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Archetype models upscale understanding of natural pest control response to land-use change

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Abstract

Control of crop pests by shifting host plant availability and natural enemy activity at landscape scales has great potential to enhance the sustainability of agriculture. However, mainstreaming natural pest control requires improved understanding of how its benefits can be realized across a variety of agroecological contexts. Empirical studies suggest significant but highly variable responses of natural pest control to land-use change. Current ecological models are either too specific to provide insight across agroecosystems, or too generic to guide management with actionable predictions. We suggest getting the full benefit of available empirical, theoretical and methodological knowledge, by combining trait-mediated understanding from correlative studies with the explicit representation of causal relationships achieved by mechanistic modeling. To link these frameworks, we adapt the concept of archetypes, or context-specific generalizations, from sustainability science. Similar responses of natural pest control to land-use gradients across cases that share key attributes, such as functional traits of focal organisms, indicate general processes that drive system behavior in a context-sensitive manner. Based on such observations of natural pest control, a systematic definition of archetypes can provide the basis for mechanistic models of intermediate generality that cover all major agroecosystems worldwide. Example applications demonstrate the potential for upscaling understanding and improving prediction of natural pest control, based on knowledge transfer and scientific synthesis. A broader application of this mechanistic archetype approach promises to enhance ecology's contribution to natural resource management across diverse regions and social-ecological contexts.

Keywords

archetype, conservation biological control, crop, ecological model, land-use, landscape, natural enemy, natural pest control, pest, upscale

1 Introduction

Worldwide, sustainable agriculture relies on integrated pest management principles to reduce crop losses to pests through a combination of ecological understanding and technological advances (Oerke, 2006). Less sustainable agricultural practices, such as extensive pesticide use (Lechenet et al., 2017), can be complemented or even replaced by natural control of arthropod pests (Khan et al., 2014; Tschumi et al., 2015; Holland et al., 2017). Natural pest control in a crop field depends on the activity of natural enemies (e.g., predators and parasitoids) and the availability of host plants for the pests (Pedigo & Rice, 2014). Both factors are controlled not only by crop management in the field, but also by land-use patterns in the landscape surrounding the crop field (Landis et al., 2000; Tscharntke et al., 2005). In theory, landscapes can thus be designed to enhance natural pest control (Bianchi et al., 2006; Chaplin-Kramer et al., 2011). In practice, however, pest suppression and crop yields show inconsistent responses to changes in landscape composition and configuration across cases (Karp et al., 2018), with effects often being modified by diverse life histories, ecological settings and management regimes (Tscharntke et al., 2016; Dominik et al., 2018).

Mechanistic models, i.e., models of explicit causative agents, can provide understanding and predictions of ecological responses to environmental change, when such responses are difficult to anticipate based on observed correlation alone (Gotelli et al., 2009; Seppelt et al., 2013). Application of classical biological control has benefitted from predictions of mechanistic ecological models (Palladino, 2013). In contrast, the complexity and context-sensitivity of natural pest control (Tscharntke et al., 2016) exacerbate fundamental modeling trade-offs (Levins, 1966). Modelers have had to either sacrifice generality by realistically representing narrowly defined systems, or sacrifice realism through general models of largely theoretical systems (Alexandridis et al., 2021). Consequently, existing models do not provide realistic predictions of natural pest control at landscape to global scales, where multiple crop-pest-enemy systems are involved (Seppelt et al., 2020).

Sustainability science faces similar challenges of systems complexity, heterogeneity and context-dependence (Cox, 2014; Verburg et al., 2015; Magliocca et al., 2018). Researchers are increasingly addressing these challenges using archetype analysis to identify recurrent patterns among causal relationships that shape sustainability across cases (Eisenack et al., 2019). Recurrent patterns are then translated into archetypes, i.e., “context-sensitive, generalized models of sustainability problems, dynamics or strategies with case-level empirical validity” (Oberlack et al., 2019). For instance, Sietz et al. (2017) use similarities in social-ecological constraints to food security in the drylands of sub-Saharan Africa, to cluster a diverse set of farming systems into groups, or archetypes, of vulnerability. They thus find most of the studied area to benefit from relatively good governance, but suffer from both high remoteness and extremely dry and resource-constrained conditions. In systems with better agricultural potential, food security is mostly threatened by high erosion sensitivity and relatively severe undernourishment. Shared determinants of vulnerability to food insecurity allow for targeted, evidence-based promotion of strategies, such as sustainable agricultural intensification, and the transfer of knowledge among farming systems grouped into the same archetype. Recurrent patterns in causal relationships can be identified in complex spatial (e.g., Messerli et al., 2016) and temporal phenomena (e.g., Levers et al., 2018). We suggest use of an archetype approach to identify similar patterns in natural pest control, underpinning model development from landscape to global scales.

Using archetypes as context-specific representations of general mechanisms behind natural pest control can capture essential features of agroecosystem functioning, such as feedbacks between pesticide use and pest suppression (Normile, 2013) or non-linear effects of landscape complexity on biodiversity (Concepción et al., 2012). Defining a reasonable number of archetypes can strike the missing balance between model generality and realism (Alexandridis et al., 2021), and contribute towards resolving inconsistencies in natural pest control responses to agricultural management (Karp et al., 2018). Wider adoption of a mechanistic archetype approach can reduce the reliance of sustainability science on event-oriented phenomenological models (Meyfroidt, 2016) of questionable causality (Oberlack et al., 2019) that ignore feedbacks, and are thus associated with high policy resistance (Sterman, 2010). Moreover, predictions derived from underlying mechanisms should be more robust to changing environmental conditions than purely correlation-based predictions (Cuddington et al., 2013).

In the following three sections, we first describe general properties of an archetype modeling approach, towards the representation of geographically distant natural pest control systems that share key characteristics. Second, we demonstrate proof of concept for such an approach, by initially deriving two crop-pest-enemy archetypes from general ecological theory and available knowledge of American and African agroecosystems, and then testing the ability of the two archetypes to reproduce observed responses of natural pest control to changes in landscape composition and configuration across Europe. Finally, we draw conclusions to leverage the approach towards upscaling understanding and improving prediction in agroecosystems worldwide.

2 Strategy for defining and modeling archetypes of natural pest control

2.1 From traits to archetypes

The definition of archetypes for heterogeneous real-world systems requires that multiple cases of the studied phenomenon show similar responses to change, and that these cases share key attributes (Oberlack et al., 2019). Natural pest control may appear to respond idiosyncratically to land-use gradients, but life-history traits of pests and/or their enemies could mediate their responses to landscape characteristics in a predictable way (Segoli & Rosenheim, 2012). For instance, organisms in different systems often show similar responses to agricultural land-use change, when grouped according to their dietary, dispersal and overwintering traits (Martin et al., 2019). Similar to life-history traits, agronomic characteristics, such as spatial and temporal in-field crop diversity, are also expected to mediate natural pest control responses consistently across systems, due to converging crops and management practices worldwide (Woodward & Bohan, 2013; Malek & Verburg, 2020). The archetype approach can ultimately incorporate most agroecosystem properties linked to natural pest control, including climate, biogeography or baseline levels of landscape characteristics subject to land-use change.

Trait-mediated similarities in natural pest control responses to land-use gradients indicate the potential to group diverse agroecosystem components into archetypes that represent important processes behind observed patterns. Ecological theory enables such a mechanistic aggregation by linking mediating traits to underlying processes (Lavorel & Garnier, 2002; Lavorel & Grigulis, 2012; Pontarp et al., 2019). Specific values of functional (e.g., dietary, dispersal or overwintering) traits can thus describe context-specific roles of pests and natural enemies in general processes, such as reproduction, mortality, dispersal, predation, herbivory and environmental filtering driven by agricultural land-use (Alexandridis et al., 2021). Trait-based conceptual models of each archetype would represent the most salient roles of pests and natural enemies within these processes, in the form of system components and their relationships. The level at which systems are aggregated into archetypes should allow each set of components and relationships to represent multiple systems and, at the same time, generate predictions that agree with system-specific observations. Inclusion of agroecosystem properties other than biological traits in archetype definition will potentially improve a model's pertinence and predictive ability.

2.2 A robust modeling framework

Reaching archetypes' full potential for improved understanding and prediction requires use of rigorous techniques to translate trait-based archetype components and their relationships into model variables and their interactions (Ings et al., 2009; Zakharova et al., 2019). The resulting mechanistic models can leverage established knowledge from ecological theory to produce outputs of interest (e.g., pest population levels or crop yields) from existing or anticipated system inputs (e.g., changing landscape proportion of non-crop habitat or crop rotations). Predictions of archetype models can be compared with observed responses of natural pest control to land-use gradients across cases that correspond to each archetype. Agreement between predictions and observations would verify the archetypes' ecological basis (Overmars et al., 2007). Further model analysis can improve understanding of respective agroecosystems and indicate priority areas for future research (Pontarp et al., 2019).

A major challenge for model development is the typically high level of uncertainty associated with system structure, technical formulation and model parameterization. All of these sources of uncertainty can be constrained by limiting the complexity of ecological models

(Cuddington et al., 2013), with the added benefit of enhancing model transferability between systems (Yates et al., 2018). The first source of uncertainty, related to system structure, can be addressed by using allometric relationships to predict trophic interactions (Curtsdotter et al., 2019). The well-established use of body size can be complemented with other biological traits (Woodward & Bohan, 2013; Wood et al., 2015) to compensate for losses in predictive power as trophic complexity increases (Curtsdotter et al., 2019; Jonsson et al., 2018). The second source of uncertainty, regarding model formulation, can be tackled through ensemble forecasting by multiple models (Araújo & New, 2007). Alternatively, one may only consider "robust theorems" (Levins, 1966), i.e., shared predictions of models developed independently, but conditioned on the assumptions that define each archetype. We adopt the latter approach in selected examples (see below), as it offers more flexibility with respect to employed techniques, encompassing qualitative and quantitative models. Qualitative mathematical modeling requires no parameter estimation, thus circumventing the third source of uncertainty, associated with parameterization, which is prominent in quantitative modeling (Levins, 1998). Therefore, we independently develop qualitative and quantitative models for example archetypes, but acknowledge that these represent just two of many possible models for each.

2.3 Applying the archetype approach

Development of mechanistic models for each archetype, as illustrated in the following section, is an iterative process that can be divided into four main stages (Sterman, 2010): 1) The process starts with articulation of the problems that need to be addressed by an application of the archetype approach. Such problems typically arise from an inability of existing models to explain observations. Problem description indicates the spatiotemporal scales of the focal system and system components. 2) Subsequently, a set of hypotheses are combined into a mechanistic archetype, with the goal of explaining observations across systems. Here, previously identified system components are linked through causal relationships based on available mechanistic understanding. 3) The compiled hypotheses are then translated into system variables and their interactions, within models that aim to reproduce observed system patterns. Characteristics of these model elements can vary depending on the adopted modeling technique. 4) Finally, the models' predictive ability is tested against observations, in order to evaluate the underlying hypotheses and improve understanding of the system. These observations should be as independent as possible from sources of mechanistic understanding used in model development, in order to test the applicability of archetype models across systems.

3 Applying the archetype approach – a worked example

3.1 The problem

Individual components of natural pest control, and their responses to landscape-scale land-use, are often studied in isolation, impeding the understanding of observed patterns and reliable prediction. A recent synthesis of natural pest control observations across Europe (Martin et al., 2019) indicates significant, trait-mediated responses of involved organisms to changes in landscape composition and configuration. On one hand, natural enemies that are generalists in their feeding behavior, and move actively by flight or on the ground between crop and non-crop habitats, increase in abundance in response to increasing non-crop habitat proportion and field edge density (Table 1). This observation is consistent with our understanding of the facilitative role of landscape complexity for natural enemy dispersal and resource provision (Tscharntke et al., 2012). In contrast, dietary specialist enemies that may disperse passively by wind tend to decrease in abundance, or show no response to increasing landscape complexity. Therefore, dietary and dispersal traits appear to interactively dictate responses of natural enemies to land-use gradients, but the underlying mechanisms are not clear.

Martin et al. (2019) further observe distinct responses of pest abundances to land-use gradients, depending on the explanatory variable and the pests' overwintering strategy, i.e., in crop fields (resident) or non-crop habitats (transient). Only higher density of field edges in the landscape, but not higher proportion of non-crop habitat, leads to lower abundance of transient pests (Table 1). Resident pests, in contrast, do not respond to either land-use variable. The need of transient pests to move between crop and non-crop habitats appears to mediate their distinct responses (Tscharntke et al., 2012). However, the lack of impact by non-crop habitat amount cannot be explained by these traits alone, and may be related to other traits, such as invasive status (Tamburini et al., 2020). Elucidating differences in pest and natural enemy responses, and assessing the degree to which differences are influenced by, and feedback to, other system components, including crop yields, requires a system perspective that encompasses multiple trophic levels.

3.2 Combining hypotheses into archetypes

Among the many properties of complex agroecosystems that can shape natural pest control around the world, we here focus on a few key life-history traits. In the examples below, we present two archetypes that incorporate divergent natural enemy dietary and dispersal behaviors, and that differ in pest overwintering strategies along with system elements related to each strategy. Besides facilitating the following illustration of archetype definition and model development, this choice also assesses the ability of the archetype approach to parsimoniously reproduce markedly different pest and natural enemy responses to change, through simple, minimally different models.

Mechanistic understanding of natural pest control in several American and African agroecosystems was elicited from experts through participatory modeling techniques (Fulton et al., 2015), towards the formulation of four conceptual models (Figure 1a-d). These detailed models were then simplified into two archetypes of crop-pest-enemy interactions (Figure 1e,f). Simplification was achieved by only retaining system components whose traits appear to mediate natural pest control responses to land-use gradients in Europe (Martin et al., 2019) (Figure 1g). We then modeled theory-anticipated functional roles of organisms with specific values of these traits. We focused on these traits and system components in order to capture important mechanisms that shape natural pest control across systems, and to allow comparison of archetype model predictions with observations of pests and natural enemies with the respective trait values from geographically distant systems (Table 1). These objectives are further facilitated by using trait values that are well represented in empirical observations of natural pest control, while still defining archetypes that are general enough to allow the use of ecological theory and available expert knowledge.

The two conceptual models (Figure 1e,f) represent resident pest (termed A1) and transient pest (termed A2) archetypes. The resident pest (A1) stays in crop fields throughout the year, whereas the transient pest (A2) moves to non-crop habitats when crop resources are unavailable, or non-crop host plants are required (indicated as 'overwintering', even for systems that lack 'winter' per se). Pest populations grow by feeding on a specific crop without density dependence, i.e., reflecting the relative abundance of the crop. In-field agricultural management practices, such as intercropping or cover cropping, are not considered. Both archetypes include natural enemies that specialize on the pest's taxonomic family and disperse with the help of the wind (specialist enemy), as well as other natural enemies that feed on a variety of pest and non-pest herbivores and disperse by active movement (generalist enemy).

The specialist enemy in A1 is exposed to abundant pest prey in the crop, so its density reflects pest relative abundance. In contrast, pest migration to non-crop habitats in A2 forces the specialist enemy to either seek other prey (usually of the same family) within the crop, or move to more species-rich non-crop habitats. This hypothesis is supported by observed behavior and host range of the main braconid parasitoids of pests in the A2 example agroecosystems: the broccoli aphid in North America (Pike et al., 1999) and the fall armyworm in sub-Saharan Africa (Agboyi et al., 2020). As a result, the specialist enemy in A2 diversifies its diet with non-pest herbivores, thus reducing its dependence on the pest. We note that this group is nevertheless 'specialized' compared to generalists that are able to prey on a wide range of taxonomic families. Higher proportions of non-crop habitat in the landscape enhance organisms that rely directly on non-crop resources, i.e., generalist enemies in both archetypes and the pest in A2. Field edges also provide such resources, as well as interfaces for spill-over between and into crops, particularly to generalist enemies actively dispersing in short distances (Tscharntke et al., 2012).

3.3 Qualitative and quantitative models

We developed mechanistic models of archetypes A1 and A2, with the goal of yielding testable predictions from each set of hypotheses. We independently formulated qualitative (Figure 2a,b) and quantitative (Figure 2c,d) models based on the same basic assumptions for each archetype, but using system simplifications that are specific to the two modeling techniques. Qualitative mathematical models (Levins, 1998) represent interactions among crop yield and populations of pests and natural enemies, as well as the proportion of non-crop habitat and field edge density in the landscape (Figure 2a,b). This technique has been applied to improve understanding and prediction of classical biological control of crop pests (e.g., Levins, 1969; Levins & Schultz, 1996). Signed digraphs (networks depicting the direction and sign of interactions among variables) represent the structure of a system as a whole. The matrix representation of a signed digraph is a qualitatively specified (i.e., consisting of -1, 0 and 1) community matrix (linearization of a Lotka–Volterra equation at an equilibrium point) (Puccia & Levins, 1985). Standard analysis of this qualitative matrix (Dambacher et al., 2002) predicts the equilibrium responses of system variables to sustained increases or decreases in landscape proportion of non-crop habitat and field edge density (see Appendix S1).

We implemented quantitative models as sets of stochastic differential equations (e.g., Walton et al., 2016). For simplicity, below we describe the deterministic part of the model for archetype A1, in order to illustrate its basic structure (for the full stochastic A1 and A2 equations, which add structured variability to the deterministic models, see Figure 2c and Appendix S1):

$$\frac{dP}{dt} = aP - \mu_P P - \frac{f_s PS}{P + K_s} - \frac{f_g PG}{P + K_g} + \upsilon_p P_0 - \upsilon_p P$$

$$\frac{dS}{dt} = -\mu_S S + \frac{\varepsilon_s f_s PS}{P + K_s} + \upsilon_s S_0 - \upsilon_s S$$

$$\frac{dG}{dt} = -\mu_g G + \upsilon_g G_0 - \upsilon_g G$$

where P, S and G are the numbers of pests, specialist and generalist natural enemies in the crop, which suffer from natural mortality at rates μ_P, μ_S and μ_G, respectively. Pests have a population growth rate of a and suffer predation or parasitism at rate $\frac{f_s PS}{P+K_s}$, representing a functional type II response, which describes the ability of consumers to detect and consume the pests (Holling, 1959). For the parameters shown, the average time taken to handle a prey item is $1/f_s$, and the rate at which specialist enemies encounter prey per unit density is f_s/K_s. Specialist enemies convert consumed pests with efficiency ε_s. Similarly, generalist enemies prey on the pests at rate $\frac{f_g PG}{P+K_g}$, where f_g and K_g describe the generalist enemies' ability to detect and consume the pests. Note that, due to generalist enemies' direct reliance on non-crop resources, we assume that the population size of this natural enemy group is not increased by the consumption of pests. Although likely not often realistic, this assumption allows us to represent the distinction between generalist and specialist natural enemies with a parsimony that suits our demonstrative purposes. More generally, influence of non-crop resources is described in terms of both inflow and outflow of organisms, e.g., for pests $\upsilon_p P_0$ and $\upsilon_p P$, respectively. Parameters P_0, S_0 and G_0 represent the amounts of pests, specialist and generalist enemies, respectively, that non-crop habitats can sustain. Parameters υ_p, υ_s and υ_g describe the connectivity between crop and non-crop habitats, which is experienced differently by pests, specialist and generalist enemies, respectively. The model for archetype A2 is the same as for A1, except that we assume reproduction of specialist enemies not to depend on the pests, as pests overwintering in non-crop habitat exposes natural enemies to a more diverse diet. This is equivalent to assuming $\varepsilon_s = 0$ (Figure 2d).

Changes in landscape proportion of non-crop habitat and field edge density are imposed on the A1 quantitative model by changing G_0 in the former case and both G_0 and υ_g in the latter. This is the same in A2, except that changes in proportion of non-crop habitat are imposed by also changing P_0. Changes in G_0 and P_0 represent impacts of varying the quality or quantity of non-crop habitat on generalist natural enemies and pests. Quality could be enhanced, e.g., by habitat improvement, but changing the quantity of non-crop habitat might reduce crop area. Our models represent pest and natural enemy density within the crop, and, therefore, do not explicitly account for a trade-off between the amount of non-crop habitat and crop area. Values of model parameters were varied within realistic ranges, based on expert knowledge of representative systems worldwide (see Appendix S1).

3.4 Model testing – shared qualitative/quantitative predictions

Identical main hypotheses behind each archetype's pair of models resulted in consistent predictions for both qualitative and quantitative models, except for responses of the resident pest in A1 to changes in landscape characteristics (Table 2). This discrepancy stems from the quantitative model's explicit representation of crop inflow and outflow of organisms, which carries more information, but requires additional hypotheses on arthropod dispersal. Still, the difference is marginal, as the qualitative model predicts no change, compared to quantitative predictions of a slight decrease (see Appendix S1). Below, we assess the models' underlying hypotheses and their transferability across systems, by comparing model predictions in response to varied parameter values with observations of natural pest control systems in Europe along land-use gradients (Martin et al., 2019).

Shared qualitative and quantitative predictions for both the resident (A1) and transient (A2) pest archetypes (Table 2) agree with observations of increasing generalist enemy abundances in response to increasing proportion of non-crop habitat and field edge density in the landscape (Table 1). A1 models further show the specialist enemy being outcompeted by the generalist, and hence reducing in numbers. In contrast to A1, access to diverse resources in A2 allows the specialist enemy to maintain its abundance. Therefore, natural enemies that are considered broadly as specialists, but exhibit varying degrees of specialization in response to different pest overwintering strategies, show contrasting responses to the same changes in landscape characteristics. These predictions may explain the weak signal from impacts of land-use gradients on the combined, but of varying specialization degree, group of specialist enemies across Europe found by Martin et al. (2019).

A1 predictions of lower specialist enemy abundance with increasing landscape complexity lead to less effective control of the pest, despite increasing generalist enemy abundance (Table 2). The predicted lack of substantial pest responses agrees with observations of no significant change in resident pest abundances in response to varying landscape characteristics (Table 1). A2 models predict no impact of non-crop habitat changes on the pest despite its use of non-crop resources, due to conflicting influences directly on the pest (positive) and through the generalist enemy (negative). In contrast, increasing field edge density enhances the generalist enemy but not the pest, leading to effective pest control and lower transient pest abundance. The predicted distinct responses of transient pests to changes in landscape composition and configuration are a prominent pattern in observations across Europe (Martin et al., 2019). Consequently, reducing field sizes in landscapes dominated by the transient pest archetype, such as Swedish cropland with spring-sown cereals attacked by aphids (Östman et al., 2003), is a land-use strategy predicted to sustain crop yields independently from other management practices (see Appendix S1).

To summarize, our example application illustrates the use of crop-pest-enemy archetypes for context-sensitive representation of general ecological mechanisms. Different assumptions regarding pests' overwintering strategy result in striking differences in predicted responses to land-use gradients, in agreement with observations that transcend geography. Potential benefits extend beyond elucidating inconsistencies in observed patterns of natural pest control, towards generating robust predictions about quantities, such as avoided pest damage or increased crop yield, that are difficult to measure accurately across agroecosystems (Holland et al., 2017).

4 Leveraging archetypes to model natural pest control at landscape to global scales

4.1 Exploiting the potential of archetypes

The examples presented above show how crop-pest-enemy archetypes can mobilize a broad range of available knowledge to explain apparently contradictory responses of natural pest control to the same management intervention. We transfer expert knowledge across agroecosystems and synthesize general ecological theory, to build archetypes that occupy an intermediate level of generality between these two extremes (Meyfroidt et al., 2018). The resulting mechanistic understanding applies to several systems, but it is context-specific, hence more nuanced and with a greater potential for consistency across cases than general theories (Levins, 2005). For example, we show how exploitative competition among natural enemies can be rendered context-sensitive by divergent overwintering strategies of the pests.

The context of application can be extended beyond functional traits of focal organisms, to include variables such as baseline landscape characteristics or agricultural management regimes. For instance, simpler landscapes can be assumed to favor organisms represented by the resident pest archetype. More complex landscapes could similarly be associated with the transient pest archetype. Overrepresentation of each set of organisms in the respective landscape context would justify targeted application of the two archetypes to systems with both specific trait values and baseline landscape characteristics. In this case, predicted responses of specialist enemies from the A1 and A2 archetype models (Table 2) match observations from relatively simple and complex landscapes, respectively (Table 1). Therefore, defining the context of application in terms of functional traits and landscape complexity can provide a testable explanation for variable responses of specialist enemies to land-use gradients across Europe (Martin et al., 2019).

Mathematically rigorous, testable explanations of seemingly idiosyncratic patterns, as illustrated by the example archetypes, are required to mainstream natural pest control in agricultural management worldwide (Kleijn et al., 2019). By facilitating application of mechanistic modeling in more cases, archetypes can explain inconsistencies in responses of natural pest control to changing landscapes (Karp et al., 2018), and indicate empirical research that distinguishes between competing hypotheses. As land-use and climate change are predicted to increase crop losses to insect pests (Deutsch et al., 2018) and hamper natural pest control worldwide (Raven & Wagner, 2021), mechanistic archetype models can increase predictive robustness, by considering not only direct biological impacts, but also modulating biotic interactions and feedbacks with agricultural management.

Agricultural landscapes often consist of mosaics of different crops that host pests and natural enemies with different characteristics. Archetypes representing major crop-pest-enemy combinations provide the building blocks for upscaling natural pest control modeling across landscapes. Predictions of farming-system-wide natural pest control potential will facilitate management of this ecosystem service through the design of agricultural landscapes, as well as inclusion of natural pest control in frameworks that bridge ecology and agro-economics (e.g., Seppelt et al., 2020). An archetype approach to modeling natural pest control would be a valuable addition to existing tools that use detailed land-use information to map ecosystem services across 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).

4.2 Towards a global set of natural pest control archetypes

Coordination of archetype definition across agroecosystems will generate archetypes with precisely assigned context of application, and minimize the effort required for development of their models. We suggest a research agenda that builds on our examples to operationalize the definition of archetypes globally, by taking the following steps:

a) Identify determinant system attributes. Example archetypes developed here are based on evidence on the mediating role of life-history traits in natural pest control responses to land-use gradients in Europe. Similarly, we can identify functional traits, landscape characteristics and other attributes that play a significant role in the behavior of natural pest control worldwide, and collect relevant values across agroecosystems (Figure 3a). A modeled system can thus expand from a network of interacting organisms to a more inclusive set of agroecological components. Co-occurring crops, pests and natural enemies from recently compiled large-scale datasets (e.g., Karp et al., 2018; Dainese et al., 2019) provide a starting point for identification of natural pest control systems worldwide. It should be possible to explicitly link system attributes to specific processes underlying the behavior of natural pest control, based on ecological theory and expert knowledge (Lavorel et al., 2007). Empirical studies that build consensus on drivers of behavior across systems and identify attributes with cross-system explanatory potential (e.g., Martin et al., 2019; Tamburini et al., 2020) are a key resource for this task.

b) Reduce dimensionality of collected information. In the examples above, expert knowledge of diverse agroecosystems is rather arbitrarily simplified using trait-based theoretical expectations. In a more systematic approach, the dimensionality of the previously collected information can be reduced using multivariate statistical techniques (Figure 3b). The selection of specific techniques will depend on the nature of collected information. For instance, functional traits of crops, pests and natural enemies can be used to cluster a diverse set of organisms into archetypes with distinct combinations of trait values. These values should describe respective organisms' roles in trait-associated processes, such as feeding, dispersal and overwintering in the examples above. These processes can then inform the mechanistic representation of each archetype in terms of system components and their relationships (Boulangeat et al., 2012). Hierarchical classification of agroecosystem components linked to natural pest control (Sietz et al., 2017) has the advantage of flexible, case-specific determination of the aggregation level in subsequent applications, depending on the model output or spatiotemporal scales of interest and knowledge availability.

c) Set rules for definition of archetypes from attributes. The last step should establish a standardized, dynamic set of rules for the definition of archetypes and their models from combinations of trait values, landscape characteristics or other system attributes (Figure 3c). These rules will allow researchers to place any real-world system within or, if necessary, outside the previously reduced space of system attributes. In the case of systems from world regions that are underrepresented in the collected information, expert knowledge can be employed to either explore close associations with existing system groups, or independently develop conceptual models, similar to our example archetypes. In either case, rules should ensure the translatability of system-specific attributes into system components and relationships, towards model variables and interactions. The four stages of model development outlined in section 2.3 provide a potential blueprint for establishing such a rule set. Observed responses of natural pest control to land-use gradients across systems (e.g., Karp et al., 2018; Dainese et al., 2019) can then be compared with qualitative and/or quantitative model predictions, to assess each archetype's validity. An iterative process of model development and validation could identify the optimal set of archetypes worldwide (Hérault, 2007; Alexandridis et al., 2017).

5 Outlook on archetypes

As the scope of natural pest control archetypes broadens, data providing their empirical basis can take the form of a 'living' database of crop-pest-enemy combinations and associated traits, along with environmental variables, such as landscape or climate characteristics, management regimes and biogeographic regions. A consistent coding for this database will lower the bar for empirical researchers and practitioners willing to contribute with case-specific knowledge. For instance, climate scientists, geographers, agronomists, entomologists and farmers from different parts of the world will be able to feed information on rainfall, land-use, crop yield, pest abundance and pesticide application into the database in a standardized format. Data analysis will allow definition of archetypes at different scales, e.g., regional or global. Experts will then be able to use available information to place a natural pest control system of interest among identified archetypes, and apply the respective model or develop a new one. Such data will facilitate dynamic archetype definitions and systematic evaluation of the mechanistic understanding that archetypes are hypothesized to carry. Keeping this framework sufficiently flexible to constantly incorporate new knowledge will require an iterative and participatory research axis involving experts and practitioners.

The need for general modeling approaches that account for the context of application extends to many environmental areas, including major land-use issues, such as deforestation and desertification, and their interactions with climate change (Dale, 2003). An enrichment of the archetype approach with ecological principles promises to improve the mechanistic basis of models of land-use archetypes, and broaden their predictive scope (Václavík et al., 2013). A wide adoption of an archetype approach to ecological modeling will increase the use of models with similar basic assumptions and comparable output. The ensuing potential for knowledge synthesis is particularly needed in the fragmented discipline of ecology (McGill, 2010). Furthermore, context-specificity reduces the effective degrees of freedom, allowing for more robust knowledge transfer. This is crucial in case of persistent data shortages, e.g., in regions where the highest projected impacts from cumulative environmental change coincide with the least studied social and ecological systems (Beckmann et al., 2019).

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Table 1. Observed trait-mediated responses of pest and natural enemy abundances to changes in landscape composition and configuration across Europe, including different baseline levels of these landscape characteristics, in cases where such differences were linked to significant divergence in abundance responses (Martin et al., 2019). Pests overwinter in crop fields (resident) or non-crop habitats (transient). Natural enemies of pests disperse passively or actively; the former have narrow (specialist) and the latter broad (generalist) feeding preferences. Responses of these organisms to increasing landscape proportion of non-crop habitat and density of field edges are given as increases and decreases. Ellipses (…) are used to illustrate lack of responses.

Abundance responses	Increasing non-crop habitat	Increasing edge density
Resident pest	…	…
Transient pest	…	Decreasing
Passively dispersing specialist enemy		
In landscapes with relatively low density of field edges	Decreasing	
In landscapes with relatively high density of field edges	…	
In landscapes with relatively low proportion of non-crop habitat		Decreasing
In landscapes with relatively high proportion of non-crop habitat		…
Actively dispersing generalist enemy	Increasing	Increasing

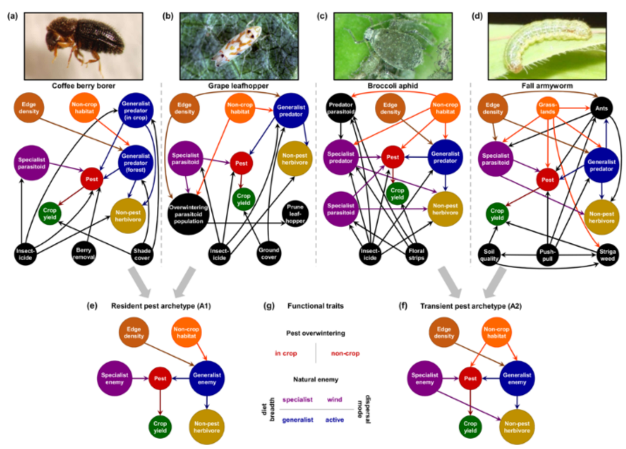
Table 2. Shared qualitative and quantitative predictions from models of archetypes A1 and A2 in response to parameter variation within globally realistic value ranges. Equilibrium responses of pest, specialist and generalist enemy abundances to imposed increases in landscape proportion of non-crop habitat and density of field edges are given as increases and decreases. Predictions of no response are illustrated with ellipses (…). Tildes indicate diverging response predictions (here, qualitative models predict no change, while quantitative models predict slightly decreasing abundances).

Abundance responses		Increasing non-crop habitat	Increasing edge density
Resident pest archetype (A1)	Pest	~	~
	Specialist enemy	Decreases	Decreases
	Generalist enemy	Increases	Increases
Transient pest archetype (A2)	Pest	…	Decreases
	Specialist enemy	…	…
	Generalist enemy	Increases	Increases

Figure 1. Conceptual models based on expert knowledge of the systems of natural control of (panel a) the coffee berry borer (*Hypothenemus hampei*) in Latin America, (panel b) the grape leafhopper (*Erythroneura* spp.) and (panel c) the broccoli aphid (*Brevicoryne brassicae*) in North America, and (panel d) the fall armyworm (*Spodoptera frugiperda*) in sub-Saharan Africa. Arrows indicate diverse causal relationships, pointing from cause to effect, and colors identify system components with pertinent similarities. Conceptual models of archetypes A1 and A2 (panels e and f) aim at representing the defining components of multiple systems with respect to natural pest control and crop yield responses to changes in landscape characteristics (non-crop habitat proportion and field edge density). Model simplification is based on theoretical expectations regarding the role of pest overwintering, and enemy dietary and dispersal traits in natural pest control (panel g). See main text for details. Photo credits: (a) Daniel S. Karp, (b) Jack Kelly Clark, courtesy University of California Statewide IPM Program, (c) Andrew Jensen and (d) Yann Clough.

Figure 2. Qualitative and quantitative modeling of archetypes A1 (left-hand panels) and A2 (right-hand panels), based on the respective conceptual models (see Figure 1e,f). Note that both modeling approaches represent a subset of the conceptual models' variables considered as necessary. Qualitative mathematical models (a and b) are shown as signed digraphs, i.e., networks of directed interactions, including loops of self-effects, with arrows for positive and dots for negative signs. Stochastic differential equations (c and d) represent the dynamics of pest (P), specialist (S) and generalist (G) enemy populations. For details, see the main text. Stochastic terms are shown in gold font, where $dB_i(t)$ represent Gaussian white noise and, for each t and $i = 1, \dots 12$, are independent draws from $N\left(0, \sqrt{dt}\right)$.

Figure 3. Steps towards operationalizing the definition of archetype models of natural pest control. First, (a) general attributes of natural pest control systems that determine their behavior should be identified, and relevant values collected across systems. A 'living' database will allow the contribution of empirical information by researchers around the world. Then, (b) multivariate statistical techniques will reduce the dimensionality of the collected information, by identifying groups of systems, potentially structured hierarchically, that share key attributes. Mechanistic understanding based on ecological theory and expert knowledge will link group attributes to specific ecological processes. Finally, (c) a standardized set of rules should use these processes to define archetypes for all combinations of system attribute values. These archetypes will comprise system components and their relationships, which will be translated into elements of mechanistic models for all major agroecosystems. Validation of these models against independent observations will evaluate available mechanistic understanding, and dictate the need to re-define system groups and their archetype models.



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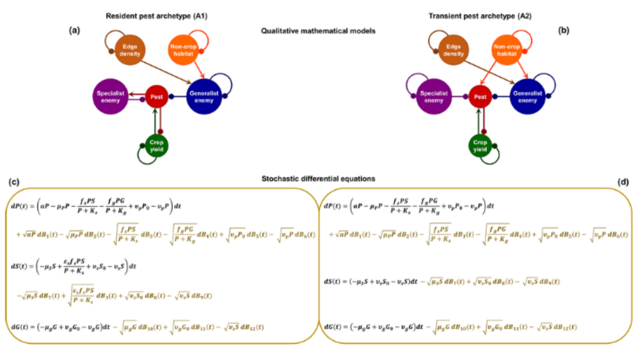

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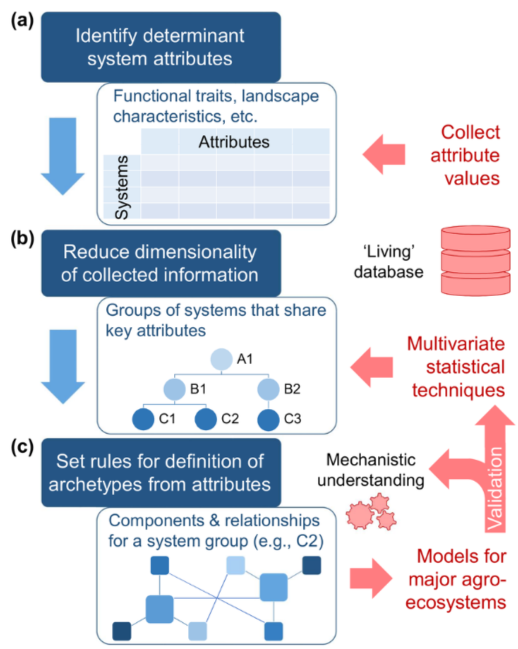

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