Bridging Levels from Individuals to Communities and Ecosystems: Including Adaptive Behavior and Feedbacks in Ecological Theory and Models

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Symposium motivation and objectives

Ecologists now recognize that the classical theory of population and community ecology is severely limited by its inability to represent the effects of individual adaptive behavior, but we are still looking for ways to accommodate adaptive behavior in models and theory. Conflicts between classical theory and adaptive behavior were brought to the forefront by analyses such as that of Abrams (1993), which showed that the fundamental assumptions of classic predator–prey trophic models are invalid when predator-avoidance behaviors are considered. Such analyses motivated the many empirical studies that documented and quantified such behaviors and their effects, for example, "trait-mediated indirect interactions" and "nonconsumptive effects," which have been a major focus of ecology since the 1990s.

At the same time, individual-based models (IBMs; also referred to as agent-based models) were recognized as a way to incorporate adaptive individual behavior and its effects in ecological models and theory. The landmark paper of Huston et al. (1988) anticipated the contributions of IBMs to new theory that unifies behavior at the individual level with population and community ecology. However, even though IBMs are widely used in ecology and many other sciences, the anticipated new theory has been slow to develop. Grimm (1999) noted that IBMs rarely addressed theory either by developing new theory or by re-evaluating existing theory. But the 2000s did see the establishment of one new approach for developing new theory that explicitly unifies individual and higher levels of ecology: the "pattern-oriented theory development cycle" (Grimm and Railsback 2005, Grimm et al. 2005) in which theory for how individuals make adaptive decisions is tested by how well it reproduces observed patterns at both individual and higher levels. This approach poses alternative hypotheses for individual behaviors and falsifies those that, in an IBM, do not reproduce important and realistic phenomena of population and community ecology. The hypothesis-testing cycle can produce (and has produced) general, reusable theory that explains higher-level ecology from individual behavior. Such theory is referred to as

"across-level" because, in contrast to strong traditions in ecology, it explicitly considers individual and higher levels at the same time.

The need to incorporate theory as part of agent-based modeling is a current issue in many sciences. This issue is the subject of a series of interdisciplinary workshops funded by the Volkswagen Foundation in Germany and co-organized by two speakers in this ESA symposium (Berger, Grimm). The first product of these workshops (Lorscheid et al. 2019) made four recommendations for how we can make more progress incorporating the effects of adaptive behavior in system-level models and theory:

- Develop theory for individual adaptive behavior by testing alternative hypotheses by how well they, when included in an IBM, reproduce patterns observed at higher levels;

- Base such theory on first principles at the individual level;

- Use IBMs to test and improve system-level theory such as the theory of population and community ecology; and

- Use standards to promote communication and learning across scientific disciplines.

The motivations for this symposium were our desires to encourage ecologists who use IBMs to address theory with them more often and, more specifically, to expose more ecologists to the ways we can incorporate adaptive individual behavior in ecological models and address it in theoretical ecology. Our objectives were to present a diversity of speakers and topics that addressed all of the above recommendations of Lorscheid et al. (2019).

The following section provides summaries of the six speakers' presentations. The first two (Harvey, Giske) provide examples of developing and applying theory at the individual level to understand systems of adaptive individuals. The remaining speakers (Berger, Semeniuk, Hagstrom, Grimm) address the use of IBMs to evaluate and improve existing ecological theory. The final section synthesizes their contributions and looks forward to new directions in the theory of ecological systems driven in part by adaptive individual behavior. The final section also summarizes topics addressed in the symposium's ending discussion period.

Presentation summaries

B. Harvey. Useful imperfection: Sub-optimal decision makers serve well in individual-based models that address real-world problems

This presentation directly addressed one of the most fundamental problems with integrating the theory of behavioral ecology with higher ecological levels: The fitness-optimization approaches that dominate behavioral ecology cannot be used in IBMs that include such fundamental elements of population ecology as competition among individuals. Much of classical behavioral theory assumes individuals make adaptive trade-off decisions (e.g., to balance feeding effort against predation risk) by optimizing

some measure of fitness over a fixed, known future period. However, when we build an IBM of populations in which individuals interact optimization is no longer possible: The best solution for each individual depends on what the other individuals do. Further, optimization is not possible in models with realistic complexities (e.g., weather and other causes of habitat variability, responses of predators to prey populations) that make the future unknowable.

The "sub-optimal" foragers referred to in the title are model individuals that use state- and prediction-based theory (SPT), a modification of the classical fitness-maximization approach that can produce realistic trade-off behaviors in population and higher-level models that include feedbacks of individual decisions. Instead of assuming a fixed set of future conditions that fitness can be maximized over, SPT assumes individuals make an explicit prediction of future conditions and then use approximation to make *good* decisions that are then updated as conditions change. Good decisions are possible even when the predictions and approximations are clearly wrong.

State- and prediction-based theory evolved from a way of modeling foraging decisions by stream salmonids in models designed for river management ecology (Railsback et al. 1999, Railsback and Harvey 2002). It was shown unique as a general type of theory for individual trade-off decisions that could reproduce behavior-driven trophic interactions such as trait-mediated indirect effects (Railsback and Harvey 2013). A forthcoming monograph (Railsback and Harvey, *in press*) provides further examples of SPT and guidance for its use in IBMs of population and communities that include individual adaptive trade-off decisions. These new examples show that SPT can produce behavior quite close to optimal under conditions simplified enough to allow optimization, but then makes much more realistic and unsimplified population models feasible.

J. Giske. Toward mechanistic theory of adaptive behavior: Integration of psychology, cognitive science, and evolutionary ecology to model behavior in realistic contexts

In his talk, Jarl Giske presented a framework for modeling populations of organisms that differ in genetics, leading to individual differences in perception, preferences, and behavior. This framework (Budaev et al. 2019) is a product of extensive experience modeling population ecology as emerging from individual behaviors that have been evolved in the computer (Strand et al. 2002, Giske et al. 2013, Eliassen et al. 2016). This theory is also across-level, but differs from SPT by representing individual adaptive decision-making explicitly as the outcome of physiological and neurological mechanisms. Giske showed that by specifying an architecture from sensing to decisions, and by evolving the gene pool of the population, this model produces virtual organisms that behave like autonomous agents. They have the ability to adjust top-down priorities in response to recent sensory information, as well as to concentrate attention on sensory information relevant to their current top-down priority.

Giske asked us to take the perspective of the animal, not the researcher. From the animal's perspective, the fundamental problems are (1) what is the best context to choose (how to interpret the situation in body and environment, e.g., shelter, company, homeostasis, mating, and parental care), (2) what is then the appropriate short-term goal, and thereafter (3) what are the relevant stimuli that require atten-

tion. This requires a cognitive architecture and machinery that enable the organism to make priorities and predictions and behave autonomously.

The modeling framework includes three essential aspects: (1) the focus on the autonomous individual, (2) the individual's goal-directed cognitive and behavioral control, and (3) its need to limit and integrate information. The resulting models integrate cognition, decision-making, and behavior in the whole phenotype that may include the genome, physiology, hormonal system, perception, emotions, motivation, and cognition.

Giske said that this modeling framework rested on three methods: (1) an IBM of a population where (2) genes controlling certain traits were evolved and adapted over many generations by a genetic algorithm, and where (3) some of these genes described the individual's cognitive architecture.

U. Berger. Individual-based modeling to discover the ecological importance of tree networks

This presentation described a particularly exciting and new example of combining modeling and field research to develop ecological understanding and theory. In forest ecology, a great deal of attention has recently been given to tree networks: There is now clear evidence that individual trees can adaptively graft their roots to the roots of neighboring trees, at a clear cost. The extent of root grafting, its benefit to individual trees, and its consequences at the forest level are much less clear. Dr. Berger addressed these uncertainties first with field observations of which trees are grafted to which other trees in a mangrove forest. She then identified several patterns in the data, such as that grafting to the nearest other tree was most common and that grafted trees tended to form small, linear networks.

Dr. Berger then modified an existing mangrove IBM, which builds on theory for how individuals interact with neighbors via competition for resources. The modified model served as a virtual forest in which she could test and contrast alternative theories for how individual trees graft roots. The alternative theories included a null model that assumed grafting is random and three that assumed trees "cooperate" by exchanging resources through the graft in different ways. Results of the model under the alternative theories were then compared to the field observations.

The initial modeling results indicate that root grafting is not random but instead adaptive. However, the results also indicate that existing understanding of the mechanisms of competition and cooperation among mangrove trees is inadequate to support models that are detailed enough to elucidate the meaning of cooperation at the stand and forest level. In other words, further empirical understanding is needed at the individual level to develop across-level theory based on first principles. Thus, this study is an excellent example of how across-level modeling and field research support and direct each other to build new theory and ecological understanding (Fig. 1).
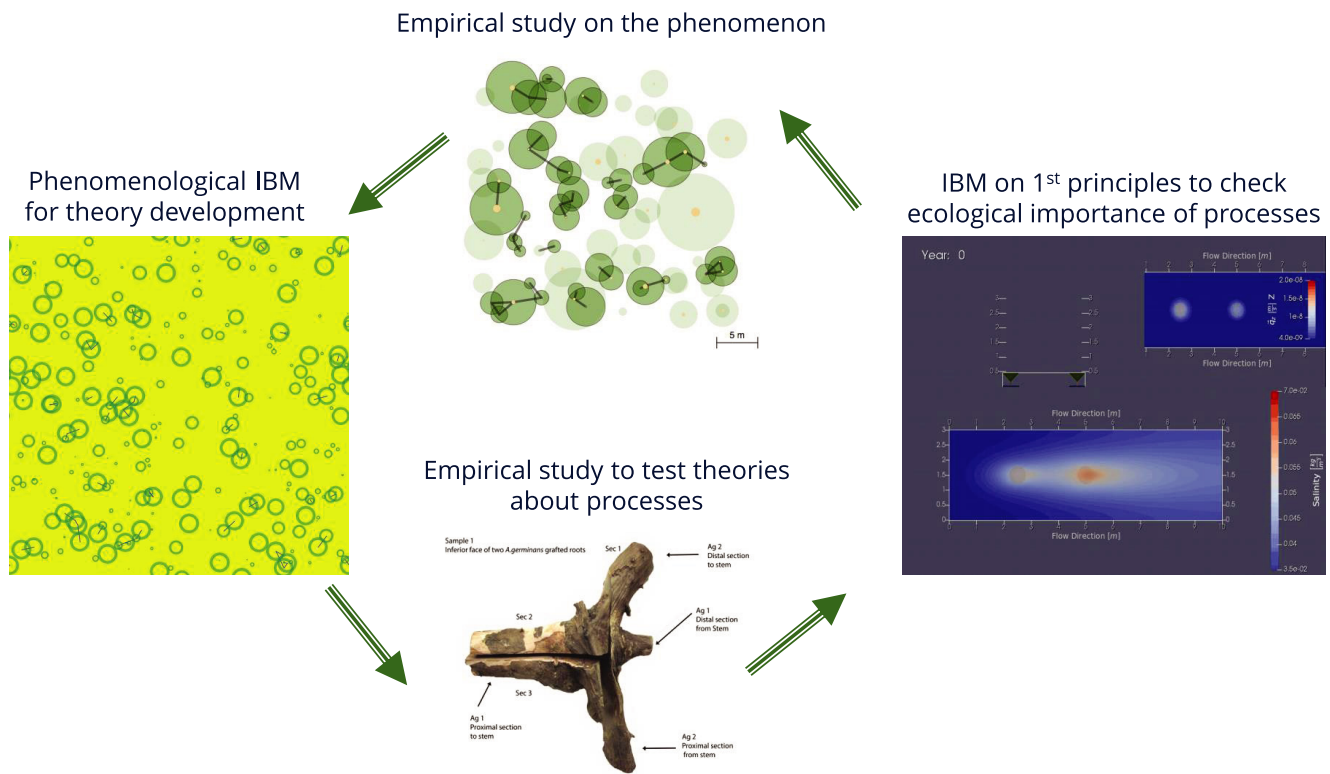
Fig. 1. The cycle of field research and modeling used in the mangrove root-graft research of Berger.

C. Semeniuk. Individual-based modeling to evaluate classical theory: Violations of the risk allocation hypothesis explained by variation in energetic state, life-history allocation, and predictive abilities of prey

This presentation illustrates the use of IBMs with individual adaptive behavior to explore and test existing theory. In this case, the existing theory is the "risk allocation hypothesis" (RAH) of Lima and Bednekoff (1999), a theory of behavioral ecology about how individuals should allocate feeding and antipredator behavior when risk varies over time.

Dr. Semeniuk explored this theory using a simple IBM that exposes simulated foragers to temporal variation in the frequency and intensity of predation risk. The model foragers sense the predation risk they are exposed to and their starvation risk, a function of their previous feeding success and energy levels. They then select among alternative behavioral strategies that differ in whether the animal feeds, whether it expends some of its effort on vigilance to reduce predation risk, and whether it moves to find more food at the cost of higher risk (Fig. 2).
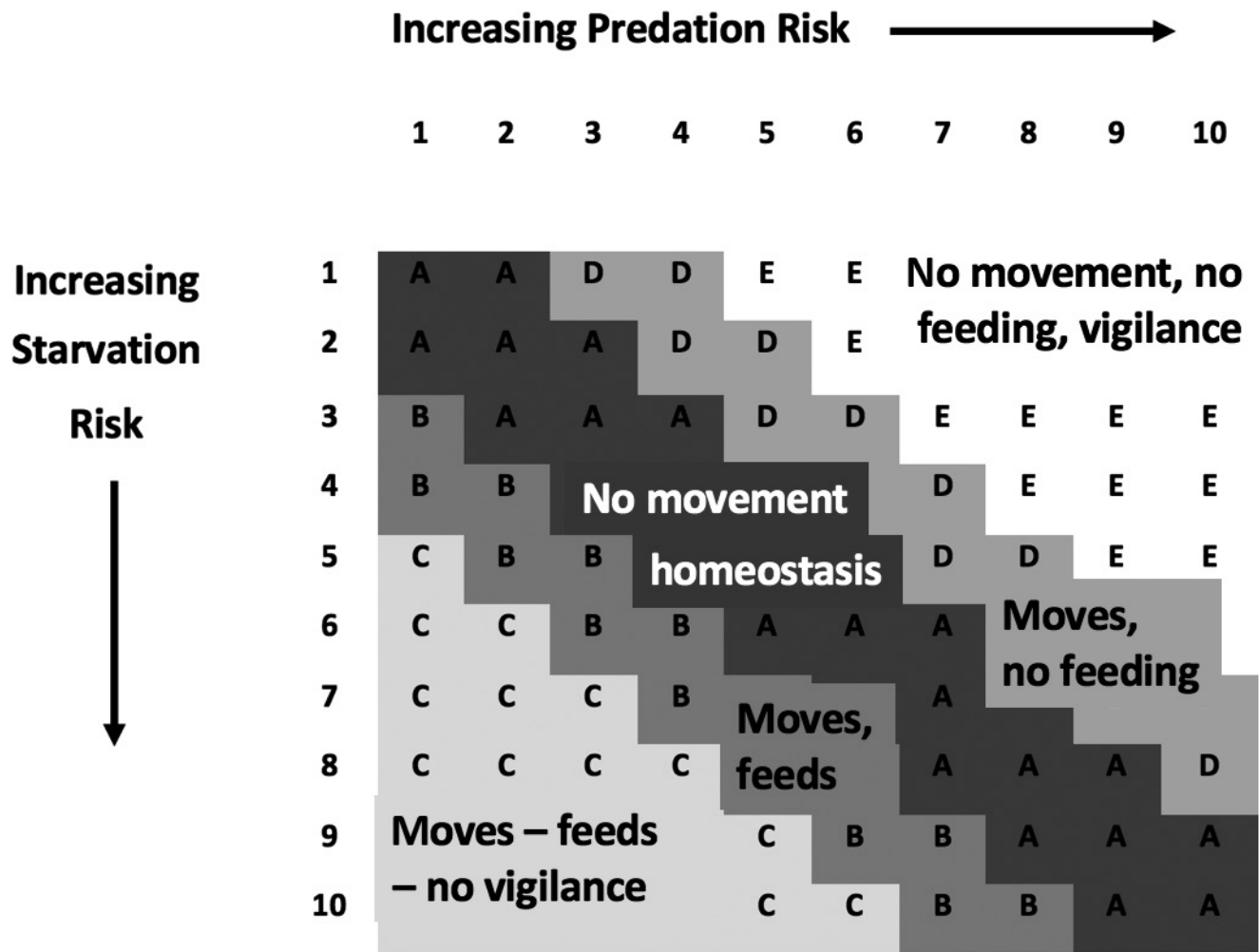
Increasing Predation Risk ⟶

	1	2	3	4	5	6	7	8	9	10
1	A	A	D	D	E	E				
2	A	A	A	D	D	E				
3	B	A	A	A	D	D	E	E	E	E
4	B	B					D	E	E	E
5	C	B	B				D	D	E	E
6	C	C	B	B	A	A	A			
7	C	C	C	B			A			
8	C	C	C	C			A	A	A	D
9					C	B	B	A	A	A
10					C	C	B	B	A	A

Increasing Starvation Risk ⟶ (vertical, downward)

No movement, no feeding, vigilance

No movement homeostasis

Moves, no feeding

Moves, feeds

Moves – feeds – no vigilance

Fig. 2. Behavior decision in Semeniuk's forager individual-based model. Increasing predation risk reduces movement and feeding and increases vigilance, while increasing starvation risk (decreasing energy reserves) increases movement and feeding and reduces vigilance.

The model's overall patterns of activity support the RAH, with the level of foraging effort responding to the magnitude and frequency of predation risk, for example, by increasing foraging over time when risk is persistently high. However, modifying the forager's risk assessment trade-offs to reflect (for example) different life-history stages caused the model to produce results that conflict with the RAH. A life stage in which growth dominates fitness can be insensitive to risk, and a life stage in which growth no longer contributes to fitness can be more sensitive to risk than predicted by the RAH.

Dr. Semeniuk also used the IBM to explore alternative models of how foragers assess and forecast predation risk and how those models affect risk allocation over time. For example, foragers can forecast future risk using weighted memory of recent predation events and use the state- and predation-based theory presented by B. Harvey to make foraging decisions. Under these more "realistic" assumptions, the IBM still produced results compatible with the RAH but less optimal when variation in risk is higher and less predictable.

G. Hagstrom. Marine bacteria behavior and the kinetics of remineralization in the ocean

This presentation provided an example of how important individual traits and their variability can be for understanding ecological problems of global significance. Dr. Hagstrom's work addresses dissolved organic matter (DOM) and its degradation by marine bacteria, a major component of the global carbon cycle. Marine DOM is an extremely large carbon reservoir, and its flux is driven by remineralization by bacteria. It is tempting to think that this extremely large system driven by simple organisms could be understood and modeled at the system level without considering individuals, but the presentation illustrated why individual variation and behavior are in fact important.

The kinetics of carbon remineralization in the ocean are driven by variation not only in the bacteria but also in the DOM itself. Much of the DOM exists as polymers and aggregations of polymers into gels, which are not readily consumed by bacteria unless they are reduced to monomers. Polymers are degraded into monomers by enzymes produced by some but not all bacteria, and this degradation takes place outside the cell so the monomers are then available even to bacteria that did not contribute to their degradation. Spatial variation in the concentration of polymers and monomers makes another key bacterial trait, motility, important.

This study modeled a bacterial community that included two environments, polymer gels and the bulk ocean, and bacteria that differed in their motility and ability to degrade polymers. This model was then used to address several fundamental questions of the marine DOC system. Example results include that motility is a successful trait of bacteria when more of the DOC is difficult to degrade and that coexistence of motile and non-motile bacteria can be explained by the monomers produced but not consumed by motile bacteria. The model and empirical research supporting it indicate several novel possibilities about the DOC system. First, motile bacteria may be responsible for most degradation of polymeric DOC by colonizing gels. Second, motile and non-motile bacteria can and do coexist throughout the ocean. Third, high diversity in the forms of DOC and the resulting limitation on the ability of bacterial enzymes to degrade it can partially explain the large reservoir of DOC that persists undegraded in oceans. This research is also important as an example of how questions dependent on individual variation and behavior can sometimes be addressed usefully with aggregated instead of fully individual-based models.

V. Grimm. It's the rare species, stupid! Coviability analysis illustrates the coevolution of individual-based modeling and ecological theory

The final presentation provided an overview and example of the role of individual-based modeling in theory development. Dr. Grimm's overview included some of the issues raised above as motivations for this symposium, including that while IBMs are widely used they remain rarely used to specifically address theory. The applicability of IBMs to theory has been limited by practices such as representing behavior via imposed rates instead of as fitness-seeking mechanisms, and designing models around single observed patterns instead of testing them against multiple patterns at different levels and scales. Further, the belief that IBMs are inherently system-specific and unsuitable for theory persists among some ecologists.

At the same time, there are reasons why IBMs are especially suited for theory and why ecology needs them for theory. Classical ecological theory often lacks standard characteristics of scientific theory such as striving for testable predictions, identifying general principles underlying the organization of sys-

tems, and providing robust general models applicable to practical problems. The traditional division of ecology into separate disciplines at different levels (physiology, behavior, populations, communities, ecosystems) has discouraged theory that addresses the links and feedbacks among levels. Individual-based models and methods are naturally suited to across-level phenomena. They can link levels from nutrients and energy through physiology and behavior to populations, communities, and ecosystems by representing the mechanisms that cause controls and feedbacks.

The example presented by Dr. Grimm addresses theory for the robustness of communities to perturbations such as invasion and habitat loss. This issue has been addressed via system-level models referred to as "Modern Coexistence Theory" (Chesson 2000). This theory is limited by its formalisms to addressing a few abundant species, stationary environments, simple situations, and long-term coexistence. However, many modern problems require consideration of many species, including the rare species often of most interest; changing environments; multiple drivers and feedbacks; transient dynamics; and species persistence. These considerations are similar to those of population viability analysis, so a new approach has been termed "Coviability Analysis" (CVA; Jeltsch et al. 2019). While population viability analysis addresses the time to extinction for a population, CVA addresses the time to critical diversity loss for a community. Using IBMs as its basis allows CVA to avoid many of the restrictions that limit Coexistence Theory.

The example CVA presented by Dr. Grimm addresses grasslands and uses a community IBM that can represent many plant species that differ in the parameters that define species characteristics and mechanisms (May et al. 2009). The CVA can produce results such as how predicted measures of diversity loss (e.g., probability of Shannon diversity decreasing to a critical level within 100 years) can vary with management measures such as seed input rate and mowing frequency.

Dr. Grimm concluded by stating that individual-based approaches, especially IBMs in which behavior emerges from first principles and mechanistic understanding, have important benefits for developing ecological theory. Foremost, they allow us to develop theory that addresses multiple scales and levels of organization. They allow us to embrace instead of ignore complexity. They are based on responses of organisms, which are easier to understand empirically and from a first-principle perspective than are responses of systems. These approaches can contain sufficient detail to make testable predictions and hence serve as a virtual laboratory in which we formulate hypotheses and test them against observations.

Synthesis

What can we learn from the ideas and analyses presented in this symposium? Foremost is that while individual-based approaches have not contributed extensively to ecological theory yet, theoretical ecology needs them. We simply have no other approaches that can represent the effects of individual adaptive behavior on populations and higher levels in a way that is tractable and useful for modeling real problems. The most straightforward way to do so is the across-level (or "individual-based"; Grimm and Railsback 2005) theory discussed above: theory for how individuals make adaptive decisions that has been tested and validated by its ability to reproduce, in an IBM, patterns observed at higher levels. There are now many examples of this approach in ecology and other fields (Railsback and Grimm 2019).

The pattern-oriented cycle used to develop individual-based theory is most often applied to specific dynamics of a specific category of systems, but the presentations by B. Harvey and J. Giske illustrate

how general types of theory can also result. Both presentations described general approaches to modeling adaptive decision-making in population contexts that arose from methods originally for specific systems and behaviors. The SPT theory presented by Harvey is a modification of the classical fitness-optimization theory of behavioral ecology, in which we assume organisms have behaviors because those behaviors convey fitness. In contrast, the theory presented by Giske seeks the actual mechanisms underlying decision-making; this quest is likely to be fruitful, given the rapid progress being made in understanding the physiology and neurology of decision-making.

The ability to link population ecology to individuals gives individual-based approaches another advantage illustrated by the presentations of U. Berger and G. Hagstrom: providing a strong and clear link between theory and empirical research. When we seek ecological theory that is based on first principles and mechanisms at the individual level, we quickly find out what we still need to know about the individuals. The modeling exercise described by Berger taught her that more must be learned about how trees share resources to understand the population consequences of root grafting. Hagstrom described an analysis of global bacterial genomes to identify a pattern (widespread coexistence of motile and non-motile bacteria) essential to the model conclusions. Railsback and Harvey (*in press*) discuss links between individual-based theory development and empirical research extensively.

The second way that individual-based approaches can contribute to ecological theory is by using IBMs to test and improve existing theory, illustrated by the work of C. Semeniuk. While it may seem counterintuitive to test ecological theory in a model instead of in the field or laboratory, Semeniuk's presentation illustrates a key benefit of doing so. Field and laboratory experiments to test ecological theory typically must use highly simplified conditions to avoid "noise" and processes not addressed by the theory, and are often limited to analysis of very few treatments. Consequently, even relatively simple IBMs often confront theory with more diverse and realistic conditions than empirical experiments have. Simulation experiments like Semeniuk's can be very valuable for defining the limitations of conventional theory.

The symposium ended with an open discussion period. One topic raised in the discussion was the effect of "big data" and sensor technologies on theory development through individual-based approaches (a topic also addressed by Railsback and Harvey, *in press*). The consensus of the speakers was that widespread availability of data on, for example, individual locations and activity, can enhance but not replace models and theory. Such data can provide only limited understanding by itself, especially for predicting future responses to novel conditions. But data, sometimes from carefully controlled experiments, can be very useful for developing theory for adaptive behavior that can be applied to novel conditions with some confidence.

A second discussion topic was how ready ecology is for new kinds of theory and for treating individual-based ecology as theoretical. The speakers with extensive experience as journal editors (Berger, Grimm) indicated that the beliefs that theory must involve system-level equations and that individual-based approaches are inherently atheoretical still persist among "gatekeepers" such as journal editors, reviewers, and academic advisors. On the other hand, the past 20 years have laid all the foundations necessary for the new approaches, including development of software and analysis tools, standards for describing models and their analysis, textbooks and guidance, numerous good examples, and (perhaps most importantly) clear evidence that new kinds of theory are needed. One basis for optimism is the high success rate of publications that explicitly treat individual-based theory development as a cycle of posing alternative hypotheses and testing them against observed patterns: When presented this way, the work is

immediately recognizable as the hypothesis-testing scientific method that we should all recognize and appreciate.

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