Comparative ecology of membracids and tenthredinids in a macroevolutionary context

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ABSTRACT

The Phylogenetic Constraints Hypothesis argues that macroevolutionary patterns provide the basis for understanding broad ecological patterns in nature involving the distribution, abundance and population dynamics of species. A phylogenetic constraint is a critical plesiomorphic character, or set of characters, common to a major taxon, such as a plant-piercing ovipositor in insects independently derived in the distantly related families of treehoppers (Homoptera: Membracidae) and the common sawflies (Hymenoptera: Tenthredinidae). Such characters limit the ecological and thus the major adaptive options in a lineage, but many minor adaptations are coordinated to maximize the ecological opportunities that can be exploited given the constraint. Such a set of adaptations is called the 'adaptive syndrome'. These characters in the adaptive syndrome, which evolve in response to the constraint, then result in inevitable ecological consequences, called 'emergent properties'. We test the hypothesis by comparing emergent properties of species of membracids and tenthredinids, such as patterns of host plant utilization and population dynamics, and by comparing their putative adaptive syndromes, especially as related to oviposition behaviour. Although the two families are very divergent phylogenetically, we argue that convergence in ovipositor structure and function sets the stage for a comparable train of effects from phylogenetic constraint to adaptive syndrome to emergent properties. We report strong similarities in critical aspects of behaviour, especially the utilization of relatively rare and vigorous, actively growing shoots of host plants. Such use of rare resources dictates the emergent properties common to both families: patchy distribution, low abundance, and relatively stable population dynamics without eruptive episodes. This macroevolutionary approach provides a perspective for the discovery of macroecological patterns in nature and their mechanistic explanation, as well as a strong predictive capability based on convergence or divergence of key plesiomorphic characters in major taxa.

Keywords: adaptive syndromes, emergent properties, Homoptera: Membracidae, Hymenoptera: Tenthredinidae, phylogenetic constraints.

INTRODUCTION

The Phylogenetic Constraints Hypothesis argues that shared ancestral characters in lineages dictate many aspects of the ecology of phylogenetically related species, such as distribution

and population dynamics (Price *et al.*, 1990; Price, 1994). Generally, some plesiomorphic character, or set of characters, common to a major taxon, limits the ecological and thus the major adaptive options for a group. Such a character(s) acts as a phylogenetic constraint around which adaptations are focused that mitigate the ecological effects of the constraint. This integrated set of adaptations has been called the 'adaptive syndrome' of a species or larger taxon (Root and Chaplin, 1976; Eckhardt, 1979): 'the coordinated set of characteristics associated with an adaptation or adaptations of overriding importance, e.g. the manner of resource utilization, predator defense, herbivore defense, etc.' (Eckhardt, 1979: 130). Root and Chaplin (1976: 139) note that, 'as organisms perfect a mode of life, their evolution is channeled so that a variety of adaptations are brought into harmony'. The adaptive syndrome includes characters such as behavioural, physiological, life-history and host plant associations, and perhaps many others. Host plant associations may include host plant specificity, plant cues used in oviposition, module choice, and so on. Although Root and Chaplin (1976) and Eckhardt (1979) make no distinction between plesiomorphic and derived character states, under the Phylogenetic Constraints Hypothesis, the adaptive syndrome should be manifested as synapomorphies amenable to cladistic tests of adaptational hypotheses (e.g. Greene, 1986; Coddington, 1988; Baum and Larson, 1991). Once the adaptive syndrome is set, then there are inevitable consequences for the ecology of the species and larger taxon, which we call 'emergent properties' (Price *et al.*, 1990; Price, 1994), such as distribution in relation to resources, abundance, demography and population dynamics. This flow of influences from phylogenetic constraints to adaptive syndrome to emergent properties, as a conceptual framework, provides a macroevolutionary basis for understanding macroecological patterns. Therefore, broadly comparative studies may be placed in the general perspective of the Phylogenetic Constraints Hypothesis with the potential for discovering broad patterns in nature. Much of the evolutionary biology of a species or larger taxon becomes integrated into a mechanistic understanding of the relevant ecology. This is a novel view for subjects involving distribution, abundance and population dynamics, which have been typically regarded as purely ecological phenomena (e.g. Hassell, 1978; May, 1981; Berryman, 1991, 1997; Royama, 1992). However, if we are to develop broadly comparative and predictive theory on population dynamics, understanding the role of phylogeny (history) is essential. That is, an argument can be made that macro-evolutionary patterns set the stage on which macroecological 'plots' can be played out, forming patterns in nature. This view is quite the reverse of Hutchinson's (1965) ecological theatre and evolutionary play, but Hutchinson focused on adaptive fine-tuning within communities rather than on macroecological patterns.

There are three important points about phylogenetic constraints in our hypothesis: (1) they are characters that are themselves constrained evolutionarily and so persist in lineages (perhaps because they are tightly integrated into developmental programs, lack genetic variation, etc.); (2) they have important ecological effects in that they set some key aspect of the niche or selective regime of a taxon; and (3) by virtue of (1) and (2), they have important evolutionary effects in that they limit the major adaptive options available to a lineage. When plesiomorphic characters that determine some key aspect of the niche of a taxon are themselves constrained, then they may set the selective regime the taxon experiences. The evolutionary effect is that many minor adaptations are brought about to ensure efficient utilization of the niche or resource dictated by the constraint. However, major adaptive changes are strongly constrained by the inherited features and hence are rare (Gould, 1980, 1989). A character is a constraint when it acts as an inherited limit on, or channel

for, current change (Gould, 1989; McKitrick, 1993). We agree with McKitrick's (1993: 309) definition of constraint: 'any result or component of the phylogenetic history of a lineage that prevents an anticipated course of evolution in that lineage'. This definition implies the absence of a course of evolution anticipated under adaptationism or functionalism (Gould, 1989). Thus, 'it is the researcher who must invent possible endpoints for a lineage in order to study evolution in this way' (McKitrick, 1993: 310). We outline this perspective for sawflies shortly.

One of the most valuable predictions of the Phylogenetic Constraints Hypothesis is that unrelated taxa with similar plesiomorphic characters (potential constraints) are likely to evolve with similar adaptive syndromes (cf. Eckhardt, 1979), with similar consequences for their plant–herbivore interactions (e.g. host taxon and specificity, module utilization, chemical ecology), distributions, abundances and population dynamics. Broad comparative studies may then be founded on distantly related taxa in which similar shared ancestral characters (potential constraints) arose independently, or on taxa with very different shared ancestral characters, and the consequent adaptive syndromes and emergent properties should reveal convergence or divergence, respectively.

We explore this comparative approach using specific species examples from one group, the free-feeding and gall-inducing sawflies (Hymenoptera: Tenthredinidae: Nematinae: Nematini), which we have studied extensively, and another distantly related group, the treehoppers (Homoptera: Membracidae), which has received little attention from our research group. We test the prediction that similar plesiomorphic characters are correlated with equivalent adaptive syndromes and emergent properties in these lineages.

The Phylogenetic Constraints Hypothesis was developed based on our studies of sawflies, so we will use this group to illustrate the logic involved. We argue that the saw-like ovipositor is a constraint for five reasons. First, it is a plesiomorphic character for the large family Tenthredinidae and, indeed, the larger Suborder Symphyta – the sawflies and horntails – which is ancestral to all the other Hymenoptera (cf. Hunt, 1999). 'Females of most Symphyta have a sawlike ovipositor used to cut slits in plant tissue for insertion of eggs' (Smith, 1993: 3). Second, the ovipositor is itself constrained, appearing in all sawflies, even if reduced in some. 'The ovipositor itself is always existing in sawflies, but sometimes it is very short . . . ' (Alexey Zinovjev, personal communication). Third, it functions as an ecological constraint, limiting oviposition to inside plant tissue. This constraint is exacerbated by wear on the 'saw' (Benson, 1963) confining most tenthredinids to oviposition in soft plant tissue, often very young developing shoots. Fourth, by acting as an ecological constraint, it has limited adaptive options. Many other variations on the ovipositor and oviposition theme have occurred (e.g. Smith, 1968; Wagner and Raffa, 1993), but the only major adaptation is gall formation. Finally, the ovipositor accounts for the shared adaptive characteristics of free-feeding and gall-inducing sawflies, indicating that feeding mode and gall induction are not the fundamental constraints.

The ovipositor appears to be central to explaining the evolution by natural selection of subsequent adaptive characters in the family Tenthredinidae. These adaptive characters, which we term the 'adaptive syndrome', include:

1. Young and soft plant tissues are selected as oviposition sites, minimizing wear on the saw.
2. The life history of univoltine sawfly species is adapted to host plant phenology, which maximizes resource availability of young shoots that are growing rapidly (Price and Clancy, 1986; Price, 1991).

3. Sensory receptors in the females that can detect long vigorous shoots and the specific host plant species (e.g. Kolehmainen *et al.*, 1994; Roininen *et al.*, 1999).
4. Oviposition preferences in the females relating to shoot length and vigour that maximize larval performance; there is a strong link between preference and performance (Craig *et al.*, 1989).
5. Being haplodiploid, a plesiomorphic character for the Order Hymenoptera, females can allocate the sex ratio of progeny according to the quality of shoots available (Craig *et al.*, 1992); such allocation has become part of the adaptive syndrome, not of course the plesiomorphic sex-determination system itself.
6. Oviposition into plant tissue predisposes a lineage to become gall inducers, and living in a gall has several adaptive features (Price *et al.*, 1987a). Our argument is that without the ovipositor for injecting eggs into plant parts, other adaptive options would also be available to nematine sawflies. These would include the possibility of using a broader range of ages of host plant tissues, decoupling of insect phenology from host plant phenology, and perhaps polyphagy.

This adaptive syndrome dictates much of the ecology of the species. Distribution of any one sawfly species depends on the distribution of its host plant species, and especially the availability of young plants or ramets with vigorous growth. Hence, disturbed sites after fire, flooding or heavy mammal browsing create patches over a landscape in which sawflies may become abundant. If, at any one site, a stable production of juvenile and vigorous ramets persists, then the population will be relatively stable through time (cf. Price *et al.*, 1995a, 1998), but without disturbance, host plants senesce, sawfly species become rare and may go locally extinct (cf. Roininen *et al.*, 1993; Price *et al.*, 1996). The flow from phylogenetic constraints to the adaptive syndrome to emergent properties results in a mechanistic under-standing of distribution and abundance based on the adaptive syndrome, and accounts for the patterns in nature we have described for tenthredinid sawflies. We argue that this hypothesis forms the basis for developing theory on the population dynamics of gall-inducing sawflies and other kinds of insect herbivores (e.g. Price *et al.*, 1995a, 1998; Price, 1996).

Broadening the comparative base of the hypothesis to other unrelated taxa is challenging because of the general shortage of critical data and directly comparable methods of study. However, we have found that, for many species, using shoot length as a synoptic character of the host plant frequently reveals distinct patterns of utilization by herbivores. When these patterns are similar to those we have found in sawflies, we can start to generalize about these emergent properties and their consequences relating to distribution and abundance. In effect, we perform a regression or gradient analysis using shoot length as the independent variable and number of insects per shoot as the response variable (e.g. Price *et al.*, 1995b). We use this approach for comparing membracids and tenthredinids in this paper.

Shoot length is a synoptic character of a host plant because length correlates strongly with many other characters: shoot diameter, leaf size, number of nodes, leaves and buds per shoot, vigour of modules, growth rate and duration, and concentration of chemical constituents (e.g. Price *et al.*, 1987a, 1989). Each herbivore species may require different characters in a shoot, but they are likely to correlate well with shoot length. For example, a sawfly requires rapidly growing shoots for gall induction, and relatively high levels of a phenolic glucoside as an oviposition stimulant; both characters are correlated positively with shoot length (Kolehmainen *et al.*, 1994; Roininen *et al.*, 1999).

First, we report on the response of four membracid species to shoot length, and then we compare this response with that of gall-inducing and free-feeding tenthredinid sawflies. We then compare life-history traits (putative components of the adaptive syndrome) of the two taxa and their ecological consequences.

ORGANISMS STUDIED

Oxyrachis tarandus is a membracid frequently encountered on *Tamarix nilotica* in Israel. This species was studied in 1998 in a parking lot adjacent to the Roman city of Caesarea, where boles of trees were pruned frequently, producing young basal shoots on which most membracids were found.

Three other species of membracid were studied in Brazil. An *Encenopa* sp. was found in 1993 on young *Caesalpinia* trees in a parking lot at the Fazenda Agua Limpa field station of the University of Brasilia. A *Leioscyta* sp. occurred on *Myrcia* sp. trees that had been pruned to clear a forest trail and then resprouted with vigorous shoots. This and the next species were studied in 1994 in the Serra do Japi Ecological Reserve near Campinas. Another membracid, *Heteronotus formicoidea* Sakakibara, occurred on young *Acacia polyphylla* trees growing in roadside ditches in a tangle of undergrowth and climbing plants.

All membracid species lived in colonies with adults and nymphs present, and all were tended by ants belonging to various genera. These species were very patchily distributed, so that study of them was opportunistic and located in landscaped areas where many members of the same host plant species co-existed, or in small disturbed sites caused by clearing the sides of roads or trails. In each of the membracid species, broods of nymphs were well developed, indicating the relative success in reproduction and survival based on the number of individuals per shoot.

Four gall-inducing sawflies of the genus *Euura* used for comparison with the membracids were studied in the United States and Finland, and these studies are reported in the literature. The stem galler, *Euura lasiolepis*, which is monophagous on *Salix lasiolepis*, was studied in the vicinity of Flagstaff, Arizona (Craig *et al.*, 1986, 1989). Another stem galler, *Euura exiguae*, monophagous on *Salix exigua*, occurred along the Weber River, Utah (Price, 1989). In Finland, in the vicinity of Joensuu, North Karelia, the bud gall inducer, *Euura mucronata* on *Salix cinerea*, and the stem galler, *Euura atra* on *Salix alba*, were studied and are treated in Price *et al.* (1987a,b) and Price *et al.* (1997a) respectively.

For comparative purposes, we also provide results from studies on free-feeding tenthredinid sawflies in the genus *Nematus*. Including these free-feeding species is important because they differ from the gall inducers in key characteristics: (1) they feed exophytically; (2) two of the species feed on *Populus* trees rather than on *Salix*; (3) they are multivoltine; and (4) eggs and larvae are frequently attacked by parasitic wasps and predators. The extent to which they share an adaptive syndrome and emergent properties with the gall inducers suggests that the causes of the patterns to adaptations and ecology we observe in the Nematini are not the result of the evolution of gall induction, but rather the result of a more primitive character or characters. All three species were studied in the Flagstaff area. One species, *Nematus oligospilus*, is a solitary feeder on *Salix lasiolepis* (Carr *et al.*, 1998), but the data presented here are provided in a new way for direct comparison with the other species. *Nematus vancouverensis*, a solitary species, and *N. iridescens*, a colonial species, both occurred on *Populus tremuloides* and were studied by Carr (1995), with a new analysis for comparative purposes presented in this paper.

As with the membracids, all the sawfly species were very patchy in distribution, with generally low population densities. Younger vigorous ramets and clones were attacked more than mature or senescent plants and, in the case of *E. atra*, heavily pruned roadside trees were attacked.

Because the hypothesis highlights the interaction of the constraint and the selective environment, we emphasize the features in common for tree hoppers and sawflies. Both families are associated primitively with woody angiosperms on which immatures live and feed. Membracids utilize stems mostly for oviposition and feeding. Tenthredinids use the leaf lamina for feeding and frequently for oviposition, but in *Euura* eggs are laid into young stems.

METHODS

The general approach for each species of membracid was to measure shoot lengths (i.e. stems plus leaves produced in the current active growing season) to obtain the distribution of shoot lengths available and the distribution of shoot lengths utilized by the insect herbivore species. Shoots were sampled haphazardly while standing at ground level until a representative sample was obtained. These methods parallel those used in studying sawflies, which are presented in detail in Craig *et al.* (1986, 1989) and Carr *et al.* (1998). Sample sizes depended on the number of plants available and their size, and are provided in the Results section (Tables 1, 2 and 3). For membracids, sample sizes of less than 100 shoots or 100 insects resulted from the typically small populations of insects and host plants encountered. In the case of sawflies, small sample sizes are the result of presenting data from one willow clone as representative of 5–10 clones used in the original study (e.g. Craig *et al.*, 1986; Price, 1989).

The data were analysed using least squares regression, with shoot length or shoot length class as the independent variable (x) and number of insects per module or group of modules (e.g. per shoot, per 100 shoots, per 100 nodes) as the response variable (y). For membracids, the percentage of shoots available per shoot length class (y) was also regressed against shoot length class (x). Equations accounting for the most variance (highest r^2) are presented.

The membracid, *Heteronotus formicoidea*, and its host plants, small *Acacia* trees, presented a special case not treated as above. Because the *Acacia* hosts had sharp thorns and shoots tangled with undergrowth and vines, with aggressive *Camponotus* ants tending the membracids, representative sampling of shoot lengths was difficult without disturbing the membracids, causing them to move to new sites. Therefore, pairwise comparisons were made between the shoot with membracids present and the nearest neighbouring shoot without membracids. Shoot lengths were then compared using the Wilcoxon matched-pairs signed-ranks test (Siegel, 1956).

After these quantitative comparisons among species, we use personal observations and information from the literature to compare the life histories, plant–herbivore interactions and female behaviour (components of the adaptive syndrome), and distribution, abundance and population dynamics (emergent properties), of membracids and sawflies.

With these two approaches, we try to test the predictions of the Phylogenetic Constraints Hypothesis and suggest other taxa on which further testing might proceed in a similar vein.

RESULTS

All host plants for membracids grew with many shoots in the shorter shoot length categories and very few shoots in the longer shoot length classes (Table 1, Figs 1–3). For the three plant species with adequate data, the relationship between shoot length class and percent of shoots per class was negative; it was significant for *T. nilotica* and the *Caesalpinia* sp., but not for the *Myrcia* sp. In the case of the latter, the heavy pruning resulted in a high proportion of moderately long shoots (Fig. 3), which is unusual in woody plants.

All species of membracid responded positively and significantly to the longer shoots available (Table 1, Figs 1–3). *Oxyrachis tarandus* used a much wider range of shoot length classes than the *Encenopa* and *Leioscyta* species, probably because the basal sprouts on pruned *Tamarix* were very vigorous, making available many shoot length classes of high quality for reproduction. And, as we have shown many times in our publications on sawflies, the response to long shoots is stronger than expected based on shoot length alone. That is the null hypothesis, that equal total shoot lengths in any shoot length class will support equal numbers of membracids. This can be roundly rejected by examining the shortest and longest shoot length classes, and we use the example of *Oxyrachis* on *Tamarix*. In the shoot length classes 0–20 cm, with 252 shoots in total and a total length of 2340 cm, no *Oxyrachis* were recorded. But in the longest shoot length classes, 121–140 cm, with 11 shoots totalling 1435 cm, 51 membracids were recorded.

In general, the distribution of shoot lengths found on host plants of the membracids was similar to that of the willow hosts published in the literature (references in Table 2). And *Euura* sawflies also showed a strong, positive and significant response to shoot length class (Table 2). Equivalent patterns were observed in the free-feeding sawflies and their host plants (Table 3).

This congruence in resource utilization is consistent with the Phylogenetic Constraints Hypothesis if membracids and tenthredinid sawflies have evolved similar adaptive syndromes under similar phylogenetic constraints. We use the published literature and personal observations for comparisons of female behaviour, oviposition, progeny development, life history, and how plant resources are utilized between the taxa.

The relevant characters for membracids and sawflies which we interpret as phylogenetic constraints and adaptive syndromes show considerable convergence from disparate phylogenetic stocks. In Table 4, we provide a comparison of general traits for each taxon as well as those that we consider as the phylogenetic constraint and the putative adaptive syndrome. Although life histories of membracids are very diverse (Wood, 1984), we concentrate on characters consistent with the four species we studied and which are widespread in the group as discussed in Hinton (1977), Wood (1984) and Loye (1992).

The phylogenetic origins of the Membracidae and Tenthredinidae are distant, the former belonging to the hemimetabolous, exopterygote Order Homoptera with haustellate mouthparts, and the latter belonging to the holometabolous, endopterygote Order Hymenoptera with mandibulate mouthparts. Thus, the two families are included in fundamentally different large sections of the neopterous insects, the Hemipteroids and the Holometabola (Borror *et al.*, 1992). Yet, a piercing ovipositor is a plesiomorphic character in both families, and we regard it as a phylogenetic constraint (cf. Smith, 1993, on sawflies in general). Membracids are members of the Suborder Auchenorrhyncha, which includes cicadas, treehoppers, froghoppers and leafhoppers, all with plant-piercing ovipositors (Carver *et al.*, 1991; Borror *et al.*, 1992).

Table 1. Statistics on the four membracid species studied

Insect species and number[a]	Host plant and number of trees and shoots[b]	Regression equation[c]	Number of shoot length classes	r^2	P
Oxyrachis tarandus, 708 insects	*Tamarix nilotica*, 10 trees, 570 shoots	(a) $y = 19.95e^{-0.02x}$ (b) $y = 0.04x - 0.17$	14 13	0.79 0.54	<0.01 <0.01
Encenopa sp., 246 insects	*Caesalpinia* sp., 7 trees, 227 shoots	(a) $y = 87.42e^{-0.08x}$ (b) $y = 0.29e^{0.07x}$	7 7	0.98 0.76	<0.01 <0.05
Leioscyta sp., 252 insects	*Myrcia* sp., 4 trees, 45 shoots	(a) $y = 20.27 - 0.16x$ (b) $(y + 0.1) = 0.04e^{0.09x}$	7 6	0.29 0.97	n.s. <0.01
Heteronotus formicoidea, 107 insects	*Acacia polyphylla*, 11 trees, 40 shoots	Matched pairs test[d]		$t = 4$	<0.01

[a]Total number of insect specimens in samples.
[b]Number of trees sampled and total number of shoots sampled on these trees.
[c]For the first three membracid species, two equations are given: least squares regressions using the independent variable shoot length class (x), and (a) percent of shoots per class (y) and (b) mean number of membracid individuals per shoot (y).
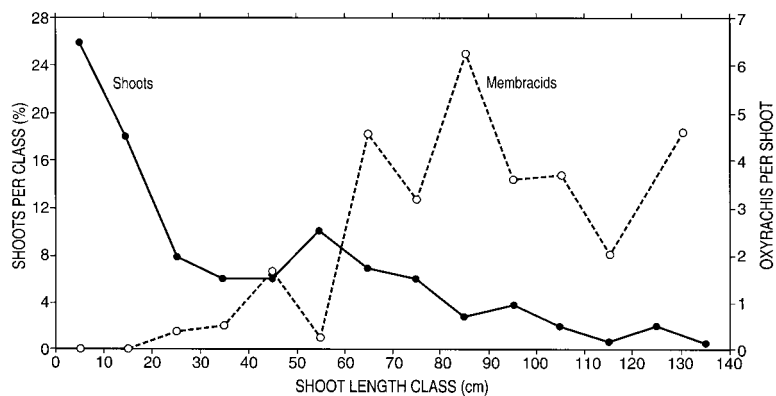[d]Data were not amenable to regression analysis.

Fig. 1. The patterns of shoot availability in *Tamarix* and utilization by the membracid, *Oxyrachis*, in Caesarea, Israel.
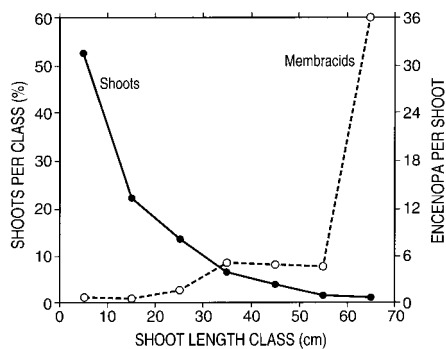

Fig. 2. The patterns of shoot availability in a *Caesalpinia* sp. and utilization by the membracid, *Encenopa* sp., at Fazanda Agua Limpa, Brazil.
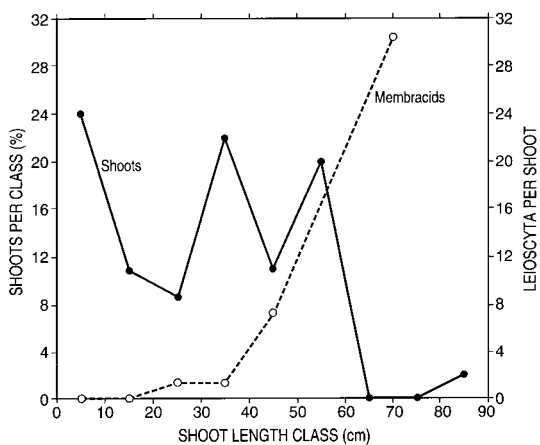

Fig. 3. The patterns of shoot availability in a *Myrcia* sp. and utilization by the membracid, *Leioscyta* sp., on Serra do Japi, Brazil.

Table 2. Statistics for four species of gall-inducing sawfly

Insect species and number[a]	Host plant and number of genets and shoots[b]	Regression equation[c]	Number of shoot length classes and class size	r^2	P	Source
Euura lasiolepis, 1270 galls	*Salix lasiolepis*, 1 clone (10), 500 shoots[d]	$y = 0.48x - 4.70$ y = no. per 100 nodes	11 10 mm	0.94	<0.001	Craig *et al.* (1986)
Euura mucronata, 52 galls	*Salix cinerea*, *c.* 10 clones, 224 shoots	$y = 0.84x - 46.70$ y = no. per 100 shoots	9 20 mm	0.93	<0.01	Price *et al.* (1987a)
Euura exiguae, 65 galls	*Salix exigua*, 1 clone (5), 40 shoots[d]	$y = 0.01x - 1.84$ y = no. per shoot	[e]	0.70	<0.01	Price (1989)
Euura atra, 81 galls	*Salix alba*, *c.* 5 trees, 151 shoots	$y = 0.41x - 89.69$ y = no. per 100 shoots	11 50 mm	0.83	<0.01	Price *et al.* (1997a)

[a]Total number of insect specimens in samples.

[b]Number of trees or shrubs sampled and total number of shoots on these plants. Numbers in parentheses indicate the total number of clones sampled in the published study.

[c]Least squares regressions using shoot length class as the independent variable (x) and number of insects per unit as the dependent variable (y). Units for y vary as stated below each equation.

[d]Two published studies provided an example for one clone, which is representative of others sampled; total samples are in parentheses.

[e]The number of individuals per shoot was used for regression, not the number of individuals per shoot length class.

Table 3. Statistics for three species of free-feeding sawfly

Insect species and number	Host plant and number of ramets and shoots[a]	Regression equation	Number of shoot length classes and class size	r^2	P
Nematus iridescens, 110 colonies	*Populus tremuloides*, >100 ramets, 5 clones, >46,000 shoots	$y = (2.89 \times 10^{-5})x^{3.11}$ y = no. per 100 shoots	9 10 mm	0.95	<0.01
Nematus oligospilus, 157 eggs	*Salix lasiolepis*, >100 ramets, 12 clones, 595 shoots	$y = 0.14x - 1.07$ y = no. per 10 shoots	10 10 mm	0.78	<0.01
Nematus vancouverensis, 353 eggs	*Populus tremuloides*, >100 ramets, 6 clones, >10,000 shoots	$y = 0.17x - 3.03$ y = no. per 10 shoots	13 10 mm	0.77	<0.01

[a]Number of ramets and clones sampled and numbers of shoots on these ramets. For *Populus tremuloides*, the number of shoots is an estimate based on a subsample of the population.

This shared but independently derived phylogenetic constraint sets the stage for parallel sets of traits in the adaptive syndrome: use of young plant modules and oviposition into soft tissues, phenology of attack correlated with rapid growth of host plants, and other characters listed in Table 4. Membracids include species that are either gregarious or solitary (Wood, 1984; Loye, 1992), just as in the tenthredinids (Smith, 1993), but our study involved only gregarious membracid species. Of course, there are also differences in other traits, such as parental care, diapausing stage and ant tending, but the key traits that determine important emergent properties are the common use of vigorous, young plant modules which are in short supply (Tables 1–3, Figs 1–3).

The emergent properties relative to members of both families appear to be very comparable (Table 4) based on our own observations and a few indications in the literature. For example, in 6 years of work on membracids at four sites in Costa Rica, Wood (1984) reported seeing only a few specimens or aggregations for many species. One of his sites was Finca La Selva in wet Atlantic tropical forest, where the only predictable site for membracids, in our experience, was in a 1 ha plot of first-year regrowth after cutting vegetation back to near ground level. This kind of distribution is characteristic of membracids we have observed in Brazil, Panama, Israel and North America. We have also emphasized the patchy nature of resources for sawflies over a landscape and the general rare or uncommon condition of populations (Price *et al.*, 1996, 1997b). Studies on the population dynamics of gall-inducing sawflies show relatively stable populations over decades on shrubs (Price *et al.*, 1995a, 1998) and only very patchy low and ephemeral populations on trees (Roininen *et al.*, 1993; Price *et al.*, 1997b). For membracids, Wolda (1979, 1982) used light traps and canopy fogging for sampling on Barro Colorado Island in Panama. On *Luehea* trees, all species of membracid showed very patchy distributions, with several found

Table 4. Comparison of traits in the membracids and tenthredinids treated in this report and in many other species

Trait	Membracids	Tenthredinids
1. Order	Homoptera	Hymenoptera
2. Family	Membracidae	Tenthredinidae
Phylogenetic constraint		
3. Ovipositor structure	Adapted for piercing plant tissue	Saw-like, for placing eggs in plant tissue
Adaptive syndrome		
4. Oviposition site	Commonly into young shoots, petioles or leaf midrib	In buds, petioles, stems or midribs, or under leaf epidermis, while tissues are soft
5. Age of module utilized	Immature, often in differentiating tissues	Immature, close to meristematic activity
6. Phenology of adults	Synchronized with new growth commonly	Synchronized with flush of new modules
7. Stage during diapause	Adult	Final instar larva with rapid development of pupa and adult in spring
Other traits		
8. Egg protection	Inside plant tissue, often protected by a white secretion	In plant tissue and developing gall tissue in relevant species
9. Egg dispersion	In clusters	Solitary or in clusters
10. Parental care	Females commonly defend eggs	Gall is initiated by female, rare cases of females defending eggs
11. Feeding	Aggregated	Solitary or in colonies
12. Ant tending	Common	Absent
13. Immature survival	Aggregations of nymphs become largest on most vigorous plant modules	Larvae survive best on largest plant modules
14. Preference–performance link	High	High
Emergent properties		
15. Resource supply	Vigorous plant modules relatively rare and patchy	Vigorous modules associated with disturbance
16. Distribution	Very patchy on young modules after disturbance	Very patchy, associated with young and vigorous shrubs or trees
17. Abundance	Low numbers over a landscape, but may become numerous locally	Uncommon to rare at the landscape level
18. Population dynamics	Stable at the landscape scale, unpredictable locally, no outbreaks	Relatively stable on shrubs, without outbreaks
19. Frequency as economically important	Very low, less than 1% of species	Moderately low, less than 3% of species

only on one or two of seven trees, and numbers in light traps from October 1975 to July 1976 were low and varied within one order of magnitude. More population sampling would be valuable. However, perhaps more convincing evidence that membracids show generally low populations comes from the north temperate literature, indicating that only a minute proportion of species ever become pests of economic importance. All authorities agree on this point, even though membracids often attack forest, woodland, orchard and landscape trees of great economic value (e.g. Baker, 1972; Furniss and Carolin, 1977; Borror *et al.*, 1992; Metcalf and Metcalf, 1993). Of the 258 species in the United States, only two are mentioned as pests (Arnett, 1993), or 0.8% of the species. In the Tenthredinidae, with some well-known and serious pests, of the 731 species described for North America, only 20 species are regarded as pests, or 2.7% (Arnett, 1993). Any compendium of injurious insects will note groups that are largely innocuous and others of major economic importance, representing basic common knowledge accumulated over decades. One example is Furniss and Carolin (1977), who note that there are no membracid forest pests in the western forests of North America and only one serious pest in the tenthredinids. They also note the many destructive species of conifer sawflies (Hymenoptera: Diprionidae) and the highly destructive bark beetles (Coleoptera: Scolytidae). (Incidentally, we expect to show in forthcoming publications how the Phylogenetic Constraints Hypothesis can account for such discrepant records on the emergent properties of forest insect groups.)

Overall, we find the argument compelling and novel that the equivalent ecology of two such disparate taxa as membracids and tenthredinids can be mechanistically explained by macroevolutionary convergence of phylogenetic constraints and consequent adaptive syndromes. However, the validity of the logic may be undermined if more parsimonious alternative hypotheses can be proposed and if exceptions to these scenarios, which inevitably exist, can be regarded as conclusive evidence falsifying the Phylogenetic Constraints Hypothesis. We discuss these issues in the next section.

DISCUSSION

We found considerable uniformity in empirical patterns of shoot length utilization among the species of membracid and tenthredinid studied, and in the evolutionary traits that are likely to account for these patterns mechanistically. That is, we have identified comparable phylogenetic patterns in putative adaptive syndromes and resultant emergent properties that may be the result of similar, but independently derived, constraints. The results are consistent with the Phylogenetic Constraints Hypothesis. However, we have not shown that the plesiomorphic character functions as a constraint on evolution in either the Tenthredinidae or the Membracidae. We also have not shown that the adaptive syndrome represents a suite of synapomorphies for either of these families (or some relevant subset thereof). Nor have we shown for either lineage that these characters arose in response to natural selection so that they are adaptive in the sense that they are improvements over ancestral states. We did show earlier, however, that these behaviours are currently adaptive in sawflies, meaning that individuals lacking these behaviours would have low relative fitness (e.g. Craig *et al.*, 1989; Carr *et al.*, 1998), and we have presented strong evidence that they are responsible for the distribution, abundance and population dynamics of sawflies (reviewed in Price *et al.*, 1990, 1995a, 1998). We have not shown for membracids that these behaviours are currently adaptive or that they lead to the population dynamics and distribution that we ascribe to them. Nevertheless, our analysis had the potential to falsify the Phylogenetic

Constraints Hypothesis. If similar plesiomorphic characters in what were probably similar past selective environments had failed to be correlated with the same suite of derived characters or emergent properties, then the Phylogenetic Constraints Hypothesis would have been modified or rejected accordingly.

Our approach brings the subject of population dynamics fully within the ambit of evolutionary biology, and places it more solidly there than earlier important initiatives (e.g. Southwood, 1975; Southwood and Comins, 1976; Northnagle and Schultz, 1987; Wallner, 1987; Barbosa *et al.*, 1989; Hunter, 1991, 1995). In addition, much of the ecology of herbivores and their behaviour must be integrated to achieve this approach, providing a strong basis for synthesis of chemical ecology, plant–herbivore interactions, life-history evolution, behaviour and, a central theme in ecology, population dynamics. Anholt (1997) asked how we should test for the role of behaviour in population dynamics, and argued that direct experimental tests are needed. We have conducted such tests on sawflies (e.g. Craig *et al.*, 1989; Carr, 1995; Carr *et al.*, 1998; Roininen *et al.*, 1999), but detailed observations on relatively sedentary animals can be equally compelling, as reported here. The evolutionary approach taken in this paper and in our earlier studies (e.g. Price *et al.*, 1990; Price, 1994, 1997) is paralleled by the initiative adopted by Wolff (1997) on population regulation in mammals. Krebs (1995) has also emphasized the validity of a mechanistic approach to understanding population dynamics, and the Phylogenetic Constraints Hypothesis provides a guide for developing approaches and achieving the goals he advocates. The hypothesis also permits many broad-based predictions and explanations of why disparate families of insects have very similar or disparate proportions of pest species. Some families have few species of economic importance, and have phylogenetic constraints in common, as in the membracids and tenthredinids. Other families have a much larger proportion of outbreak species that cause economic damage, perhaps because of other kinds of phylogenetic constraints (cf. Price *et al.*, 1990; Price, 1992, 1994, 1997). This macroevolutionary approach provides, for the first time, a strongly comparative approach in population dynamics, an ability to detect broad patterns and mechanisms, and broad predictive power.

In this paper, we have attempted to state and develop the Phylogenetic Constraints Hypothesis in such a manner that more rigorous tests should be possible, thus making the hypothesis more powerful. A combination of phylogenetic and ecological approaches would provide appropriate tests. For example, the notions of constraint and adaptation as now stated are testable in a phylogenetic framework. To test hypotheses of constraint, one can compare rates and patterns of phenotypic evolution in sister taxa with and without putative constraints, the pattern of correlation between gains and losses of putative constraints and the characters they are hypothesized to constrain, or the frequency of transitions among character states given constraints (Emerson, 1988; Maddison, 1990; Carrier, 1991; Garland, 1992; Janson, 1992; McKitrick, 1993). Phylogenies also provide the appropriate framework for devising historical and comparative tests of adaptation (Greene, 1986; Coddington, 1988), including those invoking past selective regimes (Baum and Larson, 1990). Once phylogenies are available for the taxa under consideration, claims that constraint and adaptation have occurred in a macroevolutionary context can be tested. The relationship between adaptive syndrome and emergent properties can be examined with ecological and behavioural studies, as described earlier (e.g. Craig *et al.*, 1986, 1989; Price *et al.*, 1995a; Carr *et al.*, 1998), although such studies need to be supplemented with larger-scale experiments (e.g. density manipulations).

Can the approach adopted in this paper be expanded in a comparative manner to related taxa or unrelated taxa with similar plesiomorphic characters (putative phylogenetic constraints)? Would the froghopper family (Homoptera: Cercopidae), closely related to the membracids, show consistent trends? And, would the katydids conform (Orthoptera: Tettigoniidae: Phaneropterinae and Pseudophyllinae), which have a very divergent phylogenetic origin, but with the equivalent plesiomorphic character of a plant-piercing ovipositor? These questions need detailed evaluation worthy of additional publications. But, as the comparative approach broadens, exceptions to the Phylogenetic Constraints Hypothesis are likely to increase.

Treating exceptions in the ecological literature is unfortunately more of an art than a science. The common view is that one good hypothesis can be destroyed by a single, dirty little fact. Scientists that try to generalize the most lament this view. For example, Bonner (1965: 15) stated: 'Yet when we make generalizations about trends among animals and plants . . . it is almost automatic to point out the exceptions and throw out the baby with the bath. This is not a question of fuzzy logic or sloppy thought; it is merely a question whether the rule or the deviations from the rule are of significance in the particular discussion'. The Phylogenetic Constraints Hypothesis was rejected by Berryman (1997) on the basis of a few, to him, seemingly contrary examples, and without weighing the relative bulk of evidence for and against this hypothesis. This weighing of the evidence will have to be undertaken quantitatively and objectively in the future when the kinds of explorations reported here and elsewhere (e.g. Price *et al.*, 1990, 1995a,b, 1997b, 1998; Price, 1992, 1994, 1997) are more extensive. At present, we are searching for major patterns or prevalent tendencies among large numbers of species in diverse taxa, and most biologists agree that broad theory should be based on broad and repeatable patterns in nature (e.g. Tilman, 1989), and that constraints and trade-offs are an essential aspect of theory (McKitrick, 1993).

We recognize that, during speciation within a lineage, adaptive syndromes are likely to diverge under differing selective environments. As noted by Berryman (1997), sawflies in the family Diprionidae, the conifer sawflies, include many species that are highly eruptive and damaging: about 35 of 41 species in North America, or 85% (Arnett, 1993). Cercopids, closely related to the membracids, also include many pest species, especially in the tropics (e.g. Fontes *et al.*, 1995). However, the adaptive syndrome and emergent properties can differ for different taxa within the sawflies, or any other taxon, without falsifying the Phylogenetic Constraints Hypothesis (and definitely without falsifying the view that macroevolutionary patterns are key for understanding ecological patterns). The Phylogenetic Constraints Hypothesis states that the adaptive opportunities are limited due to the ecological effects of the constraint, not that only one set of adaptations will evolve producing one set of emergent properties. In other words, the hypothesis predicts that, if we removed the phylogenetic constraint in evolutionary history, sawflies would have evolved many more suites of life histories. Furthermore, the adaptive syndrome is the result of the interaction of selection pressures and inherited design. Different selection pressures will probably interact with existing designs in different ways. Thus, sawflies and membracids feeding on woody angiosperms may have different adaptive syndromes (and resultant emergent properties) from those feeding on conifers or annual plants. The eruptive cercopids mentioned above feed primarily on herbaceous plants (often grasses), which provide very different resources from woody shrubs and set up a different selective environment than woody angiosperms. Clearly, one needs to consider the selective environment in

evaluating the Phylogenetic Constraints Hypothesis. We do recognize that finer and finer subdivisions of the selective environment (e.g. trees *vs* shrubs, tropical plants *vs* temperate plants) would eventually render the Phylogenetic Constraints Hypothesis trivial. Again, the comparisons reported here hold broadly on trees and shrubs and in tropical and temperate settings.

What sorts of results would falsify the Phylogenetic Constraints Hypothesis? What follows is a list (by no means exhaustive) of such results:

1. Failure to discern significant phylogenetic effects in the population dynamics of other taxa.
2. Failure to attribute phylogenetic effects in population dynamics to constraint.
3. Rejection of adaptational hypotheses for traits in the putative adaptive syndrome.
4. Failure of traits in a putative adaptive syndrome to account for emergent properties.
5. Lack of convergence in emergent properties given similar constraints and a selective environment.
6. Rejection of hypotheses of constraint.
7. A general finding of the inapplicability of the logic once phylogenies are known for more groups. That is, traits thought to be part of an adaptive syndrome turn out to be plesiomorphic, or cannot be explained by reference to a plesiomorphic character. Of course, constraints and adaptive syndromes may be incorrectly identified for a taxon, and this finding would falsify a particular taxon-specific formation of the Phylogenetic Constraints Hypothesis. If such local falsification were common (perhaps due to the difficulty in forming *a priori* hypotheses of constraints and adaptation using the sort of logic we outline in this paper), then the hypothesis overall may be falsified, or at best be shown not to be useful.

Alternative hypotheses have not been explored and rejected in this paper because our goal was to develop a particular point of view. However, we acknowledge that alternatives may exist. For example, an ecologist who rejects evolutionary scenarios might argue that resource abundance defines the potential abundance of exploiting species: Liebig's Law of the Minimum. This law is obviously axiomatic, but among insect herbivores on common and abundant host plants, like willows and poplars, some phytophagous species have high populations and others may be uncommon or rare. Therefore, there must be special adaptive features and constraints that dictate these very different phenomena and how any one plant and its modules are utilized. The macroevolutionary perspective is crucial in identifying the appropriate resource base and explaining why it is the relevant substrate. Other hypotheses have argued for different kinds of population regulation in tropical versus temperate environments (e.g. Dobzhansky, 1950; MacArthur and Wilson, 1963, 1967) and have employed such concepts as niche compression, *r*- and *K*-selection, and biotic and abiotic regulation of populations. However, one of the most compelling aspects of our comparison is that we observe comparable traits in a largely tropical group, the membracids, and a largely north temperate group, the tenthredinids. And a fundamental similarity between the taxa is the correlation of a plesiomorphic plant-piercing ovipositor with a suite of particular life-history traits. Surely, this is telling evidence that macro-evolutionary patterns dictate macroecological similarities and that the evolutionary basis of a group and the traits involved can override the effects of very strong ecological gradients such as latitude and climate. Although ecological interactions may be 'only partly

dependent on evolutionary strategies' (Berryman, 1997: 149), we argue that, in seeking broad patterns in nature, the macroevolutionary perspective is conducive to the advance of ecology.

We do acknowledge that a viable alternative hypothesis may emerge which argues that the plesiomorphic character we identify as the phylogenetic constraint is less central to the argument than the putative synapomorphies we call the adaptive syndrome. Like all adaptations, characters in the syndrome also act as constraints: 'Yesterday's adaptation may be today's constraint' (Ligon, 1993: 3). Therefore, identifying a key constraint is challenging, or even unrealistic, because many adaptations probably evolve rapidly once a new adaptive zone is exploited in a lineage. Furthermore, we acknowledge that we may not have identified the proper phylogenetic constraint in tenthredinids and membracids. For a structure to function as a constraint – that is, for it to determine the selective environment a lineage experiences over a long period of evolutionary time – it itself must be constrained. Its loss or radical change should require a major reorganization, which happens only rarely. On the surface, changes in or loss of a sawfly ovipositor do not seem difficult. The ovipositor does not seem to be part of some carefully integrated developmental program, for example. Another candidate for the phylogenetic constraint in sawflies is the necessity that eggs absorb water as they develop. However, considering the Hymenoptera as a whole, a central plesiomorphic character is a well-developed ovipositor used for piercing plant tissues (Smith, 1993; Hunt, 1999) and the adaptive syndrome for tenthredinids seems to derive directly from this apparently basic character. Without this morphology associating insect and plant in an intimate fashion, we would not see in the tenthredinids the evolution of strong oviposition preference for rare and vigorous plant modules, specific phytochemicals utilized as oviposition stimulants, or the emergence of the gall-inducing habit. And we would not see the evolution of embryogenesis dependent on an egg that absorbs water from plant tissue. In the sense of phylogenetic constraint preferred by McKitrick (1993), the ovipositional morphology has forced the primitive hymenopterans into a virtual straitjacket of close plant and herbivore relations not seen in the other holometabolous groups such as the Lepidoptera. For these reasons, we prefer the Phylogenetic Constraints Hypothesis over alternatives, for it provides a mechanistic flow of influences from plesiomorphic characters in tenthredinids and membracids to emergent properties of distribution, abundance and population dynamics.

Additional tests of the Phylogenetic Constraints Hypothesis, on membracids, tenthredinids or other taxa, would be most valuable, especially if conducted by others. There is a lack of information on the population dynamics of many groups at a level where generalizations can be reached, including most of the taxa we consider in this paper: membracids, tenthredinids, cercopids and katydids. The integration of an understanding of behaviours with population phenomena is poorly developed (Anholt, 1997), and strongly mechanistic approaches using experiments (Krebs, 1995) would greatly enhance our understanding of membracids, tenthredinids and other taxa and broaden the power of the comparative method. Phylogenetic hypotheses on taxa, coupled with identification of nodes at which salient traits evolved, as in Hunt (1999), are also fundamental in the development of this hypothesis. Until such data are available for 10 or 20 species in any taxa used in comparisons, we regret that more limited tests of hypotheses, as in this paper, are inevitable, even though they could advance our understanding.

ACKNOWLEDGEMENTS

REFERENCES

Anholt, B.R. 1997. How should we test for the role of behaviour in population dynamics? *Evol. Ecol.*, **11**: 633–640.

Arnett, R.H. 1993. *American Insects: A Handbook for the Insects of America North of Mexico*. Gainesville, FL: Sandhill Crane Press.

Baker, W.L. 1972. *Eastern Forest Insects*. USDA Forest Service, Miscellaneous Publication 1175. Washington, DC: US Government Printing Office.

Barbosa, P., Krischik, V. and Lance, D. 1989. Life history traits of forest-inhabiting flightless Lepidoptera. *Am. Midl. Nat.*, **122**: 262–274.

Baum, D.A. and Larson, A. 1991. Adaptation reviewed: A phylogenetic methodology for studying character evolution. *Syst. Zool.*, **40**: 1–18.

Benson, R.B. 1963. Wear and damage of sawfly saws (Hymenoptera, Tenthredinidae). *Notulae Entomol.*, **43**: 137–138.

Berryman, A.A. 1991. Population theory: An essential ingredient in pest prediction, management, and policy-making. *Am. Entomol.*, **37**: 138–142.

Berryman, A.A. 1997. On the principles of population dynamics and theoretical models. *Am. Entomol.*, **43**: 147–151.

Bonner, J.T. 1965. *Size and Cycle: An Essay on the Structure of Biology*. Princeton, NJ: Princeton University Press.

Borror, D.J., Triplehorn, C.A. and Johnson, N.F. 1992. *An Introduction to the Study of Insects*, 6th edn. Fort Worth, TX: Saunders College Publishing.

Carr, T.G. 1995. Oviposition preference–larval performance relationships in three free-feeding sawflies. MS thesis, Northern Arizona University, Flagstaff, AZ.

Carr, T.G., Roininen, H. and Price, P.W. 1998. Oviposition preference and larval performance of *Nematus oligospilus* (Hymenoptera: Tenthredinidae) in relation to host plant vigor. *Environ. Entomol.*, **27**: 615–625.

Carrier, D.R. 1991. Conflict in the hypaxial musculo-skeletal system: Documenting an evolutionary constraint. *Am. Zool.*, **31**: 644–654.

Carver, M., Gross, G.F. and Woodward, T.E. 1991. Hemiptera (bugs, leafhoppers, cicadas, aphids, scale insects, etc.). In *The Insects of Australia*, Vol. 1 (I.D. Naumann, ed.), pp. 429–509. Ithaca, NY: Cornell University Press.

Coddington, J.A. 1988. Cladistic tests of adaptational hypotheses. *Cladistics*, **4**: 3–22.

Craig, T.P., Price, P.W. and Itami, J.K. 1986. Resource regulation by a stem-galling sawfly on the arroyo willow. *Ecology*, **67**: 419–425.

Craig, T.P., Itami, J.K. and Price, P.W. 1989. A strong relationship between oviposition preference and larval performance in a shoot-galling sawfly. *Ecology*, **70**: 1691–1699.

Craig, T.P., Price, P.W. and Itami, J.K. 1992. Facultative sex ratio shifts by a herbivorous insect in response to variation in host plant quality. *Oecologia*, **92**: 153–161.

Dobzhansky, T. 1950. Evolution in the tropics. *Am. Sci.*, **38**: 209–221.

Eckhardt, R.C. 1979. The adaptive syndromes of two guilds of insectivorous birds in the Colorado Rocky Mountains. *Ecol. Monogr.*, **49**: 129–149.

Emerson, S.B. 1988. Testing for historical patterns of change: A case study with frog pectoral girdles. *Paleobiology*, **14**: 174–186.

Fontes, E.G., Pires, C.S.S. and Sujii, E.R. 1995. Mixed risk-spreading strategies and the population dynamics of a Brazilian pasture pest, *Deois flavopicta* (Homoptera: Cercopidae). *J. Econ. Entomol.*, **88**: 1256–1262.

Furniss, R.L. and Carolin, V.M. 1977. *Western Forest Insects*. USDA Forest Service, Miscellaneous Publication 1339. Washington, DC: US Government Printing Office.

Garland, T. 1992. Rate tests for phenotypic evolution using phylogenetically independent contrasts. *Am. Nat.*, **140**: 509–519.

Gould, S.J. 1980. The evolutionary biology of constraint. *Daedalus*, **109**: 39–52.

Gould, S.J. 1989. A developmental constraint in *Cerion*, with comments on the definition and interpretation of constraint in evolution. *Evolution*, **43**: 516–539.

Greene, H.W. 1986. Diet and arboreality in the emerald monitor, *Varanus prasinus*, with comments on the study of adaptation. *Fieldiana Zool. N. Ser.*, **31**: 1–12.

Hassell, M.P. 1978. *The Dynamics of Arthropod Predator–Prey Systems*. Princeton, NJ: Princeton University Press.

Hinton, H.E. 1977. Subsocial behaviour and biology of some Mexican membracid bugs. *Ecol. Entomol.*, **2**: 61–79.

Hunt, J.H. 1999. Trait mapping and salience in the evolution of eusocial vespid wasps. *Evolution*, **53**: 225–237.

Hunter, A.F. 1991. Traits that distinguish outbreaking and non-outbreaking Macrolepidoptera feeding on northern hardwood trees. *Oikos*, **60**: 275–282.

Hunter, A.F. 1995. The ecology and evolution of reduced wings in forest Macrolepidoptera. *Evol. Ecol.*, **9**: 275–287.

Hutchinson, G.E. 1965. *The Ecological Theater and the Evolutionary Play*. New Haven, CT: Yale University Press.

Janson, C.H. 1992. Measuring evolutionary constraints: A Markov model for phylogenetic transitions among seed dispersal syndromes. *Evolution*, **46**: 136–158.

Kolehmainen, J., Roininen, H., Julkunen-Tiitto, R. and Tahvanainen, J. 1994. Importance of phenolic glucosides in host selection of shoot galling sawfly, *Euura amerinae*, on *Salix pentandra*. *J. Chem. Ecol.*, **20**: 2455–2466.

Krebs, C.J. 1995. Two paradigms of population regulation. *Wildlife Res.*, **22**: 1–10.

Ligon, J.D. 1993. The role of phylogenetic history in the evolution of contemporary avian mating and parental care systems. *Curr. Ornith.*, **10**: 1–46.

Loye, J.E. 1992. Ecological diversity and host plant relationships in treehoppers in a lowland tropical rainforest (Homoptera: Membracidae and Nicomiidae). In *Insects of Panama and MesoAmerica: Selected Studies* (D. Quintero and A. Aiello, eds), pp. 280–289. Oxford: Oxford University Press.

MacArthur, R.H. and Wilson, E.O. 1963. An equilibrium theory of insular zoogeography. *Evolution*, **17**: 373–387.

MacArthur, R.H. and Wilson, E.O. 1967. *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.

Maddison, W.P. 1990. A method for testing the correlated evolution of two binary characters: Are gains or losses concentrated on certain branches of a phylogenetic tree? *Evolution*, **44**: 539–557.

May, R.M. 1981. Models of single populations. In *Theoretical Ecology: Principles and Applications* (R.M. May, ed.), pp. 5–29. Sunderland, MA: Sinauer.

McKitrick, M.C. 1993. Phylogenetic constraint in evolutionary theory: Has it any explanatory power? *Annu. Rev. Ecol. Syst.*, **24**: 307–330.

Metcalf, R.L. and Metcalf, R.A. 1993. *Destructive and Useful Insects: Their Habits and Control*. New York: McGraw-Hill.

Nothnagle, P.J. and Schultz, J.C. 1987. What is a forest pest? In *Insect Outbreaks* (P. Barbosa and J.C. Schultz, eds), pp. 59–80. San Diego, CA: Academic Press.

Price, P.W. 1989. Clonal development of coyote willow, *Salix exigua* (Salicaceae), and attack by the shoot-galling sawfly, *Euura exiguae* (Hymenoptera: Tenthredinidae). *Environ. Entomol.*, **18**: 61–68.

Price, P.W. 1991. The plant vigor hypothesis and herbivore attack. *Oikos*, **62**: 244–251.

Price, P.W. 1992. Plant resources as the mechanistic basis for insect herbivore population dynamics. In *Effects of Resource Distribution on Animal–Plant Interactions* (M.D. Hunter, T. Ohgushi and P.W. Price, eds), pp. 139–173. San Diego, CA: Academic Press.

Price, P.W. 1994. Phylogenetic constraints, adaptive syndromes, and emergent properties: From individuals to population dynamics. *Res. Popul. Ecol.*, **36**: 3–14.

Price, P.W. 1996. Empirical research and factually based theory: What are their roles in entomology? *Am. Entomol.*, **42**: 209–214.

Price, P.W. 1997. *Insect Ecology*, 3rd edn. New York: Wiley.

Price, P.W. and Clancy, K.M. 1986. Multiple effects of precipitation on *Salix lasiolepis* and populations of the stem-galling sawfly, *Euura lasiolepis. Ecol. Res.*, **1**: 1–14.

Price, P.W., Roininen, H. and Tahvanainen, J. 1987a. Plant age and attack by the bud galler, *Euura mucronata. Oecologia*, **73**: 334–337.

Price, P.W., Roininen, H. and Tahvanainen, J. 1987b. Why does the bud-galling sawfly, *Euura mucronata*, attack long shoots? *Oecologia*, **74**: 1–6.

Price, P.W., Waring, G.L., Julkunen-Tiitto, R., Tahvanainen, J., Mooney, H.A. and Craig, T.P. 1989. The carbon–nutrient balance hypothesis in within-species phytochemical variation of *Salix lasiolepis. J. Chem. Ecol.*, **15**: 1117–1131.

Price, P.W., Cobb, N., Craig, T.P., Fernandes, G.W., Itami, J.K., Mopper, S. and Preszler, R.W. 1990. Insect herbivore population dynamics on trees and shrubs: New approaches relevant to latent and eruptive species and life table development. In *Insect–Plant Interactions*, Vol. 2 (E.A. Bernays, ed.), pp. 1–38. Boca Raton, FL: CRC Press.

Price, P.W., Craig, T.P. and Roininen, H. 1995a. Working toward theory on galling sawfly population dynamics. In *Population Dynamics: New Approaches and Synthesis* (N. Cappuccino and P.W. Price, eds), pp. 321–338. San Diego, CA: Academic Press.

Price, P.W., Andrade, I., Pires, C., Sujii, E. and Vieira, E.M. 1995b. Gradient analysis using plant modular structure: Pattern in plant architecture and insect herbivore utilization. *Environ. Entomol.*, **24**: 497–505.

Price, P.W., Carr, T.G. and Ormord, A.M. 1996. Consequences of land management practices on willows and higher trophic levels. In *Southwestern Rare and Endangered Plants: Proceedings of the Second Conference* (J. Maschinski, H.D. Hammond and L. Holter, eds), pp. 219–223. USDA Forest Service, General Technical Report RM-GTR-283. Fort Collins, CO: US Department of Agriculture.

Price, P.W., Roininen, H. and Tahvanainen, J. 1997a. Willow tree shoot module length and the attack and survival pattern of a shoot-galling sawfly, *Euura atra* (Hymenoptera: Tenthredinidae). *Entomol. Fenn.*, **8**: 113–119.

Price, P.W., Roininen, H. and Carr, T. 1997b. Landscape dynamics, plant architecture and demography, and the response of herbivores. In *Vertical Food Web Interactions: Evolutionary Patterns and Driving Forces* (K. Dettner, G. Bauer and W. Völkl, eds), pp. 319–333. Berlin: Springer Verlag.

Price, P.W., Craig, T.P. and Hunter, M.D. 1998. Population ecology of a gall-inducing sawfly, *Euura lasiolepis*, and relatives. In *Insect Populations: In Theory and in Practice* (J.P. Dempster and I.F.G. McLean, eds), pp. 323–340. Dordrecht: Kluwer Academic.

Roininen, H., Price, P.W. and Tahvanainen, J. 1993. Colonization and extinction in a population of the shoot-galling sawfly, *Euura amerinae*. *Oikos*, **68**: 448–454.

Roininen, H., Price, P.W., Julkunen-Tiitto, R., Tahvanainen, J. and Ikonen, A. 1999. Oviposition stimulant for a gall-inducing sawfly, *Euura lasiolepis*, on willow is a phenolic glucoside. *J. Chem. Ecol.*, **25**: 943–953.

Root, R.B. and Chaplin, S.J. 1976. The life-styles of tropical milkweed bugs, *Oncopeltus* (Hemiptera: Lygeidae) utilizing the same hosts. *Ecology*, **57**: 132–140.

Royama, T. 1992. *Analytical Population Dynamics*. London: Chapman & Hall.

Siegel, S. 1956. *Nonparametric Statistics for the Behavioral Sciences*. New York: McGraw-Hill.

Smith, D.R. 1993. Systematics, life history, and distribution of sawflies. In *Sawfly Life History Adaptations to Woody Plants* (M. Wagner and K.F. Raffa, eds), pp. 3–32. San Diego, CA: Academic Press.

Smith, E.L. 1968. Biosystematics and morphology of Symphyta. I. Stem-galling *Euura* of the California Region, and a new female genitalic nomenclature. *Ann. Entomol. Soc. Am.*, **61**: 1389–1407.

Southwood, T.R.E. 1975. The dynamics of insect populations. In *Insects*, *Science*, *and Society* (D. Pimentel, ed.), pp. 151–199. San Diego, CA: Academic Press.

Southwood, T.R.E. and Comins, H.N. 1976. A synoptic population model. *J. Anim. Ecol.*, **45**: 949–965.

Tilman, D. 1989. Population dynamics and species interactions. In *Perspectives in Ecological Theory* (J. Roughgarden, R.M. May and S.A. Levin, eds), pp. 89–100. Princeton, NJ: Princeton University Press.

Wagner, M.R. and Raffa, K.F., eds. 1993. *Sawfly Life History Adaptations to Woody Plants*. San Diego, CA: Academic Press.

Wallner, W.E. 1987. Factors affecting insect population dynamics: Differences between outbreak and non-outbreak species. *Annu. Rev. Entomol.*, **32**: 317–340.

Wolda, H. 1979. Abundance and diversity of Homoptera in the canopy of a tropical forest. *Ecol. Entomol.*, **4**: 181–190.

Wolda, H. 1982. Seasonality of Homoptera on Barra Colorado Island. In *The Ecology of a Tropical Rain Forest* (E.G. Leigh, A.S. Rand and D.M. Windsor, eds), pp. 319–330. Washington, DC: Smithsonian Institution Press.

Wolff, J.O. 1997. Population regulation in mammals: An evolutionary perspective. *J. Anim. Ecol.*, **66**: 1–13.

Wood, T.K. 1984. Life history patterns of tropical membracids (Homoptera: Membracidae). *Sociobiology*, **8**: 299–344.