Contributed Paper

Ranking Lepidopteran Use of Native Versus Introduced Plants

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Abstract: *In light of the wide-scale replacement of native plants in North America with introduced, invasive species and noninvasive ornamental plants that evolved elsewhere, we compared the value of native and introduced plants in terms of their ability to serve as host plants for Lepidoptera. Insect herbivores such as Lepidoptera larvae are critically important components of terrestrial food webs and any reduction in their biomass or diversity due to the loss of acceptable host plants is predicted to reduce the production of the many insectivores in higher trophic levels. We conducted an exhaustive search of host records in the literature. We used the data we gathered to rank all 1385 plant genera that occur in the mid-Atlantic states of the United States by their ability to support Lepidoptera richness. Statistical comparisons were made with Welch's test for equality of means. Woody plants supported more species of moths and butterflies than herbaceous plants, native plants supported more species than introduced plants, and native woody plants with ornamental value supported more Lepidoptera species than introduced woody ornamentals. All these differences were highly significant. Our rankings provide a relative measure that will be useful for restoration ecologists, landscape architects and designers, land managers, and landowners who wish to raise the carrying capacity of particular areas by selecting plants with the greatest capacity for supporting biodiversity.*

Keywords: biodiversity, introduced plants, Lepidoptera, managed ecosystems, native plants, suburban landscapes

Clasificación del Uso de Plantas Nativas Versus Introducidas por Lepidópteros

Resumen: *A la luz del reemplazo a gran escala de plantas nativas en Norte América con especies de plantas ornamentales introducidas, invasoras y no invasoras, que evolucionaron en otra parte, comparamos el valor de plantas nativas e introducidas en términos de su habilidad para funcionar como plantas huésped de Lepidoptera. Los insectos herbívoros como las larvas de lepidópteros son componentes críticamente importantes para las redes tróficas terrestres y se predice que cualquier reducción en su biomasa o diversidad debido a la pérdida de plantas huésped aceptables disminuirá la producción de muchos insectívoros en niveles tróficos superiores. Realizamos una búsqueda exhaustiva de registros de huéspedes en la literatura. Utilizamos los datos recabados para clasificar a los 1385 géneros de plantas que ocurren en los estados del medio Atlántico de los Estados Unidos por su habilidad para soportar riqueza de Lepidoptera. Realizamos comparaciones estadísticas con la prueba de Welch para igualdad de medias. Las plantas leñosas soportaron más especies de polillas y mariposas que las plantas herbáceas, las plantas nativas soportaron más especies que las especies introducidas, y las plantas leñosas nativas con valor ornamental soportaron más especies de Lepidópteros que las ornamentales leñosas introducidas. Todas estas diferencias fueron muy significativas. Nuestras clasificaciones proporcionan una medida relativa que será útil para ecólogos restauradores, arquitectos y diseñadores de paisaje, gestores y propietarios de tierras que deseen incrementar la capacidad de carga de ciertas áreas mediante la selección de plantas con la mayor capacidad para soportar biodiversidad.*

Palabras Clave: biodiversidad, ecosistemas bajo manejo, Lepidoptera, paisajes suburbanos, plantas introducidas, plantas nativas

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Introduction

Human land use in North America has favored the widescale replacement of native plant species with plants that evolved elsewhere for over two centuries. Repeated disturbance, in combination with unintentional and purposeful importation of introduced species, has resulted in the establishment of 3427 species, many of which have become highly invasive (Pimentel et al. 2005; Qian & Ricklefs 2006). Moreover, landscaping paradigms have promoted the use of introduced ornamentals over native plants with ornamental value since colonial times. The bias toward landscaping with introduced ornamentals has been so complete that the first trophic level in suburban and urban ecosystems throughout the United States is now dominated by plant species that evolved in Southeast Asia, Europe, and South America (Mckinney 2001, 2006; Standley 2003; De Candido et al. 2004).

If introduced plants are the ecological equivalents of the native plants they replace, their addition in managed landscapes may have minimal impact on organisms at higher trophic levels that depend directly or indirectly on plants as energy sources. Nevertheless, if introduced species are not the ecological equivalents of native species, particularly in their use by herbivores that transfer energy to higher-level consumers, herbivore productivity and the diversity and biomass of organisms at higher trophic levels that depend on herbivores will be compromised in landscapes where introduced plants comprise a large portion of the plant biomass. This will be true regardless of the invasive behavior of the alien plant species in question. Most ornamental aliens are not invasive, but when they are planted by the millions throughout managed ecosystems, they dominate landscapes as if they were.

Our central goal was to categorize native and alien plant genera by their ability to support insect herbivores and, by inference, overall biodiversity. We did this by ranking all native plant genera (woody and herbaceous) by the number of Lepidoptera species recorded in the literature as using them as host plants. We hope this ranking will be used as one of the criteria for plant selections in managed and unmanaged landscapes by restoration ecologists, landscape architects and designers, land managers, and landowners who wish to raise the capacity of particular areas to support native food webs. Assembling a list of lepidopteran host records from the literature also enabled us to compare statistically the degree to which various plant groups serve as food resources for native and introduced Lepidoptera. Our comparisons included introduced versus native plant genera used as woody landscape plants, introduced versus native woody and herbaceous genera regardless of whether they are used in the ornamental trade, and woody versus herbaceous native plants.

We used Lepidoptera as surrogates for all insect herbivores because published host-plant records for this group of herbivores, although far from definitive, are more complete than host records for any other taxon of insect herbivores and because lepidopteran larvae are disproportionately valuable sources of food for many terrestrial birds, particularly warblers and Neotropical migrants of conservation concern (Morse 1989; Dunn & Garrett 1997). Although we limited our study to lepidopteran host relationships, we can think of no reason why Lepidoptera would not serve as reasonable surrogates for other folivorous insect herbivores.

Methods

We restricted our search to moths and butterflies that develop on plant genera occurring naturally or planted ornamentally in the mid-Atlantic region of North America (Maryland, Delaware, Pennsylvania, Virginia, Connecticut, Rhode Island, New York, and New Jersey) for two reasons. First, the region is sufficiently diverse in both native and alien plant genera (1385 genera; 884 native genera; 501 alien genera; USDA 2007) and in Lepidoptera species (3575 species; 122 introduced species and 3453 native species) to reveal robust patterns of host use. Second, most host-use records are only specified at the generic level. Our early attempts to compare host use of introduced and native plants in the same genus were thwarted by a lack of information at the species level.

We supplemented larval-host associations and ranges described in Forbes (1923, 1948, 1954, 1960), Tietz (1952), Covell (1984), Johnson and Lyon (1988), Robinson et al. (2002), and Wagner (2005) with records from over 400 sources in the primary literature (see Supporting Information) and occasionally with our own field collections. Because we were interested in the ability of plants to produce Lepidoptera biomass by supporting larval development, we did not record adult use of nectar sources.

The ornamentals we compared were taken from Dirr's (1977) *Manual of Woody Landscape Plants*. All plant genera with ornamental species that evolved in Europe, South America, or Asia and with no native representatives in the mid-Atlantic region were labeled as introduced (69 genera). We labeled all genera comprised of native species with geographic distributions in the mid-Atlantic region as native (103 genera), even if the genus contained one or more species that had been imported for use from Europe or Asia.

Using Levene's test for homogeneity of variance (SAS Institute 1999), we determined that the total number of Lepidoptera species, native Lepidoptera species, and introduced Lepidoptera species supported by introduced and native woody plants and by introduced and native

Table 1. Twenty most valuable plant genera ranked (from most to least) in terms of their ability to support Lepidoptera species in the mid-Atlantic (U.S.A.) region.

Rank	*Plant genus*	*Common name*	*Lepidoptera richness*
1	*Quercus*	oak	534
2	*Prunus*	cherry; plum	456
3	*Salix*	willow	455
4	*Betula*	birch	411
5	*Populus*	poplar; cottonwood	367
6	*Malus*	crabapple	308
7	*Vaccinium*	blueberry; cranberry	294
8	*Acer*	maple	297
9	*Alnus*	alder	255
10	*Carya*	hickory	235
11	*Ulmus*	elm	215
12	*Pinus*	pine	201
13	*Crataegus*	hawthorn	168
14	*Rubus*	blackberry; raspberry	163
15	*Picea*	spruce	150
16	*Fraxinus*	ash	149
17	*Tilia*	basswood	149
18	*Pyrus*	pear	138
19	*Rosa*	rose	135
20	*Corylus*	filbert	131

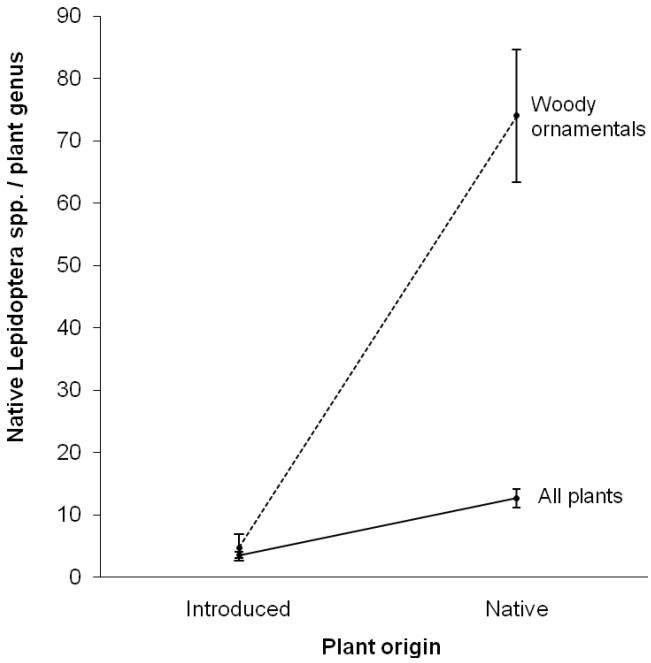

Figure 1. Number of native Lepidoptera species recorded in the mid-Atlantic states (U.S.A.) on all plant genera and on native and introduced woody plant genera used as ornamentals (bars are standard errors).

woody plants used in the ornamental industry all had unequal variance, both as raw data and after the data were log transformed. Because this violates an assumption of analysis of variance, we used Welch's test for equality of means (SAS Institute 1999) to compare the ability of introduced and native genera of woody plants and introduced and native genera of woody ornamentals to support Lepidoptera. Data are reported as means with standard errors.

Results

Our ranking of mid-Atlantic genera of vascular plants in terms of lepidopteran host use, and the actual lepidopteran host records are available (see Supporting Information). Records of lepidopteran host use were recovered for 725 plant genera (511 natives and 214 aliens). We found no records for 637 genera (363 natives and 274 introduced genera). Host records were located for 2809 lepidopteran species with ranges in the mid-Atlantic area.

All members of the top-20 most productive genera (Table 1) were woody plants with the exception of *Rubus*, which ranked 14th because it supported 163 species of Lepidoptera. All members of the top 20 ranking were also native to the mid-Atlantic region with the exception of *Pyrus*, which was ranked 19th and supported 119 native Lepidoptera and 19 introduced lepidopteran species.

Native woody plants used as ornamentals supported 14-fold more Lepidoptera (77.4 species [SE 11.0]) than introduced ornamental species (5.5 species [2.3], $F = 40.9$; $p < 0.0001$) (see Supporting Information). Several of the lepidopteran species supported by woody ornamentals were themselves introduced. Restricting the comparison to native Lepidoptera, the difference between native and introduced plants was slightly greater (Fig. 1). Fifteenfold more native Lepidoptera occurred on native ornamentals (74.1 species [10.6]) than on introduced ornamentals (4.7 species [2.1], $F = 41.2$; $p < 0.0001$).

Excluding ornamental status of the plants, native plant genera supported 3-fold more Lepidoptera (13.4 species [SE 1.54]) than introduced plant genera (3.8 species [0.6], $F = 34.3$; $p < 0.001$). Focusing only on native Lepidoptera again gave a slightly greater difference (Fig. 1). Native plant genera supported 4-fold more Lepidoptera (12.7 species [1.5]) than introduced genera (3.6 species [0.5], $F = 35.5$; $p < 0.0001$). For introduced Lepidoptera, the difference was in the same direction but was smaller. Native plant genera supported about 2-fold more Lepidoptera (0.7 species [0.1]) than non-native plant genera (0.4 species [0.1], $F = 7.1$; $p = 0.0078$).

In the comparison of woody versus herbaceous plants, woody plants supported 10-fold more Lepidoptera (41.9 species [SE 5.9]) than herbaceous plants (4.1 species [0.3], $F = 40.8$; $p < 0.0001$).

Discussion

A growing awareness of the extent to which native animals depend on indigenous plant communities is fueling a movement toward use of native plants in landscapes managed for wildlife and in residential landscapes (Burghardt et al. 2008). Our results quantified the profound differences in the lepidopteran species richness supported by indigenous plants and plants that evolved elsewhere and support the use of natives over introduced plants. Equally important, our literature review of lepidopteran host plants ranked genera of native plants in terms of their potential to support Lepidoptera and thus to support insectivores in general.

Two striking patterns emerged from our literature search of lepidopteran host use. First, woody plants supported many more Lepidoptera species than did herbaceous species. This pattern may be the result of plant apparency as envisioned by Feeny (1976). Woody plants in general are both longer lived and larger than most herbaceous plants and thus may be easier targets for insect herbivores to exploit. It is also possible that herbaceous plants are underreported as lepidopteran hosts because they are more difficult to identify and less conveniently searched by collectors. If woody plants truly support more lepidopteran species and, by inference, more biodiversity than herbaceous plants, landscapers can target woody species when attempting to maximize biodiversity.

A second pattern our data revealed was the discrepancy between the ability of native plants and species that evolved outside of North America to attract ovipositing females and support larval development in Lepidoptera. When our comparison included all plant genera, native plants supported about four-fold more species of Lepidoptera, including introduced Lepidoptera that were established in the region. This difference increased to 14- to 15-fold when we focused our comparison on plants used in the ornamental industry. The comparison of native and alien ornamentals was particularly relevant because these are the species most often intentionally planted in managed landscapes. Thus, at least in terms of supporting lepidopteran diversity, introduced ornamentals are very far from the ecological equivalents of native ornamentals. If Lepidoptera are representative surrogates for all insect herbivores, the impact of introduced ornamentals on insect diversity must be staggering in areas dominated by such plants (suburbs and cities) and in natural areas invaded by the dozens of ornamentals that have escaped cultivation (Mack & Erneberg 2002; Kaufman & Kaufman 2007).

There are several reasons these patterns of host use by Lepidoptera are predictable (Tallamy 2004). First, introduced species used by the ornamental industry in North America are not a random sample of all plants that evolved elsewhere, but rather a subset that has been specifically selected for its unpalatability to insects. An important trait historically favored by the ornamental industry is that the plant be "pest free" (Dirr 1998). This may explain why introduced Lepidoptera were recorded slightly more often on native host genera than on introduced plants.

Second, the success of introduced plants in novel landscapes is often attributed to escape from the natural enemy complexes of their homelands without accumulating equivalent complexes after introduction (i.e., the enemy release hypothesis; Williamson 1996; Crawley 1997). Definitive tests of the enemy release hypothesis have yet to be conducted (Keane & Crawley 2002), but the literature is replete with evidence that the number of herbivores associated with introduced plants in exotic habitats is only a small fraction of the historical complex of natural enemies (e.g., Morrow & LaMarche 1978; Macfarlane & van den Ende 1995; Tewksbury et al. 2002).

Third, theory backed by decades of empirical support predicts that most phytophagous insect species are restricted to eating vegetation from plant lineages with which they share an evolutionary history (e.g., Erhlich & Raven 1965; Strong et al. 1984; Berenbaum 1990) or, more precisely, plants that produce similar secondary metabolic compounds (Scriber et al. 2008). Up to 90% of all phytophagous insect species are specialists that have evolved in concert with only one or a few plant lineages (Bernays & Graham 1988; Janzen 1988; Novotny et al. 2006). What is more, many species of putative generalists, with a large list of hosts over the entire range of the species, actually specialize on only one or a few host lineages locally (Fox & Morrow 1981). Thus, most lepidopteran populations may be functionally constrained to exploiting a limited group of plants. Such restricted interactions typically require evolutionary time spans to develop (Kennedy & Southwood 1984) and have honed the ability of specialists to track their hosts in time and space, to circumvent physical and chemical defenses through behavioral and physiological adaptations, and to convert their host's tissues to insect biomass quickly and efficiently (Rosenthal & Jansen 1980; Strong et al. 1984). The evolution of specialized abilities to eat the tissues of one particular plant lineage usually, in turn, decreases an insect's ability to eat other plants that differ in phenology, chemistry, or physical structure (Erhlich & Raven 1965).

By definition, native insects have shared little or no evolutionary history with introduced plants (although some may have interacted with a species in a common genus or plants with similar phytochemistry) and thus are not predicted to possess the physiological and behavioral adaptations required to use these plants as nutritional hosts. Introduced plants have at most been available for adaptation by native insects only a few hundred years. Moreover, introduced plants may have smaller geographic ranges than most indigenous plants in North America. Both of these factors may restrict the rate at which native insects adapt to novel introduced plant lineages

(Neuvonen & Niemela 1981; Strong et al. 1984). Consequently, theory predicts that solar energy harnessed by introduced plants is largely unavailable to native specialist insect herbivores, at least in ecological time, and therefore will be unavailable to all consumers that include these insects in their diets.

There has been surprisingly little effort to measure the relationship between insect diversity and bird diversity. Although Kim et al. (2007) found that insect species richness best explains bird species richness in urban landscapes, the focus for decades has been on documenting the positive relationship between insect biomass and bird diversity (e.g., Martin 1987; Strong & Sherry 2000; Nott et al. 2002). Nevertheless, lottery reasoning predicts that the chances of encountering insect species that provide large amounts of biomass for bird consumers will be higher in communities with high insect richness than in less diverse insect communities. Thus, we are confident that the lepidopteran species richness supported by a particular plant genus is a reasonable index of that plant lineage's value to birds and other insectivores.

We encountered several records that documented native Lepidoptera use of introduced plants as hosts. In fact, introduced ornamentals supported on average about four species of native Lepidoptera. Many, if not most, of these host expansions were probably facilitated by similarities in leaf chemistry that, in turn, are the result of close phylogenetic relationships between the native host plants and the introduced ornamental on which the moth or butterfly was recorded. When this is the case, the use of novel introduced hosts may have required no evolutionary changes.

The *Ailanthus* webworm (*Atteva punctella* [Yponomeutidae]) provides a good example (Ding et al. 2006). A native of south Florida, *A. punctella* is a specialist on the paradise tree (*Simarouba glauca*), a native member of the family Simaroubaceae. When the tree of heaven (*Ailanthus altissima*), also a Simaroubaceae, was introduced to North America, *A. punctella* found its leaf chemistry and texture similar enough to its native host that it could use *Ailanthus* to complete its development successfully. *Ailanthus punctella* now reproduces on *Ailanthus* throughout its introduced range in North America.

In another example, *Pyrus*, the Old World pear genus, contains several agricultural species and supports 138 species of Lepidoptera, four times more than any other alien ornamental genus. Although 19 of these species are introduced Lepidoptera, 119 are native species that have been observed eating *Pyrus*. Again, this may be the result of phylogenetic similarities between *Pyrus* and close relatives native to North America. *Pyrus* is a member of the Rosaceae, subfamily Maloideae. This is the same lineage as the native genus, *Malus,* which supports 308 species of Lepidoptera. Eighty-two percent of the native species that develop on *Pyrus* also use *Malus* as a host plant.

The majority of Lepidoptera host records in the literature are recorded at the genus rather than species level. For example, records such as "eats oaks" prevented us from comparing the relative use of particular oak species within the genus *Quercus.* Species-level knowledge would be very useful because it is well known that specialists and generalists can discriminate among species within a particular plant genus (Scriber et al. 2006, 2007, 2008).

Our records for Lepidoptera host use necessarily reflect bias inherent in the literature. Most (95%) of the genera with no recorded Lepidoptera are comprised of ephemeral or low-profile herbaceous plants that may have been ignored by Lepidopterists over the years. It is unclear how many of these species do support Lepidoptera but have been undetected as hosts, or, in fact, do not serve as hosts for any lepidopteran species. More work on the ability of herbaceous plants to support biodiversity is clearly warranted.

Plants used in agriculture also bias host records simply because of the volume of work that exists on pests of economically important plants. This bias undoubtedly elevated our ranking of *Pyrus* (includes commercial pears), *Vaccinium* (includes blueberries and cranberries), *Prunus* (includes commercial cherries), *Rubus* (includes raspberries and blackberries), *Corylus* (filberts), and *Juglans* (walnuts and butternuts). Similarly, the Lepidoptera that develop on genera used extensively as ornamentals, including nearly all the introduced genera recorded in our study, as well as *Quercus, Betula, Populus*, *Malus, Acer, Ulmus, Pinus, Crataegus, Picea, Rosa*, and many other native genera have received more attention than those on plants with no economic value to humans. Despite these biases, our literature search of host use provides a useful first step in guiding decisions about plant choice if one of the goals of a planting is to promote biodiversity. For example, restoration ecologists in the eastern United States might be tempted to recommend *Liriodendron tulipifera* (tulip poplar) as a species for reforestation projects because of its fast growth and high survivorship. It ranked 129th, however, in its ability to support a diversity of Lepidoptera useful in supporting breeding birds and other insectivorous organisms. From this perspective, oaks (*Quercus*), willows (*Salix*), native cherries such as *Prunus serotina*, and birches (*Betula*) would all be far better choices.

In the past those determining the plant composition of managed ecosystems have not included insect productivity as a criterion guiding their choices. Landscapers, land managers, and restoration ecologists have chosen plants, respectively, on the basis of cost and aesthetics, needs of charismatic vertebrates, and environmental engineering attributes. Homeowners, arguably the group with the greatest impact on U.S. landscapes, typically choose plants on the basis of the degree to which a plant is pest free. In each of these cases the role of plants in

generating food for heterotrophs in terrestrial food webs has been ignored. This study is part of our larger effort to convince the shapers of managed ecosystems that insect herbivores are an essential component of terrestrial food webs because so many other taxa rely on them for food (Wilson 1987; Tallamy 2004). To create landscapes without knowledge of how the plants in those landscapes support insects, and thus insectivores, is to continue the practices that have decimated animal populations in managed ecosystems over the past century. Although it may be difficult to convince some homeowners to landscape with animal needs in mind, we do not believe past criteria will always trump new information about what is necessary to create productive landscapes.

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Supporting Information

Supplemental literature cited (Appendix S1), notes on using Lepidoptera and Host Plant databases (Appendix S2), the ranking of mid-Atlantic genera of vascular plants in terms of lepidopteran host use (Appendix S3) and actual lepidopteran host records (Appendix S4), number of lepidopteran species recorded on introduced woody ornamental plants in the mid-Atlantic region of the United States (Appendix S5) and number of lepidopteran species recorded using native woody ornamental plants in the mid-Atlantic region of the United States (Appendix S6) are available as part of the on-line article. The author is responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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