



The adaptive significance of insect gall morphology

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Insect galls are dramatic examples of extended phenotypes: although composed of host plant tissues, their development is largely controlled by insect genes. Adaptive explanations for gall traits should thus be expressed in terms of impacts on insect fitness, but the extent to which interspecific variation in gall structure is adaptive, and the possible selective pressures driving diversification in gall form remain controversial. In colonial aphids and thrips, gall structures probably diversified in response to selection for enhancement of the surface area available for feeding. In other taxa, such as gall wasps and gall midges, diversity is expressed predominantly in non-nutritive tissues, particularly those on the gall surface. All natural enemies attack the occupants of closed galls by penetrating gall tissue, and modifications that reduce enemy attack rates should thus be favoured. Recent studies of intraspecific variation in gall form strongly support a defensive role for several traits, but, to date, there is little empirical support for enemies as a cause of interspecific variation in gall form. Selection imposed by enemies nevertheless remains the most probable adaptive explanation for the evolution of diversity. We suggest that this hypothesis has yet to be tested explicitly, and discuss the requirements for an appropriate cross-species analysis.

Many insect groups, and an estimated 13 000 species, induce plant galls – structures composed of plant tissue within which the insect feeds, which are distinguished from other insect-generated shelters (such as rolled leaves or leaf mines) by the fact that they involve active differentiation and growth of plant tissues [1–3] (Box 1). Galls represent discrete microhabitats that support relatively closed communities of specialist inhabitants, and the ease with which galls can be collected, their occupants counted and observed, and the interactions among them inferred, have made galls important study systems in subject areas ranging from population dynamics to the evolution of altruism. In spite of the utility of insect galls as model systems, the species richness of galling taxa and the dramatic diversity of their galls, processes underlying the evolution of gall structures are still poorly understood. Recent work has established beyond doubt that galls represent the extended phenotypes of gall-inducer (galler) genes,

enabling the development of hypotheses for the adaptive significance of galls that are expressed in terms of galler fitness. The challenge facing us now is to determine which among the available hypotheses are relevant to the initial evolution of gall phenotypes, and to their subsequent diversification within and among galler lineages. Explaining variation in gall form across species remains a major challenge, requiring quantification of the impact of gall traits on galler fitness, and assessment of cross-species correlations between gall traits and fitness in a phylogenetic framework. We illustrate the approach required through discussion of the impact of natural enemies, the agents we believe to have greatest potential for driving the evolution and maintenance of gall diversity.

Gall diversity

Galling has evolved repeatedly among and within insect orders [1–3], producing species-rich lineages with fossil records extending back at least 300 million years [4–8]. The apparent success of gall induction as a life-history trait has fuelled a continuing debate about the adaptive significance of gall induction and, in particular, of gall morphology [9,10]. This debate is fuelled by observations that insect galls commonly include tissue types that are absent from ungalled host plants and that vary enormously in complexity (the extent of tissue differentiation within a single gall) and diversity (the range of gall structures induced by members of a given galler taxon) among galler lineages. Galls range in complexity from relatively open pits or folds to structures in which the galler is enclosed entirely by plant tissues (Figure 1). Such enclosed galls range from simple structures showing little variation among members of a galler taxon [such as those induced by fig wasps (Hymenoptera: Agaonidae) (Figure 1) and yucca moths (Lepidoptera: Prodoxidae) (Box 2)] to structures comprising multiple, highly differentiated layers of plant tissue that show extensive variation within a given galler taxon [1–3,11–14] (Figures 1,2). The most complex external structures, including extrafloral nectaries and coatings of hair, spines and sticky resins, are induced by gall wasps (Hymenoptera, Cynipidae) and gall midges (Diptera: Cecidomyiidae) (Figures 1–4) [9–11,13,14].

This diversity prompts the following questions: is gall morphology adaptive and, if so, which selective agents act on gall form? To what extent can differences in gall morphology within and among galler lineages be explained by selection? To answer these questions, we need to know

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Box 1. How are galls induced?

The only galls in which the molecular basis of induction is understood are bacterial, such as crown gall (induced by *Agrobacterium* spp. [46]) and the root nodules induced by nitrogen-fixing *Rhizobium* and *Frankia* spp. [47]. *Agrobacterium tumefaciens* transforms the tissues of its host by exporting plasmid DNA, and gall induction results from host expression of bacterial genes [46]. *Rhizobium* and *Frankia* export lipochitooligosaccharide signal molecules, termed nod factors. Nod-factor-like compounds have since been found to act as internal signals elsewhere in plant development, including somatic embryogenesis, illustrating the point that understanding gall induction mechanisms can be generally valuable in revealing important fundamental processes in plant development [47].

Galling insects also export gall-inducing stimuli, contained in saliva injected during feeding by aphids, in maternal secretions injected during oviposition by *Pontania* sawflies, and in larval secretions of unknown origin from cynipid gall wasps [1,48]. However, the nature and mode of action of the active compounds in these secretions, and the plant developmental pathways that they affect, remain unclear. The most commonly proposed signals are known plant growth factors, such as indole acetic acid (IAA) and other auxins, and/or zeatin and other cytokinins, or synergists thereof [1,9,15]. Proposed signals in specific

systems include amino acids (aphids in general, and *Phylloxera* in particular [49]), and protein(s) (*Pontania* sawflies [48]), whilst one intriguing theory proposes a role for mutualistic viruses and thus DNA transfer (cynipids [9]).

There are three major challenges in identifying the signal molecules involved. First, it is extremely difficult to establish suitable bioassays for plant tissue responses in many galling systems. In some cases, gall-inducing effects have been demonstrated with only very general assays, such as quantifying the growth responses of oat *Avena sativa* shoot tips to gall extracts, for which the relevance to gall induction is unclear. Second, gallers might use signal molecules that are chemically similar to (and hence difficult to separate from) those normally used in plant development (e.g. flavonoids and polyphenols, such as methyl esters of gallic acid [15,50]). Third, because exported signals from the galler are expected to induce a cascade of plant responses, a major challenge is the separation of primary morphogenetic impacts of galler origin from secondary plant responses to existing developmental pathways [45]. Major goals of current research include understanding the developmental basis of differences in gall morphology within and between galler taxa, and revealing the extent to which they exploit the same plant developmental pathways.

the extent to which the galler and its host plant control gall development (Box 1), and how variation in gall traits affects galler fitness [15].

Galls as the extended phenotypes of galler genes

The molecular basis of gall induction remains unknown in all insect galls (Box 1) and the causal roles of the insect and the plant can often be inferred only indirectly. This is significant because, until the mechanisms are known, we cannot rule out the possibility that variation in gall complexity and diversity among galler lineages might, in part, be due to differences in galling mechanisms rather than differences in selective pressures. Evidence nevertheless suggests that gallers are parasites (Box 2) that control most aspects of gall development. Galler control of gall morphology (or at least the absence of strong host plant-imposed constraints on gall form) is suggested by the fact that members of a given galling guild (such as gall wasps on oak, or gall midges on creosote bush) often induce very different galler-specific morphologies on the same plant host at the same time (Figure 4) [12–14]. In aphids,

gall midges and thrips, gall form is determined by the feeding patterns of the gall occupants, and interspecific differences in gall morphology can be linked causally to corresponding differences in feeding behaviour [1,3,16,17]. For other taxa, the extent of galler control can be inferred from analyses of phylogenetic patterns in gall evolution. If galler genes control morphology, then, on average, closely related gallers should induce structurally similar galls. Where similar structures have evolved convergently, we expect these to be of adaptive value to the galler. However, if host-plant characters place strong constraints on gall form, patterns in gall morphology should instead reflect similarities in the host plant or plant organ galled. Recent phylogenetic studies of aphids [18], thrips [17,19], sawflies [12] and gall wasps [20,21] (Figure 4) all support galler control for the major aspects of gall morphology. Where convergent evolution has been demonstrated (e.g. for surface nectaries in oak cynipid galls, or internal lamellae in thrips galls [14,17]), it involves structures of demonstrated or possible adaptive value to the galler that are entirely absent from ungalled plant tissues, and so are

Box 2. Which partner benefits from gall induction?

Galls could represent adaptations of the galler, the plant, or both. It was originally suggested that galls represent a means of isolating the damage inflicted by gallers to a specific plant part [9,10]. However, the success of galling insects, and the fact that their dependence on galls is usually obligate, shows that they must benefit from the association. Increasing experimental evidence also shows gallers to manipulate the allocation of plant resources to their advantage. Gallers can concentrate plant nutrients and metabolites in gall tissues by elevating photosynthetic rates in affected plant parts and by mobilizing resources from neighbouring plant tissues [14,22,25]. Although most insect gallers are certainly parasites, two well studied examples (agaonid fig wasps [8,51] and prodoxine yucca moths [6,52]) show that the association can become secondarily mutualistic. Both groups gall the reproductive tissues of their hosts (figs and yuccas, respectively), but also represent highly specific pollen vectors. Figure wasps and yucca moths both show behavioural and/or morphological adaptations to enhance pollination effectiveness [51,52], indicating a long-established mutualism. However, spatial variation in the cost–benefit balance of the mutualism in favour of

the galler [53], and the occurrence of parasitic nonpollinating gallers in both systems [51,52] underline the fact that parasitism is the rule.

But do gallers really damage their plant hosts? Many gallers destroy plant parts (e.g. flowers and seeds) with obvious links to host fitness, and compete with plant organs for nutrients and photosynthate. However, the population dynamic (and hence selective) impacts of such damage are variable and hard to quantify [14,15,53,54]. Costs of galling can be inferred indirectly, by looking for specific host plant responses to galler attack whose evolution implies a selective response to imposed costs [22,55–57]. The best examples of such plant defences are provided by aphids [22] and gall midges (Diptera: Cecidomyiidae) and, in particular, by the hessian fly *Mayetiola destructor*, a major pest of wheat [55,56]. In this system, specific loci in the galler control virulence, and specific loci in the host control resistance [56]. This represents a rare example of gene-for-gene correspondence between resistance and virulence in insect-plant relationships, and is evidence for a long-lasting (and costly) arms race between the organisms involved.

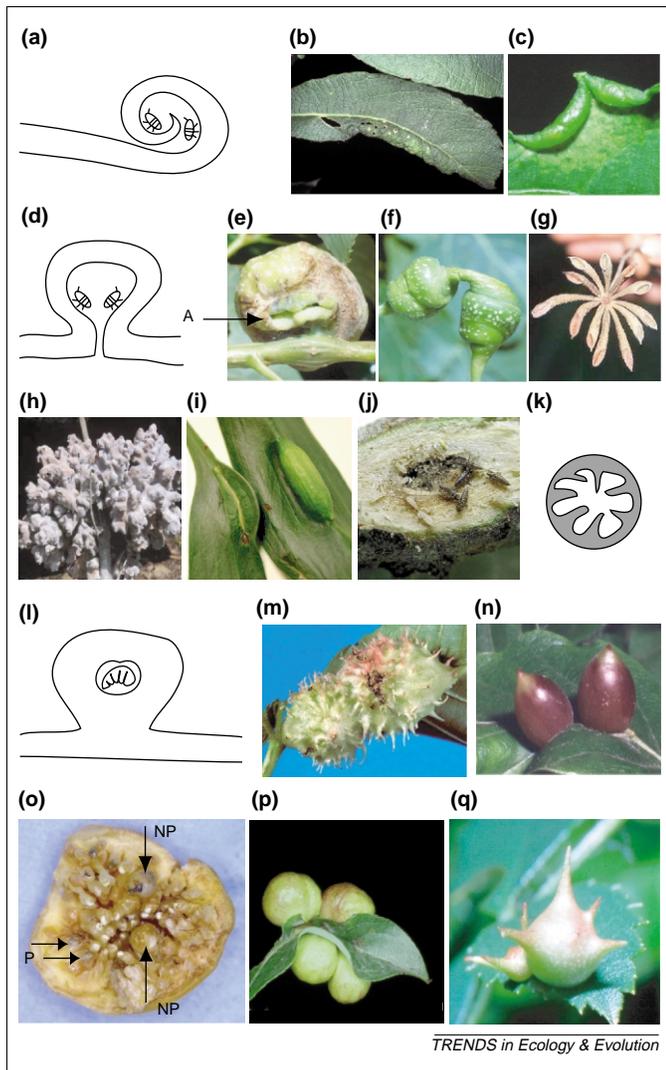


Figure 1. Morphological diversity in insect-induced galls (at different scales). (a) Cross-section of a leaf roll gall; leaf roll galls induced by (b) a sawfly *Euura weiffenbachii* on willow and (c) a gall midge *Contarinia subulifex* on oak. (d) Cross section of a pouch gall; pouch galls induced by aphids (e) *Pemphigus borealis* (note the gall aperture, A) (f) *P. spirothecae*, both on poplar in Europe; (g) *Astegopteryx styracophila* and (h) *Tuberaphis sumatrana*, both on *Styrax* in Sumatra; and (i) by a thrips *Oncothrips rodwayi* on *Acacia melanoxylon*. (j) An opened woody stem gall induced by a thrips, *Iotatubothrips* sp. on *Acacia cunninghamiana*, showing colony members. (k) Cross-section of the gall induced by an acacia thrips, *Oncothrips sterna*, showing internal lamellae to increase surface area for feeding. (l) Section of a wholly enclosed gall. Enclosed galls induced by gall midges (m) on hickory; (n) *Mikiola fagi* on beech. (o) Cryptic enclosed galls (arrows) induced inside a developing fig fruit (*Ficus rubiginosa*). Small galls (P) are induced by the pollinating wasp (*Pleistodontes imperialis*, Agaonidae), whereas large galls (NP) are induced by a nonpollinator (*Herodotia* sp. Epichrysomallinae). (p) An enclosed sawfly gall *Pontania hastatae* on willow. (q) An enclosed cynipid gallwasp gall *Diplolepis rosarum* on *Rosa*. Reproduced with permission from (b,p) Jens-Peter Kopelke; (c,e,f,n,q) György Csóka; (g,h) Utako Kurosu; (i,j) Laurence Mound, CSIRO; (m) Robert L. Anderson, USDA Forest Service. Image number 0590074 at <http://www.forestryimages.org>. (o) James Cook.

unlikely to have arisen through constraints imposed by the host plant.

For selection to act on gall morphology, galler populations must show heritable variation in traits that influence galler survival. Although this issue is central to the debate, it has rarely been examined in detail. The best evidence comes from work on a tephritid gallfly, *Eurosta solidaginis*, which galls goldenrod, *Solidago* sp. [15]. Gall size is an important predictor of galler survival

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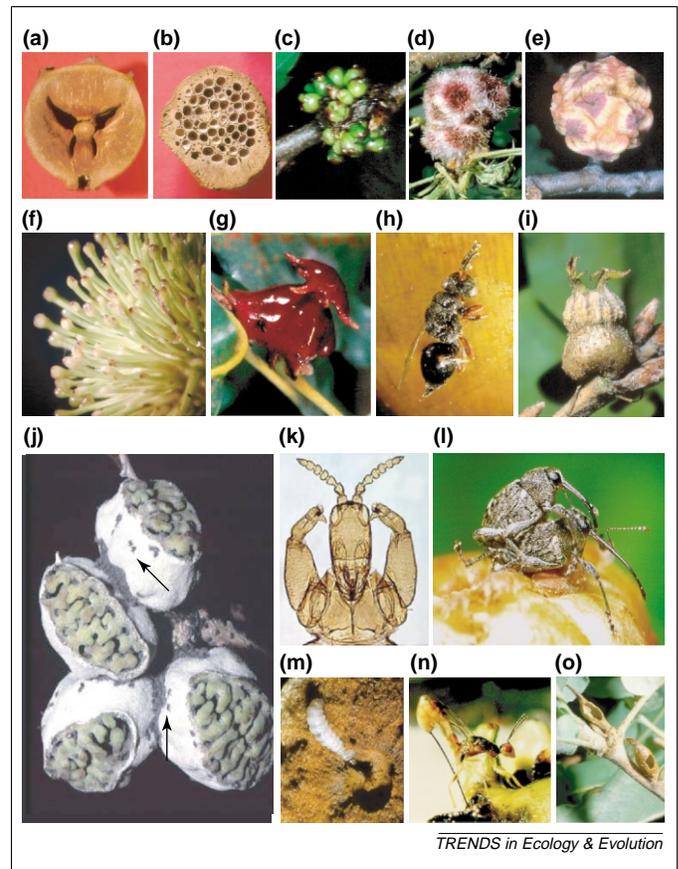


Figure 2. Gall traits of demonstrated (a–d, j) or putative (e–i) defensive value for gallers, and major groups of natural enemies (k–o) [with the exception of (j), all galls are induced by European oak cynipid gall wasps]. (a) Internal air spaces and thick outer gall tissues in *Andricus quercustozae* (longitudinal section). The larval cell containing all the nutritive tissues is in the centre. (b) Multiple larval cells in *Andricus quercusradicis* (longitudinal section). (c) Nectar secretion in galls of *Dryocosmus cerripilus*. (d) Dense coatings of hair in *Chilaspis nitida*. (e) Bright colouration in *Andricus curtisii*. (f) Dense coatings of spines in *Andricus lucidus*. (g) Surface coatings of sticky resin in *Andricus dentimitratus*, and (h) a trapped parasitoid. (i) A dummy upper chamber in *Andricus galeatus*. The larva develops in the lower part of the gall. (j) Soldier aphids (arrows) patrolling the surface of the gall induced by the ginger aphid, *Pseudoregma sundanica*. (k) A female inquiline thrip of the genus *Koptothrips*, which invades galls induced by *Kladothrips* thrips. These invading thrips kill the original gall thrips by stabbing with the teeth on the tarsi of their first pair of legs. (l) Gall weevils [*Curculio villosus* Fabr. (Coleoptera: Curculionidae)] on the gall of *Biorhiza pallida*. The larvae eat gall tissue and gallwasp larvae. (m) The caterpillar of a tortricid moth (*Pammene amygdalana*) in a gall induced by *A. quercustozae*. The caterpillar first kills the gallwasp larva to prevent lignification of the gall, and then feeds on gall tissue. (n) A parasitoid wasp (*Megastigmus stigmatizans*, Torymidae) attacking a gall induced by *Andricus quercuscalicis*. Torymids commonly use their long ovipositors to attack late in gall development. (o) Galls of *Andricus solitarius* that have been opened by birds. Reproduced with permission from (a,b,d,g,l,m,o) György Csóka; (k) Laurence Mound, CSIRO; (j) Utako Kurosu.

in this system, and detailed experiments have established that a significant proportion of the intrapopulation variance in gall size is explained by galler genotype [15]. Although host-plant genotype also has a significant impact on gall traits [15,22] (Box 2), the available evidence suggests that gall morphology should be regarded as the extended phenotype of galler genes [23]. Adaptive explanations for the genesis of gall diversity should thus be expressed in terms of galler fitness [10,14,15,17,20,21].

Hypotheses for the adaptive significance of gall induction

Of the hypotheses that have been advanced for the adaptive significance of gall induction [9,10], three are

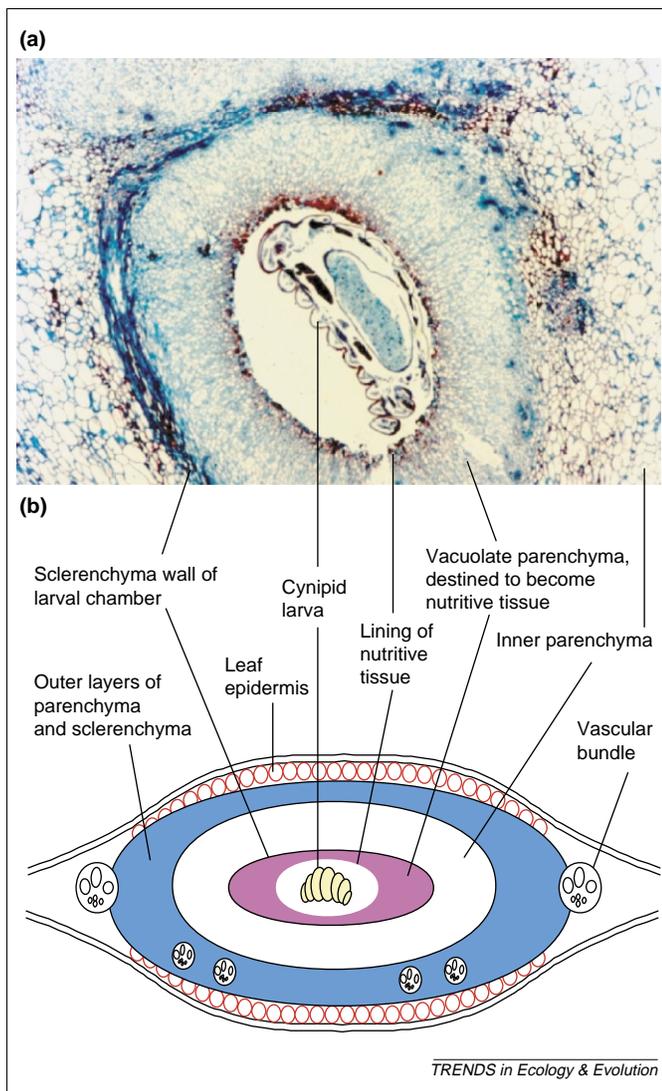


Figure 3. The distribution of nutritive and other tissues within the complex galls induced by cynipid gall wasps. **(a)** Section of the gall induced on the stem of a rose by *Diplolepis spinosa*, showing tissues immediately around the larva. The larval chamber is lined by a thin layer of nutritive tissue the development of which from vacuolate parenchyma is stimulated by larval feeding, and separated from the rest of the gall (the outer gall tissues) from a thin wall of sclerenchyma. The organization of nutritive tissues is uniform across all cynipid galls. **(b)** Distribution of tissues in the gall induced on a rose leaf by *Diplolepis rosaefolii* [14]. The tissues outside the larval chamber (outer parenchyma and epidermis) are responsible for the structural diversity seen in cynipid galls (e.g. Figure 4), and are usually transected by vascular bundles that connect the gall tissue to the plants vascular system. (a) Reproduced with permission from Joe Shorthouse.

relevant to discussions of gall morphology: the Nutrition hypothesis; the Microenvironment hypothesis; and the Enemy hypothesis. Testing these hypotheses involves two challenges. The first is to explain the adaptive value of gall induction over other modes of insect herbivory (e.g. leaf-mining or exposed feeding), and so the evolution of the first galls. The second is to identify processes generating variation in gall morphology within and among galler lineages. It is quite possible that different selective pressures have been dominant in these two phases of gall evolution.

There are three general ways of demonstrating adaptation [24]. The first is to use an argument based on functional design: if a gall is covered in sharp spines, then

reference to analogous structures suggests that these are likely to be defensive. A second, preferable, approach is to demonstrate the action of selection on the trait in question, either using natural within-population variation, or manipulated treatments: are galls with fewer or shorter spines demonstrably more vulnerable to attack by enemies? Galls are highly amenable to this approach. Third, we can use cross-species comparative analyses to examine correlations between particular gall traits and selection imposed by specific agents. Comparative approaches are particularly important when, as in many galler taxa, most of the diversity in gall traits is expressed among species rather than within them. We discuss comparative approaches in Box 3.

The Nutrition hypothesis

The Nutrition hypothesis states that galls provide enhanced nutrition over other feeding modes. With the exception of fungus-feeding gall midges, gallers feed on plant tissues or fluids. Many galls contain highly differentiated nutritive tissues (Figure 3) that are both more nourishing and less well defended than are non-gall tissues on the same plant (Box 1) [1,9,10,14,22,25], and enhanced nutrition is widely accepted as a general advantage of gall induction [9,10]. The Nutrition hypothesis also has the potential to explain diversity in gall tissues that contribute directly to galler nutrition. The strongest evidence concerns internal tissues in thrips and aphid galls. In both groups, colonies that can number thousands of individuals often occupy the gall for two or more generations [3,16] (Figure 1). The founding female and her offspring feed suctorially from internal gall tissues and gall traits that enhance feeding area or nutrient supply should be favoured by selection [3,16,17,19,22].

One way of enhancing the internal surface area in spherical galls is through the development of internal folds (Figure 1k), as found in some thrips and aphid galls. Evidence that such modification is adaptive comes from a recent comparative analysis of correlations between gall form and reproductive strategies in galling thrips [17]. Evolution of internal folds is correlated with massive enlargement of the reproductive tissues of the founding female (physogastry) and the evolution of enhanced supply is hence correlated with enhanced demand [17].

High internal surface area (relative to alternative designs of equivalent volume) can also be achieved by division of the gall into a network of hollow radiating spines or interconnected passageways, both of which are found in aphids (Figure 1g,h). To our knowledge, no comparative analysis of relationships between gall form and reproductive output in aphids has yet been carried out.

Gall midges of the genus *Asphondylia* (and of some species in the tribe Lasiopterini) represent exceptions to the rule that gallers feed on nutritive gall tissues [11]. These insects feed on a symbiotic fungus the spores of which are probably introduced by the egg-laying female. The fungal tissues can have significant impacts on gall morphology but, as discussed under the Enemy hypothesis, these are easier to interpret in terms of galler defence than in terms of galler nutrition. It remains possible,

however, that requirements of the fungus impose selection on gall structure.

In many other galler lineages, such as cynipid gall wasps and many cecidomyiid gall midges, nutritive tissues are restricted to discrete larval chambers embedded within other gall tissues that have no apparent nutritive function (Figure 3) [14]. Non-nutritive tissues account for most of the diversity in the galls induced by these groups (e.g. Figures 2,4), and their evolution cannot easily be explained by the Nutrition hypothesis [20].

The Microenvironment hypothesis

The Microenvironment hypothesis states that gall tissues act to protect the galler from unfavourable abiotic conditions, particularly desiccation [3,9,10,22,25–28]. Gallers that occupy partially enclosed structures lie within the boundary layers of moist air surrounding plant structures, and those developing within plant tissues are often directly bathed in fluid and so are buffered against water stress [1,25,26]. This hypothesis is widely accepted as a selective advantage of gall induction in general [9,10], but very little is known about the impact of variation in morphology on gall microclimate. If avoidance of desiccation has been important in the evolution of gall form, we would expect galls in xeric habitats to show adaptations protecting the galler from water stress. Possible modifications could include the evolution of fully closed galls from a partially open state, or protection of the galler by surrounding layers of waxy or corky tissue. One interesting possibility is that microclimatic considerations could influence which designs, among alternative designs of aphid and thrips galls of equivalent internal surface area, are favoured in a given habitat. For a gall of given volume, spherical galls with internal folds have a far smaller external surface area than do galls comprising hollow spines and should (all other things being equal) experience lower total rates of evaporative water loss. A prediction, then, is that spherical galls should be favoured in more arid environments. However, analyses of changes in gall form along environmental gradients have not revealed obvious patterns (e.g. [28]). It is possible that modification of gall tissue properties (e.g. reduction of permeability through deposition of resins or waxes) have been more important in any selective response to microclimate than has the modification of overall gall shape.

It has been suggested that avoidance of flooding has also been important in the evolution of gall form in high rainfall environments (U. Kurosu, pers. commun.). The gall induced by a Taiwanese aphid, *Ceratoglyphina styracicola*, has a natural aperture on its upper surface. Flooding is prevented by spine-like structures that originate from within the gall, exit the aperture and then radiate to form a cauliflower-like shield. Shedding of water (and also of honeydew) is enhanced by the deposition of wax on the velvety outer surface of the gall by individual aphids [29].

Although such examples suggest the importance of microclimatic considerations, these alone cannot explain the high diversity of gall morphologies induced by members of a single galler taxon on the same part of the

same plant at the same time, and hence occupying equivalent microclimates [12–14] (Figure 4).

The Enemy hypothesis

The Enemy hypothesis maintains that galls protect gallers from attack by natural enemies. In fully enclosed galls, all attacks must take place through gall tissues, and selection should then favour any modifications of gall morphology that enhance galler survival. Galls do provide some protection against attack by nonspecialist predators and pathogens [30], but they are far from being enemy-free space: most are attacked by communities of specialist enemies (including fungi, and the larvae of parasitoid wasps, beetles, moths and flies) (Figure 2) that often inflict high mortality [1,9,10,13–15,30–37]. For the Enemy hypothesis to be supported as a general advantage of galling, gallers should have suffered lower mortality than their nongalling ancestors at the time when galling evolved. Such an analysis is impossible for long-established galler lineages, and we can only compare data for extant galling and nongalling taxa. Ideally, we would compare patterns in galling and nongalling sister taxa (Box 3), but the availability of suitable data (particularly for mortality estimates) places strong constraints on the groups for which such comparisons are possible. The Enemy hypothesis is supported for galling sawflies [32], which are attacked by fewer parasitoid species and experience lower mortalities than do free-living forms. However, analyses over a broader taxonomic sweep have found that gallers as a trophic group are often attacked by more parasitoid species than are free-feeding forms, and the evidence for reduction in mortality is equivocal [30]. In contrast to the Nutrition and Microenvironment hypotheses, the Enemy hypothesis is thus not supported as a general long-term advantage of gall induction [9,10].

The high mortality experienced by many gallers nevertheless means that there should be strong selection for enhanced protection. Studies of the impact of intraspecific variation in gall traits on galler survival provide compelling evidence that four structural traits (increased gall hardness [14,36], increased thickness of gall tissue surrounding the galler [14,15,33,34], external coatings of hairs [35] and recruitment of ant guards through nectar secretion [15,38]) (Figure 2) significantly reduce the vulnerability of gallers to enemy attack. In the gall midge *Asteromyia carbonifera*, increased hardness is the result of growth of a symbiotic fungus, *Sclerotium asteris*, on which the galler larvae also feed [36]. Spores of the fungus are probably introduced during oviposition by the midge [11], and protection of its vector is thus of direct benefit to the fungus. Defence can also be enhanced by choices made by female gallers when laying their eggs. Many gallers induce multi-chambered (multilocular) galls by laying many eggs in the same site. The more eggs a female lays, the greater the average depth of developing larvae below the gall surface and the lower the mortality inflicted by parasitoids [14,15]. Genetic evidence shows that multilocular gall wasp galls commonly contain the offspring of several females. This raises the intriguing possibility that mothers could enhance offspring survival by contributing to the induction of a gall that is larger

Box 3. Testing correlations between gall traits and mortality inflicted by generalist enemies

Assessment of the significance of gall traits for mortality induced by generalist natural enemies involves four steps.

(1) Demonstration that morphologically indistinguishable enemies attacking different galls are members of a single generalist species

Detailed analysis of the population structure of apparently generalist enemies is needed to confirm that they actually represent a single species. Division of apparent generalists into genetically discrete ecotypes associated with different gall types would support (rather than undermine) the Enemy hypothesis. The only analysis we know to have addressed this issue in gallers concerns kleptoparasitic thrips in the genus *Koptothrips*. Two species in this genus do indeed consist of closely related sibling species or races, each invading host thrips associated with different *Acacia* species [37]. Host races are also known in hymenopteran parasitoids [58], and the same could be true for some of the highly polyphagous wasps in gall communities. Failure to incorporate such subdivision where it exists could have serious impacts in inferred relationships between gall traits and enemy attack.

(2) Quantification of mortality inflicted on each gall phenotype by each enemy

Past studies of enemy communities have predominantly generated qualitative food webs showing the presence or absence of particular trophic links [59] (Figure 1a), or semi-quantitative webs illustrating variation in the relative attack rates of different enemies [60] (Figure 1b). Most existing webs of both types are source webs [61], focused on the trophic links surrounding one host species (Figure 1a,b). Assembly of qualitative and semi-quantitative food webs for all hosts in a given galler guild reveals the existence of shared enemies and the role that each species plays in the component communities, but cannot quantify variation in mortality inflicted on alternative hosts. Analysis of links between mortality and gall traits requires fully quantified food webs, in which the interactions (usually mortality inflicted) on all available hosts by all available natural enemies are quantified for a sampled community (Figure 1c) (e.g. [62]). Interaction strengths and sets of interacting species are expected to vary in space and time, and generalization of the relationship between specific enemies and gall traits thus requires sampling at multiple sites over multiple seasons. To date, few such data

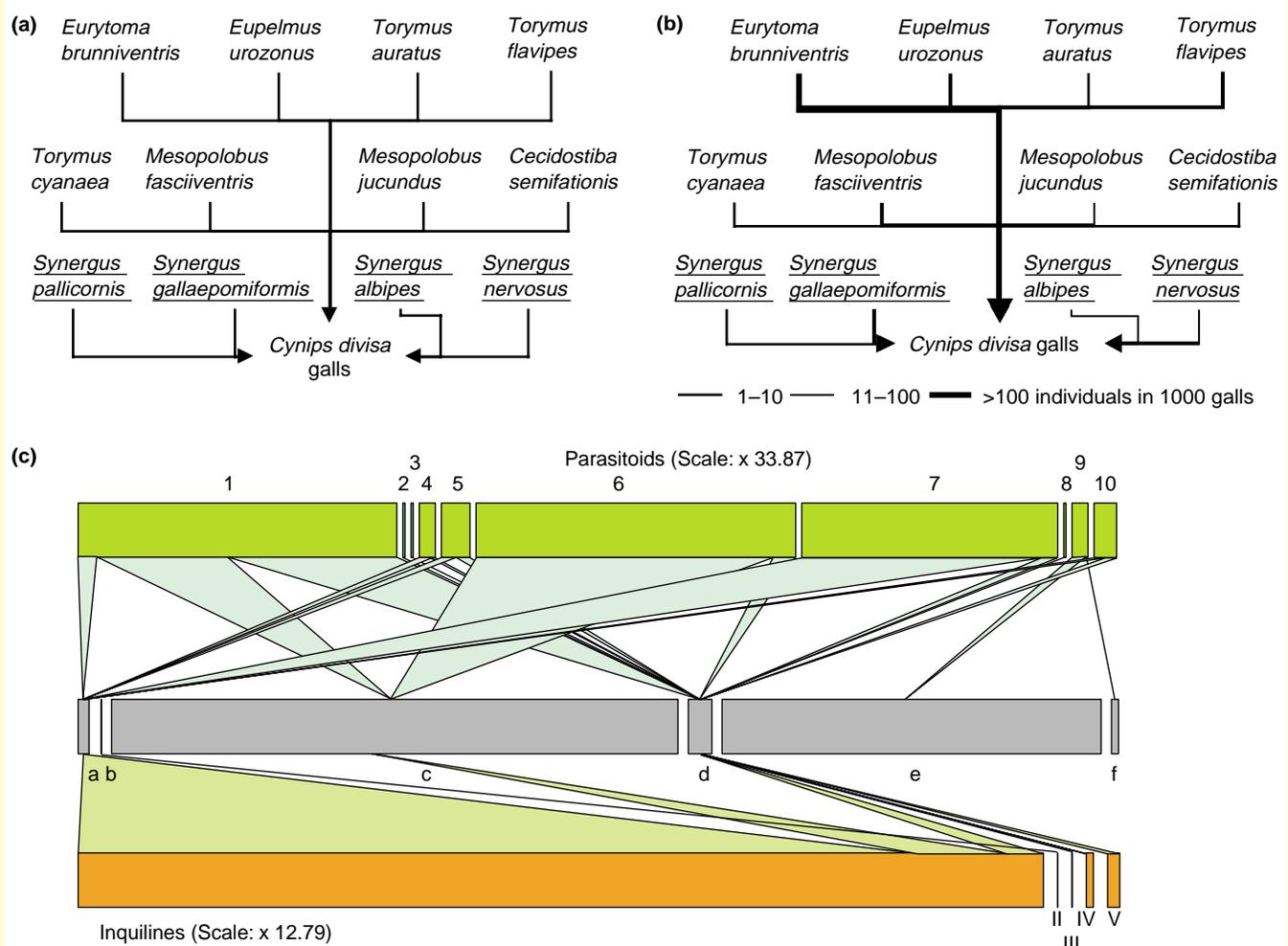


Figure 1. Different types of web displaying interactions between gall wasp hosts and their associated parasitoid and inquiline species, concentrating on the communities associated with the cynipid gallwasp *Cynips divisa* [62]. (a) and (b) are the qualitative and semi-quantitative source webs for this host. Underlined species are inquiline cynipids that inhabit galls but cannot induce their own. (c) A fully quantified web linking parasitoid species (green, species identified by numbers), cynipid gallwasp hosts [yygrey, identified by letters; *Cynips divisa* is species (d)] and inquiline cynipids (orange, identified by roman numerals). The width of the boxes shows the relative densities per area of each species. For display reasons, the total width of the bars representing all the inquilines and all the parasitoids are scaled to the same width as that of all the galls (i.e. there were 33.87 times as many galls as there were parasitoids, and 12.79 times the number of inquilines). The width of the links at the parasitoid- and inquiline side indicates the proportion of each species that emerged from each host gall.

Box 3. continued.

sets exist [63], and none has yet been generated for gallers. The sampling effort required to generate quantified webs also usually precludes detailed analysis of trophic relationships, which are best understood using both detailed source webs and fully quantified webs.

(3) The gall phenotype experienced by each enemy must be identified

See Box 4.

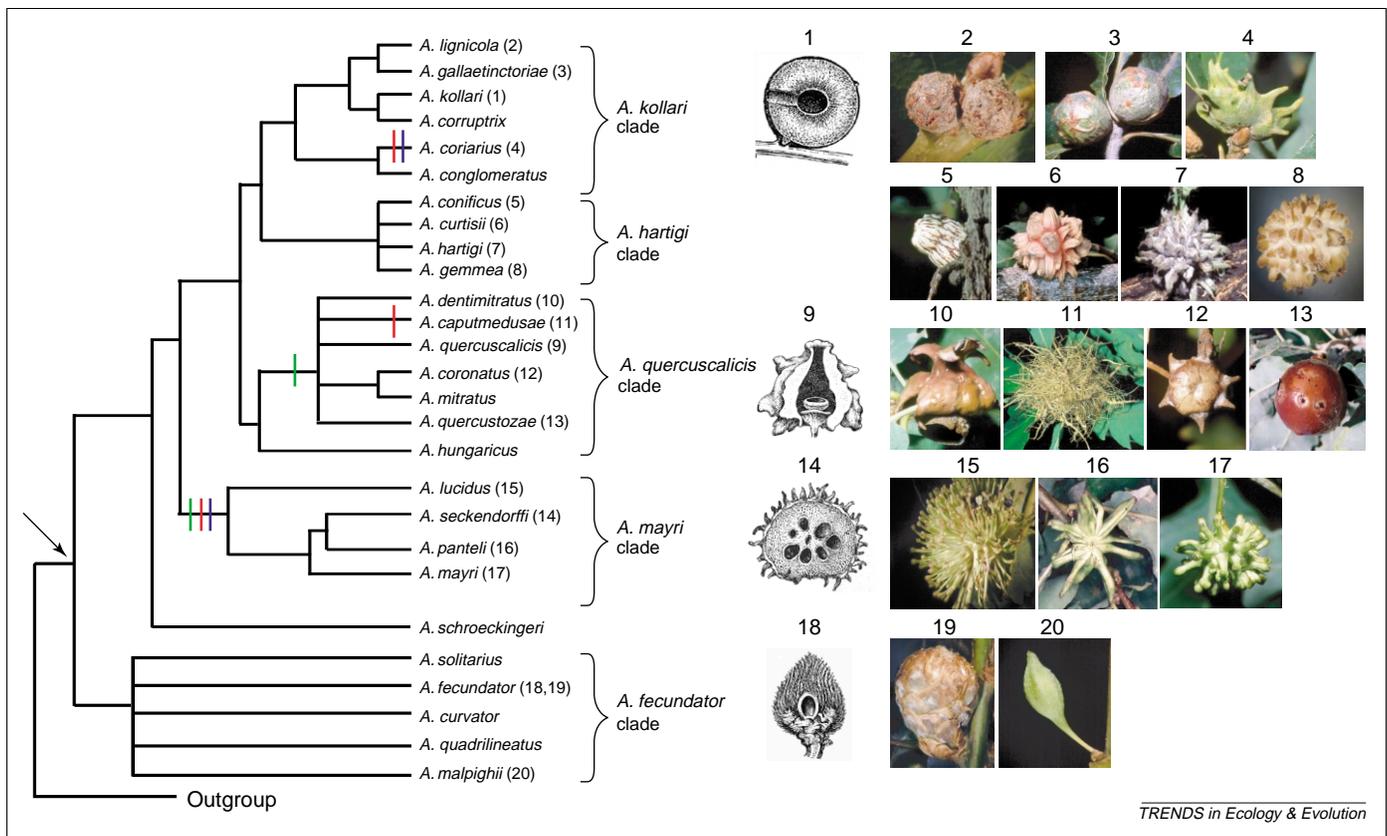
(4) Comparative analysis of mortality inflicted across alternative gall phenotypes

Once mortality data have been generated for each appropriate gall

phenotype, correlations between gall traits and mortality can be tested. Galler species are not statistically independent data points in such an analysis, but are linked by shared common ancestry. This phylogenetic nonindependence must be incorporated into the comparative analysis by testing the direction and magnitude of changes in mortality associated with divergence in gall traits from a shared common ancestor. A range of comparative techniques exists that enables appropriate contrasts to be made through incorporation of phylogenetic relationships among the taxa being compared [64]. Phylogenies have recently been constructed for a range of galler taxa [4,7,8,17,19–21,65,66], and await the generation of suitable quantified food webs.

(and so safer) than each could induce alone [39]. Defensive roles have been proposed (but not yet conclusively demonstrated) for other traits, including coatings of spines, sticky resins, the presence of false larval chambers, and larval cells that roll freely inside their gall, all of which might exclude or decrease the attack rates of insect or vertebrate enemies (Figure 2) [14,20]. Adaptive significance for these traits is further supported by their widespread convergent evolution in different galler lineages on a wide range of plant hosts [1,13,14,15,20] (Figure 4). However, gall phenotypes are not constant in time and identifying those actually experienced by natural enemies is complex (Box 4).

In the galls of aphid and thrips, selection for defence has resulted in complex interactions between gall form and individual altruistic behaviour of the insects. As well as enemies that attack through the gall wall, both aphid and thrips galls are also invaded via natural apertures (Figure 1e), which are essential for the dispersal of adults in both groups and, in many aphid galls, for the removal of excreted honeydew [3,16,31]. These openings make the galls vulnerable to invasion by a range of enemies, including nongalling kleptoparasitic aphids and thrips (Figure 2k), which otherwise lack the morphological traits necessary to open wholly enclosed galls [3,16,40]. The kleptoparasites displace or actively kill the original



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Figure 4. Patterns in the evolution of oak cynipid gall morphology for European members of the genus *Andricus*, traced over a phylogeny generated from DNA sequence data [19,20]. Numbered images correspond to species identified by the same numbers in the phylogeny. Members of each clade commonly share similar gall traits (solid woody galls in the *A. kollari* clade; an internal airspace, and an external coat of sticky resin in the *A. quercuscalicis* clade; spiny, many-chambered galls coated in sticky resin in the *A. mayri* clade). Spiny galls have evolved convergently from unspined ancestors three times (red bars), galls with many larval chambers have evolved convergently from galls containing a single larva twice (blue bars), and coatings of sticky resin have evolved convergently from non-sticky ancestors twice (green bars) during radiation from a common ancestor (marked with an arrow) that induced galls that lacked spines or resin, and contained a single larva. Images 3–5, 7, 10–12, 17 reproduced with permission from György Csóka.

Box 4. Gall development and windows of opportunity for natural enemies

Galls represent a changing resource for natural enemies. As the gall develops, not only does the resource provided by the galler larva grow, but many aspects of gall morphology (e.g. gall size, wall thickness, toughness, spine length, density of hair cover, surface stickiness and the presence of internal air spaces) also change dramatically [14,15,33,36,67–70]. These changes are associated with changes in the community of parasitoids that can exploit the gall, with small species attacking early in development, and larger, long-oviposited species attacking late in development [14,15,67–71]. Each natural enemy has a temporal ‘window of opportunity’ within which it can successfully exploit a given gall, extending from the time at which the host provides the minimum adequate resource for parasitoid development to the time at which the gall becomes impossible to attack [15,67–70]. Loss of opportunity to exploit a given host can arise in several ways: galls might become invulnerable through changes in gall morphology, inaccessible through changes in location (many galls dehisce from their host plants, and are very rarely attacked by parasitoids on the ground [14]), or emergence of the galler. In several systems, the phenology of gall development depends on environmental and/or genetic aspects of the host plant, leading to complex host-mediated effects on galler survivorship [15,69,70].

Because the phenotype encountered by a natural enemy depends crucially on when it attacks the gall, the adaptive significance of a given gall morphology must be assessed in terms of its vulnerability to attack by the enemies that are present at each stage of gall development. Where a guild of gallers shares natural enemies (as in oak gallwasp communities) [14], vulnerability will not only depend on absolute values (e.g. is the galler within reach of the ovipositor of a given parasitoid?), but also on relative values (e.g. is one gall more difficult to attack than another, and so avoided by shared parasitoids?).

The resource availability and accessibility constraints acting on natural enemies mean that gallers could potentially escape by shifting the phenology of gall development [38]. Such shifts are probably constrained by seasonal changes in the availability of suitable gall induction sites [11,14,22,72]. Furthermore, in guilds of gallers sharing enemies [13,14], escape from one set of enemies might risk encounter with another. Parasitoids can also, in principal, change the phenology of attack, and so circumvent gall defences. Resource limitation in young (but vulnerable) galls must represent a major constraint on early attack by parasitoids that halt the development of their host when the egg is laid. Selection to circumvent this constraint could explain why a range of parasitoids that attack early in gall development (and so avoid some gall defences) initially feed on gall tissue, and only later attack the galler (so reaping a larger resource) [14,67].

inhabitants and exploit the gall as a nutritional resource. In a striking example of convergent evolution, the need for protection has led to the evolution of sociality in both galling aphids and thrips, and altruistic colony defence by morphologically and behaviourally distinct soldier castes [3,37,40,41]. Soldier aphids commonly exit their gall to attack enemies on the gall surface [29,40–42] (Figure 2j). Although this behaviour often halts attacks before the gall is penetrated, it must also preclude the evolution of incompatible defences, such as coatings of sticky resins (Figure 2h). Such potential tradeoffs between alternative defensive strategies deserve further analysis. The importance of limiting the apertures available for invasion is suggested by the evolution of gall repair in aphids. The breach is sealed by (often suicidal) release of sticky secretions [42] and/or stimulation of growth in surrounding gall tissues (N. Pike and W. Foster, pers. commun.).

Natural enemies and interspecific variation in gall morphology

As discussed, neither the Nutrient hypothesis nor the Microenvironment hypothesis can explain the diversity in external gall structures induced by members of a given group of gallers on the same part of the same host plant at the same time (Figure 4). However, there are reasons to believe that selection imposed by natural enemies could, in principle, explain both the evolution and the maintenance of such diversity [37] (Box 5). For this hypothesis to be accepted, two general predictions must be supported. First, diversity should be highest in taxa in which high galler mortality is caused by enemies that penetrate gall tissues, and for which gall tissues are the primary or only defence. Second, within galler guilds, different gall morphologies should be attacked by different enemies, or experience different mortalities when attacked by shared natural enemies.

The first prediction is broadly supported: the greatest gall diversity is indeed shown by groups (e.g. gall wasps

and gall midges) that are attacked via gall tissues and (with the exception of those recruiting ant guards) have no other defence. The lower diversity of surface structures seen in aphid and thrips galls relative to these groups could result, in part, because important natural enemies enter through openings in the gall [3,37,40], effectively bypassing any external defensive structures. In aphids, surface-active soldiers also provide a defence that is incompatible with some alternative external structures. It is interesting to note that, although many nongalling aphids are ant tended, and galling aphids produce sugar-rich honeydew, no galling aphids have ant guards (U. Kurosu, pers. commun.). The low diversity and complexity of galls induced by pollinating and parasitic fig wasps can also be explained by the fact that all the enemies attacking these galls do so by ovipositing through the wall of the fig [43]. The enemies never encounter gall surface structures and, thus, there is no selection for increased complexity or diversity. Instead, the evolution of enemy traits (e.g. ovipositor length) is driven primarily by the thickness of the surrounding fig tissues [43]. There is, however, one notable exception. The eriophyiid mites are a species-rich group that induces a high diversity of galls, and has few or no known enemies [2,10]. There are two possible explanations for such exceptions. The enemies that once imposed selection on gall traits might have since disappeared, such that contemporary gall traits represent the ‘ghost of predation past’ [32]. The alternative is that this group represents a dramatic example of the impact of other, as yet unknown, factors on gall morphology. The difficulty of inferring past predation rates makes these alternative explanations difficult or impossible to test.

The second prediction is supported in its absolute form for sawflies: different gall structures are attacked by different groups of parasitoids [44]. However, this is the exception rather than the rule and parasitoid communities commonly include many species able to attack a wide

Box 5. Natural enemies and the evolution and maintenance of gall diversity

Parasites and natural enemies have long been recognized as major selective agents in the evolution and maintenance of diversity in host defences [23,37]. Several aspects of the galler–enemy interaction suggest that enemies could have a similar impact on gall diversity.

First, there are many ways of defending a gall against a given set of enemies. Different trait combinations [e.g. spherical and hard, spiny and sticky, soft and furry (Figure 4, main text)] can be regarded as alternative peaks in an adaptive landscape [23] toward which galler populations evolve, the outcome dependent on initial gall form (the starting point of the population in the adaptive landscape), the strength of selection, and any impact of nonadaptive genetic drift.

Second, although we expect the direction of selection imposed by nutritive or microclimatic requirements to be relatively constant for a given environment and group of gallers, selection imposed by enemies on a given trait can vary substantially over relatively small temporal and spatial scales. This has been shown convincingly for the size of galls induced by the gallfly *Eurosta solidaginis* [15]. Parasitoid wasps can only attack galler hosts within reach of their drilling ovipositor, and so select for increasing gall size. Birds, however, preferentially attack larger galls, and so select for decreasing gall size. Variation in the balance of these opposing selective forces results in spatial variation in favoured phenotypes [15,53,73].

Third, members of a given galling guild (such as cynipid galls on oak) are often attacked by overlapping sets of natural enemies,

some of which appear to have an extremely wide host range [13,14,44,62,74]. This creates the potential for interactions between hosts mediated by shared natural enemies. Specifically, populations of parasitoids that develop through attack of one host can impose high mortality on other, alternative hosts, leading to apparent competition among hosts for ‘enemy free space’ [74]. Apparent competition is expected to reinforce selection for improved enemy exclusion within sympatric galler guilds, and can also select for novel gall defences [75–77]. The maintenance of rare or novel gall phenotypes is favoured if, as in many host–parasite interactions, the value of any given combination of host defences is negatively density dependent [24].

Selection imposed by natural enemies can also account for three general patterns seen in the evolution of apparently defensive traits: conservation within clades, convergent evolution and a general increase in gall complexity over evolutionary time [7,12,17,20] (Figure 4, main text). Effective defensive traits should be retained during the radiation of a group from a common ancestor (conservation within clades), and when they evolve independently in separate clades (convergent evolution) [20]. If gallers are under constant attack, then, unless they can escape in other ways (e.g. by host-plant shifts [15,21,78]), we also expect gall defences and enemy counter measures (e.g. ovipositor length) to escalate over time [79].

range of gall morphologies (e.g. [13,14]). Here, the Enemy hypothesis is supported if, across species, higher values of an apparently defensive trait (e.g. hardness or spine length) are correlated with lower mortality inflicted by a given enemy. Such a cross-species comparative approach is much more challenging than a similar analysis within species and, to date, no such analysis has been completed. Crucial elements of the analysis are: (i) quantification of the mortalities imposed by specific enemies on different gall morphologies (Box 3); (ii) the identification of phenotypes actually experienced by natural enemies, and their appropriate categorization and quantification (Box 4); and (iii) analysis of correlations between the two in a phylogenetic framework (Box 3). Of these requirements, the easiest is probably the generation of the phylogeny, and the most challenging the quantification or categorization of gall traits. Although many potential cues are probably relatively constant in studies of intraspecific variation, interspecific studies require judgments of similarity and magnitude to be made from the perspective of the enemy. We know very little about the cues used by natural enemies (and particularly parasitoid Hymenoptera) to discriminate among alternative galls, and defence is in the eye (or antenna, ovipositor or beak) of the beholder.

Conclusions and goals of future research

Gall morphologies represent the extended phenotypes of galler genes, and adaptive explanations for them should be expressed in terms of galler fitness. All galls provide high-quality nutrition and protection from microclimatic fluctuation, but they do not represent enemy-free space. Diversification of some internal gall structures has probably been driven by enhancement of nutritive supply, whilst improved defence is the most probable adaptive explanation for diversification of external gall structures.

The Enemy hypothesis is supported by studies of the impact of intraspecific variation in gall traits on galler fitness, but its value in explaining variation in gall morphology across members of a galler guild remains to be established. Taxa showing low levels of enemy-induced mortality, such as the eriophyiid mites, suggest that other selective or nonadaptive processes can also generate gall diversity.

Many questions in this field remain. Studies of single systems have much to offer in determining the adaptive significance of specific gall traits, and the extent to which plant and galler genotypes determine heritable components of gall phenotypes [14,15,45]. Meaningful analysis of patterns across species requires both a detailed understanding of the way in which natural enemies interact with gall phenotypes, and the application of phylogeny-based comparative techniques. It also remains to be established whether differences in gall diversity among specific galler taxa result from variation in selection, or in other factors such as mechanisms of gall induction, or in the host plants galled. Several intriguing correlations already need explaining. Why, for example, do acacia thrips that guard their galls with soldiers also inhabit more elongate galls than do species without soldiers [17]? Exceptions (e.g. the rare examples of surface spines in the galls of acacia thrips [17]) might also help to define the rules. Finally, we need to appreciate that selection on gall morphology might well involve complex interactions between nutritive, microenvironmental and enemy impacts [10,14,15,27]. What factors limit the plant resources that gallers can direct to gall growth, and are there tradeoffs between investment in, for example, nutrition and defence?

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