010), Galegeae (Bronn) Dumort and Trifolieae (Bronn) Endl. (Delobel and Delobel 2006; Jermy and Szentesi, unpublished data). Adults at emergence leave the seeds through a chewed aperture on a dehiscent pod or the pod’s wall in the case of an indehiscent pod. With some exceptions only, a single generation develops in the Palearctic region and usually adults overwinter.

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✉ Árpád Szentesi
arpad.szentesi@ttk.elte.hu

¹ Department of Systematic Zoology and Ecology, ELTE Eötvös Loránd University, Budapest, Hungary

The taxonomic elaboration of European Bruchinae by the major taxonomic works (Hoffmann 1945; Lukianovich and Ter-Minasian; 1957; Borowiec 1987; Anton 2001, 2010) yielded ca. 160 species (not including stored product pests); however, new species and species combinations are still being described (e.g., Delobel and Delobel 2007). In addition, several alien species were introduced with exotic hosts or appeared on long-established archaeophytes (e.g., *Bruchidius siliquastris* Delobel on *Cercis siliquastrum* L. (Kergoat et al. 2007b), or *Megabruchidius* Borowiec species on *Gleditsia triacanthos* L. (Jermy et al. 2002) and *Gymnocladus dioica* (L.) K. Koch (György and Tuda 2020)).

Presumed host plant relations and distribution of Bruchinae species in European legumes have been initially mostly based on the collection of adults in the vegetation and by subsequent taxonomic identification (Hoffman 1945; Zacher 1952; de Luca 1967; Anton 2010; Borowiec 1987; Borowiec and Anton 1993, and others). However, some of these studies (e.g., Hoffman 1945) do provide host plant associations based on rearing. Such faunistic studies are extremely valuable because they demonstrate the presence of a species in an area, frequently long before the actual hosts could be detected. Seed beetles can be sweep-netted also from non-host plant species that provide nectar, pollen, or shelter (Szentesi et al. 2017). However, verifying host associations between plant and insect species is almost impossible this way. Unfortunately, many host affiliations of seed beetles remained anecdotal or inaccurate until regular and systematic pod and seed collections and subsequent rearing of seed beetles from collected samples were carried out (Bagdasarjan 1941; Lukianovich and Ter-Minasian 1957; Johnson and Siemens 1995; Szentesi and Jermy 1995; Delobel and Delobel 2006; Yus-Ramos and Romero 2011 and others). Since the spread of the “pod collection-seed beetle rearing” method, a wealth of information has been gained on the host relationships of Bruchinae. This method did not only allow the identification of host associations, but it also provided a large amount of data on distribution, life cycle, way of host use, and even on parasitoids of the seed-consuming guilds.

The largest portion of members of the Bruchinae subfamily comprises oligophagous legume seed consumers. Janzen (1980) found that the majority of the seed beetle species in a Costa Rican forest had only one host plant. Jeffs et al. (2018) recorded that 91% of pre-dispersal seed predator morphospecies were monophagous consumers in a Panamanian forest. The advent of molecular phylogenetic methods also revealed that the two major Old World seed beetle groups, *Bruchidius* Schilsky and *Bruchus* Linnaeus are phylogenetically distinct. Whereas *Bruchidius* is polyphyletic (Kergoat et al. 2004, 2005a, 2005b), *Bruchus* species constitute a monophyletic group (Kergoat et al. 2007a) and both show strong taxonomic conservatism in host use.

Concerning the leguminous hosts of the *Bruchidius* and *Bruchus* genera, more than 100 *Trifolium* L. species, out of the ca. 250 species worldwide, are native to the Mediterranean Basin (Lamont et al. 2001; Scoppola et al. 2018). However, it is also one of the distribution centers of *Vicia sativa* L., *V. faba* L., *Lathyrus odoratus* L., *Ornithopus sativus* Brot. and *Hedysarum coronarium* L. (Maxted and Bennett 2001). Another Mediterranean-type ecosystem, Transcaucasia, is the most species-rich area of the world’s largest plant genus, *Astragalus* L. (Lewis et al. 2005). Such features attempt to outline the distribution and host specialization of European seed beetles as a challenging, nevertheless scientifically profitable, task.

Despite the large amount of information on European seed beetles and their legume hosts, a continent-wide survey of their distribution is missing. This study attempts to fill this hiatus by taking into account European vegetation zones and regions and the relative species richness of native, endemic, and alien legume and seed beetle categories. It is recognised that the distribution of European legumes fundamentally determines seed beetle distribution. An equally important question is the degree of specialization of seed beetle species, which in turn is much affected by specific plant chemistry. It has long been known that leguminous species are rich in secondary plant chemicals (Bell 1958, 1972; Fowden 1970; Hegnauer 1988; Bisby et al. 1994; Wink and Mohamed 2003) affecting seed beetle distribution and survival (Rosenthal 1983; Birch et al. 1989; Wink 1992).

This paper seeks connections between the distribution of hosts and specialization of seed beetles (Coleoptera, Chrysomelidae, Bruchinae) of European Fabaceae and places emphasis on seed beetle occurrences and diversity. To achieve this aim, plant and seed beetle occurrences, based on pod collection data, were used and the following questions were investigated:

- How many leguminous species can be found in the European vegetation zones/regions?
- How are leguminous tribes, genera and species distributed in European vegetation zones/regions, and to what extent do seed beetle species follow host distribution?
- How many seed beetle species are recorded in Europe and what host specialization do they show?
- How are annual or perennial legume life cycles distributed across vegetation zones/regions and to what extent do seed beetles utilize such hosts?

Materials and methods

The European legumes (Fabaceae)

Floristic maps of Europe (Bohn et al. 2004; Lang et al. 2004; Tutin et al. 1968; ILDIS 2018 [<https://ildis.org>]; POWO

2019 [<http://www.plantsoftheworldonline.org/>]; Euro + Med Plant Base [<http://www.europlusmed.org/>]) differ in one main point, i.e., whether Transcaucasia should be included as part of Europe. In this study, this zone is involved, as—among others—it tightly coincides with the faunistic map of Löbl and Smetana (2010). In this way, records of seed beetle species can be validated with the occurrence of legume species in the same zone. Among the available vegetation maps of Europe, those of Lang et al. (2004) were used in this study.

Lang et al. (2004) differentiated six vegetation zones and 15 regions in Europe (Table 2, and Online Resource 2: Fig. 1). Among them, the Boreal zone contains three regions, the Temperate zone contains eight regions, and the Mediterranean zone contains three regions. The Arctic, Colchis-Caucasus, and Pontic-Caspian zones are not subdivided into regions. Altogether, there are 17 zones and regions. The West-Mediterranean region includes the Azores, and the East-Mediterranean incorporates most of the Aegean islands (Cyclades and Crete); however, it excludes Cyprus and islands nearby Anatolia (Rhodes, Samos, etc.). The European part of Türkiye is included. The Pontic-Caspian zone embraces parts of Azerbaijan, the Caspian shore running up to the Orenburg area of Russia, but it also extends through parts of Crimea to Romania's Black Sea shores. The Colchis-Caucasus zone includes Cis- and Transcaucasia and the southern part of Crimea. The Arctic zone, the Boreo-Russian, the Hemiboreal, and the East-European regions and the Pontic-Caspian zone are all bordered by the Ural mountain to the East.

The phylogenetic relations of tribes, genera, and species follow Lewis et al. (2005). The nomenclature of species, subspecies, and varieties is according to ILDIS, POWO, and Euro-Med Plant Base. The sources of species occurrences were floristic publications and checklists of European countries (Online Resource 1: References). These were confirmed using Tutin et al. (1968) and online plant databases and were embedded in vegetation zones/regions corresponding to countries. Native European legume species are defined in this study as those that, besides being an indigenous member of the European flora, are also present outside Europe's political borders, e.g., in North Africa, the Near East, or in some areas of Asia. There are also two kinds of endemism considered here, distinguished at two spatial scales. There are those leguminous species that occur solely in Europe, and those, that only occur in a single vegetation zone/region. The first type is called Eu-endemic, and the second is zone/region-specific endemism. To establish these categories, first, all leguminous species found in zones/regions were check listed. Then to identify the species native to Europe, all alien species were excluded. In the next step, all native species of a given zone/region shared with the other 16 zones/regions were excluded. The remaining species formed the endemics for a zone/region in question, and the sum of

these provided the number of Eu-endemic species. The procedure was repeated for all 17 zones and regions.

Each leguminous species were renamed by a six-letter code combining genus and species names. Such codenames were used for the distribution tables (Online Resource Excel File: "Szentesi_European bruchines and legumes"), giving information about native, endemic, alien, perennial, or annual statuses (biannual life cycle was not considered). Generally, only species present in Tutin et al. (1968) and ILDIS were included in this study. However, newly described species were also accepted if their validity was confirmed by more recent databases (POWO, Euro-Med Plant Base). As numerous changes in nomenclature and taxonomy have been executed since the publication of Tutin et al. (1968), the revisions were based on ILDIS. Subspecies were included only on two conditions: (1) if a species' status was changed to subspecies, or (2) if a subspecies harbored seed beetle species. Despite efforts to obtain information about their distributions, 23 plant species/subspecies/varieties could not be placed reliably into zones/regions and the life cycle (i.e., whether annual or perennial) of five species was unknown. Typically, in the former case, the difficulty was caused by the fact that the country of occurrence (e.g., Belgium, Denmark, Norway, or Sweden) was divided up into two or three vegetation zones/regions, and local checklists did not provide sufficient information on distribution.

The European seed beetles (Bruchinae)

As mentioned above, information on the presence and distribution of seed beetles was obtained in two ways: (1) collection of seed beetles from the vegetation (usually by sweep netting) or from nectar plants provenly present in a zone/region, but no host data could be deduced from it. However, these occurrences are invaluable for taxonomic purposes. Such a basic information source is Anton (2010). (2) Data originating from faunistic works based on pod collections and subsequent rearing out of adult seed beetles were the only reliable information for host plants. Until now, unfortunately, relatively few such efforts could be identified (Bagdasarian 1941; Lukianovich and Ter-Minasian 1957; Szentesi and Jermy 1995, 2003; Delobel and Delobel 2003, 2006; Delobel et al. 2004; Yus-Ramos and Romero 2011). In accordance with the above, host information was not accepted and used if it relied on method "(1)," if only the host genus name was available, or if it was an example of the serial citations of uncertain literature sources.

Globally spread stored product seed beetles, such as *Callosobruchus* species and *Zabrotes subfasciatus* Boheman, were not considered in this study, except *Acanthoscelides obtectus* Say (native to the Western Hemisphere), which lays eggs in the fields in Europe. Seed beetles whose host plants do not belong to the Fabaceae (Online Resource Excel File) were

not included in the analyses, such as members of the genus *Spermophagus* Schönherr, which are exclusively associated with Convolvulaceae and Malvoidea (Kergoat et al. 2015). However, some alien seed beetle species were also taken into consideration if their hosts were present in a vegetation zone/region. Authorities of seed beetle species names are given in Online Resource 2: Table 3.

Analysis of data

Comparing legume species compositions of vegetation zones/regions

To establish the similarity of vegetation zones/regions, paired comparisons of species lists were performed across the 17 zones/regions (152 comparisons for each native and endemic species, respectively). After counting the number of shared species, binary Sørensen indices (Magurran 2004) were calculated by the formula: $S_s = 2a/2a + b + c$, where S_s is Sørensen's similarity index, a is the number of species shared by two zones/regions, b is the number of species in the second zone/region, and c is the number of species only in the first zone/region. The resulting indices were arranged in symmetric matrices and first product-moment correlations were computed at $p=0.05$ level, then cluster analyses (UPGA method, Euclidean distance) were performed on the correlation matrices (Online Resource 2: Tables 8 and 9) using the STATISTICA program v8 (StatSoft 2007).

Frequency distribution of legume species

Frequency distributions were established by recording species' presence in 1, 2, ..., 17 zones/regions of all lists of species occurrence, then by drawing a histogram using the STATISTICA program. The histogram showed a significant fit ($p=0.0108$) approximating the geometric series.

Occurrence and number of seed beetle species in vegetation zones/regions

Anton (2010) provided the basic information source on the occurrence of seed beetles in Europe, and some corrections were considered after Yus-Ramos (2010). In addition, checklists, publications, monographs and museum records were also included if they were based on collections and rearing data. See Online Resource Excel File and Online Resource 1: References belonging to the Excel file through literature codes.

Host specialization and host use by plant life cycles of the seed beetle species

The host range data came from our collections and those of others, as well as from publications on seed beetle biology

reporting host affiliation information (Online Resource Excel File and Online Resource 1: References).

Results

Legume species

The number and distribution of leguminous species/subspecies/varieties

In this study, 1,471 species, 102 subspecies, and 11 varieties of European legumes were included, altogether 1584 species/subspecies/varieties. They belong to 107 genera and 25 tribes (Table 1) and are distributed in 17 zones and regions (Table 2). A comparison with the world's leguminous flora (Online Resource 2: Table 1) indicates that the European leguminous flora includes only a fraction (ca. 9%) of the ca. 20,000 species found globally. Tribes of Fabaeae, Genisteae, Hedysareae, Loteae, and Trifolieae are exceptions as their number of species in Europe represents half of the known species of these tribes worldwide. The most species-rich tribe in the world is Galegeae, more than 14% of which is represented in Europe, overwhelmingly in the Colchis-Caucasus and Pontic-Caspian zones.

Detailed information on the taxonomical status, distributions, and life cycle of European species included in this study can be found in the worksheets of the Online Resource Excel File. In general, species richness increases from the Arctic to the Mediterranean zones. Table 2 presents the distribution and life cycles of tribes and genera across zones/regions, and, remarkably, the number of alien species/subspecies/varieties exceeds that of the native and endemic species/subspecies/varieties in almost all zones/regions. However, these tribes and genera represent *all species* that occur in any of the zones/regions, frequently in "double statuses," i.e., being both native and alien in the same zone/region (Online Resource 2: Table 2). This is a recurrent case by the available checklists and floristic works because zones/regions include several countries where the species can be either native or alien, or both depending on the geographic size of the regions. Among the many available instances, only two are mentioned: *Lotus parviflorus* Desf. is a native species to Portugal but is considered an alien in the Azores, although both are members of the West-Mediterranean region (de Sequeira 2012). Being an Eu-endemism in Hungary, *Colutea arborescens* L. is at the same time an alien species in the Czech Republic. (Pyšek et al. 2012), although both occur in the Central-European (Tc) region of the Temperate zone. The frequency distribution by the number of zones/regions of all species/subspecies/varieties is illustrated in Online Resource 2: Fig. 2, and those further subdivided by plant life cycles are shown in Online Resource 2: Table 2.

Table 1 Number of tribes, genera, species, subspecies, and varieties of legumes (Fabaceae) of Europe, and those of the seed beetle genera and the number of species whose hosts are known

| Leguminous tribes ^a | No. of legume genera | No. of legume species | No. of legume subspecies | No. of legume varieties | No. of bruchine species | Seed beetle genera (Bruchinae) |
|--------------------------------|----------------------|-----------------------|--------------------------|-------------------------|-------------------------|--|
| Cercideae Bronn | 2 | 5 | | | 1 | <i>Bruchidius</i> Schilsky |
| Cassieae Bronn | 2 | 8 | 1 | | | |
| Caesalpinieae Rchb. | 7 | 12 | | | 2 | <i>Megabruchidius</i> Borowiec |
| | | | | | 1 | <i>Penthobruchus</i> Kingsolver |
| | | | | | 1 | <i>Caryedon</i> Schoenherr |
| | | | | | 1 | <i>Amblycerus</i> Thunberg |
| Mimoseae Bronn | 4 | 4 | | | 1 | <i>Bruchidius</i> |
| Acacieae Dumort. | 1 | 18 | 1 | | 1 | <i>Bruchidius</i> , |
| | | | | | 1 | <i>Mimosestes</i> Bridwell, |
| | | | | | 4 | <i>Caryedon</i> , |
| | | | | | 1 | <i>Pseudopachymerina</i> Zacher |
| Ingeae Benth. | 4 | 10 | | | 1 | <i>Bruchidius</i> |
| Sophoreae Spreng. ex DC. | 2 | 2 | | | | |
| Thermopsidae Yakovlev | 3 | 6 | | | 2 | <i>Bruchidius</i> ^b |
| Crotalariae (Benth.) Hutch. | 2 | 4 | | | | |
| Genisteae (Bronn) Dumort. | 18 | 227 | 18 | 3 | 9 | <i>Bruchidius</i> , |
| | | | | | 1 | <i>Bruchus</i> Linnaeus |
| Amorpheae Boriss. | 1 | 5 | | | 1 | <i>Acanthoscelides</i> Say |
| Dalbergieae Bronn ex DC. | 3 | 3 | | | 3 | <i>Caryedon</i> |
| Indigofereae Benth. | 1 | 4 | | | | |
| Millettieae Miq. | 1 | 2 | | | | |
| Phaseoleae (Bronn) DC. | 8 | 10 | 1 | 1 | 1 | <i>Acanthoscelides</i> , |
| | | | | | 1 | <i>Bruchidius</i> , |
| | | | | | 1 | <i>Bruchus</i> |
| Desmodieae (Benth.) Hutch. | 2 | 5 | | | | |
| Psoraleeae Lowe | 2 | 6 | | | | |
| Sesbanieae (Rydb.) Hutch. | 1 | 3 | | | | |
| Loteae DC. | 13 | 136 | 17 | | 8 | <i>Bruchidius</i> |
| Robinieae (Benth.) Hutch. | 1 | 4 | | 1 | | |
| Galegeae (Bronn) Dumort. | 10 | 435 | 17 | | 17 | <i>Bruchidius</i> , |
| | | | | | 1 | <i>Palaeobruchidius</i> Egorov, |
| | | | | | 1 | <i>Paleoacanthoscelides</i> Borowiec, |
| | | | | | 1 | <i>Bruchus</i> |
| Hedysareae DC. | 8 | 119 | 5 | | 1 | <i>Kytorhinus</i> Fischer von Waldheim, |
| | | | | | 8 | <i>Bruchidius</i> ^c , |
| | | | | | 2 | <i>Paleoacanthoscelides</i> |
| Cicereae Alef. | 1 | 5 | | | 1 | <i>Acanthoscelides</i> , |
| | | | | | 1 | <i>Bruchus</i> |
| Trifolieae (Bronn) Endl. | 5 | 286 | 15 | 3 | 21 | <i>Bruchidius</i> |
| Fabeae Rchb. | 5 | 151 | 27 | 3 | 31 | <i>Bruchus</i> , |
| | | | | | 7? | <i>Bruchidius</i> , |
| | | | | | 1 | <i>Kytorhinus</i> |
| In total: 25 | 107 | 1470 | 102 | 11 | 135 ^d | 13 |

^aPhylogenetic order of tribes by Lewis et al. (2005)^b*Bri. marginalis* (Bagdasarian 1941)^c*Bri. cisti* (Hoebeke et al. 2009) (misidentification?)^dThe same seed beetle species can occur in more than one host species

Table 2 The number and distribution of legume plant tribes, genera, and life cycles across European vegetation zones and regions

| Vegetation zone/region ^a | Number of legume tribes and genera | | | | | | | | | | | |
|-------------------------------------|------------------------------------|-------|-----------------|-------|-----------------|-------|-----------------|-------|-----------------|-------|-----------------|-------|
| | Np ^b | | Na ^c | | Ep ^d | | Ea ^e | | Ap ^f | | Aa ^g | |
| | Tribe | Genus | Tribe | Genus | Tribe | Genus | Tribe | Genus | Tribe | Genus | Tribe | Genus |
| Arctic zone (A) | 4 | 6 | 1 | 1 | 2 | 3 | | | 2 | 3 | | |
| Boreo-Atlantic r. (Ba) | 5 | 12 | 3 | 3 | 3 | 3 | | | 7 | 14 | 3 | 4 |
| Fennoscandic r. (Bb) | 5 | 12 | 2 | 2 | 3 | 6 | | | 11 | 27 | 7 | 17 |
| Boreo-Russian r. (Bc) | 5 | 11 | 2 | 2 | 2 | 3 | | | 7 | 13 | 2 | 4 |
| Hemiboreal r. (Ta) | 6 | 16 | 3 | 6 | 5 | 8 | | | 14 | 31 | 6 | 15 |
| Atlantic r. (Tb) | 7 | 24 | 5 | 15 | 5 | 15 | 2 | 2 | 19 | 51 | 8 | 19 |
| Central-European r. (Tc) | 8 | 26 | 5 | 17 | 6 | 22 | 2 | 3 | 23 | 56 | 8 | 22 |
| East-European r. (Td) | 8 | 23 | 5 | 10 | 6 | 17 | 1 | 1 | 17 | 34 | 7 | 14 |
| Balkan r. (Te) | 12 | 35 | 6 | 19 | 6 | 21 | 2 | 3 | 18 | 39 | 6 | 11 |
| region of Pyrenees (Tf) | 7 | 20 | 5 | 10 | 6 | 17 | 2 | 3 | 4 | 4 | 3 | 3 |
| region of Alps (Tg) | 7 | 22 | 3 | 6 | 5 | 18 | 2 | 2 | 12 | 18 | 5 | 11 |
| region of Carpathians (Th) | 5 | 11 | 2 | 2 | 5 | 9 | | | 2 | 2 | | |
| Colchis-Caucasus zone (K) | 12 | 39 | 5 | 16 | 6 | 19 | 3 | 4 | 19 | 34 | 6 | 11 |
| Pontic-Caspian zone (P) | 11 | 38 | 5 | 15 | 6 | 20 | 3 | 3 | 17 | 32 | 7 | 13 |
| West-Mediterranean r. (Ma) | 9 | 36 | 6 | 22 | 6 | 20 | 4 | 6 | 17 | 40 | 8 | 18 |
| Central-Mediterranean r. (Mb) | 10 | 32 | 6 | 21 | 6 | 20 | 3 | 6 | 19 | 34 | 7 | 12 |
| East-Mediterranean r. (Mc) | 11 | 28 | 6 | 21 | 7 | 14 | 3 | 7 | 8 | 10 | 3 | 6 |

For a clearer view, zeros are not signed in empty cells

^aAccording to Lang et al. (1994)

Life cycles: ^bNp= native perennial; ^cNa= native annual; ^dEp= endemic perennial; ^eEa= endemic annual; ^fAp= alien perennial; ^gAa= alien annual; r= region

In contrast to the above, the realistic, zone/region-specific number of leguminous species is presented in Table 3 subdivided by life cycles. There are 717 species/subspecies/varieties occurring only in single zones/regions, and 665 of these are native and endemic. The remaining 867 species/subspecies/varieties are present in two, three, ..., 16 zones/regions. The most widely spread are three perennial species (*Medicago lupulina* L., *Vicia cracca* L., and *V. hirsuta* (L.) Gray) and one annual species (*Trifolium arvense* L.), which can all be found in 16 zones/regions (no species occur in all 17 zones/regions). Among the perennials, *Lotus corniculatus* L., *Trifolium repens* L., *T. fragiferum* L., *Lathyrus pratensis* L., *L. sylvestris* L., and *Vicia sepium* L. inhabit 15 zones/regions. Nevertheless, some annual species are also widely distributed: *Lathyrus aphaca* L. in 12, *Trifolium dubium* Sibth. in 13, *Vicia villosa* Roth and *V. sativa* subsp. *nigra* (L.) Ehrh. in 14 and *Trifolium campestre* Schreb. in 15 zones/regions. Regions of the Boreal zone and the European mountainous areas (Pyrenees, Alps, and Carpathians) hardly have any specific native species/subspecies/varieties but do have some zone/region-specific endemics, such as *Lotus norvegicus* (Chrtkova) Miniaev in the Fennoscandic region, or *Cytisus emeriflorus* Rchb. in the region of Alps. The number of Eu- and zone/region-specific endemic species/subspecies/varieties of all zones/regions is substantially

more than the native ones: 380 vs. 284, respectively. The inventory is completed with 52 alien species/subspecies/varieties (Table 3).

There are interesting distributional patterns of some leguminous genera in the vegetation zones/regions: 66.7% of the *Anthyllis* L. species inhabit the West-Mediterranean region, 56.7% and 17.6% of the *Astragalus* species are present at Colchis-Caucasus (K) and Pontic-Caspian (P) zones, respectively; 72.6% of the *Genista* L. species can be found in the West-, Central- and East-Mediterranean regions; 88.2% of the *Hippocrepis* L. species occupy the West-Mediterranean region; 57.9% of the *Onobrychis* Mill. species occupy the Colchis-Caucasus; 76.9% of the *Ononis* L. species the West-Mediterranean region; and 44.4% of the *Trifolium* L. species the Balkan region (Te).

Composition, species richness, and similarities of vegetation zones/regions

The Online Resource Excel File gives detailed information on the composition and species richness of vegetation zones/regions. Correlation coefficients (Online Resource 2: Tables 8 and 9) of pairwise product-moment comparisons of native and endemic leguminous species richness, respectively, between vegetation zones and regions based on

Table 3 The number of legume species that occur only in a single vegetation zone/region (see Table 2 for full names)

| Vegetation zone/region ^a Number of legume and seed beetle species in | | | | | | | | | | | | | | |
|---|--------------|------------------|--------------|------------------|--------------|------------------|--------------|------------------|--------------|------------------|--------------|------------------|-------------------------|----------------------|
| | Np plant sp. | Sb sp. in Np sp. | Na plant sp. | Sb sp. in Na sp. | Ep plant sp. | Sb sp. in Ep sp. | Ea plant sp. | Sb sp. in Ea sp. | Ap plant sp. | Sb sp. in Ap sp. | Aa plant sp. | Sb sp. in Aa sp. | Total no. of plant spp. | Total no. of Sb spp. |
| Arctic z. (A) | 2 | | | | | | | | | | | | 2 | |
| Boreo-Atlantic r. (Ba) | | | | | 1 | | | | 1 | | | | 1 | |
| Fennoscandic r. (Bb) | | | | | 1 | | | | 1 | | | | 3 | |
| Boreo-Russian r. (Bc) | | | | | 1 | | | | | | 1 | | 1 | |
| Hemiboreal r. (Ta) | | | | | 1 | | | | | | 1 | | 2 | |
| Atlantic r. (Tb) | 1 | | | | 7 | | | | 6 | 2 | 2 | | 16 | 2 |
| Central-European r. (Tc) | | | 1 | | 8 | | | | 8 | 1 | 7 | | 24 | 1 |
| East-European r. (Td) | 1 | | | | 1 | | | | | | | | 2 | |
| Balkan r. (Te) | 15 | 2 | 8 | | 43 | | 5 | 1 | 4 | | | | 75 | 3 |
| r. of Pyrenees (Tf) | | | | | 8 | | | | | | | | 8 | |
| r. of Alps (Tg) | | | | | 1 | | | | 1 | | | | 2 | |
| r. of Carpathians (Th) | | | | | 1 | | | | | | | | 1 | |
| Colchis-Caucasus z. (K) | 91 | 7 | 7 | 1 | 113 | | 2 | | 1 | | | | 214 | 8 |
| Pontic-Caspian z. (P) | 35 | 4 | 5 | | 35 | | 1 | | 3 | 1 | 1 | | 80 | 5 |
| West-Mediterranean r. (Ma) | 50 | 5 | 27 | 4 | 72 | | 5 | | 5 | | | | 159 | 9 |
| Central-Mediterranean r. (Mb) | 6 | 3 | 4 | 2 | 49 | | 4 | 1 | 6 | | 1 | | 70 | 6 |
| East-Mediterranean r. (Mc) | 14 | 2 | 17 | 2 | 17 | | 6 | | 2 | | 1 | | 57 | 4 |
| Total number | 215 | 23 | 69 | 9 | 358 | 1 | 23 | 1 | 38 | 4 | 14 | 14 | 717 | 38 |

Highlighted digits refer to the number of seed beetle species associated with vegetation zones/regions

Life cycles: Np=Native perennial; Sb=seed beetle (Bruchinae); Aa=Native annual; Ep=Endemic perennial; Ea=Endemic perennial; Ap=Alien perennial; Aa=Alien annual; For a clearer view, zeros are not signed in empty cells. r=region; z=zone; sp.=species

^aAccording to Lang et al. (1994)

Sørensen's similarity index indicated several close associations and divergences among zones and regions. The native species compositions of the Boreal zone and the Boreo-Russian region create a similar floristic group with highly significant correlation coefficients (Online Resource 2: Table 8). As a clear consequence of this, significant negative correlations separate this group from the Colchis-Caucasus (K), Pontic-Caspian (P), and Mediterranean zones/regions. To the contrary, abundant similarities can be detected in the leguminous species composition between the Central-European (Tc) and the Balkan (Te) regions and the Colchis-Caucasus (K), Pontic-Caspian (P), and Mediterranean zones, including some elements of the East-European region. As could be expected, there is a high level of similarity between Colchis-Caucasus and Pontic-Caspian, and among regions of the Mediterranean zone, respectively, whereas the mountainous areas are detached from the rest. A subsequent cluster analysis performed on the correlation matrix of native species corroborated the above results (Online Resource 2: Fig. 3), making clearer the associations about, e.g., the close floristic connection of the Balkan and the Mediterranean regions.

The comparison of Eu- and zone/region-specific endemic leguminous flora showed reasonably restrictive connections (Online Resource 2: Table 9). Nevertheless, regions of the Boreal zone, those of Central- and East-Europe, regions of the Pyrenees and Alps, and Colchis-Caucasus and Pontic-Caspian, respectively, were similar in endemic species composition. The Central-European (Tc), Balkan (Te), and even the Alpine region (Tg) show connections with the Central-Mediterranean (Mb) leguminous flora. Results of the cluster analysis (Online Resource 2: Fig. 4) generally strengthen the presence of similar groups but also create several surprisingly new ties. For instance, there is a close connection between the easternmost Mediterranean region and the Caucasus. The westernmost Mediterranean region stands alone with many zone/region-specific endemic species. Taking all the zones/regions together, the number of zone/region-specific endemic species is greater than or equal to the number of native species in several zones/regions (Table 3).

Undoubtedly, the most species-rich zones of leguminous species in Europe are the Colchis-Caucasus, Pontic-Caspian, and Mediterranean zones (and the western region within the latter), followed by the Balkan and Central-European regions (Table 4). Concerning the dominant genera, there is a clear tendency: *Astragalus* and *Onobrychis* are most numerous in the Colchis-Caucasus and Pontic-Caspian zones, whereas *Trifolium* is most abundant in the Mediterranean and the Balkan, followed by *Genista*, *Hippocrepis*, *Lotus* L. and *Ononis* (Table 4). In contrast, *Lathyrus* L., *Medicago* L., and *Vicia* L. are present in all zones/regions in more-or-less similar numbers. The most species-rich genus is *Astragalus*, represented by 334 species and 16 subspecies in this study.

The next most species-rich genus is *Trifolium* (123 species, two subspecies, and three varieties), followed by *Genista* (108 species and two subspecies) and *Vicia* (80 species, 18 subspecies, and three varieties).

Distribution of perennial and annual leguminous species in Europe

The number of leguminous species increased towards the southern floristic regions. The number of annual species increased towards the south but stayed always lower than that of perennial ones (Table 3). No native annual species could be found in the Arctic and Boreal zones, and even in two Temperate regions (Hemiboreal and Atlantic), only alien annuals occurred. Genera such as *Cytisus* Desf. (34 species), *Genista* (72 species), *Onobrychis* (38 species), and *Oxytropis* DC. (32 species) consisted only of perennials, whereas other major genera (*Lathyrus*, *Lotus*, *Medicago*, *Ononis*, and *Vicia*) harbored these in 43–84%. However, in some cases, the prevalence of annuals was conspicuous among European- or zone/region-specific endemic species. The larger portion, i.e., 65.9% of the 123 European *Trifolium* species is annual, and more than half (55.9%) of the 34 species found in the southern zones/regions (Balkan, Mediterranean, Colchis-Caucasus, and Pontic-Caspian) are also annual. As another example, out of the 32 *Trigonella* L. species, almost entirely localized in the Mediterranean and to Colchis-Caucasus and Pontic-Caspian zones, only a single species (*Trigonella strangulata* Boiss.) is known as perennial. The number of endemic annual species is extremely low, 3% (22 species) of all leguminous species of Europe and restricted to the Balkan region, Colchis-Caucasus, Pontic-Caspian zones, and floristic regions of the Mediterranean zone.

Alien leguminous species

The number of alien leguminous species (naturalized and neophytes) is ca. 52 (38 perennial and 14 annual), mainly among the Acacieae, Caesalpinieae, Cassieae, Cercideae, Ingeae Mimoseae, and Sophoreae tribes. The species are usually ornamentals from tropical and subtropical countries, and although they are more abundant in the Mediterranean regions, not at all are restricted there. For instance, *Senna occidentalis* (L.) Link, a member of the circumtropical genus, can be found in the Fennoscandic, or *Sophora flavescens* Aiton, a resident of SE-Asia, in the Atlantic region.

Besides environmental factors limiting the occurrence of species, e.g., in high mountainous regions, the lack of thorough investigations or the availability of information hinders completing a full picture of European leguminous vegetation.

Table 4 The number and distribution of leguminous species among the most species-rich genera in the European vegetation zones and regions

| Vegetation zones/ regions ^a | <i>Anthyllis</i> | <i>Astragalus</i> | <i>Cytisus</i> | <i>Genista</i> | <i>Hedysarum</i> | <i>Hippocrepis</i> | <i>Lathyrus</i> | <i>Lotus</i> | <i>Lupinus</i> | <i>Medicago</i> | <i>Onobrychis</i> | <i>Ononis</i> | <i>Oxytropis</i> | <i>Trifolium</i> | <i>Trigonella</i> | <i>Vicia</i> |
|---|------------------|-------------------|----------------|----------------|------------------|--------------------|-----------------|--------------|----------------|-----------------|-------------------|---------------|------------------|------------------|-------------------|--------------|
| Arctic z. (A) | 1 | 7 | | 1 | | 4 | | | 3 | | | 4 | 8 | | | 4 |
| Boreo-Atlantic r. (Ba) | 3 | 3 | 1 | 1 | | 7 | 3 | 1 | 3 | | | 1 | 3 | 15 | | 10 |
| Fennoscandic r. (Bb) | 5 | 8 | 3 | 3 | 1 | 16 | 8 | 5 | 10 | | 1 | 3 | 5 | 17 | 2 | 19 |
| Boreo-Russian r. (Bc) | 2 | 6 | 2 | 1 | 1 | 10 | 4 | 1 | 3 | | 1 | 1 | 3 | 11 | | 13 |
| Hemiboreal r. | 6 | 7 | 4 | 5 | | 20 | 8 | 5 | 9 | | 3 | 3 | 2 | 22 | | 24 |
| (Ta) | | | | | | | | | | | | | | | | |
| Atlantic r. (Tb) | 9 | 16 | 10 | 20 | 1 | 4 | 27 | 8 | 9 | 22 | 1 | 13 | | 49 | 6 | 41 |
| Central-European r. (Tc) | 8 | 43 | 24 | 13 | 4 | 6 | 37 | 14 | 11 | 33 | 9 | 15 | 9 | 72 | 14 | 53 |
| East-European r. | 3 | 41 | 17 | 6 | 4 | 1 | 24 | 9 | 7 | 10 | 6 | 4 | 9 | 34 | 5 | 35 |
| (Td) | | | | | | | | | | | | | | | | |
| Balkan r. (Te) | 6 | 5 | 27 | 23 | 5 | 7 | 38 | 18 | 11 | 30 | 22 | 16 | 3 | 91 | 12 | 52 |
| r. of Pyrenees (Tf) | 4 | 18 | 7 | 9 | 1 | 7 | 11 | 7 | 1 | 10 | 7 | 8 | 10 | 24 | | 19 |
| r. of Alps (Tg) | 5 | 14 | 6 | 7 | 1 | 3 | 19 | 7 | 3 | 12 | 3 | 8 | 8 | 31 | 2 | 33 |
| r. of Carpathians (Th) | 2 | 13 | 2 | 2 | 1 | 1 | 8 | | | 1 | 1 | | 7 | 9 | | 6 |
| Colchis-Caucasus z. (K) | 4 | 17 | 6 | 17 | 16 | 5 | 34 | 10 | 2 | 36 | 43 | 4 | 12 | 53 | 12 | 50 |
| Pontic-Caspian z. (P) | 1 | 11 | 155 | 13 | 15 | 2 | 35 | 10 | 7 | 36 | 26 | 6 | 20 | 45 | 9 | 40 |

Table 4 (continued)

| Vegetation zones/ regions ^a | <i>Anthyllis</i> | <i>Astracantha</i> | <i>Astragalus</i> | <i>Cytisus</i> | <i>Genista</i> | <i>Hedysarum</i> | <i>Hippocrepis</i> | <i>Lathyrus</i> | <i>Lotus</i> | <i>Lupinus</i> | <i>Medicago</i> | <i>Onobrychis</i> | <i>Ononis</i> | <i>Oxytropis</i> | <i>Trifolium</i> | <i>Trigonella</i> | <i>Vicia</i> |
|---|------------------|--------------------|-------------------|----------------|----------------|------------------|--------------------|-----------------|--------------|----------------|-----------------|-------------------|---------------|------------------|------------------|-------------------|--------------|
| West-Mediterranean r. (Ma) | 22 | 1 | 41 | 19 | 43 | 5 | 22 | 34 | 29 | 6 | 36 | 14 | 49 | 1 | 60 | 7 | 54 |
| Central-Mediterranean r. (Mb) | 9 | 4 | 42 | 9 | 40 | 4 | 8 | 34 | 23 | 8 | 34 | 6 | 26 | 5 | 72 | 5 | 56 |
| East-Mediterranean r. (Mc) | 4 | 1 | 29 | 4 | 7 | 3 | 6 | 26 | 11 | 5 | 27 | 5 | 16 | 49 | 15 | 33 | |

For the authors' names of genera see Online Resource 2: Table 3. For a clearer view, zeros are not signed in empty cells

z = zone, r = region. Plant species can occur in more than one zone/region

^aLang et al. (1994)

The seed beetles

Literature search and published collection data yielded 175 seed beetle species of the Bruchinae subfamily in Europe. Among these, 140 native and 35 introduced species could be found. Table 1 lists the number of bruchine genera and species of leguminous tribes. Online Resource 2: Table 3 provides the list of seed beetles found in European legume tribes and genera. Among the 35 introduced seed beetle species, seven were stored products pests and were excluded from the present analysis apart from *Acanthoscelides obtectus* Say that lays eggs both in stores and in the field (Jarry and Chacon 1983). Seven species of the 175 were marked as *incertae sedis*. (See „Bruchines in Europe” worksheet in the Online Resource Excel File.) There were 99 *Bruchidius* and 31 *Bruchus* species found (see 10 additional species of other genera in Table 1).

Based on literature and collection data, 364 (23%) leguminous plant taxa have been scanned for the presence of seed beetles and 276 (17.4%) of the total (1584) were found to harbor seed beetles registered above. Naturally, the number of samples collected must have been several thousand; however, the species' representation of legumes seems low, and the distribution of sampled genera is uneven. For instance, of the 110 *Genista* species, 10; from 28 *Hippocrepis* species, five; from 48 *Lotus* species, 17; from 52 *Oxytropis* species, three; from 27 *Astracantha* Podlech species, one; from 349 *Astragalus* species, 41; from 35 *Hedysarum* species, three; from the 72 *Onobrychis* species, 12; and of the 56 *Ononis* species, only three species were documented as collected and examined for the presence of seed beetles. Genera of Trifolieae and Fabaeae were somewhat better surveyed: of the 128 *Trifolium* species 41, of the 70 *Medicago* species 25, of the 101 *Vicia* taxa 60, and of the 69 *Lathyrus* species 30 species were collected. Online Resource 2: Table 1 provides information on the number of leguminous species collected and that of the species from which the seed beetles were reared across tribes.

Distribution of seed beetles among zones/regions

Online Resource 2: Table 2 presents distributional data of seed beetles according to zones/regions, whether their hosts are native, endemic or alien, as well as perennial or annual. Taking into consideration single occurrences per zone/region, there were 104 seed beetle species present in 15 zones/regions. The most frequently occurring (widespread) species were *Bru. atomarius* Linnaeus at 13 zones/regions, *Bru. loti* Paykull and *Bru. affinis* Frölich at 12, *Bri. marginalis* Fabricius, *Bri. lividimanus* Gyllenhal, *Bri. villosus* Fabricius, and *Bru. lentis* Frölich at 10 zones/regions. The rarest seed beetles (14 native and three alien species), e.g., *Bri. bernardi* Delobel and Anton, *Bri. fallaciosus*

Iablokoff-Khznoria, *Bru. brisouti* Kraatz, or *Bru. ibericus* Anton, are only known from single zones/regions. The remaining species are present in two to nine zones/regions. From the table, the Arctic zone and the Boreo-Atlantic region seem depauperate, whereas the Fennoscandic, Boreo-Russian, Hemiboreal, and mountainous regions can be characterized by a low number of seed beetle species. Even among these, and in the regions of the Temperate zone, the number of two groups of seed beetles increases to a greater extent: (1) those that live in legumes that became “aliens,” despite being native elsewhere in the same region, e.g., *Bri. villosus* in *Lupinus angustifolius* L., *Bruchus atomarius* L. in *Lathyrus latifolius* L., or in *L. tuberosus* L., and (2) several introduced species, such as *Caryedon longipennis* Pic, *C. serratus* Olivier and others, whose host affiliation is not properly known, or species like *Bruchidius cisti* Fabricius that live on Cistaceae in the Atlantic (Tb) region. By the host species richness, the number of seed beetle species also increases toward the Mediterranean.

Of the 717 legume species occurring in single vegetation zones/regions, only 30 species and three subspecies were associated with 38 seed beetle species (Online Resource 2: Table 4). Among the 38 seed beetle species, eight were present in two legume species and one has not yet been identified. Remarkably, among the legume species, there were seven native annuals, one endemic annual, and one endemic perennial. The number of seed beetle species restricted to a single zone/region—these may be called zone/region-specific seed beetles—was 51 (38 native and 13 introduced) species (Table 3 and Online Resource Excel file). They were present in only eight zones/regions, especially in those, where legume species richness was high (Colchis-Caucasus and the Mediterranean regions).

Host plant relations

The host plants of 44 seed beetle species are unknown (Online Resource Excel File), and a further 12 are not leguminous feeders and can only be found in plant families such as Apiaceae, Cistaceae, Compositae, and Geraniaceae. Furthermore, the two recognized European species of the *Rhaebus* Fischer von Waldheim genus develop in *Nitraria* L. species (Nitrariaceae, Sapindales). *Bruchidius* species inhabit twice as many (162) leguminous species than *Bruchus* (80 species), and nine host species are shared by the two genera. No seed beetle species have been found in *Astracantha*, *Melilotus* Mill., and *Ulex* L. species and surprisingly low numbers (one or two species) in *Hedysarum*, *Ononis*, *Oxytropis*, and *Trigonella* genera. Relative to the plant species richness, few seed beetle species have been reared from species of the *Astragalus* and *Genista* genera. The frequency distribution of seed beetles according to how many species utilize a single legume species is given in Table 5.

The majority (139 species) occur in one legume species/subspecies/variety; however, at the extreme, at least three legume species (*Pisum sativum* L., *Trifolium angustifolium* L. and *Vicia cracca*) are inhabited by seven different seed beetle species in Europe. 124 hosts were utilized by 2–6 seed beetle species. About 47% of host use overlap, meaning that on average 3 ± 1.3 (\pm SD) seed beetle species develop in the same host plant.

Members of the subfamily Bruchinae are oligophagous, restricted in host range to the Fabaceae with some exceptions listed above. However, within the legume seed-consuming species, there seems to be 34 mono-, 35 sensu stricto (*s. s.*), and 35 sensu lato (*s. l.*) oligophagous members using two to four and five to 20 host plants, respectively, in Europe (Table 6), following the definitions given earlier. The exclusive use of the species-rich Galegeae and Trifolieae tribes—besides others represented with only few species in Europe—by members of the genus *Bruchidius* is remarkable (Table 1).

As for the relationship with legume life cycles, of the 104 seed beetle species, 33 species feed on seeds of only perennial, 52 species on both perennial and annual, and 19 only on annual hosts (native, endemic and alien lumped together). Among the last, nine species were strictly monophagous (e.g., *Bri. murinus* Boheman, *Bri. lineatus* Allard, *Bri. annulicornis* Allard, *Bru. laticollis* Boheman, *Bru. perezi* Kraatz, etc.). However, one of the unusual associations, *Bri. lineatus* utilizing the annual *Lathyrus aphaca* (Fabaceae), might be a misidentification. On the one hand, concerning the three host specialization categories, Online Resource 2: Table 5 demonstrates that, in general, the seed beetles use perennial and annual leguminous hosts alike. On the other hand, 58 *Bruchidius* species used a mean of 2.4 ± 0.3 (\pm SE) native perennials, 1.7 ± 0.3 native annuals, 0.4 ± 0.1 endemic perennials, 0.02 ± 0.02 endemic annuals, 0.1 ± 0.03 alien perennials and 0.1 ± 0.04 alien annual legume species. Thirty *Bruchus* species consumed a mean of 2.7 ± 0.5 native perennials, 3.4 ± 0.7 native annuals, 0.4 ± 0.2 endemic perennials, no endemic annuals, 0.1 ± 0.1 alien perennials, and 0.4 ± 0.1 alien annuals, respectively. *Bruchus* species use more legume species as hosts, a wider range of plant life cycles, as well as significantly more annual legumes than those of *Bruchidius*. [Mean (\pm SE) number of legume species used: *Bruchidius* 4.6 ± 0.6 , *Bruchus* 7.0 ± 1.1 , $N = 58$ and 30 , t -test: 2.1132 , $df = 86$, $p = 0.03375$, Levene-test: $F_{1,86} = 3.4314$, $p = 0.0674$; mean (\pm SE) number of native annual legume species used: *Bruchidius* 1.7 ± 0.3 , *Bruchus* 3.4 ± 0.7 , $N = 58$ and 30 , t -test: 2.4496 , $df = 86$, $p = 0.0163$, Levene-test: $F_{1,86} = 7.3265$, $p = 0.0082$]. Interestingly, however, members of both genera utilize native and endemic annuals in very low or in almost negligible numbers. The distribution of these among the leguminous life cycles can be found in Table 6.

Besides some genus-level cases, there must have been several possible and surprising major host shifts noted at the plant tribe level among seed beetles (Online Resource 2: Table 6). For example, *Bri. incarnatus* Boheman on Phaseoleae and Fabaeae, *Bri. longulus* Schilsky on Genisteae and Trifolieae, *Bri. pallidulus* Reitter, and *Paleoacanthoscelides gilvus* Gyllenhal on Galegeae and Hedysareae, *Bri. poupillieri* Allard on Loteae and Hedysareae, *Bru. ulicis* Mulsant and Rey on Genisteae and Fabaeae, and *Bri. villosus* on Genisteae and Thermopsidae.

Alien seed beetle species

Some of the 35 alien seed beetle species followed the already naturalized hosts in time. For example, *Amorpha fruticosa* L. has been present in Hungary since the early twentieth century. The associated seed beetle, *Acanthoscelides pallidipennis* Motschulsky followed it ca. 70 years later (Szentesi 1999). Others, supported by the more favorable environmental conditions, moved to northern regions. Such recent invasions are *Bri. terrenus* Sharp of East Palearctic origin on *Albizia julibrissin* Durazz. (Bodor and György 2014; Yus-Ramos et al. 2014; Mouttet et al. 2016) and *Bri. siliquastri* Delobel on *Cercis siliquastrum* L. (Kergoat et al. 2007b; Stojanova et al. 2011) in the Central- (Tc) and East-European (Te) regions, or the two *Megabruchidius* species of South-Asian origin on the naturalized *G. triacanthos* L. (Jermy et al. 2002) or on *Gymnocladus dioicus* (L.) Koch (György and Tuda 2020) at several parts of Europe. The number of alien seed beetle species is presented in Table 3 and Online

Resource 2: Table 2 by zones/regions and according to legume life cycles.

Discussion

As aptly mirrored in this study too, there are hiatuses and uncertainties in providing a satisfactory picture of the distributions of legumes in Europe. The primary cause of this can be the lack of checklists based on a generally harmonized and accepted vegetation map of Europe. The distributions are influenced by political borders (countries) or, the most, by large geographic units (e.g., Asia). The most important plant databases (ILDIS, POWO, Euro-Med Plant Base) also follow this line. Although Lang et al.'s (2004) vegetation map proved very useful for this study, the above-described way of area division made it difficult to place many species into the appropriate zone or region. The obstacles were even higher in cases where a country was divided up into three vegetation zones or regions, like in the case of Norway or Sweden, and available checklists did not help elucidate doubtful distribution ranges.

Within the European vegetation zones/regions, the Mediterranean Basin undoubtedly is the most species-rich zone of leguminous species. Important environmental characteristics and plant diversity components influence species richness in this zone. Among others, strong climatic and high topographic heterogeneity, fire regimes, etc., define legume species richness (Cowling et al. 1996). These authors estimate

Table 5 Distribution of seed beetles (Bruchinae) among leguminous host plant species (Fabaceae) in Europe

| The number of seed beetle species that use the same legume plant species/subsp./variety | Plant life cycles | | | | | | Sum of plant species/subspecies/variety ^a |
|---|-------------------|-----------------|------------------|----|----|----|--|
| | Np ^b | Na ^c | E ^d p | Ea | Ap | Aa | |
| 1 | 66 | 43 | 14 | 7 | 7 | 2 | 139 |
| 2 | 25 | 34 | 3 | | 1 | 1 | 64 |
| 3 | 11 | 11 | 1 | | 2 | 2 | 27 |
| 4 | 8 | 4 | 1 | | 1 | | 14 |
| 5 | 6 | 6 | | | | | 12 |
| 6 | 2 | | | | | 2 | 4 |
| 7 | 1 | 2 | | | | | 3 |
| Total | 119 | 100 | 19 | 7 | 11 | 7 | 263 ^e |

Native and alien seed beetle species were lumped

For a clearer view, zeros are not signed in empty cells

^aIncludes 14 uncertain hosts (see the Online Resource Excel File “Szentesi_European bruchines and legumes”)

^bPerennial

^cAnnual

^dEndemic

^eThis value does not contain 13 host data specified at the genus level only

Table 6 Host-plant range of seed beetles (Bruchinae) on leguminous plants (Fabaceae) in Europe

| | How many legume species/subspecies/variety does a seed beetle use? | Number of legume species with life cycles | | | | | | Total no. of plant species/subspecies/variety ¹ | Number of bruchine species showing the relationship |
|---|--|---|-----------------|------------------|----|------------------|----|--|---|
| | | N ² p ³ | Na ⁴ | E ⁵ p | Ea | A ⁶ p | Aa | | |
| 1 | (monoph.) | 12 | 9 | 1 | | 10 | 2 | 34 | 34 |
| 2 | (s. s. oligoph.) | 11 | 6 | | | 2 | 1 | 20 | 10 |
| 3 | | 18 | 8 | 1 | | 3 | 3 | 33 | 11 |
| 4 | (s. l. oligoph.) | 26 | 24 | 4 | | | 2 | 56 | 14 |
| 5 | | 12 | 7 | 1 | | 1 | 4 | 25 | 5 |
| 6 | | 9 | 6 | | | | 3 | 18 | 3 |
| 7 | | 20 | 12 | 1 | | | 2 | 35 | 5 |
| 8 | (s. l. oligoph.) | 12 | 11 | | 1 | | | 24 | 3 |
| 9 | | 12 | 11 | 2 | | 1 | 1 | 27 | 3 |
| 10 | | 6 | 11 | 2 | | 1 | | 20 | 2 |
| 11 | | 5 | 5 | 1 | | | | 11 | 1 |
| 12 | | 6 | 3 | 3 | | | | 12 | 1 |
| 13 | | 7 | 15 | | 4 | | | 26 | 2 |
| 14 | | 12 | | 2 | | | | 14 | 1 |
| 15 | | 4 | 11 | | | | | 15 | 1 |
| 16 | | 11 | 20 | 1 | | | | 32 | 2 |
| 17 | | 27 | 12 | 8 | | 1 | 3 | 51 | 2 |
| 18 | 14 | 20 | 1 | | 1 | | 36 | 3 | |
| 19 | - | - | - | - | - | - | - | - | - |
| 20 | 5 | 11 | | 2 | | 2 | 20 | 1 | |
| The sum of legume and seed beetle species | | 229 | 202 | 28 | 7 | 20 | 23 | 509 | 104 |

²N = native, ³p = perennial, ⁴a = annual, ⁵E = endemic, ⁶A = alien; monoph. = monophagous; s. s. oligoph. = *sensu stricto* oligophagous, s. l. oligoph. = *sensu lato* oligophagous. For a clearer view zeros are not signed in empty cells

that the percentage of endemic species reaches 50% of all plant species, the annual species comprise 15%, and there are ca. 450 *Astragalus* species. In the present work, 37.5% of all legumes were found to be endemic, 18.1% annual and 349 *Astragalus* species/subspecies occurred. The difference concerning the number of *Astragalus* species (Cowling et al. 1996) must have originated from the North-African and Middle East (Türkiye, Levant region, part of Iran) areas, which, however, are not parts of the European vegetation map. The global legume diversity assessment (Yahara et al. 2013) lists 73 legume genera for the Mediterranean region, whereas 107 genera were found in this study. According to Buirra et al. (2017), 104 endemic legume species occur at Ma (the Iberian Peninsula and the Balears), 53 at Mb (Italy), and 35 at Mc (Greece). Comparable numbers of zone/region-specific endemic perennial and annual legume species are provided for the Mediterranean region in Table 3. Of the 10 diagnostic species given by Buirra et al. (2017) belonging to the *Adenocarpus*, *Cytisus*, *Genista*, *Onobrychis* and *Ulex* genera, none harbors seed predators based on a literature search in this study. The tie between the East-Mediterranean (Mc) region and the Colchis-Caucasus and Pontic-Caspian zones concerning Eu- and zone/region-specific endemisms

might refer to the biogeographical influence of the Middle East and Colchis-Caucasus, the last one extending to parts of Crimea and the Balkans. The Mediterranean region is also remarkable as a diversity center of legume species (Maxted and Bennett 2001) and especially those of *Trifolium* species. Scoppola et al. (2018) found 104 *Trifolium* species of which 37 were considered endemic for the Mediterranean regions. However, the difference concerning the similar data of this work can be attributed to the delimitation of vegetation vs. biogeographic borders and to definitions of native or endemic statuses, as well as the number of subspecies not included in this study (see conditions above).

The predominant leguminous life cycle is perennial in Europe. This way of life provides survival in the cold seasons and predictability of resources for seed beetles. Annuality is equally affecting seed beetle biology; nevertheless, it is an interesting question, why it is so frequent in some leguminous genera, especially among *Trifolium* species (ca. 66%) in southern Europe (Scoppola et al. 2018 and this work). One obvious reason for its abundance lies in climatic conditions (Bennett and Maxted 2001).

There is a higher number of alien species in the Boreal and in most Temperate regions in comparison with the

Mediterranean zones/regions, including Colchis-Caucasus and Pontic-Caspian (Online Resource 2: Table 2). A possible explanation can be that species with wide environmental tolerance (numerous *Lathyrus*, *Lotus*, *Vicia*, etc.) get further north from southern habitats. In addition, intentional or inadvertent introductions, e.g., in the Atlantic (Tb) region, substantially increased the number of exotic leguminous species from the Acacieae, Cassieae, and Ingeae tribes. On the contrary, Mediterranean zones/regions share many species as native with the surrounding larger floristic domains outside Europe, e.g., North Africa and the Middle East.

The distribution of major European seed beetle groups corresponds to their leguminous hosts at the tribe level (Jermy and Szentesi 2003; Kergoat 2004; Kergoat et al. 2008) and see Table 1. Ideally, the number of known species should correlate with the intensity of research on the host associations. Unfortunately, however, research efforts do not seem proportional to the species richness. 23% of European legumes collected for such purpose is generally low, and one of the most species-rich genera, *Astragalus*, is deeply under-investigated (Online Resource 2: Table 1).

The distribution of seed beetles generally follows that of host plants. However, this is not always the case. For instance, *Astragalus exscapus* L. is also present in Hungary (Tc), but, in contrast to data by Delobel et al. (2004), *Bruchidius myobromae* Motschulsky has never been reared from it. A similar example is *A. contortuplicatus* L. and *Bri. poecilus* Germar. It means that yet unknown factors also play a role in whether a host is utilized by seed beetles in a zone/region.

Of the 174 European seed beetle species of Bruchinae, ca. 68% utilize leguminous hosts (with ca. 26% of the hosts unknown and ca. 6% live in non-leguminous hosts). The levels of host specialization (mono-, oligo- and polyphagy) of phytophagous insects are difficult to define with precision and, as in this study, it is somewhat artificial. One reason is that the spectrum of hosts utilized in nature is rarely known exactly, and as soon as the ecology of a species is better acquainted, new data can modify the previous tag. In this sense, categories of specialization become subjective. The suggestions to make the limits of host affiliations more accurate, e.g., in the case of seed beetles by Yus-Ramos (2018) or by indices based on phylogenetic distances of hosts (Jorge et al. 2017), might help determine specialization with higher precision. In this work, based on the available information on the host plant range of seed beetles, the categories of mono- and oligophagy are used, with two stages of the latter: *s. s.* and *s. l.* oligophagy, as in many recent publications (e.g., Schoonhoven et al. 1998; Altermatt and Pearse 2011; Jermy and Szentesi 2003). Within phylogenetically determined oligophagy, several seed beetle species show an “ecological” mono- or oligophagous host range (Fox and Morrow 1981), which is specific to a given zone/region due

to the lack of some leguminous species utilized elsewhere. Such examples are *Bri. marginalis*, *Bri. picipes* Germar, *Bri. poupillieri*, and *Bri. pusillus* Germar, and others are present in Central Europe (Tc), however, having even restricted or extended host ranges in other zones/regions. In this sense, oligophagy in Bruchinae is only a subfamily character. Furthermore, the use of alternative hosts locally in the absence of the major host plant is also a type of ecological specialization (Östergard and Ehrlén 2005).

Host associations of Bruchinae seed beetles can be characterized by strong taxonomic host conservatism (Kergoat et al. 2005b). Results of the present work confirm earlier data that the *Bruchidius* and *Bruchus* seed beetle genera have different host ranges, and it is the host tribe level that best describes host specialization (Jermy and Szentesi 2003; Kergoat et al. 2004). *Bruchus* species have generally been thought to be more specific because they are restricted in host use to the tribe Fabaeae only. Within the tribe, however, each species utilizes several hosts, and monophagous species are not confirmed. In contrast, *Bruchidius* species are *s. l.* oligophagous, because they colonize species within 11 leguminous tribes in Europe, although individual species are more prone to be monophagous. For instance, *Bri. bituberculatus* Schilsky, *Bri. lineatus* Allard, *Bri. murinus* Boh., *Bri. nudus* Allard, *Bri. siliquastris* Delobel, *Bri. terrenus* Sharp, and some others are known to consume seeds of a single host, respectively. (The fact that there are species in both genera that consume seeds of 14–18 different host species does not negate the above statement.) Egg-laying was found as a proximal cause of host specificity by Siemens et al. (1991), highlighting the importance of green pods in host selection in *Bruchidius* and *Bruchus*.

The recognition and acceptance of hosts are also regulated by an array of compounds of plant origin, providing the basis of specialization in bruchines (Kergoat et al. 2005b). Several legume tribes produce, besides an abundance of chemicals (Bisby et al. 1994), major groups of compounds characteristic of the tribe (Hegnauer and Grayer-Barkmeijer 1993; Wink 2013). The chemotaxonomical correspondence between the occurrence of quinolizidine alkaloids within the Genisteeae (Wink and Mohamed 2003) and the distribution of the seed beetle, *Bri. villosus*, among the species of the tribe is conspicuous (Kergoat et al. 2004). *Bri. villosus* develops in 16 plant species of Genisteeae native to Europe (Online Resource 2: Table 5), plus in one introduced species, *Baptisia australis* (L.) R. Br. (it is controversial whether it is a member of Thermopsidae or Sophoreae, Shi et al. 2017) that also contains quinolizidine alkaloids (Wink and Mohamed 2003). The use of the latter probably must be based on preadaptation (Janzen 1985). Whether *Bri. villosus* relies on quinolizidine alkaloids as token stimuli for host recognition is not known, but it may take advantage of them in defense by sequestration of the alkaloid (Szentesi and Wink

1991). A similar connection can be assumed with *Bri. lividimanus*, a relative to *Bri. villosus* (Kergoat et al. 2004) that occurs in 14 host species within the Genisteae and shares 10 of them with *Bri. villosus*. Nevertheless, host ranges of the two *s.l.* oligophagous species are still meager in comparison with the number of quinolizidine alkaloid-containing 232 European species of Genisteae. Other external factors must play a role in utilizing a host in the tribe. For instance, neither of the two seed beetle species can be found in the 16 *Ulex* species, whereas *Calicotome villosa* (Poir.) Link. harbors both, despite both plant genera having a very low level of alkaloids (Wink and Mohamed 2003). Still, one cannot find a generally valid diagnostic correspondence between the distribution of chemical factors and those of the seed beetles.

The distribution of seed beetles among leguminous taxa is probably affected by the presence of mutually exclusive major groups of compounds, such as alkaloids and “non-protein amino acids”. The latter group is characteristic of both *Lathyrus* and *Vicia*, however with no overlap (Fowden 1970) and they are important factors in plant defence (Janzen et al. 1977; Bell et al. 1978). Members of the monophyletic *Bruchus* genus feast on both plant genera, but with some exceptions, depending on detoxifying abilities (Rosenthal 1983; Akihara et al. 2018). On the other hand, *Bruchidius* species avoid *Lathyrus* and *Vicia* with rare exceptions (see below). The conspicuous lack or a low number of seed beetle species in several genera (*Hedysarum*, *Melilotus*, *Ononis*, *Trigonella*, and others) might equally be attributed to the lack of collections among the hosts or to the presence of compounds having hitherto not known roles in keeping off seed beetles. For example, except for *Bri. longulus* in *Trigonella grandiflora* Bunge, the possible factors affecting/inhibiting the utilization of these sometimes widespread or even cultivated species might include steroidal sapogenins (Brenac and Sauvaire 1996; Taylor et al. 1997).

Although—according to the classical approach—one of the major factors is host chemistry in defining host specialization, several additional important constraints (interspecific competition, neural limitations, seasonal availability of the host, and others) are also important (Morse and Farrell 2005). For generalists, chemical factors allow species-level recognition, whereas more specialized consumers might be directed by intraspecific chemical cues (Castells and Berenbaum 2008). Nevertheless, the occurrence and concentrations of toxic plant secondary compounds can determine host use (Rasmann and Agrawal 2011). Wink and Mohamed (2003) found that the contradiction between tribe- and genus-level secondary chemistry does not allow a correlation with the host specificity of seed beetles. Recently, however, molecular genetic approaches raised the likelihood of environment-dependent gene expression plasticity as a possible way of adaptation and host specialization in herbivorous insects (Birnbaum and Abbot 2020). Whereas

generalists can possess greater genomic flexibility, specialists rely on a more specific and effective detoxifying system.

Host shifts are defined as expanding the host range (Jermy 1991; Jermy and Szentesi 2021 and references therein). According to this study, host shifts might have possibly taken place among genera within a tribe and between tribes too (Online Resource 2: Table 6). It can happen to phylogenetically related plants having similar secondary chemistry or between chemically dissimilar plants (Kergoat et al. 2005b) requiring reshuffling of the genetic constitution to be able to metabolize xenobiotics in the new host (Bass et al. 2013). However, while most host range extensions in phytophagous insects happen by host shifts (Nyman 2010), they do not necessarily lead to speciation (de Vienne et al. 2013) and demand microevolutionary adaptations only. Several mechanisms (Jermy 1984; Janzen 1985; Janz 2011) can promote acceptance of a new host. Kergoat et al. (2005b) successfully demonstrated with African *Bruchidius* seed beetles that conservatism in host use was strictly coupled with host seed chemistry. Nevertheless, major host shifts occurred between subfamilies. Considering the remarkable differences in plant secondary chemistry within the Fabaceae (Bisby et al. 1994; Wink and Mohamed 2003) and host use in distantly related legume tribes corroborates the view that neither phylogenetic proximity nor chemical similarity ultimately limits host range expansion, although the uncertainty of host use does not allow to draw a firm consequence in some cases. Two further features are worth mentioning: (1) tribe-level host shifts seem to be less common in *Bruchus* than in *Bruchidius*. The higher species richness and polyphyletic nature of *Bruchidius* provide more opportunities for host shifts (Kergoat et al. 2004), and (2) tribe-level host shifts are nil to hosts between *Bruchidius* and *Bruchus*, except for *Bri. lineatus* Allard and *Bri. holosericeus* Schoen., having a very unusual association with species of the tribe Fabeae, the first with *Lathyrus aphaca* (Delobel and Delobel 2007), and the second with *Lathyrus latifolius* L. Nevertheless, the question is still open whether the legume species not attacked by seed beetles are those effectively defended by chemicals or have not been collected so far to prove the presence of pre-dispersal seed predator bruchines. In Hungary, there were seed beetles present in only $51.5 \pm 19.7\%$ (SD) of 676 samples of the most frequent and bruchine-infested 11 legume species.

Specific features and a wide range of hosts can lead to ecological specialization which might open the way to speciation (Tybirk 1991). Such is the case of *Bri. villosus* on several hosts in the Genisteae tribe, possibly promoting genetic differentiation among hosts (Haines et al. 2007). These authors found a sample of *Bri. villosus* of Hungarian origin quite separated from other European populations by molecular analysis. The differentiation process of this species might have been taking place in certain parts of Europe governed

Table 7 Components of life cycles in an annual (*Vicia sativa* ssp. *nigra*) and a perennial (*Vicia tenuifolia*) species in Hungary potentially affecting seed beetle infestation success (Data from Szentesi, unpubl. results, Szentesi 2006, Szentesi and Jermy 2003, Szentesi et al. 2006)

| Plant traits | <i>Vicia sativa</i> subsp. <i>nigra</i> | <i>Vicia tenuifolia</i> |
|--|---|---------------------------|
| Vegetative propagation | No | Yes |
| Pollination | Self-pollinated | Uutbreeder |
| Inflorescence | None | Large |
| Single flower | Large | Small |
| Extrafloral nectaries | Yes | No |
| Apparency sensu Feeny ^a | Low | High |
| Protection from ants | Yes | No |
| Predictability | Low | High |
| Plant spatial distribution | Single plants, random | Many in large patches |
| Biomass of single plants ^b | 2.6 ± 0.2 g d.w. (n = 40) | 6.9 ± 0.7 g d.w. (n = 40) |
| Pods/plant ^b | 11.0 ± 0.7 | 29.6 ± 4.6 |
| Seeds/pod | 10–15 | 4–5 |
| Seed mass ^b | 15.1 ± 0.3 mg (n = 47) | 23.6 ± 0.7 mg (n = 69) |
| Seed bank | Yes (transient) | No |
| Pod availability for egg-laying | Continuous | Limited |
| Germination rate | > 55% | 13% |
| Recruitment | High | Low |
| Recruitment before winter | Frequent | No |
| Ratio of generative/somatic parts ^b | 55.0 ± 2.3% (n = 40) | 38.5 ± 2.8% (n = 18) |
| Seed and pod abortion | Low | High |
| Post-dispersive seed predation | Not known | Very high |
| Seed beetles (Bruchinae) | One species | 3-(4) species |

^aFeeny (1976)

^bMean ± SE; d.w. dry weight

by specific host preferences. *Bruchidius villosus* was found restricted to *Genista monspessulana* (L.) L.A.S. Johnson in Spain despite the presence of *Cytisus villosus* Pourr., and in southern France on *Spartium junceum* L. in the presence of *G. monspessulana* (Sheppard and Thomann 2003). Furthermore, the relative environmental isolation of one of the host plants of *Bri. villosus*, *Genista pilosa* L. in Hungary that prefers calcareous habitats and its small seed size create a phenotypically different sample of beetles whose body lengths are substantially smaller (1.68 ± 0.04 mm, $n = 8$) in comparison with populations developing in other hosts (e.g., *Laburnum anagyroides*: 3.02 ± 0.03 mm, $n = 35$) (Szentesi, unpublished data). Paynter et al. (2016) also found substantial body size differences in *Bri. villosus* measured by the elytron area, at different habitats in New Zealand on broom (*Cytisus scoparius* (L.) Link) and concluded that the seed beetle performs better on larger seeds. Although bruchine species show remarkable plasticity in body mass (Center and Johnson 1974; Szentesi, unpublished data), smaller body size and the yet unproved exclusive preference for *G. pilosa* might promote reproductive isolation (Egan et al. 2013).

The life cycles of legume hosts create advantages and constraints for seed beetles. The annual or perennial strategies of legume species can affect the extent of seed consumption and specialization of seed beetles. For instance, the

annual character of some *Astragalus* clades made possible plant speciation and occupation of different geographic areas (Azani et al. 2017), which in turn could affect seed beetle colonization. The characteristic traits of two representatives of annual and perennial plant life cycles, and how they might affect seed beetle host use are presented in Table 7 (Szentesi, unpublished data). The spatial distribution of annual species might require larger energy investments and hold a larger risk of predation for the seed beetles while searching for hosts in comparison with perennial hosts. The annual life cycle creates unpredictability of the presence of plant species on a given area due to seed banks from which individuals can germinate randomly and elapse for several years. If annuals are *r*-strategists (such as *V. sativa* subsp. *nigra*, *V. grandiflora* Scop., and *V. villosa*) and maintain large, scattered populations, host specialization can be reserved regionally, but not necessarily in all vegetation zones. For instance, *Bru. luteicornis* only attacks *V. sativa* subsp. *nigra* and *V. grandiflora* in Hungary, whereas in other vegetation regions, it develops in further five species plus in four subspecies (Delobel 2014; Delobel and Delobel 2007), of which five are also present in Hungary; however, *Bru. luteicornis* has not been reared from them so far.

It is an intriguing question why some annual leguminous species harbor so few seed predators and suffer a

lower level of seed damage despite being more abundant in comparison with perennial ones (Table 3). For example, *V. sativa* subsp. *nigra* showed ca. 3.5% seed loss to *Bru. luteicornis*. In contrast, the perennial *Vicia tenuifolia* suffered ca. 14% seed damage by four *Bruchus* species (Szentesi et al. 1996). The predictability of perennial hosts allows the maintenance of a larger seed beetle population (Szentesi 2006). However, it is unclear how general these patterns are, because, e.g., many perennial *Astragalus* species also create seed banks (Soltani et al. 2021).

Definitions used in this paper: **Native (N)** = non-introduced, indigenous legume plant species, subspecies, varieties, and seed beetles within Europe's biogeographical regions. **Endemic (E)** = (1) "Eu-endemic" species occur only within the vegetation zones/regions of Europe; (2) "zone/region-specific" and "zone/region-endemic" species are localized to a single zone/region. **Alien** = all introduced, non-indigenous species/subspecies or variety, regardless of whether archaeophyte, neophyte, or naturalized. **Monophagous**: utilizing only a single plant species. **Oligophagous**: utilizing species of a plant family. **Polyphagous**: utilizing species of several plant families.

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Data Availability The datasets used and/or analyzed during the current study are available. Additional information is available in Online Resource Tables and Figures.

Declarations

Competing interests Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Ethical approval This article does not contain any work with protected animal species; therefore, no ethical approval/permission was necessary from an appropriate ethics committee/review board local, regional or national board, to carry out sampling and experiments described in the Methods.

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