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Fast and slow advances toward a deeper integration of theory and empiricism

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Abstract

In this article, we present a modern commentary on Ludwig, Jones, and Holling's classic paper, "Qualitative analysis of insect outbreak systems: the spruce budworm and forest," published in the Journal of Animal Ecology in 1978. In contrast to papers that become classics for advancing one big idea, Ludwig et al.'s contribution is striking for its breadth of impact. It has become a foundational reference in areas as disparate as insect ecology and management, alternative stable states, the effects of natural enemies, and the separation of time scales between fast- and slow-changing variables. Interestingly, the paper is not generally remembered as an attempt to bridge the divide between theoretical and empirical ecologists, as we will show, even though this is how the authors motivated their work. In this commentary, we examine the expected and unexpected ways Ludwig et al. (*J Anim Ecol* 47:315–332, 1978) have found a place in modern ecological thought.

Keywords Alternative stable states · Insect outbreaks · Ludwig et al. (1978) · Qualitative analysis · Separation of timescales · Spruce budworm · Theory and empiricism

Introduction

Don Ludwig, Dixon Jones, and Buzz Holling open their 1978 classic paper by stating a problem:

> "As in all sciences, ecology has its theoretical and its empirical school. Perhaps because of the complexity and variety of ecological systems, however, both schools seem, at times, to have taken particularly extreme positions. And so the empiricists have viewed the theoretical school as designing misleading constructs and generalities with no relation to reality. The theoreticians, in their turn, have viewed the empirical school as generating mindless or mind-numbing analysis of specifics and minutiae." (p. 315)

After framing the issue in this way, the authors continue on to present a three-part analysis of spruce budworm dynamics that illustrates how detailed empirical expertise and standard theoretical analyses can be productively integrated. While this paper did not, of course, close the theory-empiricism divide once and for all (see e.g. Caswell 1988; Fawcett and Higginson 2012; Huston 2014; Kilpatrick et al. 2014, and others), it remains one of the clearest examples on how to merge empirical data and intuition with theory. It is also so much more.

As the roughly 500 scholarly works that cite Ludwig et al. (1978) collectively illustrate, this paper has become a classic for several rather distinct reasons (Fig. 1). Some of these overlap with the authors' stated goals for the paper, while others are quite different. In this commentary, we highlight some of the far-reaching impacts Ludwig et al. (1978) has had in modern ecology.

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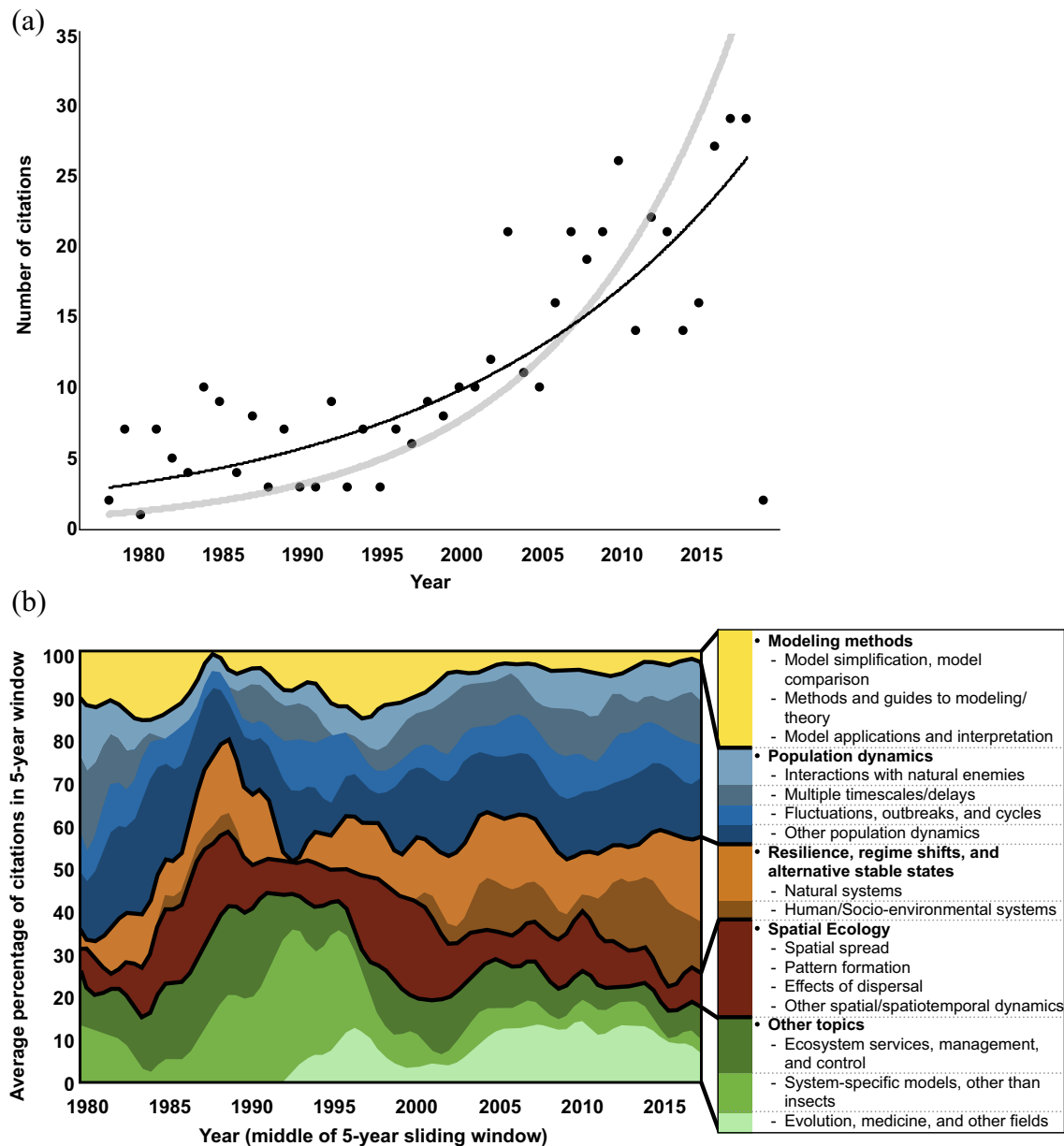
(a)

(b)

Fig. 1 Summary of papers citing Ludwig et al. (1978), based on all 476 citing articles returned by Web of Science in a January 15, 2019 search. **a** Total citations per year are shown by black points (with black exponential curve fitted to 1978–2018 counts). The gray line shows the overall increase in articles on the topic "Ecology" over the same time frame, according to Web of Science (exponential trend fitted to rescaled counts (35×[annual publications]/[maximum annual publications]) for display on this *y*-axis). **b** Proportion of citing articles on each major topic, listed at right, during rolling 5-year windows. Each article was counted only once in what we judged to be its primary subject area. These judgments were made based on article title, journal title and, as was feasible, familiarity with the paper

Themes in the citing literature

The yearly number of papers citing Ludwig et al. (1978) nearly tracks the overall increase in ecological publishing since 1978 (Fig. 1a, black versus gray curves), suggesting a consistent impact through time. However, the nature of this impact has shifted. For instance, the authors presented their study as a "how-to-do-it" (p. 316) guide to the application of mathematical models, and prior to 2000 the paper was regularly cited for this contribution (Fig. 1b, yellow region). After 2000, such citations have become proportionately more rare. Instead, there are significantly more references in these more recent years to the model's alternative stable states and related topics (light and dark brown regions). The proportion of references to Ludwig et al. (1978) in papers on spatial ecology increased in the late 1980s through 1990s (dark red region). We suspect that each of these patterns follows broader trends in ecological research.

In addition to being a how-to guide, Ludwig et al. (1978) is clearly very much a study of population dynamics. Population dynamics is also a prominent topic among the citing articles (Fig. 1b, various shades of blue), with three particular areas of emphasis that stand out: the effects of predators and other natural enemies on prey dynamics, the presences of multiple time scales, and the pattern of large amplitude outbreaks or other cycles and fluctuations. Interestingly, the proportion of citing articles on these topics has remained relatively even despite shifting research priorities over the past four decades.

We therefore perceive two different kinds of patterns in Ludwig et al.'s legacy, as told through its citation history: those that, in our opinion, track popular trends in ecology (e.g., spatial ecology and alternative stable states) and those that do not (e.g., multiple time scales and outbreaks). We find both of these observations to be compelling. As hot topics come in and out of popularity, it is noteworthy that authors continue to feel that Ludwig et al. (1978) has something to contribute to the dialog. The staying power of other ideas is likewise noteworthy.

In the sections that follow, we highlight a few select topics and discuss the role Ludwig et al. (1978) has played. These topics—fast and slow timescales, outbreaks, and alternative stable states—were chosen subjectively based on our opinions about where Ludwig et al.'s impact has been the most profound, but they also emerge from our examination of the citing literature. We bookend our discussion of these select topics by addressing the original authors' own stated objectives: to provide an instructive case study in model building and analysis and, of course, to narrow the theory-empiricism divide.

A case study in three levels

The authors introduce their study as a demonstration of "how far … mathematical tools can be pushed to give insight" (p. 315) and as a means of assessing the "value in compressing the detailed explanation contained in a simulation model into an analytically tractable" model (p. 316). They accomplish these goals through a case study of spruce budworm (*Choristoneura fumiferana*) and balsam fir (*Abies balsamea*) dynamics using three differential equations that describe changes in budworm density, average fir age, and overall tree health. The paper is divided into three parts, representing three levels of analysis that use increasingly detailed information about the spruce budworm system. Each level uses the same underlying qualitative assumptions, such as logistic budworm growth and a sigmoidal functional response of generalist predators. These phenomena are quite general, and subsequent authors have used the same or a similar set of assumptions to model taxa as diverse as plankton, fish, wildlife, plants, and even tumor cells (Spencer and Collie 1995; Chattopadhayay et al. 2002; Bulte 2003; Jiang et al. 2016; Ding et al. 2017). Budworm dynamics are assumed to occur on a much faster time scale than forest dynamics, but this is about as system specific as the model gets.

The least detailed level, Level I, is an archetypal theoretical analysis in the vein of MacArthur or May (except for the presence of multiple time scales, which adds an interesting aspect to their analysis as discussed below). The authors find and characterize equilibria and discuss asymptotic budworm and forest dynamics in a general way, without assuming any quantitative knowledge about demographic rates or the values of other parameters included in the model. The increasingly detailed Level II analysis uses the same model equations as Level I, but imposes rough parameter estimates that could be derived from cursory natural history knowledge of the system. Level III again uses the same model, now with parameter estimates derived from an extensive 15-year field study on spruce budworm in Eastern Canada (Morris 1963) and an associated, detailed simulation model (Jones 1979).

There is much to like in this three-level approach. It shows that the level of detail present in the system being modeled need not dictate the level of detail included in the model, a lesson that was reiterated (and attributed to Ludwig et al. 1978) by Simon Levin at the conclusions of his MacArthur Lecture on pattern and scale (Levin 1992). The three-level approach also illustrates the value in studying a constellation of mechanisms without necessarily worrying about the details. It portrays modeling and analysis as "a process and not a product" (p. 328). In this way, Ludwig et al. (1978) has become a textbook example of heuristic analysis (Boccara 2010; Enns 2010; Zhao 2017). The breadth of ideas that arise across the three levels of analysis has given this paper a long-lasting place in the theoretical ecology classroom (appearing in that role as early as 1979 in Simon Levin's class; S. Ellner, personal communication).

Has Ludwig et al.'s three-level recipe endured? Not exactly. Qualitative analyses like Level I remain routine in theoretical ecology, and many studies that use this kind of analysis incorporate parameter estimation akin to Level II to ground-truth the theoretical results or tie them to a particular system of interest (Carpenter et al. 1999; Fung et al. 2011). However, the idea of taking very detailed empirical data and using them to fit very generic models (as in Level III) seems odd by today's standards. Instead, it has become quite common for researchers to fit model functions, not just parameter values, to data (Turchin et al. 2003; Kendall et al. 2005; Pritchard et al. 2017). In this sense, the increased use of model selection and related tools in ecology has blurred the line between theoretical (qualitative) and statistical (quantitative) modeling (Boersch-Supan et al. 2017; Pritchard et al.

2017; Rosenbaum and Rall 2018). Meanwhile, increased computing power allows researchers with certain types of in-depth system knowledge to employ more intensive approaches like individual-based models (Grimm and Railsback 2005; DeAngelis 2018), which address a different level of complexity than Ludwig et al.'s I–III.

Even though the "levels" have diversified, the power of progressing from comprehensive and general to more system specific, and of operating in the right range of this progression for the question at hand, has retained its place in ecology (Bascompte and Solé 1995; Dwyer et al. 2000; Stephens et al. 2002; Fussmann et al. 2005; Getz et al. 2017). Also highly relevant is Ludwig et al.'s illustration of how multiple types of analyses can be combined to strengthen insights (Harmsen and Sibbald 1984; Sturtevant et al. 2015). Using numerical exploration of more realistic models to confirm analytical results derived from simpler, tractable models is a strategy that is still very much in use (e.g., Abbott 2011; Snyder and Ellner 2018). The broad agreement between the three levels in the budworm case
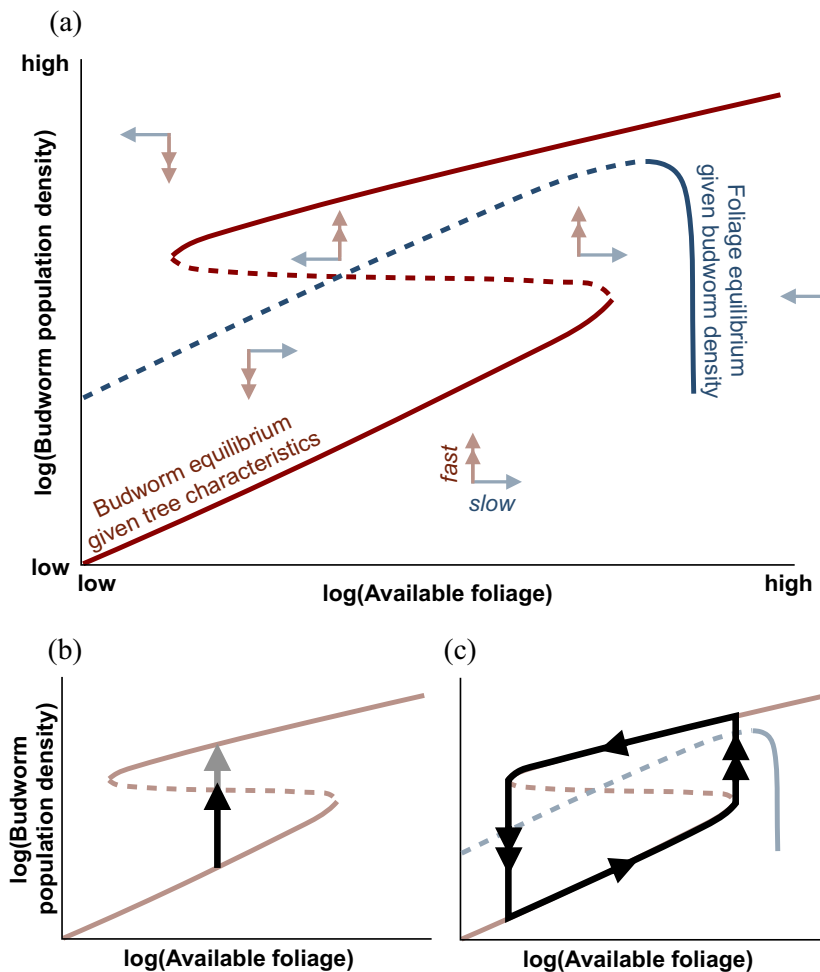

Fig. 2 The mechanisms behind outbreaks in the Ludwig et al. model. **a** Equilibria for the fast and slow variables in the model; solid lines are stable equilibria, dashed lines are unstable equilibria, and arrows show the direction of change in each part of the graph. The budworm population density changes quickly, so the fast-slow framework assumes that the systems dynamics are, to the extent possible, confined to the stable equilibria for budworm density (solid red lines). For the Level III parameter values, these stable equilibria fall on either side of the unstable foliage equilibrium (dashed blue line) that determines whether or not foliage will grow toward the stable high-foliage equilibrium (solid blue line); from most points below the blue lines foliage slowly grows, and above the blue lines foliage slowly declines. (Foliage dynamics are also influenced by a second slow variable, representing the trees' energy reserves, that is not shown because the basis for outbreaks can be understood without considering it directly.) **b** Illustration of how a stochastic outbreak can occur. Even absent any change in the tree's foliage characteristics, a random increase (black arrow) in a low-density budworm population can push the population across the unstable equilibrium, after which the population will recover (gray arrow) to the upper equilibrium. **c** Illustration of how fast-slow outbreaks occur. Dynamics are mostly confined to the budworm's stable equilibria, and populations at these equilibria will experience a slow increase or decrease in foliage abundance, depending on whether they are below the dashed blue line or above it. When the foliage abundance crosses a tipping point where the lower (or upper) budworm equilibrium is lost, the system is expected to quickly transition to the upper (or lower) equilibrium. Because this transition causes the populations to cross the dashed blue line, the foliage dynamics then reverse direction

study suggests that the more phenomenological Level I model should be adequate for most questions not involving quantitative prediction. Skeptics, however, might need the Level III model in-hand before believing Level I. Herein lies the catch: do we need detailed, system-specific data just to reassure ourselves that we don't need it? This conundrum does not reveal a shortcoming of the three-level approach per se, but it might explain why this line of inquiry has not been more definitive in resolving the tension between theory and empiricism.

Outbreaks and alternative stable states

Understanding the patterns in and mechanisms behind spruce budworm outbreaks is a long-standing challenge (Morris 1963; Royama et al. 2005; Navarro et al. 2019). On a fast enough time scale that foliage abundance can be thought of as fixed, Ludwig et al. (1978) propose that budworm population dynamics are governed by logistic growth with additional type III mortality due to unmodeled generalist predators. This single-species differential equation has become a go-to model for studying alternative stable states. The type III predation term creates the potential for both a low-density equilibrium point stabilized by generalist predation and a high-density equilibrium point stabilized by the fact that the forest, in its current state, can support a particular, finite budworm carrying capacity. These two stable equilibria coexist for intermediate foliage levels (red curves, Fig. 2a).

Outbreaks—sudden shifts from the low-density equilibrium to the high-density one—can occur in a few different ways in systems like the budworm model (Beisner et al. 2003). Stochasticity can cause outbreaks if perturbations allow the budworm density to move between the two equilibria's domains of attraction (Fig. 2b). The relative importance of top-down versus bottom-up processes in driving the population dynamics of herbivorous insects was debated ad nauseam in the late twentieth century (Hairston et al. 1960; Walker and Jones 2011), before ecologists more or less agreed that neither prevails over the other in general. Stochastic outbreaks in the budworm model exemplify the inevitability of this compromise: these outbreaks can only be explained when we acknowledge that both generalist predators (responsible for creating the low-density equilibrium) and foliage availability (creating the high-density equilibrium) play an indispensable role, and that their relative importance switches back and forth through time. Another important dichotomy (one that is no less false but has likewise motivated productive research) is the relative role of deterministic nonlinearities versus extrinsic stochasticity in shaping population dynamics (Nicholson 1933; Andrewartha and Birch 1954; Pascual and Levin 1999; Ziebarth et al. 2010). The budworm model has contributed here as well, as its relatively simple structure allows a close examination of how its nonlinearities (logistic density dependence, type III predation) interact with properties of the stochasticity (variance, autocorrelation) to determine outbreak frequency and duration (Sharma et al. 2015).

In Ludwig et al.'s original application, periodic outbreaks occur through a different mechanism that involves the slow forest dynamics (Fig. 2c). Slow changes in the tree population drive the budworm population across a bifurcation at which the low-density equilibrium disappears (leaving the high-density equilibrium as the only one remaining). The outbreak ends after the tree characteristics have changed back to where the low-density equilibrium has been regained and eventually past another bifurcation where the high-density equilibrium disappears. Dynamics of this type—where a population is driven across a fold bifurcation, causing a regime shift with hysteresis—have become very widely studied in ecology (Scheffer et al. 2001) and form the basis for most of the proposed early warning signals of ecosystem collapse (Boettiger et al. 2013). Because the slow forest changes are not exogenous, but are instead gradual responses to the faster budworm dynamics, outbreaks in Ludwig et al. (1978) have an additional layer of complexity not present in most other regime shift studies. We discuss this further in the next section. Meanwhile, the logistic/type III budworm model has become a standard in alternative stable states research (Dennis and Patil 1984; Sharma et al. 2015; Zeng et al. 2016; Přibylová 2018). Although this model was actually first published in May (1977), May cites "D. Ludwig, D. Jones and C. S. Holling, to be published" (p. 472) and subsequent uses of the model generally attribute it to Ludwig et al. (1978).

Fast and slow ecological processes

An important element of Ludwig et al.'s Level I analysis is the separation of time scales. On fast time scales (measurable in spruce budworm generations), the budworm population has a carrying capacity determined by what the current population of trees can support. At this time scale, tree characteristics are effectively fixed. On slower time scales (measurable in balsam fir generations), average tree age and health change in response to budworm herbivory. Given how relatively quickly budworm dynamics occur, the budworm population can be assumed to track these changes by equilibrating to the current tree characteristics with no meaningful lag. The presence of two very different time scales therefore greatly enhances the tractability of the Level I analysis because tree characteristics are constant on the fast time scale, and budworm densities, though changing, simply track tree dynamics directly on the slow time scale.

While Ludwig et al. (1978) were not the first to present an ecological analysis involving a separation of time scales (see e.g., Nisbet et al. 1977), they were perhaps among the first to publish such an analysis in a mainstream ecological journal, and their clear and intuitive exposition of the approach likely helped broaden awareness.

The presence of multiple time scales in ecological systems leads to more than a convenient analytical trick; it also produces distinct dynamics of great ecological relevance. During periods when changes in the slow variable have relatively little impact (e.g., during the slow phases of the trajectory shown in Fig. 2c), the fast variable can appear static. However, a larger change in response to the slow variable—and, in turn, a dramatic shift in the fast one—can occur without any disturbance to the underlying processes. This is how budworm outbreaks occur in the budworm-forest model (Fig. 2c). More generally, the interaction between fast and slow processes is an important way that long ecological transients can arise (Rinaldi and Scheffer 2000; Hastings 2004; Hastings et al. 2018). A stable fast-slow cycle (known in some fields as a relaxation oscillation) may, during the slow phases, appear to be at a point equilibrium for a long time even though this state is ultimately transient (Rinaldi and Muratori 1992). An unstable fast-slow cycle may transiently look like a stable cycle, until it suddenly stops repeating (Muratori and Rinaldi 1992). Figure 3 shows examples of both of these transient phenomena in fast-slow systems.

Short-lived forest insects and long-lived trees are certainly not unique in their mismatched time scales and the dynamical phenomena that can result: a similar separation of fast and slow processes occurs in other interactions, such as corals and algae (Crépin 2006), caribou and habitat (Wilman and Wilman 2017), pollinators and flowering plants (Revilla 2015), and plants and soil microbes (Abbott et al. 2015). Local and global metapopulation dynamics (Eriksson et al. 2014), behavioral and demographic process (Fahse et al. 1998), and disease transmission versus predation (Hall et al. 2005) can also occur at different enough rates for a separation of time scales to be used. In evolutionary biology, adaptive dynamics has very fruitfully employed the simplifying assumption that new mutations arise on a much longer time scale than fixation of favored traits (Waxman and Gavrilets 2005).

The theory-empiricism divide, then and now

Ludwig et al. (1978) clearly perceived a gap between theory and empiricism, given how they chose to present their work. To see how today's ecologists perceive this divide, we conducted an informal, unscientific survey on the social media platform, Twitter (https://twitter.com/lifedispersing/status/1090291757852643328). We provided the opening paragraph from the paper (quoted in the first paragraph of our "Introduction") and asked ecologists when they thought

Fig. 3 Illustration of two types of long transients (circled in **b**, **d**) in fast-slow systems. (**a**) is similar to Fig. 2 but here, the slow portions of the cycle are especially close to horizontal. During these slow phases, the fast variable will appear to be at a steady state (**b**). In (**c**), the equilibrium states of the fast variable are plotted as a surface, a function of two slow variables. Each fast transitions takes the system to a slightly different spot on the upper or lower equilibrium, slowly marching toward the front of the surface, where there is only a single stable state. In this example, the cycles are transient (**d**)
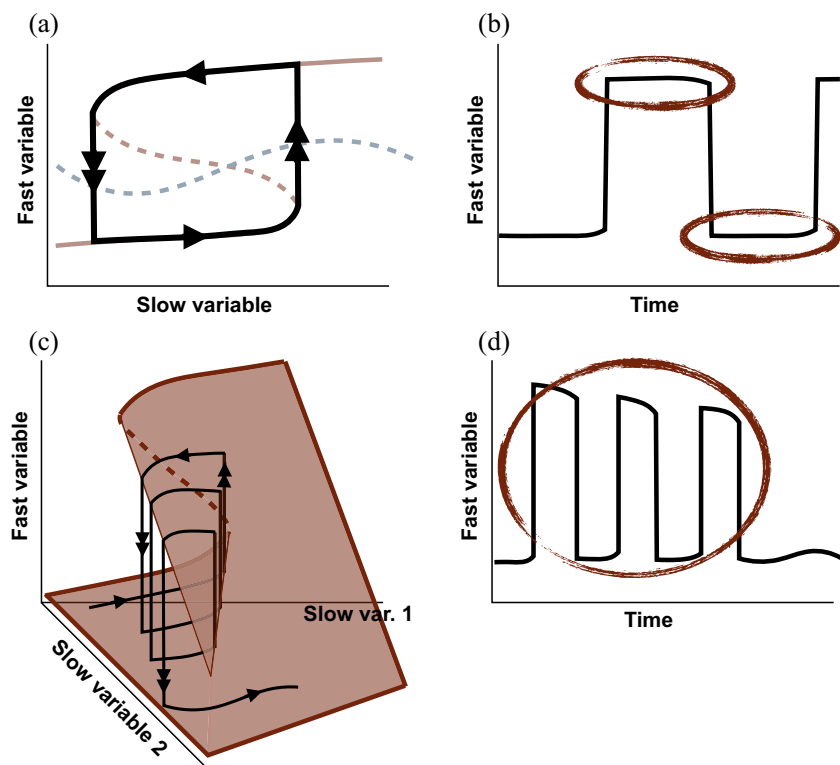
the paragraph was written. Respondents were allowed to choose between four options (the maximum allowed by Twitter): 1940–1959, 1960–1979, 1980–1999, and 2000–2019. A total of 785 people voted over 7 days in early 2019. If respondents perceived that the theory-empiricism gap has been shrinking, we would expect them to place the paragraph into one of the earlier time frames. Respondents who think the paragraph is more recent likely perceive that the gap has been widening. Evenly distributed votes would suggest that the field generally see the divide as timeless.

Figure 4 shows the results of the poll. To our surprise, the correct choice and the two subsequent time periods received roughly equal numbers of votes, and the most frequent response was that the paragraph was written sometime within the past 20 years. This supports our sentiment that Ludwig et al. (1978) were not, unfortunately, particularly successful in narrowing the theory-empiricism divide. (Of course, balancing this criticism is our admiration that they were bold enough to frame their paper in that light.) One Twitter user indeed wrote, "…that passage looked 'timeless'."

Nobody admitted to recognizing the paragraph. One person tweeted "Oh no! I answered wrong despite having cited this" and some of us could have said the same before we discussed the paper in depth to prepare this commentary. This response, in a way, speaks to the richness of ideas in the paper, which overshadow the attempt at reconciling theory and empiricism.

Why the theory-empiricism divide has persisted is a complex question, but Ludwig et al. (1978) may have identified a prime reason in their own concluding sentence: training. Their paper ends with the observation that "in principle, the methods which were applied to the budworm do not go beyond first year calculus; however, their effective use requires considerable mathematical confidence" (p. 330). Just as we would not expect a scientist
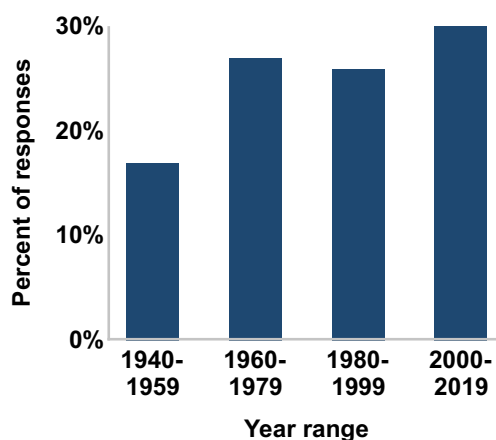
to take a couple of lecture-based courses in experimental methods then be ready for a career as a field ecologist, we cannot expect our students to master theoretical methods from a semester or two of college calculus. "Mathematical confidence" comes from exposure, practice, and mentoring, and the latter can come from formal mentor-mentee relationships or from collaborators and peers. Bruce Kendall credited interdisciplinary synthesis centers (specifically NCEAS, but the same could be said of NIMBioS, SESYNC, and others) for fostering a deeper integration of quantitative methods and data (Kendall 2015). These and other efforts that support broad-based training and interdisciplinary collaboration may prove to be how we prevent the theory-empiricism divide from becoming truly timeless.

Concluding remarks

History has shown that Ludwig, Jones, and Holling framed their landmark paper in terms both too broad and too narrow. The work did not really serve to bring ecology's theoretical and empirical schools into greater harmony; this framing was too ambitious. The paper has also faded from its role as a how-to example; other approaches for merging models and data have come along. In effect, the authors could be judged as having missed both marks established in their own introduction. Instead, their work has found a much greater place in modern ecology, providing us with specific models, general methods, and a range of broad concepts that have served as inspiration for hundreds of advances in the past four decades. We look forward to tracking its impact through the next four.

Fig. 4 Results from Twitter poll showing that respondents most commonly thought that the opening paragraph from Ludwig et al. (1978) was written within the past 20 years

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