Parasites help find universal ecological rules

Ryan F. Hechinger¹

Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92093

Approximately half of all species are parasites. Further, parasites can strongly influence individuals, populations, and even communities. It should therefore be axiomatic to consider parasites in efforts to develop ecological principles meant to characterize all species (1, 2). However, all too often, our general empirical and theoretical work neglects parasites. Although my colleagues and I might bemoan this neglect, as evidenced in PNAS by Lagrue et al. (3), it does give us something to do.

Indeed, ecology has been making headway by considering parasites simultaneously with free-living species in our most cohesive frameworks. For instance, recognizing parasites as consumers and resources alongside free-living species has recently enhanced our understanding of the properties of food webs (4, 5), which are maps of who eats whom in any given ecosystem. Similarly, considering parasites has helped generalize the metabolic theory of ecology, including the development of a broadly applicable rule for the abundance of all species, whether they be

plants, predators, grazers, or parasites (2, 6). The importance and utility of parasites, in tandem with the promise of further developing metabolic theory in a food web context, has fostered efforts to collect extensive data for parasites and free-living species in local ecosystems. It is an exciting time, as such data permit substantial empirical and theoretical advances.

Lagrue et al. break new empirical ground using an extensive dataset on the density and body sizes of most aquatic animals in the shallow waters of four New Zealand lakes. To put parasites and free-living species on equal footing, they follow an approach that was recently used (6) and express both parasites and free-living species densities as individuals per square meter. A novel aspect of the article by Lagrue et al. is that, not only do they examine parasites alongside free-living species, but they also group free-living species into either parasitized or unparasitized species (those in which Lagrue et al. did not detect parasites).

Lagrue et al. document that each of the three animal groups follow three ecological power laws (Fig. 1). Power laws are fascinating. Despite their immense complexity, ecological systems are regularly characterized by emergent, simple patterns, which often take the form where one focal variable scales with another raised to a power as $Y \propto X^b$, which is usually examined in log-log space where the exponent is provided by the slope (7). These pervasive relationships are important, most particularly because they may reflect fundamental processes and they therefore provide material for generating theory explaining why the patterns exist.

The first power law documented by Lagrue et al. is well known and often referred to as Taylor's law. This law states that the variance of population density increases with mean population density. The slope of the power relationship tells us whether individuals are randomly distributed or aggregated together (7, 8). Before Lagrue et al., this pattern had not been documented for parasite numbers in space (e.g., square meters), although much prior research—including Taylor's (8), when he first documented the law—has shown it for parasite numbers per host. In fact, ecological parasitologists have long cherished the strong aggregation of macroparasites among hosts, where the exponent of this law can be related to numerous epidemiological processes (9, 10). Now, thanks to Lagrue et al., we know that parasites are also strongly aggregated in space, and in a way similar to their free-living hosts in the same communities.

Lagrue et al. further explore their parasites and free-living species in the context of Damuth's law, where species density decreases with body size (11). This law has had much theoretical attention because body size can be related to density via its link to metabolic rates and individual resource requirements (12). In fact, it was previously shown that this law applies reasonably well to parasites and free-living species in the same communities and that apparent differences between parasites and free-living species were readily accounted for by also considering temperature and

Fig. 1. The empirical patterns presented in Lagrue et al. (3) provide rich fodder for the testing and development of explanatory theory, including that based on host and parasite energetics. (A–C) Condensed and annotated representation of their main results documenting three ecological power laws involving abundance and body size for animals in four New Zealand lakes. Trend lines and analysis use species' mean values among seasons and lakes. (D–F) My analysis of their data indicates that the probability that a species is parasitized increases with density (at a given body size), with body size (at a given density), or with the amount of energy flowing through the population [energy flux estimated using metabolic scaling equations in ref. (12)] Statistics represent likelihood-ratio tests for each effect.

Author contributions: R.F.H. wrote the paper.

The author declares no conflict of interest.

See companion article on page 1791.

¹Email: rhechinger@ucsd.edu.

the loss of energy up trophic levels (6). Consistent with those findings, in the results of Lagrue et al., parasites are rarer for their body sizes than the parasitized species (Fig. 1B), as expected because parasites are at higher trophic levels. It would be useful to more precisely apply and test preexisting theory using Lagrue et al.'s density-body size data, but that will have to wait for additional information on trophic levels or resource supply.

Lagrue et al. then consider combining information from the above two power laws to explore a third relationship involving how density variance relates to body size. Although this pattern is simply and algebraically derived from the other two laws (7, 13), it is lacking in empirical demonstration for anything other than oak trees! Lagrue et al. provide the first documentation of this pattern for animals of any sort. A next step is to determine whether the pattern is just a correlation or if population variance is mechanistically linked to body size [perhaps via its effects on maximum population growth rates (14)].

Overall, perhaps the most striking finding from Lagrue et al. is that unparasitized species consistently appear to be the deviant category concerning power law slopes (Fig. 1A–C). What explains this? Lagrue et al. hypothesize that the divergent scaling arises because parasitism increases the density variance of parasitized species. We could easily test this idea by using information on parasite body sizes and abundances to estimate the total energy taken by parasites from each host (15), followed by incorporating the energetic impacts of parasites into scaling theory and asking whether that helps explain the density of free-living species.

However, inspection of the data from Lagrue et al. leads me to a very different (although not necessarily mutually exclusive) explanation for the divergent scaling of parasitized and unparasitized species: that the scaling plots capture aspects of host biology that affect the chance of being parasitized. Although it is true that unparasitized species exhibit lower population variances, this is primarily so for smaller-bodied species (Fig. 1C). These unparasitized

species are the same ones that have relatively low densities in the density vs. body size plot (Fig. 1B). Finally, the rarest unparasitized species also have relatively large density variance (Fig. 1A). Being relatively rare, unstable, small-bodied, and unparasitized is consistent with generally documented trends

The empirical relationships documented by Lagrue et al. improve our understanding of basic and pervasive ecological patterns.

and epidemiological models where smaller-bodied species and those that reach low population densities have fewer parasites (16–18). Indeed, a logistic regression on Lagrue et al.'s data confirms that the odds of a species being parasitized decreases 2.1-fold for every 10-fold drop in density (holding size constant) and 2.8-fold for every 10-fold drop in body size (holding density constant) (Fig. 1D and E). Hence, future work should tease out how the ecological scaling relationships are relatively influenced by the impacts of parasites and by attributes of free-living species that make them less likely to be parasitized.

The position of parasitized species in the density-body size plot (Fig. 1B) further suggests a metabolic explanation for the risk of parasitism. Because density and body size directly link to levels of energy flowing through populations (11, 12) and the parasitized species tend to be more common and larger, parasites may tend to infect species characterized by large energy fluxes. Indeed, a logistic regression using energy flux estimates derived from Lagrue et al.'s data shows that the odds of a species being parasitized drops 3.0-fold for every 10-fold decrease in energy flux (Fig. 1F). This further highlights the promise of developing an energetics-based theory of ecological parasitology that is grounded in how both parasite and host metabolic rates scale with body size and temperature (2, 15, 19).

The empirical relationships documented by Lagrue et al. improve our understanding of basic and pervasive ecological patterns. The inclusion of parasites alongside free-living species, and the recognition of the unparasitized animal group, provides rich fodder for hypothesis generation and testing. Such theoretical development will enhance our understanding of the role of parasites in ecosystems and help us find better rules and mechanistic principles that apply to most life forms on Earth.

- 1 Arneberg P, Skorping A, Read AF (1998) Parasite abundance, body size, life histories, and the energetic equivalence rule. *Am Nat* 151(6): 497–513.
- 2 Hechinger RF, Lafferty KD, Kuris AM (2012) Parasites. *Metabolic Ecology: A Scaling Approach*, eds Sibily RM, Brown JH, Kodric-Brown A (Wiley, Oxford, UK), pp 234–247.
- 3 Lagrue C, Poulin R, Cohen JE (2015) Parasitism alters three power laws of scaling in a metazoan community: Taylor's law, density-mass allometry, and variance-mass allometry. *Proc Natl Acad Sci USA* 112:1791–1796.
- 4 Dunne JA, et al. (2013) Parasites affect food web structure primarily through increased diversity and complexity. *PLoS Biol* 11(6): e1001579.
- 5 Lafferty KD, et al. (2008) Parasites in food webs: The ultimate missing links. *Ecol Lett* 11(6):533–546.
- 6 Hechinger RF, Lafferty KD, Dobson AP, Brown JH, Kuris AM (2011) A common scaling rule for abundance, energetics, and production of parasitic and free-living species. *Science* 333(6041):445–448.
- 7 Marquet PA, et al. (2005) Scaling and power-laws in ecological systems. *J Exp Biol* 208(Pt 9):1749–1769.
- 8 Taylor LR (1961) Aggregation, variance and the mean. *Nature* 189(476):732–735.
- 9 Shaw DJ, Dobson AP (1995) Patterns of macroparasite abundance and aggregation in wildlife populations: A quantitative review. *Parasitology* 111(Suppl):S111–S127.
- 10 Morand S, Krasnov B (2008) Why apply ecological laws to epidemiology? *Trends Parasitol* 24(7):304–309.
- 11 Damuth J (1981) Population-density and body size in mammals. *Nature* 290(5808):699–700.
- 12 Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. *Ecology* 85(7):1771–1789.
- 13 Cohen JE, Xu M, Schuster WSF (2012) Allometric scaling of population variance with mean body size is predicted from Taylor's law and density-mass allometry. *Proc Natl Acad Sci USA* 109(39): 15829–15834.
- 14 Savage VM, Gillooly JF, Brown JH, Charnov EL (2004) Effects of body size and temperature on population growth. *Am Nat* 163(3): 429–441.
- 15 Hechinger RF (2013) A metabolic and body-size scaling framework for parasite within-host abundance, biomass, and energy flux. *Am Nat* 182(2):234–248.
- 16 Poulin R, Morand S (2004) *Parasite Biodiversity* (Smithsonian Books, Washington, DC), pp viii, 216.
- 17 Combes C (2001) *Parasitism: The Ecology and Evolution of Intimate Interactions* (Univ of Chicago Press, Chicago), pp xiii, 728.
- 18 Hudson PJ, Rizzoli A, Grenfell BT, Heesterbeek H, Dobson AP (2002) *The Ecology of Wildlife Diseases* (Oxford Univ Press, New York), pp xii, 197.
- 19 George-Nascimento M, Munoz G, Marquet PA, Poulin R (2004) Testing the energetic equivalence rule with helminth endoparasites of vertebrates. *Ecol Lett* 7(7):527–531.