stressful conditions, when ROS production is thought to be increased. Yet Johnston *et al.* report no marked change in leaf ascorbate contents or plant phenotypes in mutants for *MDHAR6* grown without TNT. Either this enzyme plays a relatively minor role in ascorbate regeneration or, when it is no longer present, the plant engages other pathways in order to compensate for its loss. As well as ascorbate-independent antioxidant systems such as peroxiredoxins, alternative pathways include different mechanisms of ascorbate regeneration (*2–4*, *11*). Loss of *MDHAR6* function could be compensated in the plastids by reduction of MDHA to ascorbate by ferredoxin and, in both plastids and mitochondria, by enzyme-dependent and chemical regeneration of ascorbate from dehydroascorbate that is secondarily formed from MDHA. Ongoing studies of mutants for MDHAR and other enzymes may help to clarify the importance of specific antioxidant pathways in different growth conditions.

Military and industrial activities have led to TNT pollution at many sites throughout the world, potentially endangering human health and having a negative impact on ecological and agricultural systems. Plants could be used to clean up undesirable compounds such as TNT by extracting them from the soil and concentrating them within their tissues (phytoremediation). Depending on the nature of the resistance mechanism, plants able to thrive on polluted soils are likely to be more effective phytoremediators. Previous studies have focused on biochemical systems in plants that enhance resistance by chemically modifying TNT (*12*). This new report identifies a promising alternative strategy for making plants more resistant to this compound, by modifying or knocking out the activity of *MDHAR6*. Further, apart from the specific question of TNT resistance, initial observations suggest that this strategy could also be useful in conferring plant specificity to herbicides that may act through similar mechanisms (*1*). ∎

REFERENCES

1. E. J. Johnston *et al.*, *Science* **349**, 1072 (2015).
2. K. Asada, *Plant Physiol.* **141**, 391 (2006).
3. C. H. Foyer, G. Noctor, *Plant Physiol.* **155**, 2 (2011).
4. N. Smirnoff, *Adv. Bot. Res.* **59**, 107 (2011).
5. G. Creissen *et al.*, *Plant Cell* **11**, 1277 (1999).
6. Y. Han *et al.*, *Antioxid. Redox Signal.* **18**, 2106 (2013).
7. T. Hackenberg *et al.*, *Plant Cell* **25**, 4616 (2013).
8. C. Miyake, U. Schreiber, H. Hormann, S. Sano, A. Kozi, *Plant Cell Physiol.* **39**, 821 (1998).
9. O. Chew, J. Whelan, A. H. Millar, *J. Biol. Chem.* **278**, 46869 (2003).
10. J. Dowdle, T. Ishikawa, S. Gatzek, S. Rolinski, N. Smirnoff, *Plant J.* **52**, 673 (2007).
11. J. Awad *et al.*, *Plant Physiol.* **167**, 1592 (2015).
12. V. Gunning *et al.*, *Plant Physiol.* **165**, 854 (2014).

All about energy. In trophic terms, the lupin plant is the producer, providing energy through photosynthesis. The savannah sparrow and its insect prey are the consumers.

ECOLOGY

Energy flows in ecosystems

Relationships between predator and prey biomass are remarkably similar in different ecosystems

By **Just Cebrian**[1,2]

All organisms in an ecosystem can be placed on a trophic level, depending on whether they are producers or consumers of energy within the food chain (see the photo). Ecologists have long debated what regulates the trophic structure and dynamics of ecosystems (*1*). This is important because trophic structure and dynamics regulate many of the goods and services that ecosystems provide to wildlife and humankind, such as the production of harvestable food and energy, carbon sequestration and modulation of climate change, and nutrient uptake and control of global biogeochemical cycles (*2*). A study by Hatton *et al.* on page 1070 of this issue (*3*) and a recent report by Lafferty *et al.* (*4*) represent important advances toward a unified theory of trophic structure that captures observed trends across all ecosystems.
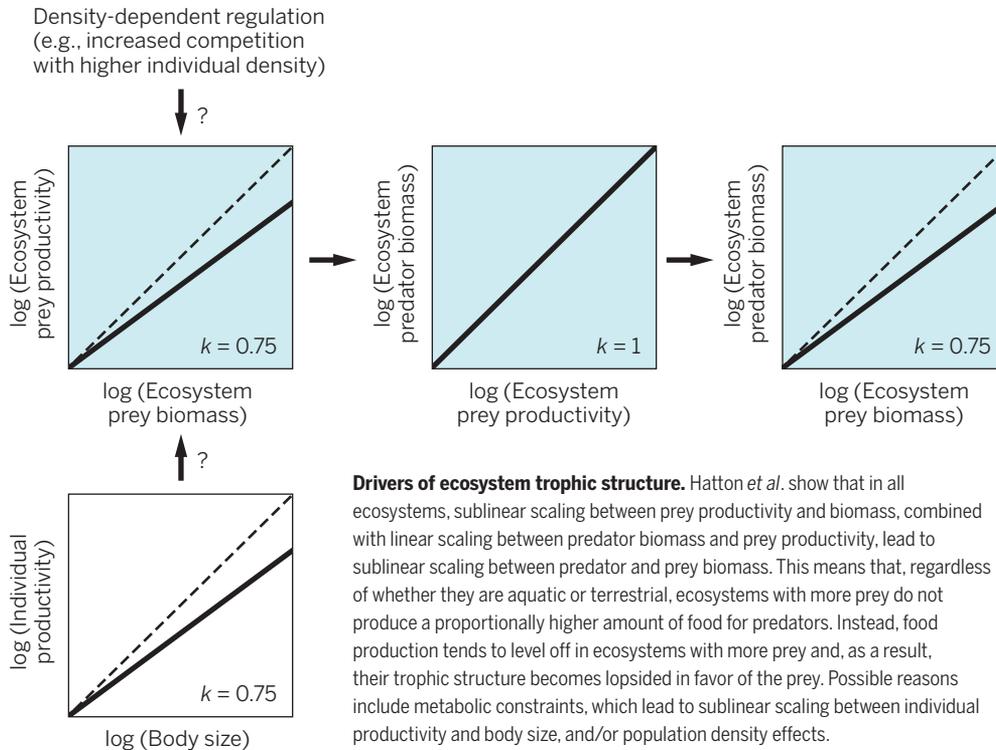
The ratio of predator-to-prey biomass is a key element of trophic structure that has been studied intensively given its importance for understanding biomass distributions and energy cycling in ecosystems. The nature and control of this ratio have been controversial, but a growing body of literature shows the ratio to be more bottom-heavy in ecosystems with higher prey biomass. In other words, as prey biomass increases, the ratio of predator-to-prey biomass decreases in ecosystems. This pattern has, however, only been demonstrated for specific types of ecosystems, such as planktonic systems (*5*), and its generality has remained uncertain. Hatton *et al.* show that this pattern—that is, a decreasing predator-to-prey biomass ratio with increasing prey biomass—applies universally in both aquatic and terrestrial ecosystems. Furthermore, they demonstrate that this universal pattern emerges from a sublinear scaling ($k = 0.75$, see the graph) that is independent of the ecosystem considered.

Where does this sublinear pattern stem from? Prior research has shown that, in

aquatic and terrestrial ecosystems, consumer biomass is linearly related to the consumption of basal resource, which in turn is linearly related to the productivity of the basal resource (6, 7). Thus, predator (consumer) biomass and prey (basal resource) productivity are linearly related, and if predator biomass is sublinearly related to prey biomass, then prey productivity should also be sublinearly related to prey biomass. In a series of elegant calculations with simple trophic models and fits to empirical data, Hatton et al. demonstrate the universality

mass), with a sublinear scaling coefficient of $k = 0.75$ (10). Thus, if ecosystems with higher prey biomass are also composed of larger-size prey, it follows that metabolic constraints on body size could explain the sublinear scaling between prey productivity and biomass in ecosystems. Recent evidence (11) has shown this to be the case across ecosystem types differing widely in individual prey size. For instance, when comparing phytoplankton communities to seagrass beds, shrublands, and forests, increasing individual prey size explains the

The numerous avenues of new and exciting research opened by Hatton et al. are heightened by the results of Lafferty et al. In an impressive compilation, the authors show that all trophic models published to date, including the seminal Lotka-Volterra predator-prey equations (12), can be unified into a general consumer-resource population model. The general model contains several quantifiable state variables for consumers and their resources. It can thus be adapted to explain diverse trophic dynamics, ranging from classical examples where the consumer is a predator to cases where the consumer is a micropredator, parasitoid, or parasite. Trophic models that may have been regarded as disconnected and exclusive now emerge as variants of the same conceptual framework. Adaptation of the general model to specific models reveals the simplifications and assumptions that are idiosyncratic to each of them. This provides an accurate procedure to evaluate the focus, limitations, and applicability of all trophic models.

Lafferty et al. bring the patterns found by Hatton et al. to a new level of scrutiny, providing a test for whether such patterns are truly universal. The general trophic model of Lafferty et al. indicates that all consumers and their resources follow the same fundamental principles that govern energy transfer and trophic structure in ecosystems. Thus, the sublinear biomass scaling reported by Hatton et al. for predators and their prey could also apply to any other type of consumer and its resource, including micropredators and parasites. Such patterns could in turn invariably emerge from sublinear scaling between resource productivity and biomass. Confirming these hypotheses would mark a major milestone in ecosystem science. ∎

Drivers of ecosystem trophic structure. Hatton et al. show that in all ecosystems, sublinear scaling between prey productivity and biomass, combined with linear scaling between predator biomass and prey productivity, lead to sublinear scaling between predator and prey biomass. This means that, regardless of whether they are aquatic or terrestrial, ecosystems with more prey do not produce a proportionally higher amount of food for predators. Instead, food production tends to level off in ecosystems with more prey and, as a result, their trophic structure becomes lopsided in favor of the prey. Possible reasons include metabolic constraints, which lead to sublinear scaling between individual productivity and body size, and/or population density effects.

of these processes (see the graph). Previous studies have found similar trends in some aquatic and terrestrial ecosystems (6–9), but Hatton et al. now generalize their occurrence in nature, thereby advancing substantially our understanding of ecosystem trophic dynamics and structure.

The question follows why prey productivity is scaled sublinearly to prey biomass. If we can answer this question, then we would understand the mechanisms underlying the universal trophic cascade processes shown by Hatton et al. The authors consider tenets of the metabolic theory of ecology. According to this theory, metabolic constraints with increasing individual size generate a sublinear scaling between individual growth (biomass production) and size (bio-

sublinear scaling between ecosystem prey productivity and biomass.

However, when Hatton et al. compared communities within the same ecosystem type, they found that individual prey size does not increase with ecosystem prey biomass and, thus, cannot account for the sublinear scaling pattern. Instead, prey density was higher in ecosystems with higher prey biomass. The authors suggest that processes that depend on prey density, such as competition for resources and other negative interactions among prey species, can result in the sublinear scaling between ecosystem prey productivity and biomass (3). Another interesting idea is that higher ecosystem biomass, regardless of the size of the prey in the ecosystem, could be subject to the same metabolic constraints on individual body size, thereby averting the need to invoke density-dependent processes to explain the sublinear scaling.

¹Dauphin Island Sea Lab, Dauphin Island, AL, USA. ²Department of Marine Sciences, University of South Alabama, Mobile, AL, USA. E-mail: jcebrian@disl.org

REFERENCES

1. V. Volterra, *Nature* **118**, 558 (1926).
2. O. J. Schmitz et al., *Ecosystems (N. Y.)* **17**, 344 (2014).
3. I. A. Hatton et al., *Science* **349**, aac6284 (2015).
4. K. D. Lafferty et al., *Science* **349**, 854 (2015).
5. J. M. Gasol, P. A. del Giorgio, C. M. Duarte, *Limnol. Oceanogr.* **42**, 1353 (1997).
6. J. Cebrian, J. Lartigue, *Ecol. Monogr.* **74**, 237 (2004).
7. J. Cebrian, *Ecol. Lett.* **7**, 232 (2004).
8. J. Cebrian, *Am. Nat.* **154**, 449 (1999).
9. C. M. Duarte, C. L. Chiscano, *Aquat. Bot.* **65**, 159 (1999).
10. J. H. Brown, J. F. Gillooly, A. P. Allen, V. M. Savage, G. B. West, *Ecology* **85**, 1771 (2004).
11. J. R. Schramski, A. I. Dell, J. M. Grady, R. M. Sibly, J. H. Brown, *Proc. Natl. Acad. Sci. U.S.A.* **112**, 2617 (2015).
12. A. J. Lotka, *Elements of Physical Biology* (Dover, New York, 1924).