Reducing ecological complexity using the archetype approach – an application to natural pest control

Nikolaos Alexandridis[1,*], Emily A. Martin[2], Glenn Marion[3], Rebecca Chaplin-Kramer[4], Matteo Dainese[5], Johan Ekroos[1], Heather Grab[6], Mattias Jonsson[7], Daniel S. Karp[8], Carsten Meyer[9,10], Megan E. O'Rourke[11], Mikael Pontarp[12], Katja Poveda[6], Ralf Seppelt[13,14], Henrik G. Smith[1,12], Yann Clough[1]

[1]Lund University, Centre for Environmental and Climate Research (CEC), Lund, Sweden

[2]University of Würzburg, Department of Animal Ecology and Tropical Biology, Würzburg, Germany

[3]Biomathematics and Statistics Scotland, Edinburgh, UK

[4]Stanford University, Woods Institute for the Environment, Stanford, USA

[5]Eurac Research, Institute for Alpine Environment, Bozen/Bolzano, Italy

[6]Cornell University, Department of Entomology, Ithaca, USA

[7]Swedish University of Agricultural Sciences, Department of Ecology, Uppsala, Sweden

[8]University of California, Department of Wildlife, Fish, and Conservation Biology, Davis, USA

[9]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

[10]University of Leipzig, Faculty of Biosciences, Pharmacy and Psychology, Leipzig, Germany

[11]Virginia Polytechnic Institute and State University, Department of Horticulture, Blacksburg, USA

[12]Lund University, Department of Biology, Lund, Sweden

[13]Helmholtz Centre for Environmental Research – UFZ, Department of Computational Landscape Ecology, Leipzig, Germany

[14]Martin Luther University Halle-Wittenberg, Institute of Geoscience & Geography, Halle (Saale), Germany

* Corresponding author: nikos.alexandridis@cec.lu.se

Abstract

Complexity and context-dependence in ecological and socioecological phenomena often cause inconsistent or seemingly idiosyncratic responses. This apparent lack of generality presents a challenge to the implementation of ecological principles in environmental management. We mostly rely for prediction on data-hungry correlative models that offer little mechanistic understanding. The alternative of process-based modelling is knowledge-intensive and has limited applicability across systems, due to a trade-off between generality and realism. Here, we present an archetype approach, combining trait-mediated mechanistic understanding into ecological models of intermediate generality, as a way to overcome these limitations. We demonstrate its potential in the case of natural pest control across crop-pest-enemy systems. After reviewing the current modelling approaches and their shortcomings, we show that similar responses of natural pest control in cases that share key characteristics indicate the potential for context-sensitive generalizations. Example archetypes show great promise for improved understanding and prediction. We outline how statistical analysis of available data and rule sets for model development will allow systematic definition of archetypes representing the key processes of all major crop-pest-enemy systems of the world. In this and other applied cases, the use of archetype

approaches is a major step forward in facilitating both scientific synthesis and uptake of ecological knowledge in environmental management. Archetype approaches can enhance the application of ecological principles not only to crop pest control, but also to the management of a wide range of natural resources that have been affected by fragmentation of ecological research.

1 | INTRODUCTION

Ecology increasingly informs management of the natural environment, but much potential remains untapped (Dale, 2003). Ecological applications have been partly restricted by our inability to bridge between reductionism, which helps us understand a system by looking ever deeper into its constituent elements, and holism, through which we investigate the properties of a system in its entirety (Jørgensen, 2002). Modelling, an ideal tool for the synthesis of ecological knowledge, has been marred by this polarization. General deductive models often fail to match empirical evidence, while inductively formulated models are accused of providing limited understanding (Levins, 1968). Most researchers, implicitly and following disciplinary tradition, adopt elements of both approaches (Overmars et al., 2007). Still, methodological divisions hinder ecological synthesis, calling for an approach that bridges this divide. In the case of agricultural pest management, such restrictions are amplified by the need to model complex socioecological phenomena with direct links to human well-being that often result in counter-intuitive observations. Not surprisingly, pest management has been a major battleground for proponents of the two modelling approaches (Palladino, 2013).

A substantial portion of crops around the world is consumed by invertebrate pests, with ensuing yield losses predicted to increase in response to climate warming

(Deutsch et al., 2018). Control of crop pests by their natural enemies, such as arthropod predators and parasitoids, is an essential ecosystem service valued at US$4.5 billion/year in the USA (Losey & Vaughan, 2006). Natural pest control holds the potential to partially or completely replace intensive agricultural practices aimed at pest regulation, including wide-spread pesticide use (Khan et al., 2014; Tschumi et al., 2015; Holland et al., 2017). Mainstreaming natural pest control into agriculture calls for simple and reliable tools that can predict its response to the way land is managed (Kleijn et al., 2019). The continuing decline of biodiversity in agricultural landscapes poses a threat to many natural enemy organisms (Pe'er et al., 2014), adding urgency to this call.

Widely applicable, stakeholder-friendly tools already exist to map a range of ecosystem services on the basis of detailed land-use maps, including crop pollination by invertebrate organisms (Sharp et al., 2014). Similar to pollinators, the abundance and diversity of natural enemies and their potential to provide ecosystem services are largely regulated by agricultural land use (Tscharntke et al., 2005). In contrast to pollination, pest and enemy biology and the associated impacts on crops can be extremely diverse across regions and systems (Tscharntke et al., 2016). This has restricted the potential to link specific landscape characteristics to enhanced pest suppression (Englund et al., 2017). As a result, efforts to assess natural pest control on the basis of spatially-explicit land-use information have had limited predictive scope (e.g., Rega et al., 2018). Currently, no widely accepted model for assessment of the natural pest control potential of agricultural landscapes exists. In addition, the usefulness of existing models outside the systems for which they were developed is largely unknown.

Here, we aim to provide a new perspective on the application of ecological principles in environmental management. Similar to minimum realistic models from marine ecosystem management, our approach aims at including only key variables and interactions, not of a specific ecological system (Punt & Butterworth, 1995), but of an ecological phenomenon across several systems. To illustrate the approach, we focus on modelling natural pest control across agricultural landscapes. We first review landscape-scale models of natural control of invertebrate pests in agricultural systems, critically examining model characteristics and predictive potential, highlighting strengths and weaknesses. We then outline how the concept of 'archetypes', combining functional traits and empirical knowledge about crops, pests and natural enemies, can resolve the complexities of pest control in heterogeneous systems and represents a unifying step towards a general predictive tool. We concretize our approach by independently developing qualitative and quantitative mathematical models of example archetypes. We use these models to explore the ability of the archetype concept to contribute towards initially understanding and ultimately predicting the potential of land-use strategies to manage natural pest control across agricultural landscapes. A successful application of this approach to natural pest control will contribute to wider scientific synthesis and lower the bar for the use of ecological principles towards improving the management of the natural environment.

2 | A REVIEW OF MODELS OF NATURAL PEST CONTROL

A search of the Core Collection of ISI Web of Science with the topic argument: model* AND land* AND (biocontrol OR "biological control" OR "pest control" OR "natural control") returned 448 publications (search date: 25 June 2018). We

reviewed their abstracts, discarding non-modelling studies and studies of non-crop systems, anthropogenic biocontrol and plant or vertebrate pests. We thus retained 172 studies modelling natural control of invertebrate pests in agricultural systems. Of the respective models, 105 are formulated on the basis of observed correlations (correlative) and 67 are based on the explicit representation of specific processes (mechanistic) (Figure 1a). Mechanistic approaches dominated the early models of natural pest control. The picture has been reversed in recent years, as an increase in modelling applications has been primarily driven by correlative approaches (Figure 1c).

2.1 | Correlative models

The main objective of correlative models has been the assessment and development of general theories explaining the responses of natural pest control to agricultural land use at scales ranging from field to region. A fundamental model assumption is that compositional (e.g., proportion of non-crop habitat) and/or configurational (e.g., field edge density) complexity of the landscape surrounding a field, enhances in-field activity of natural enemies by providing them with limiting resources, such as nesting sites and alternative food sources (Landis et al., 2000).

Meta-analyses of empirical studies show positive effects of landscape complexity on the diversity and abundance of natural enemies but, critically, the responses of pest suppression and crop yield are rather inconsistent (Bianchi et al., 2006; Chaplin- Kramer et al., 2011). Analyses of recent large-scale correlative models corroborate the inconsistent nature of natural pest control responses to landscape characteristics. These studies identified system-specific (Karp et al., 2018)

and trait-mediated differences in responses (Martin et al., 2019) as a major underlying cause of discrepancies.

As a general understanding of natural pest control currently eludes us, the use of correlative models for predictive purposes requires the development of models for each system of interest. This task involves extensive collection of data, including an array of land-use, agronomic, abiotic and biotic environmental variables, hindering the derivation of accurate predictions across agricultural landscapes. Furthermore, correlative models typically make several assumptions that may not hold in novel or non-equilibrium contexts associated with environmental change (Dormann, 2007).

2.2 | Mechanistic models

Models based on processes that underlie natural pest control are an alternative to data-hungry correlative prediction (Gotelli et al., 2009). Increasing a model's mechanistic basis allows for more reliable interpolations and extrapolations in space and time; deviations of predictions from observations can generate knowledge about the role of specific processes and indicate the most productive areas for future research (Soetaert & Herman, 2009).

The amount of knowledge on system processes that is required for the formulation of mechanistic models would exclude less-studied systems, while data requirements for model parameterization and validation can prove just as challenging as for correlative approaches (Dormann et al., 2012). It is not surprising that the general trend among mechanistic models of natural pest control towards more processes per model, has been checked by attempts at simpler system representations (Figure 1b; 2a).

Various techniques have been applied for mechanistic modelling of natural pest control, involving trade-offs in the ability to represent different processes, the ease of analysing model output and the computational resources required (Table 1). Most of the models are dynamic and represent space either explicitly or implicitly. Time steps vary from 1 s to 1 y and temporal extent from 1 min to 600 y. Spatial resolution and extent similarly vary from 0.01 mm to 500 m and from 4.5 m to 700 km, respectively.

The majority of mechanistic models of natural pest control represent the general ecological processes of reproduction, mortality, dispersal, environmental filtering (or species sorting) and predation, in combination with other ecological processes, as well as the anthropogenic processes of land use and agricultural management (Figure 2b). More specialized ecological and socioeconomic processes form unique combinations that are represented by only a few models (Figure 2b).

Most mechanistic models represent specific crop-pest-enemy systems (Figure 1a) and are ideal for applications in case-specific management (Levins, 1966). While such models generally include the largest number of processes per model (Figure 1b), they have only been developed for a few combinations of crops, pests and their enemies around the world (Figure 3). Moreover, model output has primarily comprised ecological components of natural pest control and to a smaller extent its agronomic and economic benefits, which are most relevant to farmers (Figure 2c).

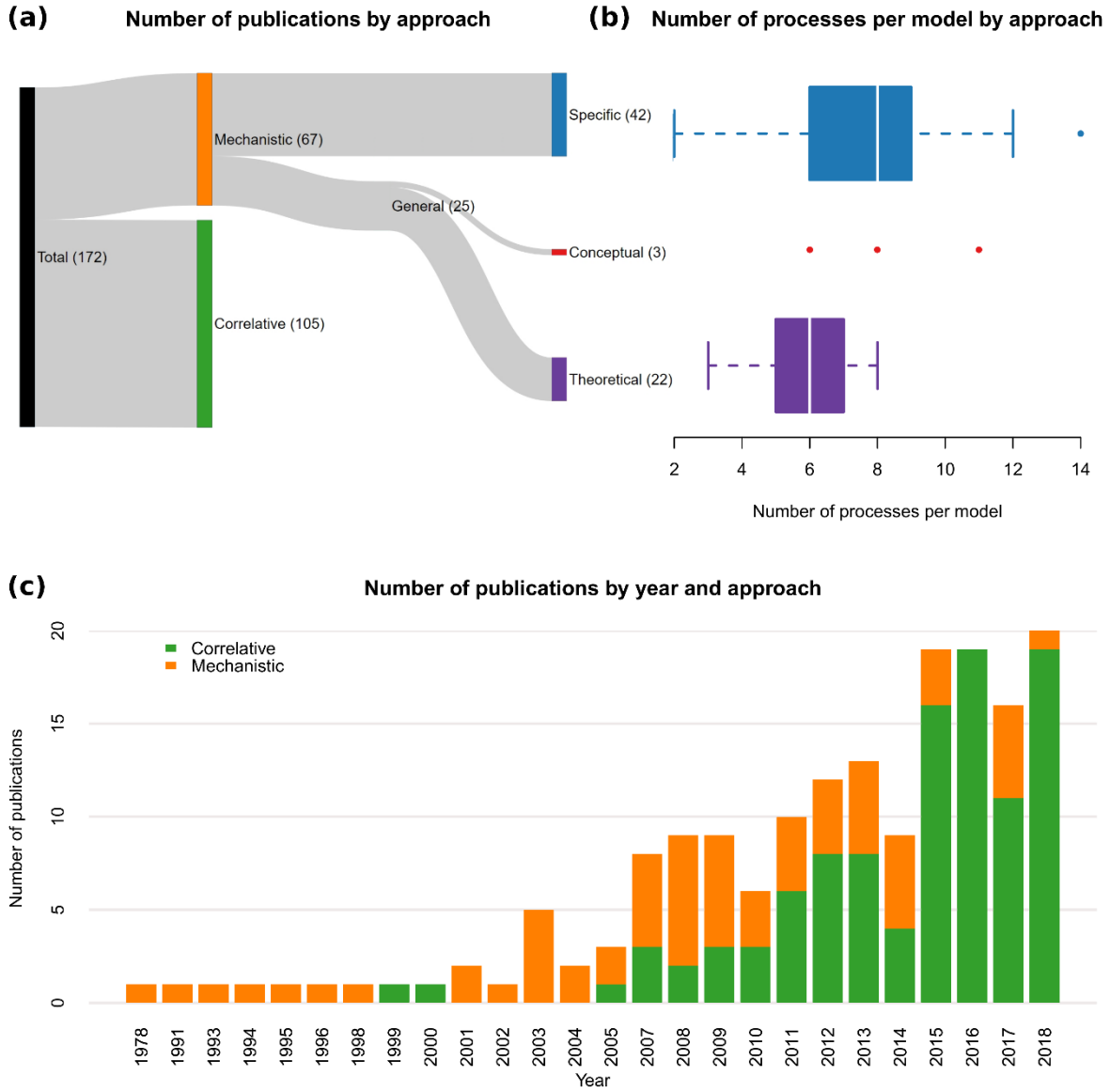

FIGURE 1 (a) Number of reviewed publications following contrasting modelling approaches, sequentially separated based on their mechanistic basis, generalization potential and approach to generality. (b) Number of processes represented per reviewed model, among models following three contrasting mechanistic approaches. Box bands, lower and upper edges represent 2nd, 1st and 3rd quartiles, respectively. Whiskers extend to the most extreme values within 1.5 × interquartile range from the box; more extreme values are indicated with dots. (c) Number of reviewed publications featuring correlative and mechanistic models for each publication year

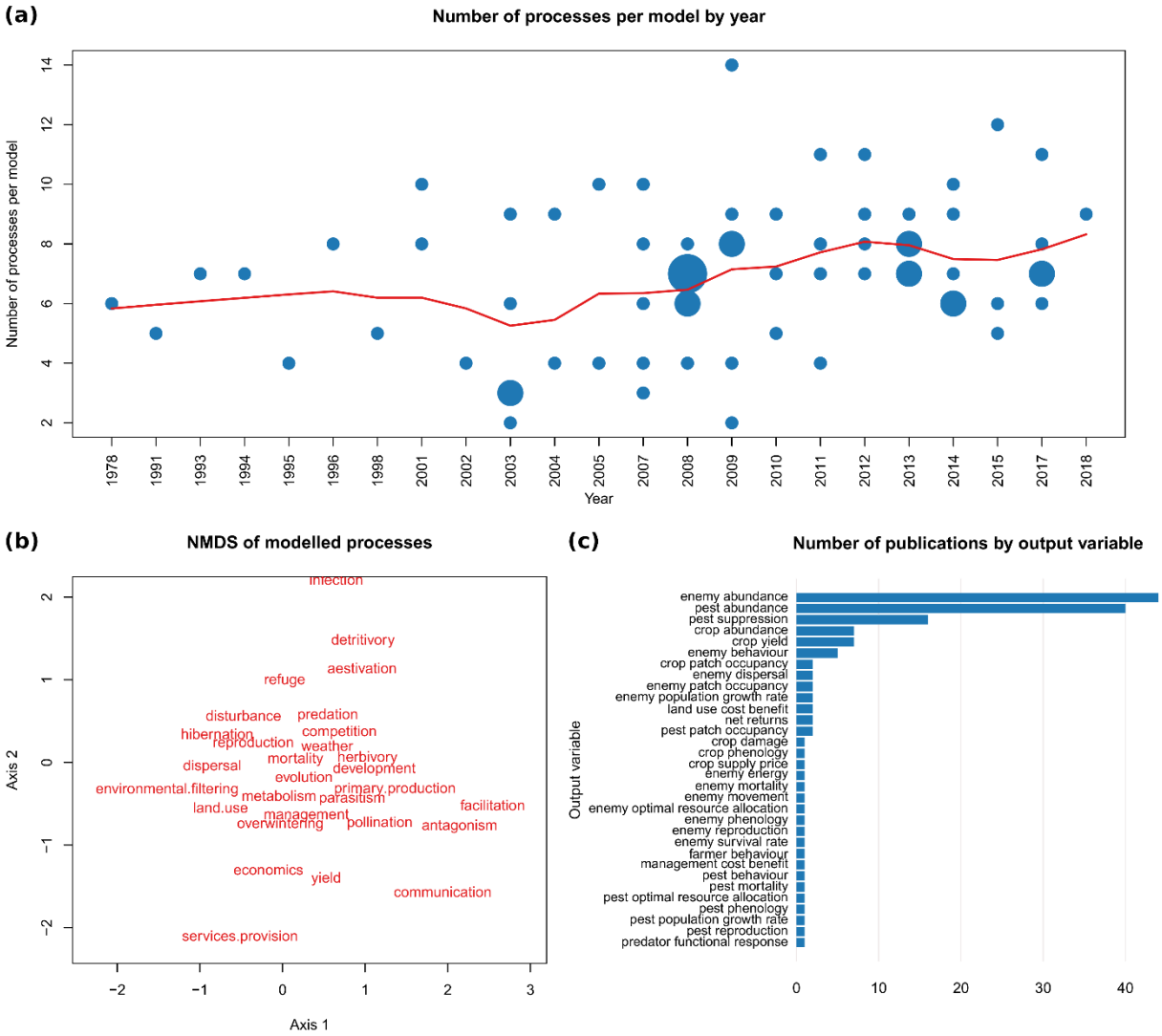

FIGURE 2 (a) Number of processes represented per reviewed mechanistic model for each publication year. Small, medium and large circles indicate 1, 2 and 3 models, respectively, with identical values. The red lowess curve was fitted to the data with a smoother span of ¼. (b) Nonmetric multidimensional scaling (NMDS) showing the associations of processes represented among reviewed mechanistic models (stress = 0.2). The closer the processes are, the more often they are represented together. (c) Number of reviewed publications having each variable as the main output of their mechanistic models. Single models may have several variables as their main output

TABLE 1 Examples of deterministic (always producing the same output given a particular input) and stochastic (including random elements) techniques used in mechanistic models of natural pest control. Technique classification is further based on the degree of explicitness in the representation of space and the distinction between discrete and continuous time representations, all viewed as key factors in modelling ecological processes. Relative strengths (+) and weaknesses (–) were assigned to each technique with respect to the following desired qualities of a modelling procedure: formulation flexibility (FF), analytical tractability (AT) and algorithmic efficiency (AE). Individual- and agent-based models differ in that the former pool and equate individuals, while the latter track agents independently

	Deterministic						Stochastic					
	Discrete time			Continuous time			Discrete time			Continuous time		
Non-spatial	Difference equations (DEs) (Zhang & Swinton, 2009)			Ordinary differential equations (ODEs) (Glaum, 2017)			Individual-based models (IBMs) (Meyer et al., 2012)			Stochastic differential equations (Dwyer et al., 2004)		
	FF	AT	AE	FF	AT	AE	FF	AT	AE	FF	AT	AE
	–	+	+	–	+	+	+	–	–	–	–	+
Spatially implicit	Meta-population DEs (Legrand et al., 2011)			Meta-population ODEs (Chatterjee et al., 2009)			Spatially implicit IBMs (Wajnberg et al., 2012)			Agent-based models (Thomas et al., 2003)		
	FF	AT	AE	FF	AT	AE	FF	AT	AE	FF	AT	AE
	–	+	+	–	+	+	+	–	–	+	–	–
Spatially explicit	Coupled map lattices (Riolo et al., 2015)			Partial differential equations (PDEs) (Halley et al., 1996)			Stochastic cellular automata (Kondoh, 2003)			Stochastic PDEs (Banks & Yasenak, 2003)		
	FF	AT	AE	FF	AT	AE	FF	AT	AE	FF	AT	AE
	+	–	–	–	–	+	+	–	–	–	–	+

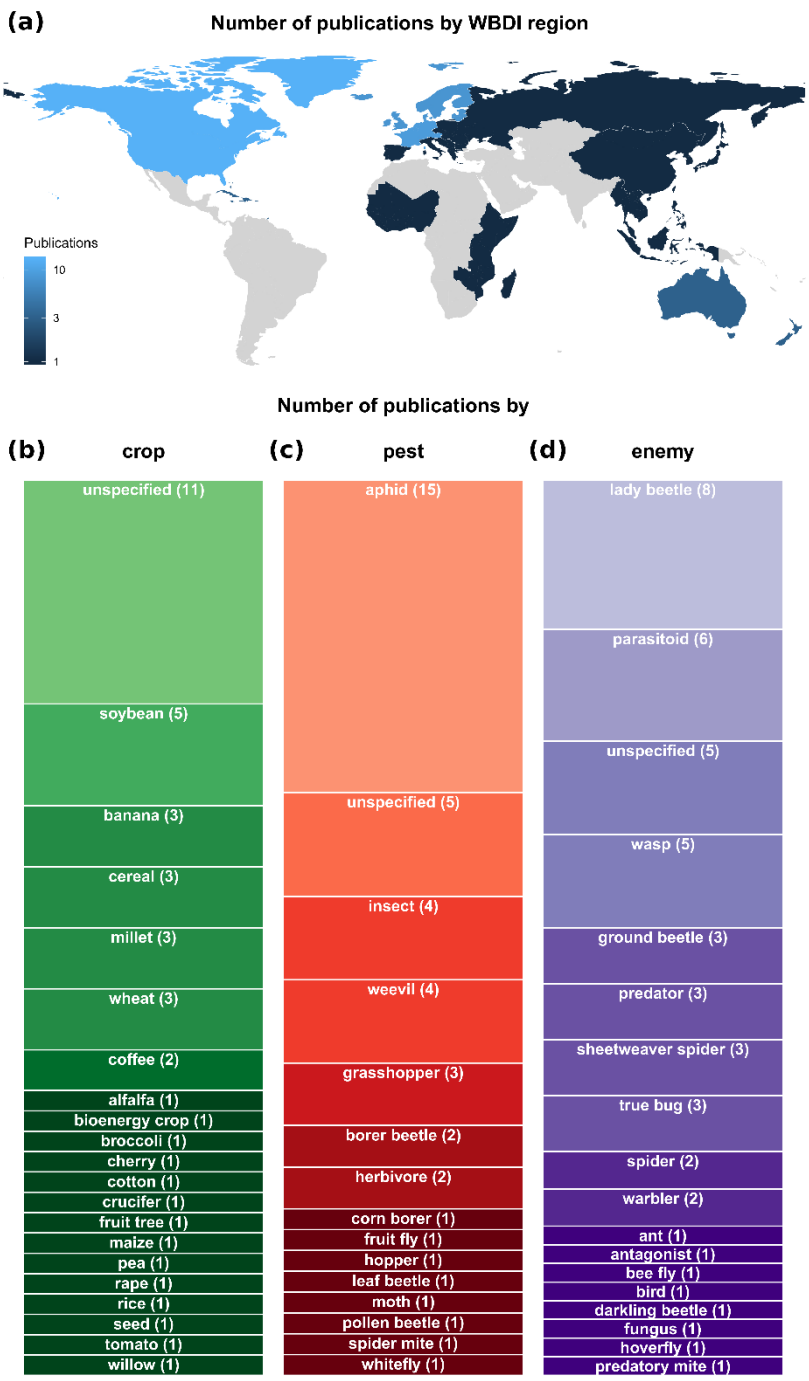

FIGURE 3 Number of reviewed publications featuring mechanistic models of specific systems (a) geographically belonging to each region defined in the World Bank Development Indicators (WBDI) and representing different (b) crop, (c) pest and (d) natural enemy organisms. Certain models do not represent all categories of organisms, others represent more than one organism in a category and, in some cases, organisms are part of the model but not identified (indicated as unspecified)

The fewer theoretical models (Figure 1a) focus on essential features of natural pest control, producing general understanding and predictions that may apply to many systems (Levins, 1966). However, these models have a narrower mechanistic basis on average (Figure 1b) and they consistently approximate modelled processes by averaging over space. The resulting qualitative mismatch with observed phenomena reduces the applicability of theoretical models of natural pest control.

Conceptual models aiming at a more holistic system representation can be more realistic (Figure 1b). However, their abstract nature often prevents translating their representation of a system into specific responses to environmental change, therefore hindering the comparison of model predictions with observations of a system under change (Levins, 1998). This, in turn, prevents model validation and analysis towards mechanistic understanding and reliable prediction. Overall, there is a lack of realistic models with testable predictions that can be applied across systems to predict the potential for natural pest control in managed landscapes.

3 | POTENTIAL OF THE ARCHETYPE APPROACH

Predictions of natural pest control potential can be currently generated either from data-hungry correlative models of limited utility in understanding the underlying causes, or from process-based models that occupy the extremes of an apparent trade-off between generality and realism, and have little applicability as predictive tools across systems. We propose that filling this methodological gap requires an approach akin to middle-range theories, providing explanations that are valid in multiple cases, but within a narrower range of conditions than grand theories (P. Meyfroidt et al., 2018). Similar needs in sustainability research have led to an

increase in the use of so-called archetypes, i.e., “context-sensitive, generalized models of sustainability problems, dynamics or strategies with case-level empirical validity” (Oberlack et al., 2019). Archetype approaches are particularly useful for capturing the critical details of a phenomenon with highly heterogeneous cases and for employing these details towards contextually explicit generalizations.

We suggest that, and illustrate below how, archetypes derived inductively from empirical research and expert knowledge of causal mechanisms can facilitate knowledge upscaling and its transfer across cases, tackling fragmentation in the research of natural pest control. Combining empirical knowledge with theoretical expectations, archetypes also have the potential to inform deductively the formulation of predictive models, which can be applied to cases with limited data availability (Figure 4; Figure 5). Deriving a reasonable number of archetypes of existing, diverse pest control systems can thus strike the missing balance between generality and realism in predictions of natural pest control. Furthermore, generally accepted archetypes can tackle methodological fragmentation and channel the increasing interest in model development (Figure 1c) towards a concerted effort to better understand and predict natural pest control around the world.

3.1 | Archetypes of crop-pest-enemy systems

The derivation of archetypes of heterogeneous real-world systems requires that multiple cases be similar with respect to defining features of the studied phenomenon and that these cases share some key attributes (Oberlack et al., 2019). Natural pest control seems to respond idiosyncratically to land-use gradients across different systems, but cases show similar responses when grouped according to system characteristics and functional traits (Karp et al., 2018; Martin et al., 2019). For

instance, dietary, dispersal and overwintering traits of pests and their enemies mediate these organisms' responses to landscape characteristics (Martin et al., 2019), while other traits, such as invasiveness, contribute under certain conditions (Tamburini et al., in prep.).

These trait-mediated similarities in responses indicate the critical role of processes linked to the traits through ecological theories. The generality of these theories and niche conservation among related organisms broaden the pertinence of such processes across different systems (Evans et al., 2015). The challenge of an archetype approach to natural pest control then consists in combining heterogeneous information on functional traits to define system components and their relationships. The level of abstraction in defining these elements is crucial, as each archetype should be able to represent multiple systems and its predictions should agree with system-specific observations.

3.2 | Predictive tools of natural pest control

The models that make up archetypes in sustainability research are typically simple linear chains from causes to effects, both of which are of qualitative nature. Most archetype models thus fall short of reproducing key characteristics of socioecological systems, such as hysteresis, thresholds and feedbacks. These limitations can be partly attributed to the disproportionate focus of sustainability research on causal effects rather than causal mechanisms (Patrick Meyfroidt, 2016), which has led to additional concerns with respect to model causality (Oberlack et al., 2019).

Archetype models of natural pest control can incorporate trait-based mechanistic understanding and minimize concerns in the treatment of causality by

calling on established knowledge in ecological modelling (Ings et al., 2009). If defined at the level of elements of mechanistic models, i.e., system variables and their interactions, archetype models can produce output of interest (e.g., pest population levels) from existing or anticipated system input (e.g., changes in landscape proportions of non-crop habitat). Critically, this allows the representation of essential features of the modelled systems, such as non-linear dynamics and feedback loops.

4 | DEFINING CROP-PEST-ENEMY ARCHETYPES

The definition of archetypes of natural pest control, each producing mechanistic understanding and reliable predictions for multiple crop-pest-enemy systems, requires the incorporation of knowledge and methods from different approaches. Trait-based correlative models contribute general understanding of potentially important processes behind pest control responses to landscape characteristics (Martin et al., 2019). Multivariate statistical techniques help reduce complex socioecological systems to the fewest possible elements that describe the identified processes across systems (Sietz et al., 2017). The role of these processes can be confirmed through their explicit representation by mechanistic models that can reproduce observed pest control responses to changes in landscape characteristics (Overmars et al., 2007). This model verification and further validation with independent observations will allow models to be transferred to cases with similar characteristics.

The result should be similar to minimum realistic models, a method representing only key elements of complex managed marine ecosystems (Punt & Butterworth, 1995). The formal definition of archetypes will allow this method to extend beyond a single system, towards the representation of a phenomenon across systems.

Developing models of ecological systems involves high levels of uncertainty with respect to model structure, formulation and parameterization. Luckily, there appears to be a limit to the effective structural complexity of ecological systems (Yodzis, 1998; Levin, 2005; Chave, 2013). Uncertainty in model formulation can be addressed by only considering 'robust theorems', i.e., shared predictions of independently developed models of the same system. Truth is thus approached as "the intersection of independent lies" (Levins, 1966). Parameter uncertainty can be reduced by using qualitative modelling for one of the independently developed models, as this technique requires no parameter estimation (Levins, 1998).

4.1 | Example archetypes

We illustrate the application of crop-pest-enemy archetypes in predicting natural pest control across systems, by building mechanistic models of the resident pest (A1) and migrating pest (A2) archetypes. Models were based on the following basic assumptions, illustrated in the respective conceptual models (Figure 4e,f). Both archetypes represent the responses of populations of pests with specialist and generalist natural enemies to changes in landscape characteristics. The proportion of non-crop habitat and density of field edges in the landscape enhance generalist enemies in both archetypes, by providing alternative resources and facilitating dispersal. The two archetypes differ in that the pest is also enhanced by non-crop habitat in A2, as it migrates there when crop resources are not available. This behaviour of the pest is further associated with a diversification of the specialist enemies' diet in archetype A2. For details about model assumptions, see Figure 4.

We formulated qualitative (Figure 5a,b) and quantitative (Figure 5c,d) models of archetypes A1 and A2, using the same basic assumptions for each archetype, but

based on method-specific simplifications. Qualitative models follow a holistic approach (equilibrium/landscape), compared to quantitative models' reductionist approach (growing season/crop field). We focus on shared qualitative and quantitative model predictions, in order to increase predictive robustness. For model verification, predictions are compared with the responses of organisms with the respective trait values to changes in landscape characteristics, as revealed by the analysis of observations across Europe (Martin et al., 2019).

These observations indicate a consistent increase in the abundance of generalist enemies in response to increasing non-crop habitat and edge density, in agreement with our predictions (Figure 5e,f). Observed responses of specialist enemies to the same changes vary from decreasing abundances in intensely farmed landscapes, to no change in more complex landscapes. The former agrees with model predictions for the A1 archetype, where specialists are outcompeted by generalist enemies (Figure 5e), while the latter agrees with model predictions for the A2 archetype (Figure 5f), where specialist enemies maintain their abundance, thanks to access to diverse resources. This distinction is in accordance with our expectation for simple landscapes to favour resident pests (A1) and complex landscapes to favour migrating pests (A2) and the respective systems. Finally, observations indicate distinct responses of pests to landscape characteristics, depending on their overwintering strategy. Resident pests show no response to all landscape changes, same as migrating pests in response to changes in non-crop habitat proportion. Only the abundance of migrating pests decreases as the density of field edges increases. Our models generally predict this distinction in the responses of resident (Figure 5e) and migrating pests (Figure 5f). Reduced specialist enemy abundances in A1 prevent effective control of the resident pest. In A2, changes in non-crop habitat have no

impact on the migrating pest, due to conflicting influences directly on the pest and through the generalist enemies. On the other hand, edge density only enhances generalists, allowing the non-competing specialist enemies to control the pest effectively, as they maintain their abundance through their reliance on diverse resources. Thus, increasing the density of field edges in landscapes dominated by the migrating pest archetype is the only land-use strategy leading to qualitative predictions of higher crop yields.

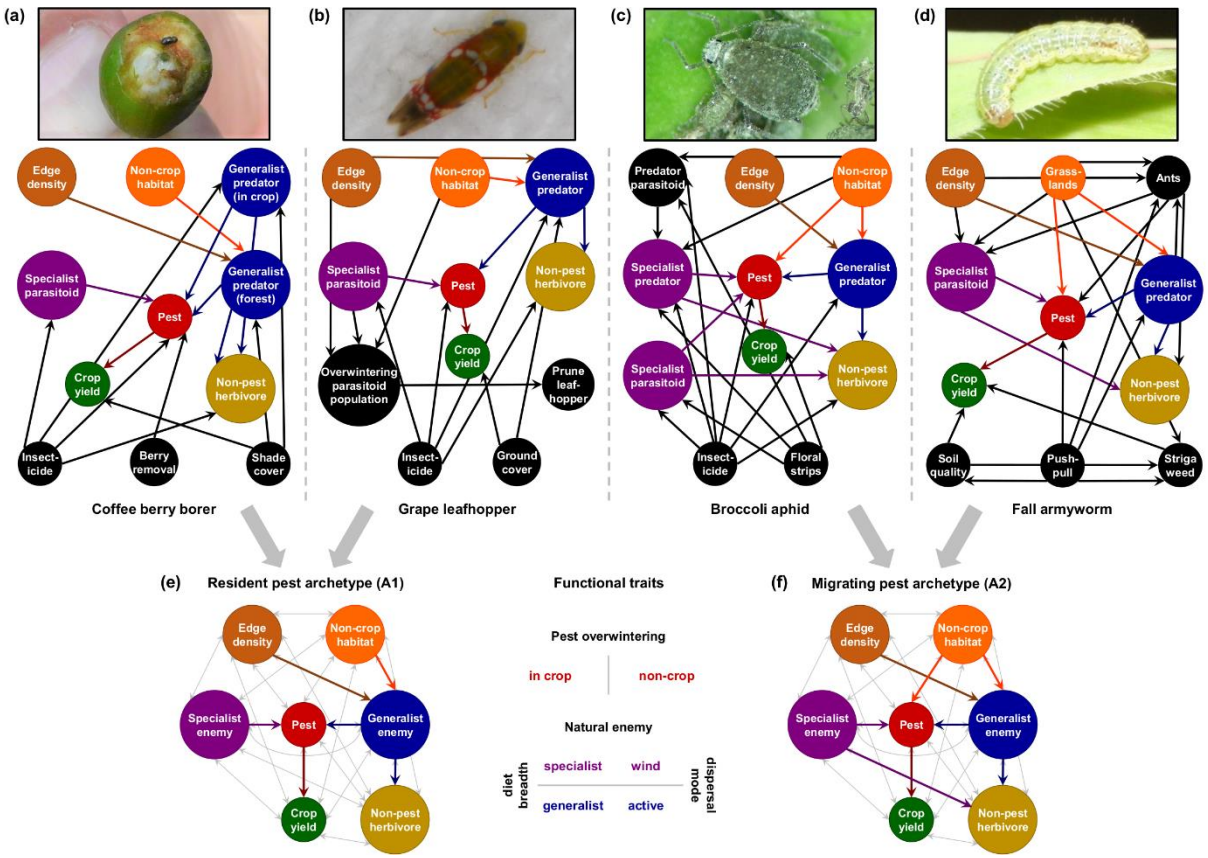

FIGURE 4 Conceptual models based on expert knowledge of the systems of natural control of (a) the coffee berry borer in Latin America, the Californian (b) grape leafhopper and (c) broccoli aphid and (d) the fall armyworm in Sub-Saharan Africa. The arrows indicate causal relationships, pointing from cause to effect. Conceptual models of archetypes A1 and A2 (e and f) aim at representing the defining

components of multiple systems with respect to natural pest control and crop yield responses to landscape characteristics (edge density and non-crop habitat). Model simplification is based on empirical evidence regarding the role of pest overwintering, and enemy dietary and dispersal traits in the behaviour of natural pest control (Martin et al., 2019). Trait-based and expert knowledge reduces model complexity from all possible relationships (thin grey arrows) to a few (thick coloured arrows) key drivers of the behaviour of real-world systems of natural pest control. In the resident pest archetype (A1), the pest stays in crop fields throughout the year, while, in the migrating pest archetype (A2), it moves to non-crop habitats when crop resources are unavailable. Pest populations grow by feeding on a specific crop without density dependence. Both archetypes include natural enemies that specialize on the pest family and disperse with the help of the wind (specialist enemy) and natural enemies that feed on a variety of non-pest herbivores and disperse through active movement (generalist enemy). Specialists in A1 are, therefore, dependent on the pest, while pest migration to more diverse non-crop habitat in A2 exposes specialists to more family members and makes them similar to generalists. Increased proportion of non-crop habitat in the landscape enhances organisms that rely on its resources, i.e., generalist enemies in both archetypes and the pest in A2. Field edges can also provide such resources, especially to short-distance, actively dispersing generalist enemies entering the crop. Photo credits: (a) CGIAR/CCAFS, (b) Lee Elliott, (c) Andrew Jensen and (d) Yann Clough

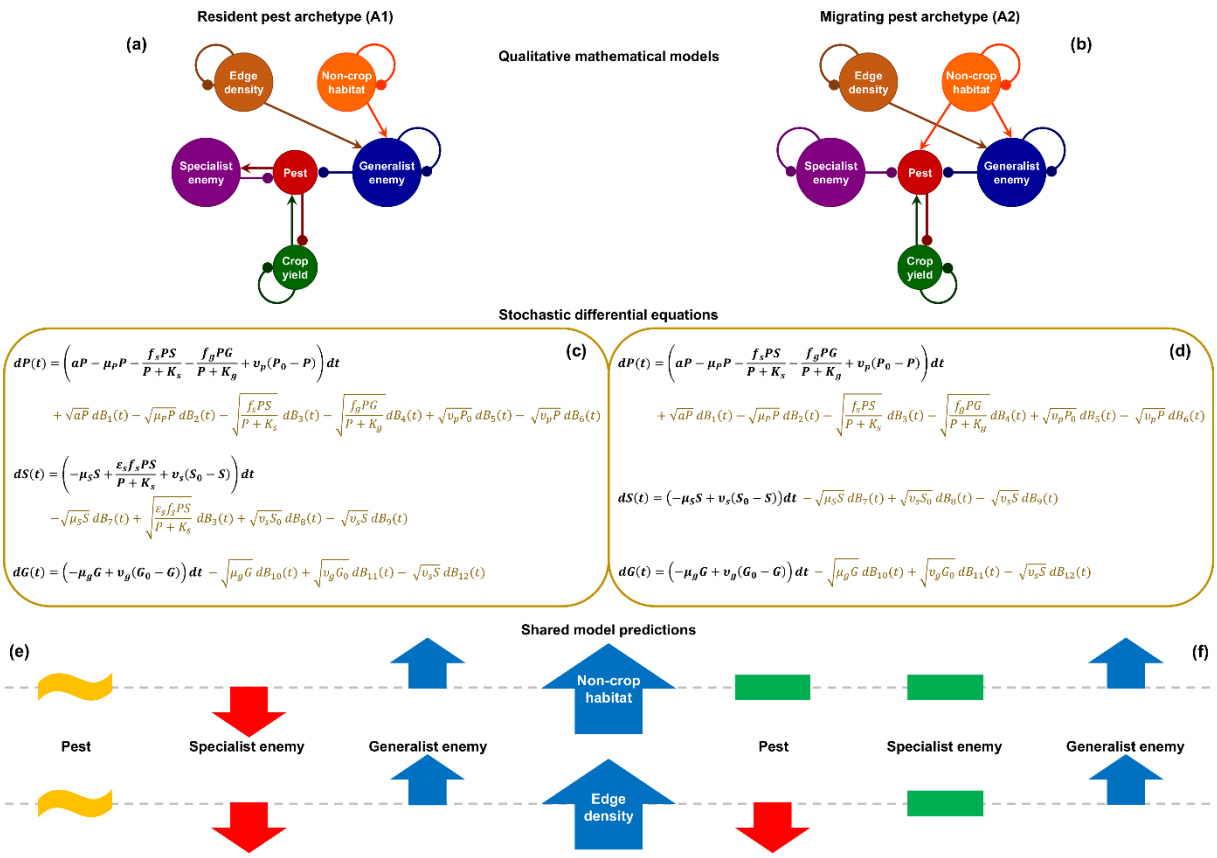

FIGURE 5 Qualitative and quantitative modelling of archetypes A1 and A2, based on the respective conceptual models (see Figure 4e,f). Note that both approaches represent a subset of the conceptual models' variables considered as technically necessary. Qualitative mathematical modelling, or loop analysis, was used (a for A1 and b for A2) to represent the equilibrium levels of crop yield and populations of pests and natural enemies, along with landscape characteristics. Signed digraphs (networks of the direction of interactions, with arrows for positive and filled circles for negative interaction sign) represented the structure of the system as a whole (Levins, 1998). Analysis of the equivalent representation of qualitatively specified community matrices (Dambacher et al., 2002) predicted the equilibrium responses of system variables to sustained changes in the proportion of non-crop habitat and edge density in the landscape. Stochastic differential equations (Marion et al., 2002) were used (c for A1 and d for A2) to represent the dynamics of pest (*P*), specialist (*S*) and

generalist (*G*) enemy populations during a growth season, along a gradient of landscape characteristics. Stochasticity is represented through terms in gold font, but model structure is more easily explained by the deterministic terms in bold black. The equations include terms for reproduction, mortality and predation or parasitism, based on the type II functional response (Holling, 1959). Dispersal was represented implicitly, through terms of inflow and outflow of organisms with respect to the crop. These terms describe the influence of landscape-scale non-crop habitat and edge density on the pools of immigrating populations and the connectivity between crop and non-crop habitats. Model parameters were given generally realistic values, based on expert knowledge. Shared model predictions (e for A1 and f for A2) about the responses of pest, specialist and generalist enemy abundances to increases in the landscape proportion of non-crop habitat and density of field edges are given as upward and downward facing arrows for increases and decreases, respectively. Predictions of no response are illustrated with horizontal lines. Tildes indicate different predictions (qualitative of no change and quantitative of a slight decrease), arising from distinct simplifying assumptions used in the former (holistic) and the latter (reductionist) approach's system representation

4.2 | Next steps

We suggest operationalizing the definition of natural pest control archetypes that represent all major agroecosystems, by taking the following steps:

1) Identify the organismal traits and landscape characteristics that play the most determinant role in system functioning and collect relevant values across systems. Crop-pest-enemy combinations that feature in recently compiled large-scale datasets (Karp et al., 2018; Martin et al., 2019; Dainese et al., 2019) can provide a pertinent

collection of systems. The identified features should be linked explicitly to specific processes that are known to underlie the behaviour of a system, based on ecological theory and expert knowledge. Empirical studies that build consensus on drivers of behaviour across systems and identify traits with cross-system explanatory potential are a key resource for this task.

2) Reduce the dimensionality of the previously collected information using multivariate statistical techniques. The goal is to classify agroecosystems based on the trait values of their organisms, and, hence, trait-associated processes. A hierarchical classification (Sietz et al., 2017) has the advantage of allowing for a flexible, case-specific determination of the aggregation level in subsequent applications, depending on the availability of knowledge and the spatiotemporal scales/model output of interest.

3) Establish a standardized, dynamic set of rules for the definition of archetypes and their models from combinations of trait values and landscape characteristics. These rules will allow researchers to place real-world systems within or, if necessary, outside the previously reduced trait space. In either case, the rules should ensure the translatability of system-specific trait levels and landscape characteristics into model variables and interactions.

Qualitative and quantitative modelling techniques can be used in combination or interchangeably, depending on the research question, the features of the system and the availability of information. For instance, a quantitative approach would be preferable in case of expected non-linearities with hysteretic effects and threshold values (Marzloff et al., 2013). On the other hand, a qualitative approach would be more amenable to an expansion of the modelling scope with the inclusion of

socioeconomic, along with agronomic and ecological processes (Dambacher et al., 2007).

5 | FUTURE RESEARCH

Example archetypes show the potential of the approach for improved understanding and prediction of natural pest control responses to landscape characteristics across systems. Expanding the approach to define a set of archetypes that represent the major crop-pest-enemy systems across the world will allow mainstreaming natural pest control in both agricultural applications and research. An archetype-based approach to modelling natural pest control would be, for instance, a valuable addition to existing tools that use detailed land-use information to map ecosystem services in a variety of landscapes (Sharp et al., 2014), or to global assessments of nature's contributions to people under different scenarios of environmental change (Chaplin-Kramer et al., 2019). This expansion of the archetype approach will create new challenges and opportunities in the research of natural pest control and environmental management in general.

5.1 | Natural pest control

Defining multiple archetypes that cover all major crop-pest-enemy combinations will facilitate modelling natural pest control across whole agricultural landscapes, which often consist of mosaics of different crops that host pests and natural enemies with different characteristics. This would contribute to a better agronomic and economic assessment of farming-system-wide natural pest control potential, which is currently deficient (Figure 2c). Furthermore, modelling landscapes that consist of multiple archetypes facilitates their spatially explicit representation, which is a

prerequisite for ecosystem services management based on spatial planning of agricultural landscapes. The choice of an appropriate technique of spatially explicit modelling will have to consider a likely trade-off between the representation of disparate processes and the computational resources required (Table 1).

As the scope of the archetype approach broadens, the data that provide the empirical basis of the approach can take the form of a 'living' database of crop-pest-enemy combinations and the associated traits, along with variables of context, such as climate features, biogeographic region, landscape characteristics and management regime. A consistent coding for this database will lower the bar for empirical researchers and practitioners willing to contribute with case-specific knowledge. The rule set for translating empirical knowledge into archetypes and the associated models can also be a dynamic element of the approach. Changes in the rule set may be preferably implemented through an incremental instead of a continuous process, as it should require some scientific consensus. Finally, the dynamic character of the approach will facilitate the systematic evaluation of the mechanistic understanding that the archetypes are assumed to carry against independent observations. Keeping the framework sufficiently flexible to constantly incorporate new knowledge will constitute an iterative and participatory research axis involving experts and practitioners, with implications for how the archetypes and their models are developed and refined.

5.2 | Environmental management

The need for general ecological models that account for the context of application extends to other environmental areas, including major land-use issues, such as deforestation and desertification, and their interaction with climate change

(Dale, 2003). An enrichment of the archetype approach with ecological principles will improve the causal basis of models found in land-use archetypes and broaden their predictive scope. A wide adoption of an archetype approach to ecological modelling will increase the number of researchers building models on similar basic assumptions, with comparable output, irrespective of their reductionist or holistic view of ecology predisposing them in favour of general or realistic approaches. The ensuing potential for synthesis of knowledge is particularly needed in the fragmented landscape of ecological research (McGill, 2010). It is, furthermore, especially helpful in case of data shortages, as context-specificity reduces the required degrees of freedom and allows for more robust knowledge transfer between cases. Ultimately, archetype approaches will increase the potential for ecology to contribute towards higher environmental security, especially in regions that combine the highest projected impacts from cumulative environmental change with the lowest levels of economic development and the least studied and, hence, modelled socioecological systems.

6 | CONCLUSIONS

The application of ecological principles in environmental management is restricted on the one hand by inconsistent empirical evidence and on the other hand by trade-offs in ecological models' approach to generality. We suggest filling this gap by combining the trait-mediated general understanding produced by correlative models with the explicit representation of causal relationships that can be achieved by mechanistic modelling. To bridge these contrasting approaches, we adapt the archetype concept from sustainability research, where it is being increasingly employed towards contextually explicit generalizations. We demonstrate an

application of the approach to natural control of crop pests, an ecosystem service with great promise for improving the sustainability of agricultural production. Effective management of natural pest control is impaired by observed inconsistencies and methodological limitations. Nevertheless, similar responses in cases where organisms share key traits indicate general processes that drive system behaviour. Exploratory archetypes based on these processes show potential for improved understanding and prediction across systems. Building on these results, we suggest the use of correlative and mechanistic techniques in order to define archetype models for all major agroecosystems. A broader application of the archetype approach promises to enhance ecology's contribution to the management of natural resources across a wide range of environmental issues and geographic areas of the world.

REFERENCES

Banks, J. E., & Yasenak, C. L. (2003). Effects of plot vegetation diversity and spatial scale on Coccinella septempunctata movement in the absence of prey. *Entomologia Experimentalis et Applicata*, *108*(3), 197–204. https://doi.org/10.1046/j.1570-7458.2003.00083.x

Bianchi, F. J. J. A., Booij, C. J. H., & Tscharntke, T. (2006). Sustainable pest regulation in agricultural landscapes: A review on landscape composition, biodiversity and natural pest control. *Proceedings of the Royal Society of London B: Biological Sciences*, *273*(1595), 1715–1727. https://doi.org/10.1098/rspb.2006.3530

Chaplin-Kramer, R., O'Rourke, M. E., Blitzer, E. J., & Kremen, C. (2011). A meta-analysis of crop pest and natural enemy response to landscape complexity.

Ecology Letters, *14*(9), 922–932. https://doi.org/10.1111/j.1461-0248.2011.01642.x

Chaplin-Kramer, R., Sharp, R. P., Weil, C., Bennett, E. M., Pascual, U., Arkema, K. K., Brauman, K. A., Bryant, B. P., Guerry, A. D., Haddad, N. M., Hamann, M., Hamel, P., Johnson, J. A., Mandle, L., Pereira, H. M., Polasky, S., Ruckelshaus, M., Shaw, M. R., Silver, J. M., … Daily, G. C. (2019). Global modeling of nature's contributions to people. *Science*, *366*(6462), 255–258. https://doi.org/10.1126/science.aaw3372

Chatterjee, S., Isaia, M., & Venturino, E. (2009). Spiders as biological controllers in the agroecosystem. *Special Issue: Mathematics in Biointeractions*, *258*(3), 352–362. https://doi.org/10.1016/j.jtbi.2008.11.029

Chave, J. (2013). The problem of pattern and scale in ecology: What have we learned in 20 years? *Ecology Letters*, *16*(s1), 4–16. https://doi.org/10.1111/ele.12048

Dainese, M., Martin, E. A., Aizen, M. A., Albrecht, M., Bartomeus, I., Bommarco, R., Carvalheiro, L. G., Chaplin-Kramer, R., Gagic, V., Garibaldi, L. A., Ghazoul, J., Grab, H., Jonsson, M., Karp, D. S., Kennedy, C. M., Kleijn, D., Kremen, C., Landis, D. A., Letourneau, D. K., … Steffan-Dewenter, I. (2019). A global synthesis reveals biodiversity-mediated benefits for crop production. *Science Advances*, *5*(10), eaax0121. https://doi.org/10.1126/sciadv.aax0121

Dale, V. H. (2003). *Ecological modeling for resource management*. Springer Science & Business Media.

Dambacher, J. M., Brewer, D. T., Dennis, D. M., Macintyre, M., & Foale, S. (2007). Qualitative Modelling of Gold Mine Impacts on Lihir Island's Socioeconomic

System and Reef-Edge Fish Community. *Environmental Science & Technology*, *41*(2), 555–562. https://doi.org/10.1021/es0610333

Dambacher, J. M., Li, H. W., & Rossignol, P. A. (2002). Relevance of Community Structure in Assessing Indeterminacy of Ecological Predictions. *Ecology*, *83*(5), 1372–1385. https://doi.org/10.1890/0012-9658(2002)083[1372:ROCSIA]2.0.CO;2

Deutsch, C. A., Tewksbury, J. J., Tigchelaar, M., Battisti, D. S., Merrill, S. C., Huey, R. B., & Naylor, R. L. (2018). Increase in crop losses to insect pests in a warming climate. *Science*, *361*(6405), 916–919. https://doi.org/10.1126/science.aat3466

Dormann, C. F. (2007). Promising the future? Global change projections of species distributions. *Basic and Applied Ecology*, *8*(5), 387–397. https://doi.org/10.1016/j.baae.2006.11.001

Dormann, C. F., Schymanski, S. J., Cabral, J., Chuine, I., Graham, C., Hartig, F., Kearney, M., Morin, X., Römermann, C., Schröder, B., & Singer, A. (2012). Correlation and process in species distribution models: Bridging a dichotomy. *Journal of Biogeography*, *39*(12), 2119–2131. https://doi.org/10.1111/j.1365-2699.2011.02659.x

Dwyer, G., Dushoff, J., & Yee, S. H. (2004). The combined effects of pathogens and predators on insect outbreaks. *Nature*, *430*, 341.

Englund, O., Berndes, G., & Cederberg, C. (2017). How to analyse ecosystem services in landscapes—A systematic review. *Ecological Indicators*, *73*, 492–504. https://doi.org/10.1016/j.ecolind.2016.10.009

Evans, T. G., Diamond, S. E., & Kelly, M. W. (2015). Mechanistic species distribution modelling as a link between physiology and conservation. *Conservation Physiology*, *3*(1). https://doi.org/10.1093/conphys/cov056

Glaum, P. (2017). A theoretical basis for the study of predatory syrphid fly ecology. *Theoretical Ecology*, *10*(4), 391–402. https://doi.org/10.1007/s12080-017-0336-1

Gotelli, N. J., Anderson, M. J., Arita, H. T., Chao, A., Colwell, R. K., Connolly, S. R., Currie, D. J., Dunn, R. R., Graves, G. R., Green, J. L., Grytnes, J.-A., Jiang, Y.-H., Jetz, W., Lyons, S. K., McCain, C. M., Magurran, A. E., Rahbek, C., Rangel, T. F. L. V. B., Soberón, J., … Willig, M. R. (2009). Patterns and causes of species richness: A general simulation model for macroecology. *Ecology Letters*, *12*(9), 873–886. https://doi.org/10.1111/j.1461-0248.2009.01353.x

Halley, J. M., Thomas, C. F. G., & Jepson, P. C. (1996). A Model for the Spatial Dynamics of Linyphiid Spiders in Farmland. *Journal of Applied Ecology*, *33*(3), 471–492. https://doi.org/10.2307/2404978

Holland, J. M., Douma, J. C., Crowley, L., James, L., Kor, L., Stevenson, D. R. W., & Smith, B. M. (2017). Semi-natural habitats support biological control, pollination and soil conservation in Europe. A review. *Agronomy for Sustainable Development*, *37*(4), 31. https://doi.org/10.1007/s13593-017-0434-x

Holling, C. S. (1959). Some Characteristics of Simple Types of Predation and Parasitism1. *The Canadian Entomologist*, *91*(7), 385–398. https://doi.org/10.4039/Ent91385-7

Ings, T. C., Montoya, J. M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C. F., Edwards, F., Figueroa, D., Jacob, U., Jones, J. I., Lauridsen, R. B., Ledger, M. E., Lewis, H. M., Olesen, J. M., Veen, F. J. F. V., Warren, P. H., & Woodward,

G. (2009). Review: Ecological networks – beyond food webs. *Journal of Animal Ecology*, *78*(1), 253–269. https://doi.org/10.1111/j.1365-2656.2008.01460.x

Jørgensen, S. E. (2002). *Integration of Ecosystem Theories: A Pattern*. Springer Science & Business Media.

Karp, D. S., Chaplin-Kramer, R., Meehan, T. D., Martin, E. A., DeClerck, F., Grab, H., Gratton, C., Hunt, L., Larsen, A. E., Martínez-Salinas, A., O'Rourke, M. E., Rusch, A., Poveda, K., Jonsson, M., Rosenheim, J. A., Schellhorn, N. A., Tscharntke, T., Wratten, S. D., Zhang, W., … Zou, Y. (2018). Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. *Proceedings of the National Academy of Sciences*, 201800042. https://doi.org/10.1073/pnas.1800042115

Khan, Z. R., Midega, C. A. O., Pittchar, J. O., Murage, A. W., Birkett, M. A., Bruce, T. J. A., & Pickett, J. A. (2014). Achieving food security for one million sub-Saharan African poor through push–pull innovation by 2020. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1639), 20120284. https://doi.org/10.1098/rstb.2012.0284

Kleijn, D., Bommarco, R., Fijen, T. P. M., Garibaldi, L. A., Potts, S. G., & van der Putten, W. H. (2019). Ecological Intensification: Bridging the Gap between Science and Practice. *Trends in Ecology & Evolution*, *34*(2), 154–166. https://doi.org/10.1016/j.tree.2018.11.002

Kondoh, M. (2003). Habitat fragmentation resulting in overgrazing by herbivores. *Journal of Theoretical Biology*, *225*(4), 453–460. https://doi.org/10.1016/S0022-5193(03)00279-0

Landis, D. A., Wratten, S. D., & Gurr, G. M. (2000). Habitat Management to Conserve Natural Enemies of Arthropod Pests in Agriculture. *Annual Review of Entomology*, *45*(1), 175–201. https://doi.org/10.1146/annurev.ento.45.1.175

Legrand, A., Gaucherel, C., Baudry, J., & Meynard, J.-M. (2011). Long-term effects of organic, conventional, and integrated crop systems on Carabids. *Agronomy for Sustainable Development*, *31*(3), 515–524. https://doi.org/10.1007/s13593-011-0007-3

Levin, S. A. (2005). Self-organization and the Emergence of Complexity in Ecological Systems. *BioScience*, *55*(12), 1075–1079. https://doi.org/10.1641/0006-3568(2005)055[1075:SATEOC]2.0.CO;2

Levins, R. (1966). The strategy of model building in population biology. *American Scientist*, *54*(4), 421–431.

Levins, R. (1968). *Evolution in changing environments: Some theoretical explorations*. Princeton University Press.

Levins, R. (1998). Qualitative mathematics for understanding, prediction, and intervention in complex ecosystems. *Ecosystem Health*, 178–204.

Losey, J. E., & Vaughan, M. (2006). The Economic Value of Ecological Services Provided by Insects. *BioScience*, *56*(4), 311–323. https://doi.org/10.1641/0006-3568(2006)56[311:TEVOES]2.0.CO;2

Marion, G., Mao, X., & Renshaw, E. (2002). Convergence of the Euler Scheme for a Class of Stochastic Differential Equation. *International Mathematical Journal*, *1*(1), 9–22.

Martin, E. A., Dainese, M., Clough, Y., Báldi, A., Bommarco, R., Gagic, V., Garratt, M. P. D., Holzschuh, A., Kleijn, D., Kovács-Hostyánszki, A., Marini, L., Potts, S. G., Smith, H. G., Hassan, D. A., Albrecht, M., Andersson, G. K. S., Asís, J. D.,

Aviron, S., Balzan, M. V., … Steffan-Dewenter, I. (2019). The interplay of landscape composition and configuration: New pathways to manage functional biodiversity and agroecosystem services across Europe. *Ecology Letters*, *22*(7), 1083–1094. https://doi.org/10.1111/ele.13265

Marzloff, M. P., Johnson, C. R., Little, L. R., Soulié, J.-C., Ling, S. D., & Frusher, S. D. (2013). Sensitivity analysis and pattern-oriented validation of TRITON, a model with alternative community states: Insights on temperate rocky reefs dynamics. *Ecological Modelling*, *258*, 16–32. https://doi.org/10.1016/j.ecolmodel.2013.02.022

McGill, B. J. (2010). Towards a unification of unified theories of biodiversity. *Ecology Letters*, *13*(5), 627–642. https://doi.org/10.1111/j.1461-0248.2010.01449.x

Meyer, K. M., Vos, M., Mooij, W. M., Hol, W. H. G., Termorshuizen, A. J., & Putten, W. H. van der. (2012). Testing the Paradox of Enrichment along a Land Use Gradient in a Multitrophic Aboveground and Belowground Community. *PLOS ONE*, *7*(11), e49034. https://doi.org/10.1371/journal.pone.0049034

Meyfroidt, P., Roy Chowdhury, R., de Bremond, A., Ellis, E. C., Erb, K.-H., Filatova, T., Garrett, R. D., Grove, J. M., Heinimann, A., Kuemmerle, T., Kull, C. A., Lambin, E. F., Landon, Y., le Polain de Waroux, Y., Messerli, P., Müller, D., Nielsen, J. Ø., Peterson, G. D., Rodriguez García, V., … Verburg, P. H. (2018). Middle-range theories of land system change. *Global Environmental Change*, *53*, 52–67. https://doi.org/10.1016/j.gloenvcha.2018.08.006

Meyfroidt, Patrick. (2016). Approaches and terminology for causal analysis in land systems science. *Journal of Land Use Science*, *11*(5), 501–522. https://doi.org/10.1080/1747423X.2015.1117530

Oberlack, C., Sietz, D., Bürgi Bonanomi, E., de Bremond, A., Dell'Angelo, J., Eisenack, K., Ellis, E., Epstein, G., Giger, M., Heinimann, A., Kimmich, C., Kok, M., Manuel-Navarrete, D., Messerli, P., Meyfroidt, P., Václavík, T., & Villamayor-Tomas, S. (2019). Archetype analysis in sustainability research: Meanings, motivations, and evidence-based policy making. *Ecology and Society*, *24*(2). https://doi.org/10.5751/ES-10747-240226

Overmars, K. P., de Groot, W. T., & Huigen, M. G. A. (2007). Comparing Inductive and Deductive Modeling of Land Use Decisions: Principles, a Model and an Illustration from the Philippines. *Human Ecology*, *35*(4), 439–452. https://doi.org/10.1007/s10745-006-9101-6

Palladino, P. (2013). *Entomology, Ecology and Agriculture: The Making of Science Careers in North America, 1885-1985*. Routledge.

Pe'er, G., Dicks, L. V., Visconti, P., Arlettaz, R., Báldi, A., Benton, T. G., Collins, S., Dieterich, M., Gregory, R. D., Hartig, F., Henle, K., Hobson, P. R., Kleijn, D., Neumann, R. K., Robijns, T., Schmidt, J., Shwartz, A., Sutherland, W. J., Turbé, A., … Scott, A. V. (2014). EU agricultural reform fails on biodiversity. *Science*, *344*(6188), 1090–1092. https://doi.org/10.1126/science.1253425

Punt, A. E., & Butterworth, D. S. (1995). The effects of future consumption by the Cape fur seal on catches and catch rates of the Cape hakes. 4. Modelling the biological interaction between Cape fur seals Arctocephalus pusillus pusillus and the Cape hakes Merluccius capensis and M. paradoxus. *South African Journal of Marine Science*, *16*(1), 255–285. https://doi.org/10.2989/025776195784156494

Rega, C., Bartual, A. M., Bocci, G., Sutter, L., Albrecht, M., Moonen, A.-C., Jeanneret, P., van der Werf, W., Pfister, S. C., Holland, J. M., & Paracchini, M.

L. (2018). A pan-European model of landscape potential to support natural pest control services. *Ecological Indicators*, *90*, 653–664. https://doi.org/10.1016/j.ecolind.2018.03.075

Riolo, M. A., Rohani, P., & Hunter, M. D. (2015). Local variation in plant quality influences large-scale population dynamics. *Oikos*, *124*(9), 1160–1170. https://doi.org/10.1111/oik.01759

Sharp, R., Tallis, H., Ricketts, T., Guerry, A., Wood, S., Chaplin-Kramer, R., Nelson, E., Ennaanay, D., Wolny, S., & Olwero, N. (2014). InVEST user's guide. *The Natural Capital Project: Stanford, CA, USA*.

Sietz, D., Ordoñez, J. C., Kok, M. T. J., Janssen, P., Hilderink, H. B. M., Tittonell, P., & Dijk, H. V. (2017). Nested archetypes of vulnerability in African drylands: Where lies potential for sustainable agricultural intensification? *Environmental Research Letters*, *12*(9), 095006. https://doi.org/10.1088/1748-9326/aa768b

Soetaert, K., & Herman, P. M. J. (2009). *A Practical Guide to Ecological Modelling: Using R as a Simulation Platform*. Springer Science & Business Media.

Thomas, C. F. G., Brain, P., & Jepson, P. C. (2003). Aerial activity of linyphiid spiders: Modelling dispersal distances from meteorology and behaviour. *Journal of Applied Ecology*, *40*(5), 912–927. https://doi.org/10.1046/j.1365-2664.2003.00844.x

Tscharntke, T., Karp, D. S., Chaplin-Kramer, R., Batáry, P., DeClerck, F., Gratton, C., Hunt, L., Ives, A., Jonsson, M., Larsen, A., Martin, E. A., Martínez-Salinas, A., Meehan, T. D., O'Rourke, M., Poveda, K., Rosenheim, J. A., Rusch, A., Schellhorn, N., Wanger, T. C., … Zhang, W. (2016). When natural habitat fails to enhance biological pest control – Five hypotheses. *Biological Conservation*, *204*, 449–458. https://doi.org/10.1016/j.biocon.2016.10.001

Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters*, *8*(8), 857–874. https://doi.org/10.1111/j.1461-0248.2005.00782.x

Tschumi, M., Albrecht, M., Entling, M. H., & Jacot, K. (2015). High effectiveness of tailored flower strips in reducing pests and crop plant damage. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1814), 20151369. https://doi.org/10.1098/rspb.2015.1369

Wajnberg, E., Coquillard, P., Vet, L. E. M., & Hoffmeister, T. (2012). Optimal Resource Allocation to Survival and Reproduction in Parasitic Wasps Foraging in Fragmented Habitats. *PLOS ONE*, *7*(6), e38227. https://doi.org/10.1371/journal.pone.0038227

Yodzis, P. (1998). Local trophodynamics and the interaction of marine mammals and fisheries in the Benguela ecosystem. *Journal of Animal Ecology*, *67*(4), 635–658. https://doi.org/10.1046/j.1365-2656.1998.00224.x

Zhang, W., & Swinton, S. M. (2009). Incorporating natural enemies in an economic threshold for dynamically optimal pest management. *Ecological Modelling*, *220*(9), 1315–1324. https://doi.org/10.1016/j.ecolmodel.2009.01.027