IN FOCUS

All ecological models are wrong, but some are useful

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Abstract

In Focus: Curtsdotter, A., Banks, H. T., Banks, J. E., Jonsson, M., Jonsson, T., Laubmeier, A. N., … Bommarco, R. (2019). Ecosystem function in predator-prey food webs—Confronting dynamic models with empirical data. *Journal of Animal Ecology*, 88, https://doi.org/10.1111/1365-2656.12892

Species' population dynamics are influenced by a variety of abiotic and biotic factors. Curtsdotter et al. (2019) used a food web model to investigate the role of predator–prey interactions in the population dynamics of the bird cherry-oat aphid *Rhopalosiphum padi.* Their analysis hinged on linking the observed population dynamics to a mathematical description of the multi-species system via inverse methods—an approach less utilized in ecology but that allows one to search a wide space of possible parameterizations and identify best-fit model parameters. By scrutinizing the fit of this model to observed aphid population dynamics in 10 separate barley fields, they identified fields in which predation was the key driving force; in others, they found that accurate predictions depended on the existence of an unpredictable and unidentified extrinsic driver of aphid mortality. By scrutinizing areas where the model gave poor or biologically counterintuitive fits, their study provides a path forward to better link ecological theory to ecosystem function.

KEYWORDS
allometric scaling, ecological modelling, food-web theory, functional responses, inverse methods, population dynamics, predator–prey interactions

Species interactions are central to the modern ecological paradigm (Sutherland et al., 2013), and a large body of research therefore has the explicit goal of disentangling the link between interactions and emergent community and ecosystem properties (Thompson et al., 2012). As the number of species under consideration grows, there is a tendency for such studies to rely on model-centric approaches, for example to determine when interactions are in fact essential to make useful predictions (Iles & Novak, 2016) or to better understand why and how so many species coexist (Serván, Capitán, Grilli, Morrison, & Allesina, 2018). Despite mathematical models' proven ability to provide general insights into various ecological phenomena, their use is predicated on researchers' ability to answer two key questions. First, when is the mathematical structure of a model sufficiently "realistic" to be trusted (Bascompte, Jordano, & Olesen, 2006; Holland, Okuyama, & DeAngelis, 2006)? Second, how should that model be

parameterized to best match "realistic" settings (Rohr, Saavedra, & Bascompte, 2014)? Unfortunately, the answers to these questions can often appear rather arbitrary or, worse yet, determined solely by the capricious inclinations of individual researchers (and their peer reviewers). Even when these questions can be answered confidently, *validation* of the predictions made by these models via comparison to population dynamics of real assemblages remains surprisingly rare (Boit, Martinez, Williams, & Gaedke, 2012; Jonsson, Kaartinen, Jonsson, & Bommarco, 2018; Rip, McCann, Lynn, & Fawcett, 2010; Schneider, Scheu, & Brose, 2012).

In this issue, Curtsdotter et al. (2019) outline a novel approach to follow this road less travelled. Namely, they fit a dynamic food web model using data about predator–prey interactions and observed population dynamics of (a) an aphid herbivore, (b) its known predators and (c) those predators' alternative prey. They then exploited

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this data-informed model to examine the role predation plays in driving aphid population dynamics across 10 Swedish barley fields. By applying their model to 10 different fields, the authors were able to assess the consistency, and lack thereof, of observed food web dynamics. Though their model focuses exclusively on dynamics of the aphid population, solving this problem was no small feat. Indeed, it involved consideration of predation pressure from 10 different types of consumers exerted on the aphids and 14 alternative prey. Intriguingly, their model was able to capture a substantial amount of the temporal variation in aphid abundance in half of the fields surveyed. It also provided better than average qualitative fits in a majority of fields. The authors leveraged these results to emphasize the importance of body size-based predation pressure and extrinsic sources of increased mortality in explaining the temporal variation in aphid population size.

In most situations, model-based prediction like the one performed here operates as a "forward problem": Given a model and its parameters, one can analytically or computationally determine the expected system-level state (Figure 1). Of course, this approach is only practical when the model and its parameters can be robustly underpinned with laboratory or field data. In contrast, the authors here tackled the "inverse problem" that required *starting* from a set of observations and then identifying the factors (e.g., model parameters) that likely produced them (Figure 1). It may go without saying, but this process is less straightforward than performing a regression or an ANOVA. Even so, inverse methods allow one to reliably search within a large parameter space when more conventional approaches are infeasible or impossible (Tarantola, 2004). Of course, the greater the complexity of the problem at hand and the more limited the observed data, the more a search conducted via inverse methods can mirror the proverbial search for a needle in a haystack. To make their search easier, Curtsdotter et al. (2019) therefore built their parameterization around the assumption of allometric scaling of the model parameters (Kalinkat et al., 2013; Schneider et al., 2012; Yodzis & Innes, 1992). On the one hand, the pay-off was clear, as this implied identifying only a handful of best-fit parameters per field rather than the hundreds of parameters corresponding to all pairwise predator–prey interactions. On the other, this simplification was not without a corresponding cost since it required assuming that differences in the biology of a suite of predators could all be distilled down to differences in their average body size.

At first glance, the fact that the authors' "allometrically-simplified" model performs well for only half of the fields in their study can appear a bit underwhelming. However, appearances can be deceiving; indeed, one of the highlights of the authors' study is the way they turn this apparent weakness into a bona fide strength. In particular, rather than extensively repeat many ways in which their results matched previous research, they instead provide a wonderfully transparent vivisection of the various places that their results motivate future empirical *and* theoretical research questions. After all, there were strong a priori reasons to expect that predation plays a key role in their system, and a test of just that hypothesis was unlikely to break novel ground. In contrast, the very way in which
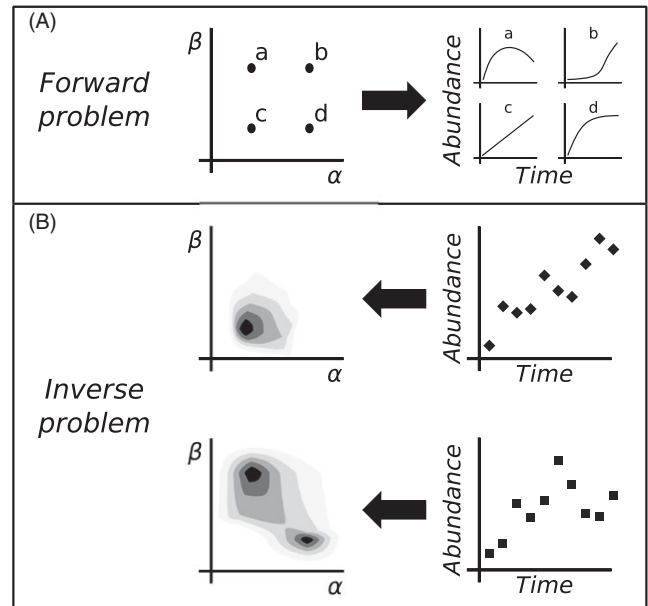

FIGURE 1 Studies of complex ecological models usually proceed as either forward or inverse problems. (A) Given a mathematical model with two parameters, α and β, the forward problem is often tackled by selecting a representative set of parameter combinations (points a, b, c, and d) and then determining the corresponding model behaviour (e.g., analytically or via simulation). In the example shown here, each combination of α and β provides qualitatively and quantitatively different predictions about how some species' abundance varies over time. (B) Rather than taking the mathematical model and its parameters as the starting point, inverse problems typically begin from the model and observed data. Researchers then apply inverse methods to search the model's parameter space and identify the parameter combination or combinations that best reproduce the observed data. In the two hypothetical examples shown here, regions of parameter space that provide better fits to the data are indicated by darker colours. For the dataset on top, the observed behaviour could have most plausibly emerged from the model within a single region of parameter space; for the dataset on bottom, two regions of parameter space are equally consistent with the observations. Conceptually, we can think of both (i) the contrasts between datasets and (ii) the contrasts within parameter space as providing alternative hypotheses about the underlying biology of the system. Inverse methods allow us to isolate scenarios such as these which can then be explored to greater depth or may be further disambiguated with additional data

the effects of predation varied across fields presents strong challenges to how we balance the competing desires for models to be widely applicable and locally useful. Moreover, there were multiple instances where the best-fit parameter values defied conventional wisdom—such as unexpectedly high variability of some allometric constants across fields. In this sense, there is as much benefit to reading the study in terms of its ability to generate new hypotheses as its ability to test existing ones.

For example, the authors' model was unable to explain some rather dramatic bursts of aphid mortality observed in a few fields. These episodic events gave a strong indication that stochasticity

may play a bigger role in their system than initially anticipated or than could be accounted for in their deterministic model. Likewise, the authors' analysis incorporated laboratory-estimated aphid population growth rates that were available in the literature rather than treat them as free parameters (Curtsdotter et al., 2019). These rates ultimately overestimated growth later during the season within the study site, pointing to an under-appreciated role played by declining resource quality—a biological feature not explicitly included in their model. The variation in functional-response parameters across fields is a bit harder to reconcile (Curtsdotter et al., 2019). It is widely acknowledged that interactions between species vary as a function of a variety of biotic and abiotic drivers (Tablado, Fauchald, Mabille, Stien, & Tveraa, 2014; Tylianakis, Didham, Bascompte, & Wardle, 2008), but is it reasonable to expect that the conditions across the 10 fields varied as greatly as the best-fit parameters would have us believe? More likely, the equivocal support for non-saturating and saturating functional responses speaks to the inherent challenge of inverse problems and the possibility that best-fit parameters often only tell a small portion of the story. Exploring the optimization landscape in more depth would allow us to quantify our degree of confidence in the vanishingly small allometric handling times (h_0) and interference coefficients (c_0) inferred for some fields and thus whether these were in fact reliable indicators of the biological processes at play. Even more, it would be interesting to learn about where these singular optima fall compared to the rest of the optimization landscape. With such data-hungry methods, it is not uncommon for two or more wildly different parameter sets to provide roughly equivalent fits to the available data. Picking apart the biological plausibility and empirical support for these is one of the best ways to drive research forward since doing so can strongly reinforce or invalidate the model-generated predictions. Likewise, any lingering uncertainty should always remind us that variation across solutions to inverse problems can be either biologically meaningful, woefully idiosyncratic, completely dependent on the underlying mathematical model or, worst of all, simultaneously all of the above.

In the absence of tools like inverse methods, it is sobering to realize that a fully bottom-up approach would require sufficient replicates of 294 separate experiments in order to *empirically* estimate every parameter within the authors' functional response. The allometric assumption sidesteps this issue, but can only be stretched so far before itself being confronted by additional data. In their Discussion and Conclusion, Curtsdotter et al. (2019) rightly argue that incorporating traits beyond body size, such as hunting mode (Pawar, Dell, & Savage, 2012) or prey type (Uiterwaal, Mares, & DeLong, 2017), could help better capture residual variation in realized interaction strengths. Unfortunately, such approaches may ultimately need about as much data across predator–prey combinations as would explicit parameterization of the functional responses in the first place; that is, following this suggestion may inadvertently send us back to a scenario when a many-species problem requires a borderline-infeasible many-species solution. Alternatively, it would also be very valuable to know more about where and how particular predator or prey species (or particular predator–prey pairs) held greater leverage during the estimation process. This would allow for future data collection to be tailored in such a way that it fills in the knowledge gaps as strategically as possible, and that further exploration via the inverse method can then be iteratively fit around these additional "constraints."

There is a long-standing tradition in ecology of dissecting the forces that influence observed population dynamics (Volterra, 1926). In settings such as the paradigmatic cycles between lynx and hare, isolating the underlying drivers can appear comparatively unambiguous (Elton & Nicholson, 1942; Krebs, Boonstra, Boutin, & Sinclair, 2001; Stenseth, Falck, Bjornstad, & Krebs, 1997). Realistically, few ecological scenarios can be faithfully reduced to a mere handful of explanatory variables, even in contexts such as the agricultural landscape studied here which is relatively "simplified" (Martin, Blossey, & Ellis, 2012). Often, ecologists are therefore forced to choose sides in an equally long-standing debate: Should we follow the "reductionist" approach in which each individual component is studied in depth and later stitched together, but run the risk that the whole we obtain is more than the sum of its parts? Or should we follow the "holistic" approach in which we start from the whole and work backward to the individual components, but run the risk that we get the right result for all the wrong reasons? Within their study, Curtsdotter et al. (2019) provide a refreshing perspective of how ecologists faced with by this dilemma may sometimes be able to eat their cake and have it too.

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