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30. Single-letter abbreviations for the amino acid residues are as follows: A; Ala; C; Cys; D; Asp; E; Glu; F; Phe; G; Gly; H; His; I; Ile; K; Lys; L; Leu; M; Met; N; Asn; P; Pro; Q; Gln; R; Arg; S; Ser; T; Thr; V; Val; W; Trp; and Y; Tyr.

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## Supporting Online Material

[www.sciencemag.org/cgi/content/full/327/5973/1638/DC1](http://www.sciencemag.org/cgi/content/full/327/5973/1638/DC1)  
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## Evolutionary Trade-Offs in Plants Mediate the Strength of Trophic Cascades

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Predators determine herbivore and plant biomass via so-called trophic cascades, and the strength of such effects is influenced by ecosystem productivity. To determine whether evolutionary trade-offs among plant traits influence patterns of trophic control, we manipulated predators and soil fertility and measured impacts of a major herbivore (the aphid *Aphis nerii*) on 16 milkweed species (*Asclepias* spp.) in a phylogenetic field experiment. Herbivore density was determined by variation in predation and trade-offs between herbivore resistance and plant growth strategy. Neither herbivore density nor predator effects on herbivores predicted the cascading effects of predators on plant biomass. Instead, cascade strength was strongly and positively associated with milkweed response to soil fertility. Accordingly, contemporary patterns of trophic control are driven by evolutionary convergent trade-offs faced by plants.

Trophic cascades—the indirect positive effect of predators on plant biomass through herbivore suppression—are the best examples of the importance of indirect interactions as determinants of community structure and ecosystem function. For this reason, there has been great interest in elucidating the sources of variation in trophic cascade strength both within (1–3) and among ecosystems (4). Much of the research aimed at explaining variation in trophic cascade strength has focused on factors mediating the top-down effects of predators on herbivores, including the influences of intraguild predation (5), synergistic and antagonistic effects of multiple predators (6), trophic subsidies to predators (7), and the non-consumptive effects of predators on herbivores

(8). At the same time, it is also recognized that plant stoichiometry (9), antiherbivore defense traits (10–12), and primary productivity (13, 14) can mediate trophic cascade strength from the bottom up. Consequently, a consensus is emerging that multiple, complementary top-down and bottom-up processes determine trophic cascade strength.

Although it is recognized that plant traits can influence interactions with herbivores and herbivore-predator interactions (15, 16), there has been little consideration of how plant growth and defense strategies might result in predictable patterns of trophic cascade strength. There is wide acceptance that plant species evolve in response to fundamental trade-offs that should influence the effects of predators and productivity upon herbivore and plant biomass. For example, plant defense theory predicts that fast-growing species should have relatively low herbivore resistance as compared with slow-growing species (17, 18). Plant resistance to herbivores may in turn influence the indirect effects of predators on plants by altering herbivore susceptibility to

predators (19, 20). Similarly, plant growth strategies influence tolerance to herbivory (21, 22), again showing potential to alter the strength of trophic cascades. Although trophic cascades are rightly considered community-level phenomena (23), an understanding of how plant traits influence such dynamics requires first documenting the influence of plant traits on component, species-level cascades.

We conducted a field experiment in which we grew 16 species of milkweeds (*Asclepias* spp., Apocynaceae) (Fig. 1), factorially manipulated predator access and soil fertility, and monitored plant biomass and populations of the potent herbivore *Aphis nerii* (Aphididae, Hemiptera), a specialist on the Apocynaceae that occurs naturally on the studied milkweeds (24). It has previously been shown that milkweed species influence this aphids' population dynamics and interactions with parasitoids (16, 25). We tested whether there are indirect consequences of such variation in trophic dynamics for plant growth as well as whether trade-offs between milkweed growth strategy and herbivore resistance predictably influence the top-down effects of predators. Because all plants were grown in a single environment, any variation in the effects of predators and growth strategy can be attributed to plant species traits. By interpreting these patterns of interspecific variation in trophic structure from a phylogenetic perspective, we link the outcome of fundamental evolutionary trade-offs to contemporary community dynamics.

We first tested for variation among milkweed species in the effects of predators and soil fertility on both plant biomass and herbivore abundance using general linear models. Where species varied in such responses, we then quantified effect sizes for individual species [log response ratios (26)] in order to examine the relationships among species using phylogenetically independent contrasts (27).

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The 16 milkweed species varied in herbivore resistance (quantified here as  $-1 \times$  aphid density in the absence of predators) (fig. S1 and table S1) and the top-down effects of predators on herbivore density and plant biomass (Fig. 1 and table S1). This variation in top-down control among species is equivalent in magnitude to that previously observed among ecosystem types (4). That such variation occurs among closely related species in a single abiotic environment, with the same herbivore species and with a common guild of predators, underscores the powerful influence of plant traits upon trophic structure.

Milkweed species also differed strongly with respect to two aspects of the plants' growth strategy, growth rate [which is defined as mean species biomass at the conclusion of the experiment (fig. S1 and table S1)], and the growth response to increased soil fertility (Fig. 1 and table S1). The strength of soil fertility effects on plant biomass was stronger when predators were absent than when present (fig. S2 and table S1), but these dynamics were consistent among milkweed species (table S1). Despite the species-specific effects of soil fertility on milkweed growth, the indirect positive effect of soil fertility on aphid density was indistinguishable among milkweed species (Fig. 1 and table S1). Accordingly, there was asymmetry in how milkweed species influenced top-down and bottom-up trophic dynamics: Predator effects on both herbivore density and plant biomass were species-specific, whereas species variation in soil fertility

effects were limited to the direct influence on plant biomass.

Having shown milkweed species differences in growth strategies, resistance, and the top-down effects of predators, we examined the relationships among these species traits while controlling for phylogenetic history (27). Variation in herbivore density among milkweed species was determined by means of a combination of top-down and bottom-up processes. Although theory and data predict that herbivore resistance in plants should influence predator-herbivore interactions (19, 20), predator effects on herbivores were unrelated to milkweed resistance (fig. S3). In addition, the strength of predator effects on herbivores did not vary as a function of milkweed growth or growth response to soil fertility (table S2). However, both components of milkweed growth strategy convergently traded off against resistance so that species that were fast growing and responsive to soil fertility had low resistance (meaning, higher herbivore densities) (Fig. 2 and table S2), which is consistent with predictions from plant defense theory (17, 18). Thus, herbivore density was jointly and independently determined by means of interspecific variation in the top-down effect of predators and the bottom-up effect of milkweed growth strategies.

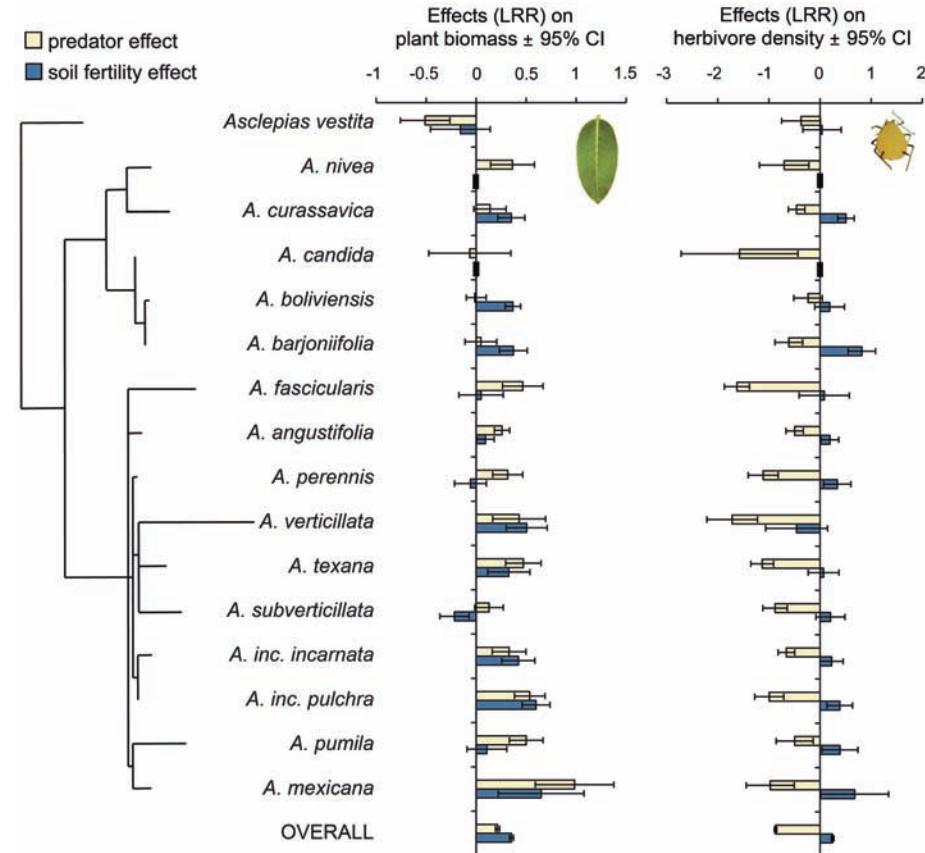
Surprisingly, predator effects on plant biomass were unrelated to either predator effects on herbivores or herbivore density (resistance) (table S2). Instead, plant growth response to soil fertility predicted more than half of the variation

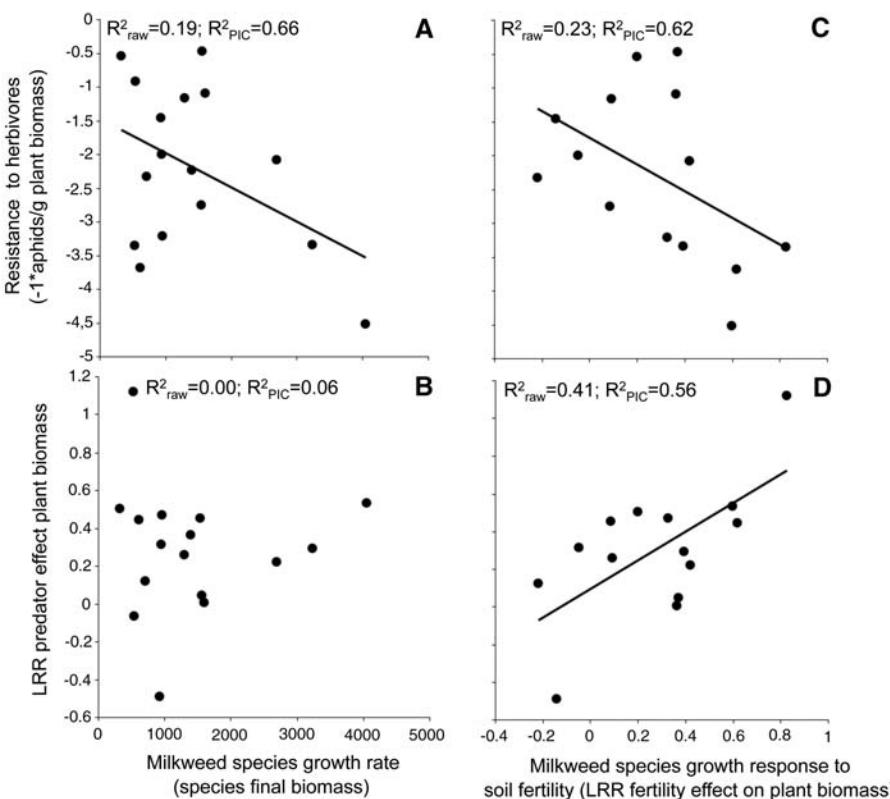
in the top-down effects of predators on plant biomass (Fig. 2). At the same time, milkweed growth rate was not predictive of predator effects on plant biomass [and growth rate and response to soil fertility themselves are uncorrelated (table S2)]. Because the impact of predators on plant biomass was not related to the strength of herbivore suppression, variation in the indirect effects of predators on plants is probably attributable to variation in tolerance of milkweed species to herbivory. Consequently, an evolutionary trade-off leads to an association between high growth in response to soil fertility, low tolerance to herbivory, and an increase in predator effects on plant biomass.

Of several plant traits assayed, we found evidence suggestive of one mechanism behind the observed variation in the top-down effects of predators on plants. Plant emissions of sesquiterpene volatile organic compounds (VOCs) were significantly positively correlated with the top-down effects of predators on plant biomass (fig. S4 and table S3). Sesquiterpenes are a group of VOCs that can play a key role in indirect defense through recruitment of predators to plants (28). Therefore, variation among species in trophic cascade strength may be driven at least in part by interspecific variation in this ecologically important group of volatile compounds.

We have documented wide variation in top-down regulation of plant and herbivore biomass among a group of closely related species; this variation corresponded with a fundamental evo-

**Fig. 1.** Effect sizes for influence of predators and fertilization on herbivore density (calculated per gram of plant dry biomass) and final plant biomass. Black bars for *A. nivea* and *A. candida* indicate that soil fertility was not manipulated for these species. Effects are natural log response ratios (LRRs) with 95% confidence limits. Predator effects are calculated across both levels of soil fertility, soil fertility effects are calculated across both levels of predation, and all effects are based on manipulation and control sample sizes of  $n = 10$  plants each. LRRs of 1.0, 2.0, and 3.0 correspond to changes of 2.7-fold, 7.4-fold, and 20-fold, respectively. Predator effects on both herbivore density and plant biomass differ significantly among species, whereas fertilization effects differ for plant biomass but not for herbivore density (table S1). To the left of the effect sizes, the phylogenetic relationship of the studied milkweeds is presented (29).





**Fig. 2. (A to D)** Relationship between milkweed species' growth rate, growth response to soil fertility, resistance to herbivores, and predator effects on plant biomass. For ease of interpretation, raw data are depicted with both raw and phylogenetically corrected  $R^2$  values indicated in each panel. Where the phylogenetically independent correlations were significant [conducted by using generalized least-squares methods (27)], a linear best fit is shown through the raw data. Growth rate and response to soil fertility themselves are uncorrelated (table S2).

lutionary trade-off faced by plants. Interspecific variation in herbivore density was determined jointly and independently through variable effects of predators and two components of plant growth. In contrast, the cascading effects of predators on plant biomass were not tied to predator-herbivore interactions but instead fell along a probable trade-off between tolerance to herbivores and the bottom-up effects of soil fertility. Whereas food web models have predicted the correspondence of top-down and bottom-up effects on the basis of thermodynamic principles of energy flow (13, 14), we show here that such dynamics can similarly arise from convergent trade-offs faced by plants over evolutionary time. Our results underscore the importance of considering the plant-herbivore linkage as a determinant of trophic cascade strength, and the dynamic interplay between past evolutionary processes and contemporary ecological dynamics.

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#### Supporting Online Material

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Materials and Methods

Figs. S1 to S4

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References

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## A Peroxidase/Dual Oxidase System Modulates Midgut Epithelial Immunity in *Anopheles gambiae*

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Extracellular matrices in diverse biological systems are cross-linked by tyrosine covalent bonds catalyzed by the peroxidase/oxidase system. We show that a peroxidase, secreted by the *Anopheles gambiae* midgut, and dual oxidase form a tyrosine network that decreases gut permeability to immune elicitors. This network protects the microbiota by preventing activation of epithelial immunity. It also provides a suitable environment for malaria parasites to develop within the midgut lumen without inducing nitric oxide synthase expression. Disruption of this barrier results in strong and effective pathogen-specific immune responses.

Insects, like most metazoa, harbor large numbers of commensal bacteria within their guts. Midgut epithelial cells need to pro-

tect the host from pathogenic organisms but must do so without mounting immune responses against the normal microbiota. This is

instead they observed two. Although this result may not be exciting from a statistical point of view, it has been met with excitement in the field. For years, experiments have produced null results, providing only upper limits on cross sections of WIMP-nucleon interactions. The two detection events have raised hopes that more sensitive detectors may soon shed light on dark matter.

Because target materials can be made very pure, most radioactive backgrounds come from the surface of a detector, and instrumental effects are also stronger near detector edges. Continuing their two-decade long effort building improved detectors, the CDMS II Collaboration developed thicker germanium targets to improve the surface-to-volume ratio, and with more efficient phonon collection to better reject surface events. This increases the acceptance of these new detectors to dark matter events and allows them to take the next step in sensitivity that is required to clarify the result reported.

Meanwhile, other experiments use differ-

ent technologies, each with its own difficulties and advantages. Some use liquid noble gases as target material and read out the scintillation light that is created in a particle interaction. If electrons liberated in the interaction drift through the liquid and are measured as well, this allows for background discrimination similar to CDMS. The major advantage of these liquid target detectors is that they can be made large, hence decreasing the surface-to-volume ratio. The first of these to challenge the CDMS lead of the field was the XENON10 experiment (4). There, a large reduction of the radioactive background was achieved using only the innermost 5.4 kg from a 15-kg liquid xenon target. This year should see rapid progress, with at least three major liquid noble gas experiments expected to take and release data. Even ton-scale detectors will be feasible within a few years.

With all these highly sensitive detectors being or becoming operational, we can expect to learn soon whether or not CDMS observed dark matter and, with a bit of luck, what it

is made of. Further, we expect that, should dark matter be WIMPs, we will detect many of them within only a few years and be able to estimate of their mass. Then the real fun will begin, as WIMP astronomy will allow us to infer otherwise inaccessible information. For example, due to their feeble interactions, the energy distribution of WIMPs in our galaxy, the Milky Way (see the figure), preserves features more than a billion years old that arose during collisions with other galaxies (5). Hence, measuring this WIMP energy distribution with direct dark matter detectors would open the history book of our galaxy.

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#### ECOLOGY

## A Green or a Prickly World?

Peter A. Hambäck

Is the world a green place where plant biomass abounds for herbivores to devour, or a prickly place where herbivores struggle to locate the few edible plant pieces? The answer to this question has crucial consequences for broad ecological and evolutionary questions. On page 1642 of this issue, Mooney *et al.* (1) show how evolutionary trade-offs among plant traits affect responses to herbivores and higher trophic levels.

If plant biomass is accessible but not consumed, herbivore numbers, and thus their consumption, may be regulated from the top by their natural enemies. If, in contrast, plant biomass is a nasty resource, then plant resistance to herbivory is central to understanding the greenness of the world. This dichotomy suggests a straightforward answer, but in nature, top-down forces interact in complicated ways with plant traits in determining the strength of species interactions. To address these issues, Mooney *et al.* have studied 16 related milkweed species. The results show that top-down effects from predator presence to plant biomass were determined not by plant resistance

or by interaction strengths between herbivores and their natural enemies, but rather by a trade-off between plant growth strategy and resistance to herbivory.

The evolution of species traits depends on the main selective factors determining fitness. Populations facing high risks of predation will evolve different traits than populations where food limitation and starvation is common. In nature, this dependence is not unidirectional (even though most experiments are so), and traits themselves likely feed back to affect the species interactions and the fitness landscape. When we try to understand the role of certain species interactions in a specific ecological situation, what we see is a product of the evolutionary history of involved species and the proximate ecological factors. The interplay between these temporal scales for indirect interactions is only beginning to be disentangled by work such as that of Mooney *et al.*

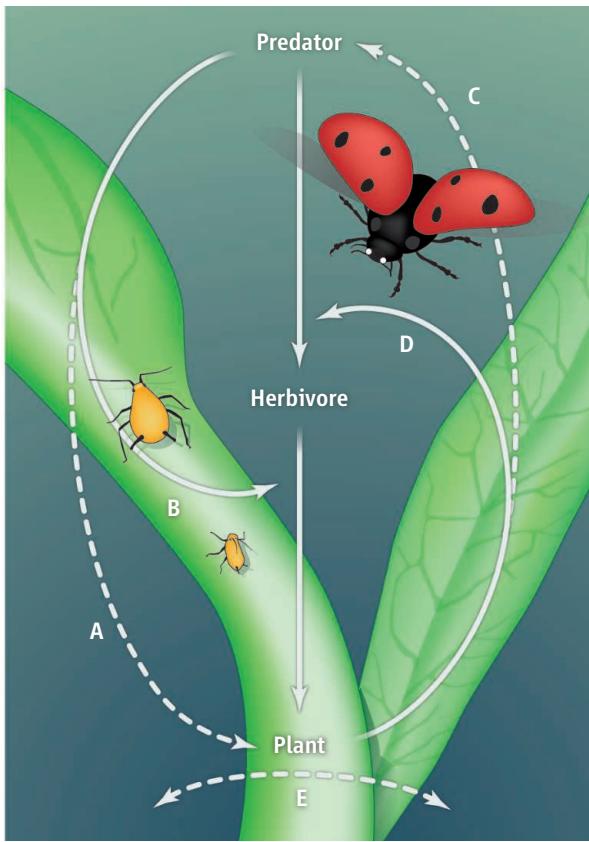
In many insect-dominated ecological systems, plants emit volatile compounds to attract predators. These emissions create feedbacks between predators and herbivores that affect plant biomass and fitness (2). Predators and parasitoids attacking herbivorous insects use the chemical cues provided

**The evolution of plant traits shapes complex interactions with herbivores and their predators.**

by plants at the time of herbivore attack to locate their prey. Mooney *et al.* (1) suggest that differences in volatile production—particularly of sesquiterpenes, which affect natural enemy attraction (3)—correlate with the effect of removing predators. Milkweed species that produced higher amounts of sesquiterpenes showed a larger difference in plant biomass with or without lady-bird beetles and other aphid predators, apparently because these species also differed in their tolerance to herbivory.

Most studies on the role of volatiles (the infochemical web) in plant-arthropod interactions have focused on mechanisms and chemical backgrounds, providing limited insights into the wider consequences for natural communities. Overlaying food webs with the infochemical web will increase our understanding of complex species interactions. In addition to the top-down effects on trophic cascades studied by Mooney *et al.*, this was illustrated in a recent study of two related herbivorous beetles, their respective host plants, and a shared parasitoid (4). Field surveys suggested that mortality rates of one beetle species (*Galerucella tenella*) were higher when the other species (*G. calmariensis*) was pres-

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**A complex web.** Food web interactions involve direct (solid lines) and indirect (hatched lines) effects. Predators and herbivores directly affect their resources through consumption, creating indirect effects of predators on plants (A). Predators also affect herbivore behavior and, indirectly, plant consumption (B) (8). Plants affect predator growth through effects on herbivore biomass and quality (C) (9) and predator search through damage-induced volatiles (D). Mooney *et al.* (1) suggest that trade-offs between plant growth strategy and resistance to herbivory moderate top-down effects (E).

to the scent of flowering meadowsweet (*Filipendula ulmaria*), host plant to *G. tenella*, and deposited more eggs in *G. tenella* larvae. As a result, attack was reduced and seed set increased on meadowsweet when growing together with the host plant of *G. calmariensis*, purple loosestrife (*Lythrum salicaria*). Herbivory from *G. tenella* can be very strong, defoliating the host plant, and selects for increases in defensive chemicals (5). This strong selection would presumably not occur in the presence of purple loosestrife.

Predators and parasitoids provide important ecosystem services to mankind and food production by reducing pest densities. Estimates suggest that up to 15% of food production is lost to arthropod pests (6), and the global cost of biological

control is estimated at US\$417 billion/year (7). Yet, little is known about how to improve the conditions and efficiency of natural enemies in cropping systems. This development hinges on our detailed understanding of how complex interactions between plants, herbivores, and their predators determine the loss of plant tissue and the ability of plants to compensate for such losses. The integration of trophic dynamics and infochemical webs promises to provide deep additional insights to this end.

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ent in the neighborhood. Seemingly, *G. calmariensis* was the better host for parasitoids, but adult parasitoids were nevertheless attracted

pest densities. Estimates suggest that up to 15% of food production is lost to arthropod pests (6), and the global cost of biological

#### CHEMISTRY

## Less Costly Catalysts for Controlling Engine Emissions

James E. Parks II

Lowering the fuel consumption of transportation vehicles could decrease both emissions of greenhouse gases and our dependence on fossil fuels. One way to increase the fuel efficiency of internal combustion engines is to run them “lean,” in the presence of more air than needed to burn all of the fuel. It may seem strange that engines are usually designed to run with fuel and air at stoichiometric balance, or even fuel rich. However, the way emissions have been controlled with catalytic converters has required some unburned fuel in the exhaust, especially for controlling the nitrogen oxide pollutants NO and NO<sub>2</sub> (called

NO<sub>x</sub>). On page 1624 of this issue, Kim *et al.* (1) report encouraging results for catalysts that can process NO<sub>x</sub> in lean-burn engines. These perovskite oxide catalysts may help reduce or even eliminate the need for expensive and scarce platinum group metals (PGMs) in emission-control catalysts.

Commercially available vehicles with lean-burn technology have either diesel (2) or gasoline direct injection engines (3), and typically have additional costs of \$1000 to \$5000 compared with stoichiometric engine vehicles (4). A large part of the extra cost is due to engine modifications and exhaust catalysts that enable compliance with emission regulations.

Lean engines produce oxygen-rich exhaust, which prevents the reduction of NO<sub>x</sub>

via the “three-way” catalyst commonly used for stoichiometric engines. The new combustion and catalyst technologies for lean engines must meet NO<sub>x</sub> emission standards as well as those for carbon monoxide, hydrocarbons, and particulate matter (soot). For diesel engines, special exhaust filters have eliminated the unsightly plumes of soot emissions from diesel exhaust.

Two catalyst technologies for controlling NO<sub>x</sub> emissions from lean-burn engines are urea-based selective catalytic reduction (SCR) and the lean NO<sub>x</sub> trap (LNT), also known as the NO<sub>x</sub> storage and reduction catalyst. Urea SCR’s main disadvantages are related to the requirement of onboard storage of the urea reductant and the need to heat the urea in cold weather. The issue of how

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## Trophic Trade-Offs >>

There have been many attempts to document and explain the effects of predators on plant biomass in so-called "trophic cascades." Theory suggests that fast-growing plants are relatively undefended and suffer more from herbivory, which implies a functional trade-off between investment in traits relating to growth and defensive strategies. **Mooney *et al.*** (p. 1642; see the Perspective by **Hambäck**) compared responses to fertilization and aphid predators in 16 milkweed species. As predicted, interspecific variation in the strength of top-down control in terms of a tradeoff with growth was observed.



## Platinum-Free Diesel

The efficiency advantages inherent in diesel-based combustion engines are counterbalanced by the production of pollutants such as nitrogen oxides ( $\text{NO}_x$ ). Currently, expensive precious metals, such as platinum, are required to remove these pollutants. **Kim *et al.*** (p. 1624; see the Perspective by **Parks**) show that a strontium-doped perovskite catalyst, prepared from more abundant (and cheaper) elements, may help to lower the cost of  $\text{NO}_x$  treatments and thus ultimately make diesel a more cost-effective automotive fuel. Under conditions realistically simulating exhaust streams, the catalyst rivaled platinum in accelerating  $\text{NO}_x$  decomposition.

## Iron Exposure

The macrocyclic heme motif coordinates iron ions in proteins and plays a widespread role in biochemical oxidative catalysis. **Bezzu *et al.*** (p. 1627) prepared crystals in which analogous iron-centered macrocycles were aligned in pairs. The outer faces of the pairs exposed the iron ions to vacant cavities, where ligand exchange could take place; the inner faces were bound together by rigid bridging ligands lending the crystals structural integrity. The stability and high porosity of these crystals lend themselves to potential catalytic applications.

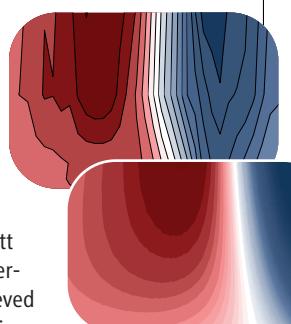
## Preventing Radiation Damage

Inside a nuclear reactor, long-term exposure to radiation causes structural damage and limits the lifetimes of the reactor components. **Bai *et al.*** (p. 1631; see the Perspective by **Ackland**) now show, using three simulation methods able to cover a wide range of time and length scales,

that grain boundaries in copper can act as sinks for radiation-induced defects. The boundaries are able to store up defects, in the form of interstitials, which subsequently annihilate with vacancies in the bulk. This recombination mechanism has a lower energy barrier than the bulk equivalent, and so provides a lower-cost route for the copper to self-heal.

## Fermion Behavior in an Optical Lattice

Due to their extreme tunability, optical lattices loaded with fermions and bosons are expected to act as quantum simulators, answering complicated many-body physics questions beyond the reach of theory and computation. Some of these many-body states, such as the Mott insulator and the superfluid, have been achieved in bosonic optical lattices by simply changing the characteristic depth of the lattice potential wells. Now, **Hackermüller *et al.*** (p. 1621) describe an unusual effect in an optical lattice loaded with fermions: When the strength of the attraction between the fermions is increased adiabatically, instead of contracting, the gas expands in order to preserve entropy.



## Perfect Mismatch

Heteroepitaxy, or the overgrowth of one crystalline material onto a second crystalline material, is a key fabrication method for making thin

films and nanoparticles. But if the lattice mismatch between the two materials is too large or messy, fractured interfaces result. **Zhang *et al.*** (p. 1634) describe a synthesis strategy to obtain spherical nanoparticles with a core-shell architecture that does not depend on heteroepitaxy. Silver was deposited and converted to various semiconductors through a series of chemical transformations to yield structurally perfect single-crystal semiconductor shells on a gold core, despite mismatches approaching 50%.

## Lipid Kinase Revealed

The lipid kinase, Vps34, makes the key signaling lipid phosphatidylinositol 3-phosphate [PI(3)P] and has essential roles in autophagy, membrane trafficking, and cell signaling. It is a class III PI 3-kinase, a class against which there is currently no specific inhibitor. **Miller *et al.*** (p. 1638) now describe the crystal structure of Vps34. Modeling substrate binding and combining structural data with mutagenesis suggests a mechanism in which Vps34 is auto-inhibited in solution, but adopts a catalytically active conformation on membranes. Structures of Vps34 with existing inhibitors might allow for the generation of inhibitors with high affinity and specificity.

## Mosquito Double Act

Peroxidase/dual oxidase (duox) systems act in concert to catalyze the nonspecific formation of dityrosine bonds, which cross-link a variety of proteins. Knowing that these reactions are involved in fine-tuning insect immune responses, **Kumar *et al.*** (p. 1644, published online 11 March) investigated how the peroxidase/duox system in malaria-vector mosquitoes pro-

1   **SUPPLEMENTARY MATERIALS**

2   Methods

3                 Six-week old plants of 16 closely related milkweed species (*SI*) were out-planted  
4         to a plowed field near Ithaca, NY USA on 7 June 2007. Fourteen species were in a two-  
5         by-two factorial experimental design of soil fertilization and predator manipulation, while  
6         *A. candida* and *A. nivea* were only in the latter treatment due to limited sample size. The  
7         native range of these milkweeds spans North to South America, including a variety of  
8         open habitats. Seeds came variously from commercial seed sources and field collections.  
9                 We obtained seedlings of *A. mexicana* adjacent to mature plants in the collection of the  
10        U.C. Berkeley Botanical Garden and *A. barjonifolia* was propagated from cuttings of  
11        mature plants maintained in a greenhouse.

12                 The aphid predators observed in this experiment were dominated by larval and  
13         adult coccinellids (Coccinellidae: Coleoptera) and larval syrphids (Syrphidae: Diptera),  
14         both of which are generalists that feed upon aphids world-wide (*S2*). There were few  
15         visible signs of aphid parasitism. *Aphis nerii* is notable for the fact that it reproduces  
16         exclusively via parthenogenesis and is thus genetically uniform (*S3*). Consequently, the  
17         arthropod community associating with milkweeds at the field site in Ithaca is similar to  
18         that occurring in the native ranges of the studied species.

19                 In the field, fertilized plants received 5.0 g of slow-release 14-14-14 NPK  
20         fertilizer. Predator density was reduced by 77% using buried spun polyester bags, with  
21         control plants receiving identical bags with vertical slits to allow predator access. There  
22         were five plants of each milkweed species in each experimental treatment, and  
23         assignments of all treatments to positions within the experimental plot were random.

24 Colonies of 12 *Aphis nerii* aphids were initiated on 19 June. Aphid analyses are based  
25 upon counts made on 13 July, during peak aphid density, and above-ground plant  
26 biomass was harvested on 1 August. Relatively few aphids were of winged dispersal  
27 morphs, suggesting that aphid movement among plants was relatively unimportant.  
28 Milkweed herbivores other than *A. nerii* were rare, with individuals being observed in  
29 only 3% of plant surveys.

30 Data on species cardenolide concentration, trichome density, and specific leaf  
31 area were taken from other experiments on the same milkweed species (S4, S5). Volatile  
32 emissions were measured on 2-3 July from 3 to 5 randomly selected individuals of each  
33 species in treatments exposed to predators and without fertilizer. Aphids infested all  
34 plants, but damage by other herbivores was minimal. Volatiles were collected on  
35 activated charcoal adsorption tubes (Supelco, Bellefonte, PA, USA), eluted with  
36 dichloromethane and analyzed by gas chromatography-mass spectrometry as described  
37 elsewhere (S6). Individual compounds were classified into compound classes of  
38 monoterpenes (ocimene, myrcene and linalool), green leaf volatiles (*Z*3-hexenal and *Z*3-  
39 hexenyl acetate) and sesquiterpenes including trans- $\beta$ -caryophyllene, farnesene, nerolidol  
40 and 5 unidentified sesquiterpenes based on their mass spectra.

41 Tests were performed for effects of milkweed species, fertilization, predator  
42 exclusion and their two- and three-way interactions on aphid density (transformation for  
43 normality of residuals =  $\ln([\text{aphid count}+1]/\text{plant dry biomass})$  and plant biomass  
44 (transformation for normality of residuals =  $\text{plant dry biomass}^{0.5}$ ) by ANOVA. Results  
45 for plant biomass were qualitatively identical when based upon a log transformation.

46 Where ANOVA showed species differences, raw and phylogenetically corrected  
47 correlations were performed among log response ratio (LRR) effect sizes and species  
48 traits (S7). Effect sizes for predator effects were calculated across both soil fertility  
49 treatments, as were soil fertility effects calculated across both predation treatments. In  
50 some cases (those shown in Table S2) LRRs and species means for herbivore resistance  
51 and growth were non-independent due to their calculations being based on some of the  
52 same data (e.g., plant biomass was a component of both aphid density and plant growth  
53 rate). Consequently, the significance of these raw correlations was tested by  
54 randomization (S8). In these randomization tests, the species means for plant biomass  
55 and aphid abundance from each level of the predator exclusion and soil fertility  
56 treatments were randomized across species, after which all dependent variables and  
57 correlation coefficients were recalculated. The observed correlation coefficients were  
58 then compared to the distribution of 999 correlations generated through this  
59 randomization process.

60 Phylogenetic analyses were only performed where randomization tests showed  
61 the raw correlations to be significant ( $P < 0.05$ ) and unbiased (i.e. a mean randomized  
62 correlation coefficient not differing significantly from 0) because there are no developed  
63 methods for controlling for such bias in phylogenetic independent contrasts. Where the  
64 pairs of correlated variables were independent (those shown in Table S3), phylogenetic  
65 analyses were performed for all correlations. Phylogenetic analyses were conducted  
66 with the Continuous module of BayesTraits ([http://www.evolution.rdg.ac.uk/  
67 BayesTraits.html](http://www.evolution.rdg.ac.uk/BayesTraits.html)) (S9) and the generalized least squares phylogenetically corrected  
68 correlations were parameterized to equal the traditional independent contrast.

69 Correlations were performed among LRR of predator effects on aphid density and  
70 plant biomass, LRR of soil fertility effects on plant biomass, milkweed species mass and  
71 herbivore resistance (quantified as -1 x aphid density in the absence of predators). Among  
72 these 10 correlations, five were significant, which is statistically improbable by chance  
73 alone ( $P<0.0001$ , binomial expansion test). Similar analyses were performed between  
74 species traits and LRR of predator effects on aphid density and plant biomass, LRR of  
75 soil fertility effects on plant biomass and herbivore resistance. Among these 28  
76 correlations five were significant, which is statistically improbable by chance alone  
77 ( $P=0.009$ , binomial expansion test).

78

79 Tables

80 **Table S1.** ANOVA tables for results of statistical tests for milkweed species,  
81 predator and fertilization effects on herbivore density and milkweed growth response.

82 **Table S2.** Correlations among growth, resistance and milkweed response to  
83 manipulation of predators and soil fertility.

84 **Table S3.** Phylogenetically corrected correlations of milkweed species traits with  
85 herbivore performance and predator and soil fertility effects.

86

87 Figures

88 **Figure S1.** Mean  $\pm$  1SE herbivore density (bars, left Y axis,) and herbivore  
89 abundance (circles, right Y axis) for each of 16 milkweed species. Herbivore means are  
90 across all levels of soil fertility and predator manipulations. Milkweed species are

91 arranged in order of increasing size, with mean species g dry biomass listed in  
92 parentheses.

93 **Figure S2.** Interactive effects of predators and soil fertility on milkweed biomass.

94 Mean  $\pm$  1SE plant biomass in each treatment.

95 **Figure S3.** Relationship between milkweed species' resistance to herbivores and  
96 the strength of predator effects on those herbivores. For ease of interpretation, raw data  
97 are depicted and raw and phylogenetically corrected R<sup>2</sup> are indicated.

98 **Figure S4.** Relationship between milkweed species' production of sesquiterpene  
99 volatiles and the strength of predator effects on plant biomass. For ease of interpretation,  
100 raw data are depicted and raw and phylogenetically corrected R<sup>2</sup> are indicated.

101

102 References

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Table S1. ANOVA tables for results of statistical tests for milkweed species, predator and fertilization effects on herbivore density and plant biomass.

	Source	Degrees of freedom	Sums of squares	Mean Square	F Value	P
Aphid density	Model	59	261.93	4.44	3.5	<.0001
	Error	251	318.57	1.27		
	Corrected Total	310	580.50			
	Pred	1	41.93	41.93	33.04	<.0001
	Fert	1	10.68	10.68	8.41	0.0041
	Pred*Fert	1	0.05	0.05	0.04	0.8412
	Species	15	151.65	10.11	7.97	<.0001
	Pred*Species	15	35.75	2.38	1.88	0.0258
	Fert*Species	13	5.22	0.40	0.32	0.9892
Plant biomass	Pred*Fert*Species	13	14.68	1.13	0.89	0.5647
	Model	59	55530.28	941.19	14.61	<.0001
	Error	245	15787.21	64.44		
	Corrected Total	304	71317.49			
	Pred	1	1691.86	1691.86	26.26	<.0001
	Fert	1	2083.96	2083.96	32.34	<.0001
	Pred*Fert	1	311.12	311.12	4.83	0.0289
	Species	15	44161.50	2944.10	45.69	<.0001
	Pred*Species	15	2485.98	165.73	2.57	0.0014
	Fert*Species	13	2643.06	203.31	3.16	0.0002
	Pred*Fert*Species	13	698.22	53.71	0.83	0.6243

Table S2. Correlations among growth, resistance and milkweed response to manipulation of predators and soil fertility.

	growth rate	herbivore resistance	predator LRR on herbivores	predator LRR on plant biomass	fertilization LRR on plant biomass
	-0.81**	--	--	--	--
<u>growth rate</u>					
herbivore resistance	-0.44*		--	--	-0.79**
predator LRR on herbivores	0.20	0.49		--	--
predator LRR on plant biomass	0.02	-0.55	-0.35		0.75**
fertilization LRR on plant biomass	0.30	-0.48*	-0.22	0.64**	

1. Phylogenetically corrected correlation coefficients (above diagonal) are shown when raw correlation coefficients (below diagonal) are statistically significant in randomization tests. Randomization tests were used because variables are non-independent due to their being based on some of the same data (See Methods in the Supplement for details).

2. Sample size for correlations with fertilization LRR on plant biomass are N=14, all others are N=16.

3. \* P<0.05; \*\* P<0.01; \*\*\*P<0.001

4. Correlations with fertilization effects on herbivores are not shown because these effects did not vary significantly among milkweed species (Table S1).

Table S3. Phylogenetically corrected correlations of milkweed species traits with herbivore performance and predator and soil fertility effects.

Species trait	<u>Species effect</u>	<u>Predator Effect</u>		<u>Fertilization effect</u>
	aphid density	aphid density	plant biomass	plant biomass
Plant dry biomass	0.65*	0.33	0.24	0.63*
Cardenolide equivalents	-0.05	0.27	-0.06	0.07
Specific Leaf Area	0.04	-0.09	0.28	-0.52*
Trichome density	-0.25	0.24	-0.12	-0.03
Volatile monoterpenes	0.08	0.11	0.04	0.13
Green leaf volatiles	0.23	-0.14	0.36	0.39
Volatile sesquiterpenes	0.25	-0.03	0.58*	0.44(*)

1. (\*) P>0.05 and P<0.10; \* P<0.05

Figure S1

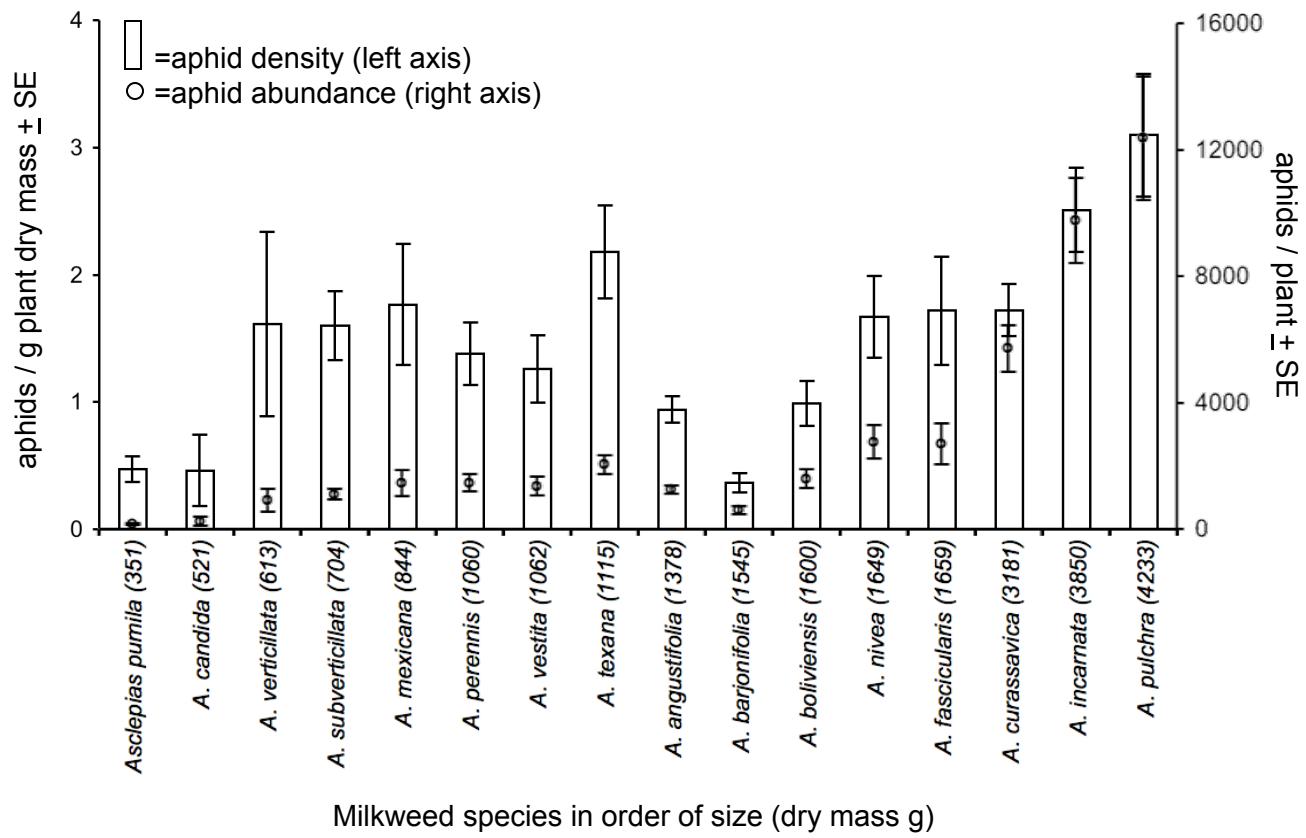


Figure S2

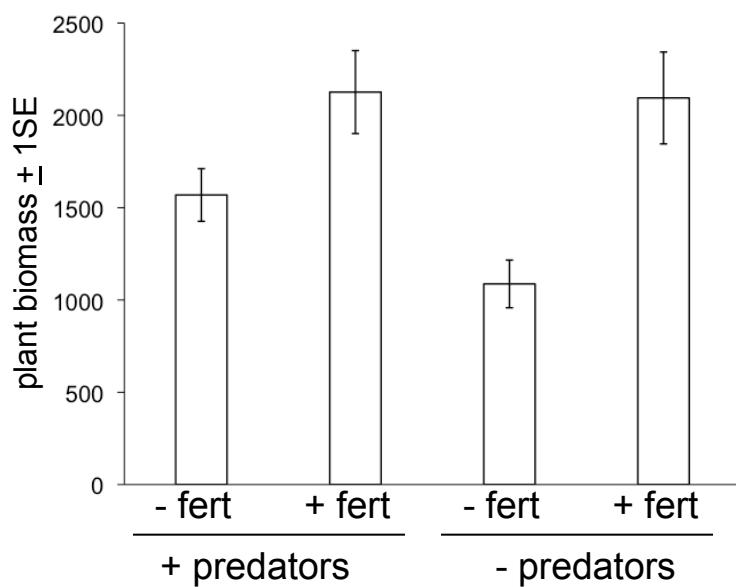


Figure S3

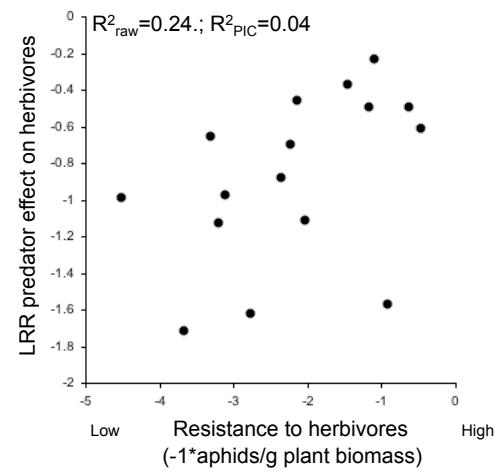


Figure S4

