

Differentiating and Defusing Theoretical Ecology's Criticisms: a Rejoinder to Sagoff's Reply to Donhauser (2016)

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Abstract

In a (2016) paper in this journal, I defuse allegations that theoretical ecological research is problematic because it relies on teleological metaphysical assumptions. Mark Sagoff offers a formal reply. In it, he concedes that I succeeded in establishing that ecologists abandoned robust teleological views long ago and that they use teleological characterizations as metaphors that aid in developing mechanistic explanations of ecological phenomena. Yet, he contends that I did not give enduring criticisms of theoretical ecology a fair shake in my paper. He says this is because enduring criticisms center on concerns about the nature of ecological networks and forces, the instrumentality of ecological laws and theoretical models, and the relation between theoretical and empirical methods in ecology that that paper does not broach. Below I set apart the distinct criticisms Sagoff presents in his commentary and respond to each in turn.

Key Words

Theoretical Ecology; Lotka-Volterra models; Ecological laws; ceteris paribus conditions

Mark Sagoff pursues a practically-motivated approach to environmental philosophy that I greatly appreciate. In several works, he critically analyzes the foundations of theoretical methods in ecology, and questions whether they can be usefully applied for public policy and resource management decision-making (Sagoff 1997; 2000; 2003; 2013; 2016). Such analysis is crucially important because leading environmental advisory organizations have cast ecology as an objective guide for significant policy and management decisions.¹

In some recent papers, I examine how different inferential methods in theoretical ecology work and how they can (and cannot) be usefully applied for practical decision-making. In my (2016), "Theoretical Ecology as Etiological from the Start," I dispel claims that theoretical ecological

¹ See Donhauser 2016a and Donhauser 2016b and the sources cited therein for more discussion of ways in which ecology has been bestowed this guiding role.

research is unscientific and of no value for practical decision-making because it is supposed to rely on teleological thinking. Therein, I spotlight comments made by Sagoff (2013) as expressions of the criticisms I had in mind.

I was pleased to see Sagoff's formal response, and sincerely appreciate his endorsement of my positive arguments in my recent paper. In a kind fashion, he says: "Donhauser admirably succeeds in showing that several founders of ecological theory, including Lindeman (1942) and Hutchinson (1948), had 'efficient' rather than 'final' causality in mind." So, although he lodges complaints later on, Sagoff confirms that I succeed in showing that ecologists abandoned robust teleological views long ago, and use teleological characterizations of ecological phenomena as metaphors that aid in developing mechanistic accounts of the underlying causes of observable ecological "network-level" dynamics. He also takes no issue with my operational account of the role of teleological metaphors in certain reasoning processes commonly employed in ecology after Hutchinson (1948) (pp. 71-2). Moreover, Sagoff does nothing to undermine my contention that modern ecologists generally embrace a thoroughgoing instrumentalist and metaphysic-neutral view on the nature of ecological networks and properties (pp. 68-9; 74). In fact, most of his reply concerns not what I argue in my paper but what it left him wanting me to say about the nature of ecological networks, so-called ecological "forces," and theoretical models of such things.

Sagoff's negative appraisal is that I have been uncharitable in my treatment of criticisms of theoretical ecology. According to him, this is because enduring criticisms center on interrelated concerns about the existential status of ecological networks and forces, the instrumentality of ecological laws and models derived therefrom, and the relation between theoretical and empirical methods in ecology that not discussed in that paper. Yet, despite his initial comments about the ways I succeed in the paper, Sagoff's interpretation and critique of my paper show that he and I see theoretical ecology and its criticisms very differently.

Sagoff gerrymanders the scope of my brief and narrowly focused comments about criticisms of ecology, and claims that I should have addressed several issues my paper was never meant to address. Though he frames it as a response to my claim that methods in modern theoretical ecology have always been underwritten by an etiological, rather than a teleological, understanding of ecological networks, he uses his commentary primarily as a vehicle for endorsing several independent criticisms of theoretical ecology that he runs together and that are outside the explicit scope of my paper. Unfortunately, the criticisms Sagoff defends in his reply, and his comparatively few criticisms of claims I make in my paper, are founded on mistaken assumptions about the conceptual foundations and basic workings of theoretical methods in ecology. Accordingly, I see this opportunity to respond Sagoff as an opportunity to push forward understanding of ecology's conceptual foundations and practical value.

My rejoinder to Sagoff will progress in two main steps. First, in §1, I assess Sagoff's critique of my paper, and identify problems with its set up, scope, and framing that largely belie his commentary. In §2, I then systematically defuse several independent criticisms Sagoff endorses in his commentary.

§1. Problems with Sagoff Criticism of Donhauser (2016)

1.1. A Bait-and-switch

Sagoff defends criticisms of theoretical ecology he says I unfairly brush aside via presenting what he frames as counterpoints to my contention that 'theoretical ecology has been etiological from the start.' In my (2016), I show that in "the first, and [...] archetypical, project in modern theoretical ecology" and key works directly preceding it, seminal ecologists explicitly abandoned robust teleological commitments and use "teleological metaphors to aid in generating component-to-component accounts of the mechanics of ecological network-level dynamics" (p. 73). In response, Sagoff claims that theoretical ecology has *never been* etiological. However, he does not then establish

this or even deny my point. He instead uses 'etiological' in a way inconsistent with my carefully restricted usage, and uses the slogan that 'ecology has never been etiological' to loosely pull together several independent criticisms that are tangential to the considerations of my paper.

This begins happening as he specifies that by saying 'theoretical ecology has never been etiological' he means: "[ecologists have] not presented empirical evidence of the causal forces it theorizes, such as density dependence, competitive exclusion, Lotka-Volterra predator-prey relations, the logistic relation of species abundance to resource limits, and the like" (p. 2). Sagoff brings in further tangential concerns later, but even here, at his commentary's start, he has conceded my main point and shifted to discussing concerns about "ecological forces" and the relation between theoretical and empirical work in ecology that are outside the scope my paper. After this brief clarification on the first page, Sagoff (literally) does not mention etiology, teleology, or the distinction between "top-down" and "bottom-up" thinking anywhere else in his commentary. He instead launches into a discussion of old criticisms of theoretical ecology that see it as divorced from empirical work, which he ties to independent concerns about ecological forces, regularities, and the existential status of ecological entities.

He buttresses his worry about an alleged disconnect between theoretical and empirical ecology by citing Hall (1988), who once complained that ecological principles and models are often taught, and presented in textbooks, as if they are "a priori true" even though they have known exceptions (p. 2; cf. Haskell 1940). Sagoff attaches this arguably anachronistic brand of critique lodged by Hall to the abovementioned independent issues by then pointing to an oft-cited paper by Lawton (1999); who argues that there are no ecological community-level regularities in nature because contingent local factors are so various and diverse that such regularities just do not occur. Sagoff then abruptly brings in worries about the nature of ecological networks, properties, and kinds, saying: "many of the kinds of [network-level] properties theoreticians posit and

mathematicians model are observable in principle; the critics contend, however, that these patterns or regularities are not observed in fact” (p. 1). He relates this loosely associated bundle of independent concerns back to my paper in an ad hoc fashion; by concluding that my recent demonstration that ‘modern ecologists do not rely on assumptions about teleological causes of ecological network-level properties’ is inconsequential to enduring criticisms of theoretical ecology. According to him, this is because undermining enduring criticisms requires defusing the aforementioned concerns by establishing that ecological network-level properties, the “forces” that produce them, and regularities and laws applying to them are observed in nature.

1.2. *Misjudging the Scope*

My (2016) paper’s main point is that ecologists’ use of teleological language is metaphorical and a conceptual device for helping to fill out the “bottom-up,” efficient, causal picture they presuppose. Yet, Sagoff’s commentary focuses on topics orthogonal to the questions of whether ecologists accept a robust teleology and “top-down” causes—*while he also explicitly agrees that they do not*. What’s more, he unfairly flags my comments about criticisms of theoretical ecology as uncharitable and inconsequential.

Sagoff mistakenly believes that I respond to a much broader class of criticisms of ecology than I do in my paper. He remarks that my paper’s introduction, “helpfully and accurately cit[es] a list of authors who have questioned whether the entities described in ecological theory exist in any meaningful sense at all” and others who “have argued that theoretical ecological research is empirically unfounded (even empirically unfindable)” (p. 68). Yet, I cite those criticisms early on to emphasize the juxtaposition between the unfettered embrace of ecology in policy circles and the wariness of it expressed by some academics. I do not purport to respond to the whole class of enduring criticisms, and my project is not even presented as a response to criticisms. It is presented as a historical project that provides insights into the heuristic roles of teleological metaphors in

certain sorts of theoretical research, and which has ramifications for certain misinterpretations of work in modern ecology. The explicit aim is not ‘defusing criticisms of ecology’ but ‘providing insights into the workings of certain inferential processes in ecology’ through examination of key moments in theoretical ecology’s genesis. I do say that my arguments have ramifications for *some* criticisms, but those comments are restricted to criticisms that concern teleological language used in ecology.

As I say at the top of my paper, in the final section, “I critically respond to opposing literalist construals of teleological characterizations in ecology—including enduring arguments according to which theoretical ecological research is unscientific and of no value for practical decision-making because it is supposed to rely on teleological, ‘magical,’ thinking” (p. 68). I accomplish this by providing textual and conceptual support for my prior contention that robust teleological views are not and have not been embraced as a mainstream convention within ecology since Hutchison (1948) at least. *Nowhere* do I say that my arguments in the paper have ramifications for criticisms of ecology centering on concerns other than ecologists’ ostensible appeals to teleological causes. So, since Sagoff agrees that I succeed in establishing that modern ecologists do not embrace robust teleological views, he must concede that criticisms that assume as much are indeed without basis. But, rather than conceding this, Sagoff speciously denies the force of my brief and pointed comments about such criticisms.

1.3. *Sagoff’s Misleading Appraisal*

Sagoff denies that my arguments have ramifications for criticisms of theoretical ecology by implying that *no* critics actually employ a literalist reading of teleological language used by ecologists. As he puts it, in his abstract, “Donhauser strenuously denies that theoretical ecology must have teleological foundations, but those critical of it do not assume it does. They argue instead that it lacks empirical support” (p. 1). I was flummoxed when I read these words, because Sagoff has argued that

theoretical ecology is problematic because it relies on robust teleological assumptions. Indeed, in writing my paper, I took his more recent comments that theoretical ecology relies on “magical thinking” (2013) as a nod back to such arguments in earlier work.

Though they appear in other works as well, he presents the relevant arguments most forcefully in a 1997 paper where he says:

“[T]he temptation to ascribe a purpose, order, or design to nature remains strong in spite of all the Darwinian objections against doing so[...] Ecologists themselves are loathe to let go of the notion that Nature has a nature[...] As ecologists throw teleology out the front door, they smuggle it in by the back.” (1997, p. 830)

Sagoff carries on later in that piece, claiming that “theoretical ecology blurs the distinction between science and religion” and that “[b]y dressing traditional conceptions of Creation in mathematical concepts and models, the mainstream position in theoretical ecology maintains its deeply satisfying image of nature’s orderliness and purposiveness” (1997, p. 888).

Of course, I may have mistakenly thought Sagoff’s more recent comments pointed back to these explicit critical arguments that pin teleology on modern ecologists. But surely my claim that some critics have lodged such arguments is justified nonetheless; and my brief comment that my arguments showing that literalist interpretations of teleological language fail also show that any such criticisms fail still stands. If Sagoff means what he says when he confirms that I succeed in defusing literalist interpretations, he must admit that my recent paper suffices to show that his earlier criticisms in this vein and others like them are hyperbole. Yet, after denying me this without argument, he concentrates exclusively on concerns tangential to those addressed in my paper. Since I am grateful for any opportunity to clear up enduring confusions about ecology and its practical applicability, I will now systematically disentangle and defuse the broader independent concerns Sagoff wants to discuss.

§2. Disentangling and Defusing Tangential Concerns

Sagoff begins actively defending several independent criticisms of theoretical ecology by discussing “ecological forces” he claims play key roles in reasoning processes commonly employed in theoretical ecology.² He has in mind *general* forces, which he indicates by distinguishing between “greater causes” that are operative “across environments” and “lesser causes” that are “place-specific” and accidental.³ Sagoff invokes J.S. Mill’s discussion of ‘Tidology’ to motivate a, decidedly superannuated, positivist stance; according to which genuine sciences must produce theoretical principles from which one can infer by deduction what will occur in particular situations in nature.⁴

He points to the ‘Tidology’ meta-model as an exemplary sort of model based on theoretical principles that take account of general forces that he suggests theoretical ecological models (TEMs) try to emulate. ‘Tidology’ basically explains that regular tidal patterns result from the relative positions of the Earth and Moon and their gravitational effects on each other. According to Sagoff, this “model” is accurately predictive and informative because: “[t]he gravitational forces on which the levels of the tides depend are strong, general, and wide-ranging enough that they can be distinguished in their efficiency from the incidental factors that vary place to place” (p. 2). By contrast, he says TEMs cannot be informative because: “unlike ‘Tidology’, ecology cannot distinguish between greater and lesser causes [...] The abundance and distribution of plants and animals [...] result from local, idiosyncratic, incidental, and circumstantial forces and conditions particular to a place and time” (ibid.).

In view of this, Sagoff then endorses what some call the “contingency hypothesis,” according to which individual ecological networks are sensitive to so many contingent factors that

² Sagoff’s overall presentation faces a more global issue that I will ignore in the interest of seriously engaging his arguments. In brief, this is that he speaks of theoretical methods and modeling as if there is a singular, “theoretical,” approach when in fact there is a diversity of approaches and methods and many combinations of them.

³ His use of this distinction is confusing and brings in other independent issues, as there can be accidental local causes that are dominant, or “greater,” in bringing about an effect (e.g. an aggressive invasive species could extinct a population of a certain tree species in one place and not others). The distinction also risks conflating ‘greatness’ (magnitude) and ‘generalness’ (universality).

⁴ Sagoff purports to echo Lange (2005). However, Lange invokes Mill’s discussion to make a rather different point about causality and ecological laws, and he does not endorse the sort of old-school positivism Sagoff espouses.

each is unique (Sterelny 2001, pp. 158–9).⁵ He subsequently endorses four distinct claims he contends pose a problem for the denial of broader criticisms of theoretical ecology that he attributes to me. He endorses two claims, (i) and (ii), that are supposed to follow from the contingency hypotheses:

- (i) “[in ecological research] there is no way to distinguish the signal from the noise” / ‘no distinction to be drawn between the “greater causes” and the myriad of local contingent factors’
- (ii) “ecology should be directed not toward theorizing [about] patterns and regularities that do not exist but toward building a catalogue of case studies”

Then he endorses variations of the abovementioned claims concerning “ecological forces” and the nature of theoretical ecology, that he thinks follow from (i) and (ii). These are:

- (iii) TEMs cannot usefully characterize natural target systems because the ecological forces they (allegedly) posit are not found in nature
- (iv) reasoning with TEMs cannot usefully inform questions about natural ecological phenomena, because such models are (allegedly) derived from empirically-unfounded, “a priori,” principles from which actual ecological dynamics cannot be deduced.

Recognizing key problems with (iii) and (iv) reveals mistaken assumptions that belie Sagoff’s critique of theoretical ecology while at once providing insights into how theoretical methods square with (i) and (ii) via their relationship with empirical methods.

2.1. *What ecological forces?*

Claim (iii) derives from Sagoff’s belief that theoretical reasoning and models in ecology work by appeal to *general* forces. Yet, just looking at how commonly employed TEMs work makes it clear that they do not. In fact, the physics models and ecological models that he compares do not work the same way at all. To illustrate this, let’s consider models based on the Lotka-Volterra principles; which Sagoff lists as an exemplary sort of TEMs via referring to “Lotka-Volterra relations” as an

⁵ For discussion of some practical implications of the contingency hypothesis, see Donhauser 2016a, 15-8.

example of what he considers ‘general ecological forces’ represented in TEMs.⁶ To flesh out the contrast Sagoff evokes, let’s compare the Lotka-Volterra models (LV-models) with a mathematical expression of models based on a key principle used in Tidology: Newton’s Law of Universal Gravitation, which states that any two massive bodies will exhibit gravitational pull on one another.

A classic model used to calculate the gravitational force, F , between two bodies, m_1 and m_2 (e.g. the Earth and Moon), includes the paradigmatic general force via including the gravitational constant, G , as is shown in (1).

$$F = \frac{G * m_1 * m_2}{d^2} \quad (1)$$

Here a general force plays a role in calculations and predictions via the way the variables factor with the constant— G often stands in for $6.673 \times 10^{-11} \text{ N m}^2/\text{kg}^2$. By contrast, LV-models *do not contain any* general forces.

LV-models apply general ideas from kinetics to characterize dynamical relationships between biological populations interacting as predator and prey. Variables for species-typical efficiencies, relationships, and mortality rates comprise LV-models; their values and mechanisms of realization change depending on which populations one selects to play predator and prey roles in her model predator/prey community. A simplified variation is expressible as a coupled set of equations:

$$\frac{dD}{dt} = aD - bDW \quad (2)$$

$$\frac{dW}{dt} = -cW + dDW \quad (3)$$

Here D is the number of members of a simulated prey population (e.g., a target deer population), W is the number of members of a simulated predator population for that prey population (e.g., a target wolf population), t is elapsed time since the beginning of the simulation period [T], a is the growth

⁶ Sagoff also discusses LV-models as exemplary of models that appeal to “ecological forces” in a recent paper (his 2016).

rate of the prey $[1/T]$, b is the parameter that quantifies the effect of predators on prey mortality, c is the death rate of the predator $[1/T]$, and d is the parameter that quantifies the effect of prey consumption on the growth of the predator.⁷

Models extrapolated from these basic equations help one estimate changes in a prey population's abundance across time $[dD/dt]$ by assuming that this is jointly determined by that population's species-typical growth rate and the efficiency of a predator population $[aD - bDW]$. Such models can also help estimate changes in the abundance of that predator population across time $[dW/dt]$ by assuming that is jointly determined by species-typical mortality rates and the rate at which that population's abundance increases as a result of consuming prey (that population's "conversion efficiency") $[-cW + dDW]$.⁸

LV-models are used to simulate how natural populations may change relative to one another by identifying populations that can be seen as interacting as predator and prey and then inputting population-specific variable values. Whether members of any population are effectively a predator or prey for those of another is a simple matter of whom typically eats (or otherwise hastens the mortality of) whom. For instance, dragonflies are predators for bees and at once potential prey for many species of frogs. With this simple who-eats/kills-who criterion, one can determine on the basis of observation or prior knowledge about species-typical behaviors which natural populations are predators and which are prey for an endless array of species.

⁷ I have not included units for b and d because they are complicated and their inclusion would complicate my discussion of LV-models unnecessarily; Odenbaugh 2005 provides a more detailed analysis of LV-models and discusses how certain sorts of calculations are done with them.

⁸ Lotka's (1925, pp. 92-3) original discussion of these equations is exceptionally clear and concise. Since I am here concerned only with providing a cursory idea of how LV-models works, I refer my reader to his discussion for explanation of the rationale behind their construction.

Notably, there are *no operative general forces* anywhere in the thinking behind LV-models.⁹ There are general features one might consider “constants” in LV-models. Species-typical predation and prey relationships, efficiencies, and mortality rates are key features of LV-models in general. These features also correspond to typicalities that are causally relevant to population and community-level abundance dynamics. Some would even call statements about such typicalities ecological “laws”—since some laws are generalizations about regularities. For example, ‘wolves hunt and never graze,’ ‘deer graze and never hunt,’ and statements about average species lifespans could be counted as ecological laws (see Partridge 2000, p. 86). Yet, to my knowledge, ecologists have not proposed any general force—nothing like gravity—that is supposed to produce population and community-level properties.

In my view, trying to envisage typical predator/prey interactions as general forces in the way Sagoff does is quite odd, because they are typicalities that bear on aggregate dynamics not a dominant general force operating across different contexts. Accordingly, I submit that Sagoff is mistaken in thinking that LV-models and other TEMs see such interactions as general forces; and I have not encountered anyone in the literature in ecology including such forces in methods using TEMs. There is also no reason to think ecologists must do so to show that TEMs are useful and informative, except to presuppose that reasoning with theoretical models must operate according to a very limited, and dated, positivist ideal. Sagoff’s view of theoretical ecology rest on such a presupposition.

2.2. *What “A Priori” Assumptions?*

Sagoff claim (iv) comes out as he says that theoretical ecology “proceeds by deducing the consequences of principles assumed a priori” (p. 12). He cites as an example the deduction of correlated “oscillations” in species abundances from models based on Lotka-Volterra principles. So,

⁹ There are many different kinds of scientific principles and laws, and only a limited set deal with forces; cf. Woodward 2002 and Schurz 2002.

Sagoff claims that ecologists have made up principles about general ecological forces, “a priori,” and then purport to deduce how natural populations and communities should behave with models based on such principles (cf. Sagoff 2000, pp. 70-72). Yet, even if we assume that by “a priori” Sagoff just means prior to observations—rather than the stronger sense standard in philosophical discussions—we can see his comment is off track in several ways.

I have already argued that he is mistaken about ecologists making up the general forces he says play roles in reasoning with TEMs. More importantly here though, we have also seen TEMs, LV-models, that take account of species-isomorphic typicalities. Those are not invented but derived from observations of instances of predator and prey species. In fact, LV-equations aren’t even LV-models, they are not models of anything, until species-typical values (or “toy” values) are input for their variables.¹⁰ Reasoning with such models does not assume anything *a priori*.¹¹ Even the general relationships LV-equations characterize were borne out by observations; as Vito Volterra was led to develop the core bits of LV-models only after observing predator/prey relationships, and correlated dynamics, in Adriatic fisheries (see Guerraggio & Paoloni 2010, p. 78).

One might also point out that the ecological models Sagoff asks us to consider are in a sense less removed from empirically observations than the physics models he discusses. Mechanisms that realize what we conceptualize as gravitational forces are famously opaque—imagine Newton with his hands in the air (Newton 2004, 92). By contrast, species-typical behaviors and interactions that bear on aggregate abundance dynamics are observable. For instance, members of a wolf pack eating deer is an observable mechanism for changes in that prey population’s abundance; each kill surely changes their overall abundance by one.

¹⁰ LV-models are not really predator/prey models but, more specifically, predator-species/prey-species models—where population-isomorphic differences make different LV-models.

¹¹ There are applications of other sorts of TEMs that apply selected principles to dictate what can occur in models, but even there empirical knowledge constrains thinking.

I think what Sagoff is trying to highlight with his comments about “a priority” is that ecological principles, like the LV-principles expressed via (2) and (3), are data-neutral; since they are not directly extrapolated from any particular data-set but are intended to be applied to predator and prey populations generally (cf. Levin 1980, p. 424). However, that does not count against theoretical models or methods. It is just to say theoretical models are differently related to data, and play different roles in reasoning in ecology, than models created by simply aggregating data. Indeed, Sagoff’s comments (iii-vi) rely on overlooking the complementary roles theoretical and aggregate-data models play in ecology.

TEMs basically see two general uses in ecological research: they are used to organize and interpolate data to aid in understanding observable phenomena and hypothesis development and refinement; and they are used to simulate ecological possibilities to aid in understanding and develop and refine hypotheses (both in particular cases and in general). Moreover, in practice, TEMs are often systematically modified with data and augmented with other models that track site-specific features to provide new insights into what is going on in particular cases. Accordingly, *I submit that TEMs are well characterized as adaptable tools for developing better hypotheses and theories via iterative ampliative reasoning processes*, as opposed to deductive frameworks derived from accepted theories that are applied only by some “a priori” deductive, HD, process (cf. Wimsatt 2007, Ch. 6).

Even with just an understanding of the basics of LV-models, as outlined above, one can see that such models have uses beyond just generating simulations that have nothing to do with empirical and practical considerations. For instance, imagine how a natural resource manager might devise a simple LV-model to help select species management strategies. By using such a model to organize data and/or simulate ecological possibilities, she could better estimate the likelihood of possibilities such as:

whether a wolf population could possibly annihilate a deer population (e.g., to inform wolf-control strategies);

what impacts hunting of members of a predator or prey population could have on the abundance of the other population;
how the introduction new predator or prey populations (e.g., an invasive species or a predator reintroduction) could impact population dynamics in a place.

From his (i) and (ii), I anticipate that Sagoff's response here is that, even though they may countenance empirical considerations and can be used to guide thinking about particular populations, such models are still uninformative because a 'myriad of local contingent factors' will produce local circumstances that cannot be deduced from them in any case.¹²

He is right that simple LV-models are too partial to accurately simulate how most predator and prey populations actually evolve because various factors such models ignore would need to be accounted for to produce such simulations. Diseases, anthropogenic habitat modification, in situ predator selectivity (e.g., predators culling the most abundant of multiple prey species), and topographical features (e.g., resource patchiness) are just some of the exceedingly many contingent factors that can significantly impact how natural predator and prey populations interact and evolve (cf. Allen & Greenwood 1988; Chesson 1978; Grünbaum 2012). However, that a model does not predict events due to such contingencies does not show that it is uninformative or that it cannot aid in developing better models and inferences.

2.3. *Who's afraid of ceteris paribus conditions?*

Sagoff contends that gravity is not contravened by contingent local factors as a legitimate "general force" while predator/prey effects are; such that the *ceteris paribus* conditions for TEMs are supposed to be problematically restricted in comparison to those of physics models. However, really *nothing* is contravened anywhere. Gravity does not contravene local causal factors and dominant local causal factors do not contravene gravity—neither magnetism nor jumping contravene gravity and gravity does not contravene magnetism or jumping. Likewise, even when local factors influence population

¹² In a recent article he even argues as much; Sagoff 2016, p. 3007.

abundance dynamics in ways a basic LV-model cannot predict, predator/prey interactions and dynamics are still at play. Hence, pointing out that LV-models simulate predator/prey dynamics that occur only in naturalistically improbable *ceteris paribus* conditions does nothing to show that they are uninformative or otherwise problematic.¹³

Sagoff's claim (iv) and related claims assume that models are informative only by permitting one to deduce from simulations what will occur in nature or permitting one to deduce which situation-specific contingencies need to be countenanced to explain discrepancies between a simulation and what actually occurs (see Sagoff 2013, p. 3005 and 2003, p. 532; cf. Cartwright 1989, p. 50; Lipton 2004, p. 67). Yet, the fact that LV-models often fail to accurately predict actual dynamics due to factors outside their *ceteris paribus* conditions does not even show that they do not accurately predict the outcomes of typical predator/prey interactions (what they are designed for). Nor does it provide reason to think that they cannot help identify local "aberrations" that explain case-specific dynamics. These conclusions do not follow logically, but from superannuated positivist assumptions Sagoff embraces.

Furthermore, LV-models provide insights into causally relevant typicalities and reciprocal relationships even when they cannot predict population dynamics because of impacts of unique local factors or anomalies. Imagine a tidal wave extinguishing wolf and deer populations on an island. Though a basic LV-model of the form presented above would not predict this abrupt decline in both populations, surely this does not show that the model is problematic. Impacts of such local factors may show that a model is not suited to characterizing a target system because it does not account for those local factors. Yet, this is no flaw with the model. Trying to predict the impact of

¹³ Contrary to Sagoff's suggestions, it is notable that the Universal Law of Gravitation is not actually universal. It does not hold at microphysical scales or in parts of space remote from Earth (e.g. in black holes), and it can be masked by the presence of various "greater" local cause (e.g. magnetism). These occurrences also cannot be deduced from models derived from the Universal Law; cf. Cartwright 1983; Lange 2002; Mitchell 2009, Ch. 3.

tidal waves with an LV-model is obviously a misapplication; and an LV-model would still provide insights into the wolf and deer population dynamics in the absence of catastrophic tidal waves.

That notwithstanding, many cases are not so extreme, and *in situ* predator/prey dynamics can be seen as resulting from species-typical behaviors as mitigated by unique local factors. To more instructively respond to Sagoff's (iv) and further illuminate how theoretical methods square with Sagoff's (i) and (ii), I will now outline in simplified terms how LV-models can be used in iterative and ampliative processes to: inform inferences, reinforce conclusions drawn from empirical observations, and even help 'find a signal in the noise' in particular cases.

2.4. *Building Case-specific TEMs*

Sagoff's positivist interpretation of theoretical ecology is undercut by the fact that TEMs can be, and are, used in iterative and ampliative processes of building case-specific models with value for reasoning about particular populations.¹⁴ To begin to understand how more complex and extensive case-specific TEMs can be generated, one must move beyond the idea that applying TEMs only means applying ready-made models or principles straight out of the box—or "a priori" as Sagoff says—to predict by deduction the dynamic trends that two interacting population should exhibit. I have already pushed on this idea by acknowledging that LV-equations are not models until they are imbued with species-typical values. Let's now move a bit further in thinking about potential applications of LV-models by noting that the application of simple, two-population, LV-models is a building block of more complex models and applications. This building block essentially conceptually links two interacting populations (as is represented in Figure 1) via the variables and parameters expressed in equations 2 and 3 above.

¹⁴ Since my discussion of practical applications here must be rather brief for concerns of space, I would like to note that there is plenty of literature on successful applications of TEMs and methods. That literature includes discussions of applications for practical decision-making (e.g. Van Dyne (Ed.). 1969 and Grant & Swannack 2008), discussions of generally fruitful applications of specific models (e.g. Zhang et al 2010), as well as discussions of related philosophical issues (e.g. Odenbaugh 2005).

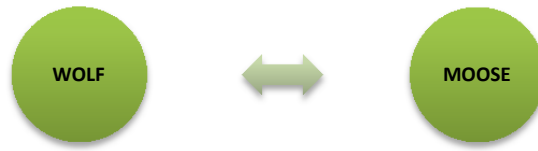


Figure 1: Conceptual diagram of typical reciprocal impacts represented as causally connecting target wolf and moose populations in a basic LV-model.

Generating more extensive TEMs, including case-specific LV-models, and running more complex possible scenario simulations, is then a matter of linking together more models.¹⁵ By doing this one can simulate the collective impacts an indefinitely large number of populations and other factors may have on selected populations of concern. For example, if a wolf population were a selected population-of-concern, one could generate a more complex case-specific LV-model by conceptually *building out from* that population a model-community; a network of LV-models that could help garner insights into how other local populations and factors might impact (or be impacted by) that population. I hope Figure 2 assists my reader in envisioning how one can go about constructing a case-specific community model by linking together basic population-to-population predator/prey models to conceptually *build out from* a population-of-concern in this way (cf. Donhauser 2014, pp. 101-2).

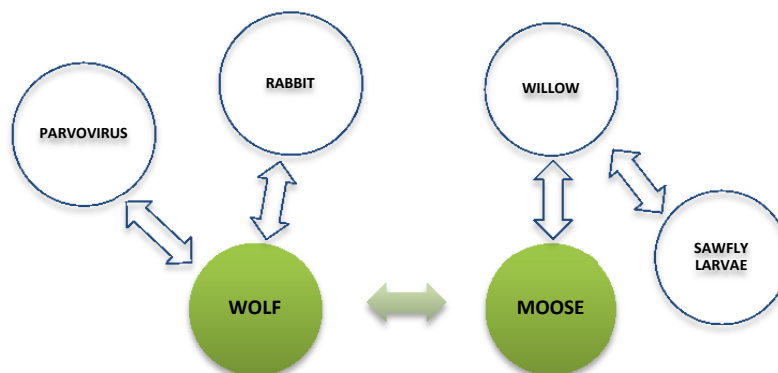


Figure 2: Conceptual diagram of the reciprocal causal impacts that can be represented as causally connecting other case-relevant populations to target wolf and moose populations in a more complex LV-model.

¹⁵ Numerous sources explain different ways to do this; Bender et al 1984 is one.

Figure 2 suggests a model that would consider impacts of wolf and moose populations on each other and also considers more indirect, or mitigated, impacts through their interactions with other populations and factors. In it, I include organic populations that are not conventionally conceived as predators or prey but that can be usefully modelled as such in LV-models to underscore the adaptability of LV-models. Indeed, ecologists continue to extend thinking far beyond conventional conceptions of ‘predator’ and ‘prey’ in applications of LV-models. Models of the LV form are used to characterize populations interacting through interspecies competition (mutually detrimental), predator/prey (beneficial/detrimental), mutualistic (mutually beneficial), amensalistic (detrimental/no-impact), and commensalistic (beneficial/no-impact) interactions—among others. Ecologists also use them to characterize reciprocal dynamics between plant populations in which one species (the ‘predator’) typically out competes the other (the ‘prey’) for light and nutrient resources (e.g., Mäkelä & Hari 1984). LV-models are even used to characterize reciprocal dynamics between infectious diseases (the ‘predator’) and different biological populations (the ‘prey’) (e.g., Holt & Pickering 1985 and Rohr et al 2006).

In view of the array of possible population-to-population and population-to-environment interactions that can be envisaged as predator/prey interactions, one can imagine building all sorts of LV-models to inform considerations in particular cases using the very basic strategy that I have suggested here alone. One can also see ways TEMs can be used to inform and augment empirical research. To illustrate some of these, let’s consider some populations at Isle Royale Sagoff discusses in recent work.

Sagoff (2016) focuses on Isle Royale to motivate claims that uniqueness and contingency in natural ecological communities render TEMs useless, as numerous unpredictable events have resulted in similarly unpredictable local wolf and moose population dynamics. Researchers documented eighty percent decline in the wolf population apparently due to an outbreak of *canine*

parvovirus and then a similar decline in the moose population apparently “due to the combined effects of a severe winter, a tick outbreak, and a catastrophic food shortage” on the island in the 1980s (2016, p. 3014). In subsequent years, researchers observed a shift in climatic factors, severe summer and winter conditions, that apparently had a more drastic effect on population abundances than species-typical predator/prey interactions at Isle Royale. Then, more recently, researchers documented a marked decline in the wolf population between 2011 and 2013 that has been attributed to the alpha male and other wolves from the local pack drowning in a flooded mineshaft in 2011 (Sagoff, p. 3015).

Notably, as with tidal waves, disease outbreaks, climate change impacts, and mineshaft accidents each fall outside the scope of a basic LV-model. Yet, again, a basic LV-model would still provide insights into the impacts of predator/prey relationship on the salient wolf and moose populations even in the wake of these events. This is because predator/prey interactions are still at play even when other factors, and even those with rather severe impacts, are also at play. Accordingly, it is reasonable to believe that generating models that incorporate various LV-sub-models to do multiple possible scenario-analyses and to test hypotheses based on observations could help better understand the populations at Isle Royale and could thereby aid in devising more robust strategies for managing and protecting the island’s wolves and moose.

One straightforward way that case-specific LV-models can be informative is by enabling retrodictive validation of hypotheses based on empirical observations. At Isle Royale, an LV-model that takes account of *parvovirus* efficiency could be compared against data-models of abundances to test the hypothesis that the disease outbreak was the leading cause of the eighty percent decline in the wolf population in the 1980’s (see Wilmers *et al* 2006). Likewise, an LV-model that accounts for tick outbreak impacts could be used to enhance understanding of the cause of the subsequent decline observed in the Moose population. An LV-model could also be constructed to help examine

whether the 2011 death of the alpha male and other pack members could indeed have produced more recent declines in the Isle Royale wolves. Additionally, LV-model simulations can be compared with abundance level data plots to help pin down time periods during which researchers should be look for significant factors other than predator/prey interactions, ‘a signal in the noise,’ to explain observed population changes. Indeed, it is precisely because they draw together species-typical relationships and provide a means of predicting general trends in predator/prey abundances *ceteris paribus*, LV-models have such applications for helping make inferences about contingent factors other than predator/prey interactions that impact those abundances.

What’s more, in direct contradiction of Sagoff’s claims that LV-models cannot inform considerations about natural populations, there are in fact LV-models of the Isle Royale wolf and moose populations that do so. These include applications of LV-models of Isle-Royale-populations that have proven useful for understanding species-typical functional responses and wolf-pack-isomorphic variations in functionality (Jost et al 2005). Then there are related LV-models that arguably *do* accurately predict (i.e. retrodict) Isle Royale population dynamic as seen in aggregate survey data (see Vucetich et al 2011). There is even a user-friendly online version of an LV-model of those populations Scott Fortmann-Roe has developed using his *Insight Maker* app, which permits one to simulate dynamic cycles at Isle Royale and compare those LV-model simulations with trends seen in sixty-years-worth of data (Isle Royale).

2.5. “Ecological network-level properties” versus Trends in Data

Finally, let me address Sagoff’s comments about the existence of ecological entities and properties. Via (ii) and related claims, he explicitly denies that ecological-networks and network-level properties exist in his commentary. He also denies the existence of observable dynamics and patterns that I refer to in my paper. Accordingly, he forefronts allegations that I “nonchalantly assume that

ecological network-level properties exist” in his abstract (p. 0). He elaborates on why he thinks I make such assumptions and why he thinks it is problematic later, saying:

Donhauser in his paper uses the term ‘network-level’ 26 times; he speaks of ‘ecological network-level dynamics;’ ‘ecological network-level phenomena;’ and ‘network level structure.’ The critics to whom he responds, however, deny that network-level phenomena, such as oscillations, are observed. If network-level properties have been observed, there must be an empirical literature documenting their occurrence, but it is elusive. (p.6)

This comment is misdirected, because criticisms centering on questions about the metaphysical status of ecological entities and properties are not among the narrow range of criticisms I directly respond to (very briefly) in my paper—as explained above (in §1). Worse though is that: Sagoff’s allegation that I presuppose the existence of ecological-network level properties in my paper is unwarranted; he mistakenly believes that I claim that ecological network-level properties are observable; and he wrongly thinks that I claim that “oscillations,” or oscillating behaviors, are properties of ecological networks.¹⁶

Although his count of the times I use variations of ‘network-level’ in my paper may be correct, Sagoff’s allegation that I assume that ecological network-level properties exist in nature derives from overlooking explicit indicators that I do not make such assumptions. In fact, I make no commitment regarding the existential status of networks or network properties in my paper, but *refer to claims and views ecologists and advisory organizations apparently hold*. Moreover, in many places I urge that they need not make such commitments. My first mention of debates about the existential status of ecological entities is even accompanied by a footnote (the first in the paper), which says: “I am sympathetic to the view that many concepts employed in ecology (e.g. ‘ecosystem’ and ‘community’)

¹⁶ Because he mistakenly believes that I assume that there are network-level properties that are irreducible to series of organism-to-organism and organism-to-environment interactions, Sagoff’s also misreads my brief comments about natural selection. He responds as if I claim that natural kinds of ecological networks are naturally selected and are subject to evolution (his §3). However, I actually say that organisms living or dying and successfully breeding or not are at once the mechanisms for species evolution and the mechanisms for changes in population abundances. I respond to this point only briefly, in this footnote, because it draws in a gaggle of worries about the nature of natural selection that are very far afield from both the considerations of my paper and from the rest of Sagoff’s comments about theoretical methods in ecology.

[...] serve as useful and practically valuable theoretical constructs even if they haven't any naturally delineated referents" (p. 67).

Furthermore, I think my deflationary account of teleology in the paper can easily be read as presupposing an eliminative stance on the metaphysical status of ecological networks and properties; such that network-level phenomena and properties are completely reducible to stochastic component-to-component interactions. This would be a natural interpretation following my claims that pioneering theoretical ecologists explicitly jettisoned the "idea that ecological networks bear irreducible causal properties" (p. 69). Accordingly, I would think one would easily read my claims about 'ecological network properties' as claims about "series of causal interactions through which biota and abiota can [...] produce dynamic patterns observable in aggregate data on relative population and nutrient abundances" (p. 70). Further still, I explicitly endorse a neutral metaphysical stance in my paper, and claim that modern ecologists can and should embrace a neutral stance on the ontological status of ecological entities and properties (pp. 69-70; 74). Thus, I argue that conceptions and talk of ecological populations, communities, and systems, and their properties are heuristically *useful ways of thinking and talking about* contingent ecological assemblages and aggregate dynamics observable in data—without saying anything about what metaphysics (realist or antirealist) one ought to choose.¹⁷

What about Sagoff's related claims that I assume that observable "oscillations" are exhibited by natural ecological networks? To begin with, I talk about "oscillations" in repetition of Hutchinson's use of this term in his 1948 paper. So, contrary to Sagoff's reading, I do not say anything about whether natural ecological networks oscillate; honestly, I am not sure I even know what that is supposed to mean. Rather, I offer an interpretation of what Hutchinson says about

¹⁷ Sagoff presupposes that concerns about establishing the existence of ecological entities and properties are inseparable from concerns about the instrumentality of ecological theories and TEMs, while, as a general point, there are many instrumentally useful theories and models that posit things that have not been shown to exist.

observable “oscillations” and explain how he appears to have used teleological metaphors in the development of bottom-up accounts of the types of mechanisms that can produce observable oscillations (pp. 71-2). Moreover, as I interpret Hutchinson in my paper, neither he nor I say anything about natural ecological networks exhibiting observable oscillating behaviors. Rather, Hutchinson (1948), and so I, use that word to refer to correlations and repeating patterns *observable in aggregated data* on population and nutrient/resource abundances. Specifically, I write that Hutchinson: “provides accounts of the mechanics that could produce correlated dynamic patterns, what he calls ‘oscillations,’ observable in data on nutrient resource and species abundances and data on the Earth’s biosphere” (p. 70).

Now Sagoff also denies that there are any such correlations and patterns observable in aggregated data. He even expresses this while criticizing my using toy data values to generate an illustrative faux data plot in my paper; claiming that one, “has to make up the values since there are no data sets—no sustained empirical evidence—that could serve the purpose” (p. 4). Yet, the confidence with which he just plain denies that there are such observable correlations is astonishing.

Surely, Sagoff does not mean to claim that there are no hydrologic cycles, weather patterns, seasons, and associated nutrient cycles; that would be absurd. It is also easy to find data correlations between nutrient and plant species abundances. Hence, I take it that his claims on this point must be restricted to data on conventionally conceived predator and prey populations. But even with this restriction, his comment does not wash.

An obvious place to look for the sorts of data sets I had in mind when discussing Hutchinson’s work is where I direct one to look in my paper. There, in the footnote that accompanies my “made up” figure, I list five places one can find discussions and plots of such data in independent works by Volterra and George Clarke. To ensure I hadn’t suffered a lapse of sanity, upon reading Sagoff’s comment I checked those citations and also looked back at another, more

well-known, counterexample to his denial of such data's existence. In my first edition of E.P. Odum's *Fundamentals of Ecology* that classical data plot on a “pure”—relatively unobstructed by other factors—predator/prey community was still there. This is the plot of the Hudson Bay Company's century-long Canadian lynx and snowshoe hare pelt-trading records, which Odum re-draws in his text and I re-draw here:

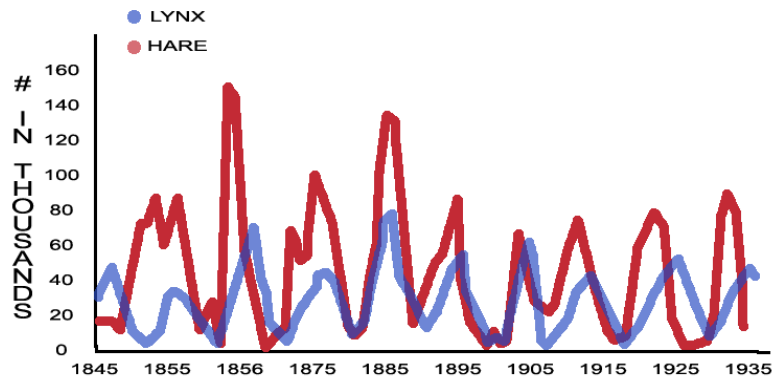


Figure 3: Redrawn from (Odum 1953, p. 134); where he says this plot shows “[c]hanges in the abundance of the lynx and snow shoe hare, as indicated by the number of pelts received by the Hudson Bay Company. This is a classic case of cyclic oscillation in population density (redrawn from MacLulich 1937).”¹⁸

This data admittedly presents a rare case, and predator/prey changes often look much messier by comparison because of local contingent factors that also impact abundance levels. Yet, even where other factors have a substantive impact on abundances, one can find correlated patterns in the comparatively messier data. As a case in point, look at the data from Isle Royale (Figure 4) that Sagoff (2016) argues says should show that there are no correlations or patterns observable in data on natural predatory/prey populations. Even there correlations and patterns *can be* found.

¹⁸ Tyson, Haines, & Hodges 2010 provide a nice discussion of how typical interactions with other species bear on typical lynx and hare dynamics and of how to account for this in models.

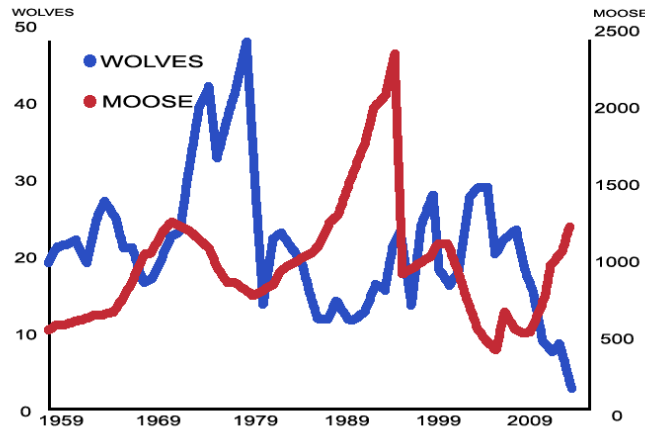


Figure 4: Adapted from Peterson & Vucetich (2016, p. 3). This figure shows “[w]olf and moose fluctuations, Isle Royale National Park, 1959-2016”; where “[m]oose population estimates during 1959–2001 were based on population reconstruction from recoveries of dead moose” and that other estimates are based on aerial surveys and track identification.

Because of the above noted disease outbreaks, extreme weather conditions, and accidents at Isle Royale, the correlations and patterns here are not as neat as the case of the lynx and hare above. Yet, there are still correlations and patterns to be found in this data. Anyone can see: when one of the population abundances is high the other is low, and this occurs while each is fluctuating in repeating upward and downward cycles. Where the patterns here are disrupted, researchers at Isle Royale have kept track of the noted dominant contingent factors that account for that.

Should we side with Sagoff and agree that, because local contingencies disrupt otherwise typical moose and wolf interactions and obscure neat patterns, such patterns are too insignificant to be counted? Robert MacArthur—who I quoted in my (2016) paper to make a related point (p. 73)—I think provides a way to square undeniable variability and the appearance of the sorts of correlations observable in both Figures 3 and 4. MacArthur (1968) writes:

Ecological patterns, about which we construct theories, are only interesting if they are repeated. They may be repeated in space or time, and they may be repeated from species to species. A pattern which has all of these kinds of repetition is of special interest because of its generality, and yet these very general events are only seen by ecologists with rather blurred vision. The very sharp-sighted always find discrepancies and are able to say that there is no generality, only a spectrum of special cases. (p. 159)

This is to say that although unique local features are clearly present in nature there are typical causal processes and interactions that produce observable correlations and patterns nonetheless. Hence, in Jay Odenbaugh's words, "some patterns are general though they will have exceptions. Nevertheless, they [...can] be explained by models which depict those causal processes which generate those patterns" (2011, p. 125). At once, MacArthur points out that if one conceptually "zooms out" on a dataset he or she can see typical correlations and patterns, but if one instead zooms in one finds nothing but deviations. Sagoff has chosen to zoom in and emphasize the deviations. However, this does not make correlations and patterns due to species-typical behaviors and interactions any less real; what we choose to pay attention to does not change the fact that there are causally relevant typicalities that play roles in how predator and prey abundances change.

As I've said (in §2.3), predator/prey interactions are *still at play* even when other factors, and even those with rather severe impacts, are also at play. Accordingly, though the noted hardships no doubt made pack hunting and foraging and breeding more difficult and less frequent, surely the remaining wolves and moose at Isle Royale still behaved in ways typical of their species. It is not a "fact that the significant causal factors in any instance are so ephemeral, transitory, extemporaneous, spontaneous, one-off, coincidental, and contingent that they may never occur twice" as Sagoff says (p. 14). Some significant causal factors are typical as well. Hence, I cannot see why ecologists should not carry on "theorizing [about] patterns and regularities" while also "building a catalogue of case studies" as they do. That's how ecology works.

§3. Conclusion

Sagoff's commentary on my (2016) paper is primarily a vehicle for rehashing concerns about theoretical ecology that are tangential to the concerns of my paper. Nevertheless, I have seriously engaged each of the concerns he raises; because the need to understand ecology's conceptual foundations and potential practical applications is not only interesting and significant but also

increasingly-urgent, as policymakers and resource management practitioners confront compounding political, ethical, and management decisions.

Sagoff and I clearly think very differently about how theoretical ecology works and how it can be usefully applied. Where he sees an empirically baseless pseudo-science that is uninformative and useless, I have endeavored to illuminate the connections between theoretical and empirical work in ecology and make plain several ways TEMs can be applied to inform policy and resource-management decision-making. Moreover, I have distinguished and systematically defused the independent criticisms Sagoff defends in his commentary—showing that they derive from a limited positivist understanding of theoretical science and that his arguments for them are exposed as problematic once stripped of that base.

Despite our diverging perspectives on methods in ecology, I respect and admire Sagoff for trying to make the tough sell and defending the unpopular critical position. I am also grateful to him for taking the time to read and respond to my work. It is my sincere hope that our exchange in these pages helps push forward dialogue about ecology's philosophical foundations and scientific and practical value, and that it provides useful resources for others interested in ecology and its applications.

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