



Review

Models of natural pest control: Towards predictions across agricultural landscapes

Nikolaos Alexandridis^{a,*}, Glenn Marion^b, Rebecca Chaplin-Kramer^{c,d}, Matteo Dainese^e, Johan Ekroos^{a,1}, Heather Grab^f, Mattias Jonsson^g, Daniel S. Karp^h, Carsten Meyer^{i,j,k}, Megan E. O'Rourke^l, Mikael Pontarp^m, Katja Poveda^f, Ralf Seppelt^{k,n}, Henrik G. Smith^{a,m}, Emily A. Martin^{o,2}, Yann Clough^{a,2}

^a Lund University, Centre for Environmental and Climate Science (CEC), Lund, Sweden

^b Biomathematics and Statistics Scotland, Edinburgh, UK

^c Stanford University, Woods Institute for the Environment, Natural Capital Project, Stanford, USA

^d University of Minnesota, Institute on the Environment, St. Paul, USA

^e Eurac Research, Institute for Alpine Environment, Bozen/Bolzano, Italy

^f Cornell University, Department of Entomology, Ithaca, USA

^g Swedish University of Agricultural Sciences, Department of Ecology, Uppsala, Sweden

^h University of California – Davis, Department of Wildlife, Fish, and Conservation Biology, Davis, USA

ⁱ German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

^j University of Leipzig, Faculty of Biosciences, Pharmacy and Psychology, Leipzig, Germany

^k Martin Luther University Halle-Wittenberg, Institute of Geoscience & Geography, Halle (Saale), Germany

^l Virginia Polytechnic Institute and State University, Department of Horticulture, Blacksburg, USA

^m Lund University, Department of Biology, Lund, Sweden

ⁿ Helmholtz Centre for Environmental Research – UFZ, Department of Computational Landscape Ecology, Leipzig, Germany

^o Leibniz University Hannover, Institute of Geobotany, Zoological Biodiversity, Hannover, Germany

HIGHLIGHTS

- We review models of natural pest control assessing usability across agroecosystems.
- Ecological complexity and context sensitivity impede correlation-based predictions.
- A trade-off of generality with realism hinders mechanistic modeling across systems.
- Similarities in causal relationships can inform contextually bound generalizations.
- This framework will allow knowledge synthesis and transfer in less studied regions.

ARTICLE INFO

Keywords:

Crop
Ecological modelling
Land use
Landscape
Natural control
Pest

ABSTRACT

Natural control of invertebrate crop pests has the potential to complement or replace conventional insecticide-based practices, but its mainstream application is hampered by predictive unreliability across agroecosystems. Inconsistent responses of natural pest control to changes in landscape characteristics have been attributed to ecological complexity and system-specific conditions. Here, we review agroecological models and their potential to provide predictions of natural pest control across agricultural landscapes. Existing models have used a multitude of techniques to represent specific crop-pest-enemy systems at various spatiotemporal scales, but less wealthy regions of the world are underrepresented. A realistic representation of natural pest control across systems appears to be hindered by a practical trade-off between generality and realism. Nonetheless, observations of context-sensitive, trait-mediated responses of natural pest control to land-use gradients indicate the potential of ecological models that explicitly represent the underlying mechanisms. We conclude that modelling

* Corresponding author at: The Ecology Building, Sölvegatan 37, 22362 Lund, Sweden.

E-mail address: nikos.alexandridis@cec.lu.se (N. Alexandridis).

¹ Current address: University of Helsinki, Department of Agricultural Sciences, Helsinki, Finland.

² These authors share senior authorship.

<https://doi.org/10.1016/j.biocontrol.2021.104761>

Received 31 December 2020; Received in revised form 28 August 2021; Accepted 1 September 2021

Available online 3 September 2021

1049-9644/© 2021 The Authors. Published by Elsevier Inc. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

natural pest control across agroecosystems should exploit existing mechanistic techniques towards a framework of contextually bound generalizations. Observed similarities in causal relationships can inform the functional grouping of diverse agroecosystems worldwide and the development of the respective models based on general, but context-sensitive, ecological mechanisms. The combined use of qualitative and quantitative techniques should allow the flexible integration of empirical evidence and ecological theory for robust predictions of natural pest control across a wide range of agroecological contexts and levels of knowledge availability. We highlight challenges and promising directions towards developing such a general modelling framework.

1. Introduction

Crop yield losses to invertebrate pests worldwide are substantial (e.g., up to 20% of major grain crops is lost to insects) and predicted to increase with ongoing climate warming (Deutsch et al., 2018). Top-down 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/yr in the US alone (Losey and Vaughan, 2006). Crop pests can also be controlled bottom-up, by the availability of their host plants in space or time (Pedigo and Rice, 2014). This bidirectional natural pest control holds the potential to at least partially 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). However, similar to the transition from calendar-based insecticide application to integrated pest management (Palladino, 2013), mainstreaming natural pest control in global agriculture would benefit from reliable predictive tools, applicable across a variety of management contexts and agroecosystems (Kleijn et al., 2019).

Applicable tools exist to model and map a range of ecosystem services, including crop pollination by invertebrates, based on detailed land-use information and biophysical characteristics of different land covers (Sharp et al., 2014). Similar to the case of pollinators and pollination, land uses surrounding agricultural fields affect the abundance and diversity of natural enemies and their potential to provide ecosystem services (Tschardt et al., 2005). In contrast to pollination, however, natural pest control involves an additional trophic level. As such, complex interactions between natural enemies, pests and crops cause diverse outcomes for crop damage and yields across agroecosystems (Tschardt et al., 2016; Karp et al., 2018). This ecological complexity has so far restricted the potential to consistently link specific landscape characteristics to enhanced pest suppression (Englund et al., 2017), with efforts to assess natural pest control based on spatially explicit land-use information having limited predictive scope (e.g., Rega et al., 2018). Consequently, we lack general models predicting the natural pest control potential of agricultural landscapes, while the transferability of pertinent ecological models outside the specific cases for which they were developed is unknown (Seppelt et al., 2020).

Here, we evaluate the ability of existing models to predict the interactions between natural enemies, pests and crops in response to land-use changes across agroecosystems. To this end, we review models of natural control of invertebrate pests, assessing the capabilities of different approaches and techniques, with a particular focus on models that represent ecological complexity. We examine the systems and processes that are modelled, as well as the main properties of model output. Based on our review, we identify and discuss major challenges and highlight promising directions for the development of models that predict natural pest control responses to agricultural land use across agroecosystems. Our ultimate goal is to help design a modelling framework for natural pest control that facilitates the transfer and synthesis of knowledge worldwide.

2. Literature search

We do not aim for an exhaustive review of models of natural pest control, but rather for a description of the available modelling approaches, with a focus on land-use and landscape-scale studies. A search

of the Core Collection of ISI Web of Science over all available years 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). Repeated follow-up review of search results suggests no qualitative shift from our conclusions. We reviewed the abstracts of the collected publications, discarding non-modelling studies as well as studies of non-crop systems, importation or augmentative biocontrol and weeds or vertebrate pests. We retained 172 studies modelling natural control of invertebrate pests in agricultural systems, published between 1978 and 2018. A list of the reviewed publications and collected information about their models are provided in the [Supplementary Material](#). Of the respective models, 105 make predictions that stem directly from correlations among system components (correlative), and 67 are based on the explicit representation of causative agents and their interrelations (mechanistic) (Fig. 1a). Although this distinction represents only extremes of the correlation-process continuum (Dormann et al., 2012), in practice, models can often be meaningfully divided into these two categories, if only in relative terms.

In the following sections, we present a more detailed examination of the collected mechanistic models of natural pest control. Although correlative and mechanistic approaches share certain strengths and weaknesses, they can complement each other in ecological research. Dormann et al. (2012) illustrate the benefits of this approach in species distribution modelling, noting that a recent decline in the number of mechanistic relative to correlative applications calls for further examination of the specific capabilities of mechanistic modelling. A similar trend in our results (Fig. 1b) supports such a focused examination in the context of natural pest control. Furthermore, mechanistic models typically have the benefit of transparent assumptions and easy interpretation (Cuddington et al., 2013). These properties warrant a deeper look into the potential of mechanistic models to address inconsistencies in observed responses of natural pest control to land-use changes (Karp et al., 2018) and indications of complex mechanisms as the underlying causes of variation (Martin et al., 2019). Efforts to better understand and predict natural pest control may thus benefit from mechanistic modelling, just as other ecological fields, such as biodiversity research (Urban et al., 2016; Pontarp et al., 2019a,b; Hagen et al., 2021), have benefitted from the development of novel mechanistic frameworks.

Mechanistic models of natural pest control were separated into three approaches (Fig. 1a), representing strategies that produce models with different characteristics. “Specific” models are developed to represent narrowly defined crop-pest-enemy systems, and are therefore assumed to lack generality. “Theoretical” models focus on essential features underlying the behaviour of natural pest control across systems, hence are assumed to be general. “Conceptual” models represent causal relationships that may apply to several systems, without quantifying them. This approach is considered as general, but also as the only one unable to generate precise predictions. We expect a trade-off between generality, precision and realism, in that in practice ecological models have to sacrifice one of these elements to retain the other two (Levins, 1966). This constraint is linked to the statistical problem of overfitting, in which appropriate model complexity is limited by the informativeness of available data (Dormann et al., 2012). We tested the expected trade-off using the number of modelled processes as a proxy for a model’s ability to represent the breadth and detail of real-world phenomena. We

built a list of potential ecological, agronomic and economic processes, and listed for each model which of these processes are explicitly represented. These general processes can be modelled at different levels of organization, using mathematical or algorithmic expressions of varying complexity, along with the respective model parameters. Consistent nomenclature was thus favoured over publication-specific terminology. The same principle was followed for the identification of main output variables. In contrast, publication terminology was adopted when assigning a set of represented crop, pest and natural enemy organisms to each model. As a result, organism categorization reflects the diversity of the reviewed publications and corresponds to various taxonomic or functional levels of biological organization. Finally, for each mechanistic model, we documented the modelling techniques employed, the spatiotemporal extent and resolution, plus spatial and stochastic characteristics.

3. Correlative models

The main objective of the correlative models captured by our selection criteria is to explore patterns and test general theories that relate

natural pest control to surrounding land use, at scales ranging from fields to regions. The search argument resulted in models primarily applied at landscape or larger scales. Early models describe relationships between predictor and response variables based on multiple linear regression (e.g., Downie et al., 1999), with random effects eventually included in mixed-effects models (e.g., Clough et al., 2005). Generalized linear (e.g., Dong et al., 2015) and additive models (e.g., Cotes et al., 2018) are increasingly used to relax statistical assumptions. More specialized techniques, such as autoregression (Bommarco et al., 2007), maximum entropy (Ceccarelli et al., 2015) and redundancy analysis (Egerer et al., 2018), are employed for temporal, spatial and community modelling, respectively. Structural equation models are at the interface between correlative and mechanistic modelling, as they allow for a significant increase in the former's mechanistic basis, towards investigating interaction networks (e.g., Diekötter et al., 2007).

Most correlative models of natural pest control expect that compositional (e.g., proportion of non-crop habitat) and/or configurational complexity (e.g., field edge density) of the landscape surrounding a field enhances pest suppression. Two mechanisms are thought to underlie these general expectations, in spite of potential inconsistencies caused

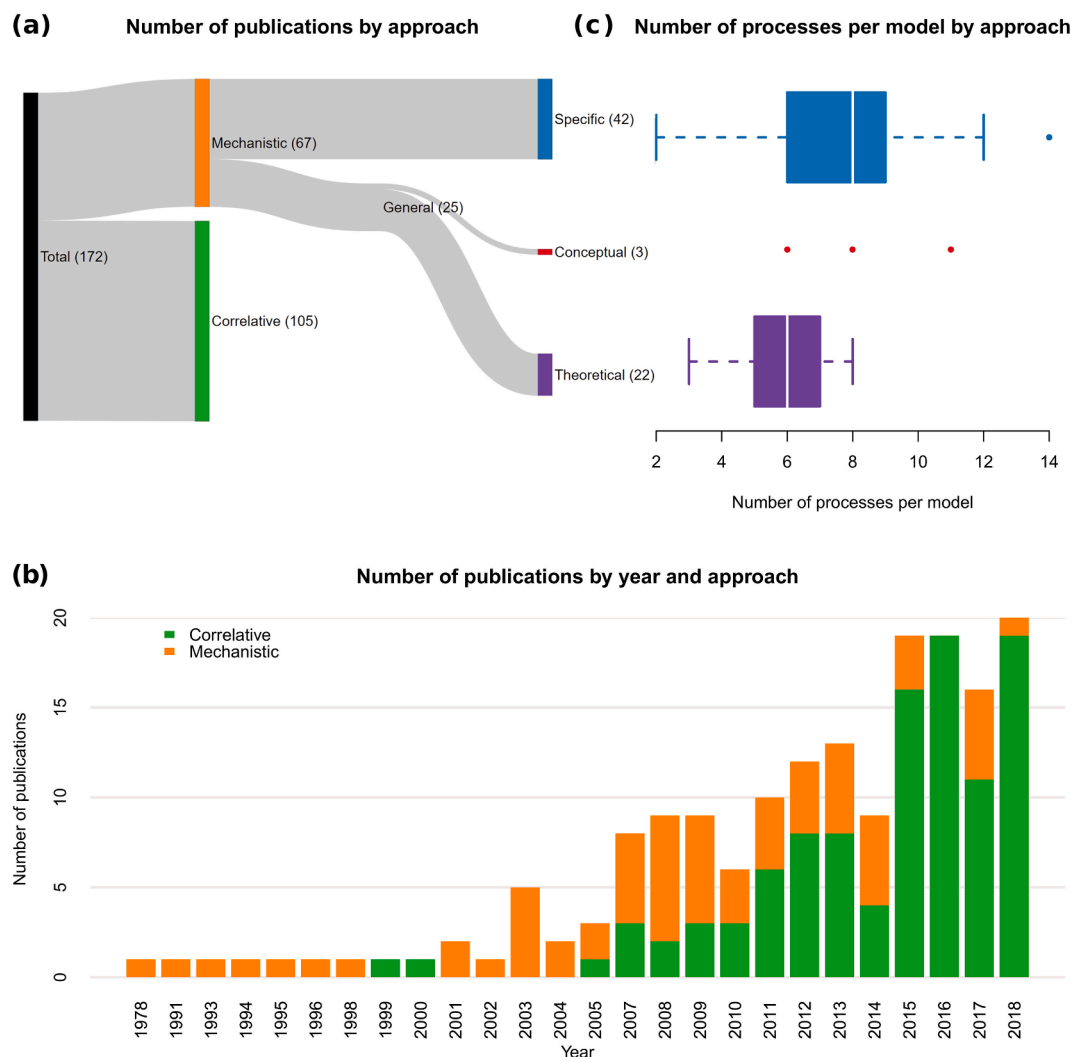


Fig. 1. (a) Number of reviewed publications following contrasting modelling approaches, sequentially separated based on their mechanistic basis, generalization potential and approach to generality (Allaire et al., 2017). (b) Number of reviewed publications featuring correlative and mechanistic models for each publication year. (c) Number of processes represented per reviewed model (for a list of processes, see Fig. 3a), among models following three contrasting mechanistic approaches: specific representation of a crop-pest-enemy system or general representation of natural pest control through conceptual or theoretical modelling. Box bands, lower and upper edges represent the 2nd, 1st and 3rd quartiles, respectively. Whiskers extend to the most extreme values within $1.5 \times$ the interquartile range from the box; more extreme values are indicated with dots (R Core Team, 2019).

by ecological complexity and context-sensitivity (Tschamtk et al., 2016). First, landscape simplification into extensive crop monocultures is expected to enhance specialist pest abundance and dispersal, by increasing the density of their host plants (Root, 1973). Second, compositional and configurational complexity is thought to enhance the activity of natural enemies by providing them with limiting resources,

such as nesting sites and alternative food sources (Landis et al., 2000), as well as resource continuity (Juliano and Gratton, 2020; Schellhorn et al., 2015). Meta-analyses of empirical studies have investigated the generality of these expectations, revealing positive effects of landscape complexity on the diversity and abundance of natural enemies but, critically, rather inconsistent responses of pest suppression and crop

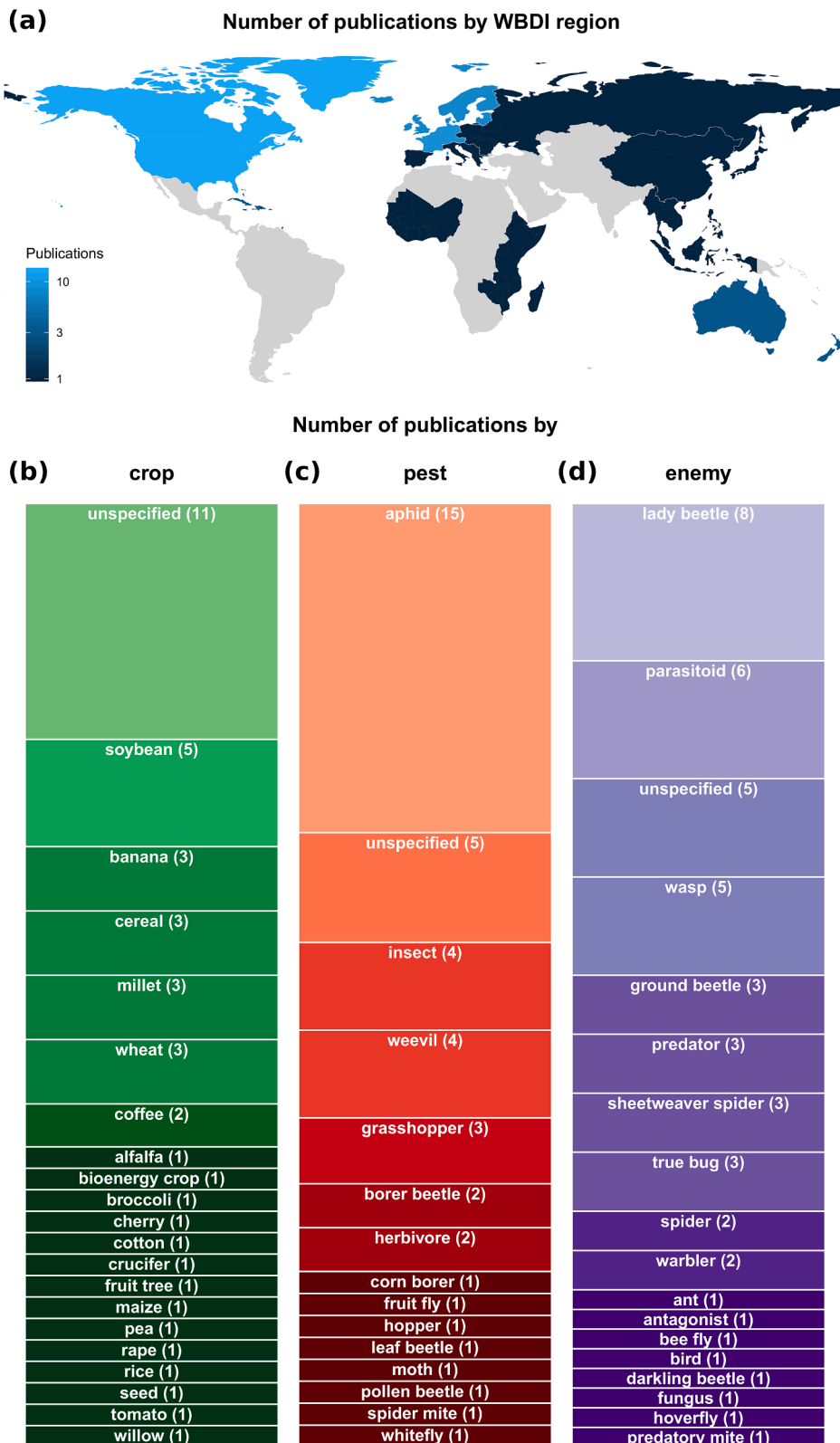


Fig. 2. Number of reviewed publications featuring mechanistic models of specific systems (a) geographically belonging to each region defined in the World Bank Development Indicators (WBDI) (Arel-Bundock et al., 2018), and representing different (b) crop, (c) pest and (d) natural enemy organisms (Wickham, 2016). Certain models do not represent all categories of organisms; others represent more than one organism in a category, and, in some cases, organisms belonging to a category are part of the model but not further identified (indicated as unspecified). Organism names may not be independent, as they reflect the nomenclature of each publication.

yield (Bianchi et al., 2006; Chaplin-Kramer et al., 2011). Analysis of recent correlative models extending to global scales indicates similar inconsistencies, suggesting the need for closer investigation of complex, context-sensitive ecological mechanisms that may lie behind them (Karp et al., 2018). Variability in responses seems to be partly mediated by functional traits of the involved organisms (Martin et al., 2019; Tamburini et al., 2020).

As a unified understanding of natural pest control currently eludes us, correlative approaches for predictive purposes require the development of distinct models for systems of interest. This task involves an extensive collection of data, including an array of land-use, agronomic, abiotic and biotic environmental variables. The logistic difficulties involved in such data collection hinder the development of predictive models for most agroecosystems. Furthermore, correlative models typically make several assumptions, such as stationarity of ecological processes or lack of adaptability, which may not hold in novel or non-equilibrium contexts often associated with environmental change (Dormann, 2007).

4. Mechanistic models

4.1. Different approaches to mechanistic modelling

Most of the reviewed mechanistic models are specific (Fig. 1a), i.e., aim at a highly realistic representation of observed crop-pest-enemy combinations. Such models include the largest number of processes per model (Fig. 1c), and typically require significant amounts of data. For instance, in order to model natural pest control of the Senegalese grasshopper along a latitudinal transect of the Sahel, Axelsen (2009) represented crop and natural vegetation, pest population dynamics and migration, competition with another grasshopper, predation by invertebrates and birds, climatic influences and different pesticide treatments. The model represents 14 ecological and agronomic processes in space and time and requires input for tens to hundreds of parameters, depending on the objectives of the application. Not surprisingly, specific models of natural pest control have only been developed for a few combinations of crops, pests and enemies around the world (Fig. 2a). These models originate (based on first author affiliation) exclusively in North America, Europe, Oceania and East Asia, the world regions with the highest GDP per capita (World Bank DataBank, 2018). The modelled systems also represent the Caribbean, South-East Asia and West and East Africa, but with a relatively small number of studies in these regions. The remaining regions are not represented at all (Fig. 2a). There is considerable variability among the represented crops (Fig. 2b). Aphids are by far the most represented pests (Fig. 2c), while enemies are, to a lesser extent, dominated by lady beetles, parasitoid wasps and spiders (Fig. 2d).

The fewer theoretical models of natural pest control (Fig. 1a) aim at increasing general understanding and predicting fundamental aspects of pest control dynamics across many systems. For instance, Hambäck et al. (2007) used a rather simple model of pest population growth and migration to reproduce broadly observed patterns of field area – aphid density relationships, and assess the impacts of nutrient availability and natural control, irrespective of absolute population numbers observed in each case. The collected theoretical models represent, on average, the fewest processes per model among the three approaches (Fig. 1c), and they consistently lack an explicit or implicit representation of space. Even when investigating spatial factors, such as field area, modelled processes are approximated by averaging their effects over space. A focus on a few crucial processes, as well as on general patterns, such as area – density relationships, instead of absolute numbers, results in a mismatch with observed phenomena, in terms of both system representation and predictive scope. This mismatch is exacerbated by the complexity of modelled phenomena, limiting the ability of theoretical models captured in our review to inform policy or management of natural pest control.

In contrast to quantitative modelling approaches, conceptual models require minimum model specification and no parameter estimation. By evading these data-hungry modelling steps that can narrow model applicability and increase uncertainty (Dormann et al., 2012), conceptual models gain higher potential for representations that are both general and holistic, in terms of the number (Fig. 1c) and nature of their processes (Levins, 1998). In one of the three reviewed conceptual models, Ekroos et al. (2014) developed a highly abstract but comprehensive representation of the processes that control the effectiveness of agri-environment schemes for biodiversity conservation and provision of ecosystem services, including natural pest control, in a variety of agroecosystems. The abstract nature of such models typically hinders translating their representation of a system into quantified responses to multifaceted socioecological change, preventing model analysis towards improved understanding and reliable predictions.

4.2. Components, spatiotemporal scale and resolution

Various techniques have been applied for mechanistic modelling of natural pest control, involving trade-offs between a model's ability to represent different processes (or formulation flexibility), ease of analyzing model output (or analytical tractability) and frugality in the use of computational resources (or algorithmic efficiency). None of the identified techniques appears to possess all of these qualities (Table 1). Spatially explicit and stochastic representations are particularly susceptible to these trade-offs, as they consistently lack analytical tractability, trading off formulation flexibility for algorithmic efficiency. Most models are dynamic, either continuous in time or with discrete steps. Time steps vary from 1 s (Lester et al., 2005) to 1 yr (Kean and Barlow, 2001), and the temporal extent varies from 1 min (Banks and Yasenak, 2003) to 600 yr (Bianchi et al., 2009). The majority of the models represent spatial processes explicitly or implicitly, with the rest averaging their effects over space. Spatial resolution varies from 0.01 mm (Lester et al., 2005) to 500 m (Milne et al., 2015) and spatial extent from 4.5 m (Provencher and Riechert, 1994) to 700 km (Milne et al., 2015), in terms of largest dimension of the respective model entities. These scale extremes represent entirely different systems, so the respective models cannot be linked through direct up- or down-scaling.

The majority of mechanistic models represent the general ecological processes of reproduction, mortality, dispersal, environmental filtering (or species sorting) and predation, along with the anthropogenic processes of land use and agricultural management (Fig. 3a). A considerable proportion of models also represent competition, biological development (or ontogeny), parasitism and herbivory. Isolated cases of specific and conceptual models combine some of these processes with socio-economic or case-specific ecological processes, which, as a result, appear at the edges of the processes ordination (Fig. 3b). The abundance of enemies, pests and, to a lesser degree, crop plants are the main outputs of the majority of mechanistic models (Fig. 3c). Crop yield, i.e., the harvested product of crop plants, is explicitly predicted by only 7 of the 67 reviewed models, as greater focus is generally put on pest suppression. A few models predict economic variables related to natural pest control (Fig. 3c), as well as parameters of population dynamics and behavioural or physiological characteristics, by simulating individual organisms.

4.3. Capabilities and limitations of mechanistic modelling

Explicit representation of causative agents of observed ecological change is a necessary, although not sufficient, condition towards extrapolations in space and time that are more reliable than those based purely on correlation (Gotelli et al., 2009). Deviation between these predictions and observations can generate knowledge about the role of specific processes and indicate the most productive areas for future research (Soetaert and Herman, 2009). Furthermore, mechanistic models based on first principles are less likely to produce the right

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 critical factors in modelling ecological processes. Relative strengths (+) and weaknesses (-) are assigned to each technique for the following desired qualities of a modelling procedure: formulation flexibility (FF), analytical tractability (AT) and algorithmic efficiency (AE). We use the terms “individual-based” and “agent-based” to distinguish models that respectively pool/equate individuals at each time step from models that constantly track each agent. (See below-mentioned references for further information.)

	Deterministic						Stochastic					
	Discrete time			Continuous time			Discrete time			Continuous time		
Non-spatial	Difference equations (DEs) (Zhang and 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 and Yassenak, 2003)		
	FF +	AT -	AE -	FF -	AT -	AE +	FF +	AT -	AE -	FF -	AT -	AE +

results for the wrong reasons, as unrealistic representations typically result in stronger bias than in purely correlative models, and hence are easier to detect (Dormann et al., 2012). However, model realism does not guarantee predictive performance, while data requirements for model parameterization and validation can prove just as challenging as for correlative approaches (Dormann et al., 2012). Correlative models can perform equally well or better than mechanistic models of the same system (Fordham et al., 2018). Optimal choice of modelling approach depends on system complexity, information availability, and the aim of the study, i.e., explanation or prediction (Robertson et al., 2003).

Lack of information can be particularly restrictive for mechanistic modelling, in situations where the generation of precise and accurate predictions relies on high levels of model complexity, as the development of complex models requires in-depth knowledge of system function and data for model parameterization (Ings et al., 2009). Complex systems analysis can benefit ecological applications, interpretation of empirical data and theory development, particularly on emergent properties of ecological systems (DeAngelis and Mooij, 2005). However, complexity can also increase uncertainty of model predictions (Cuddington et al., 2013), and limit a model’s transferability to novel systems (Yates et al., 2018). Indeed, although advances in empirical and modelling research of natural pest control have generally increased model complexity over time, the average number of processes per model has only increased by 2 over 40 years, and relatively simple system representations are still common (Fig. 1c, 3d).

5. Towards general predictive models

Elucidating the role of ecological complexity in the provision of

natural pest control would benefit from a wider adoption of mechanistic modelling approaches. However, generating reliable predictions across agricultural landscapes is a challenging task. Our findings are consistent with an anticipated trade-off between generality and realism among modelling strategies for biological populations (Levins, 1966): highly realistic models of natural pest control have to sacrifice generality by representing narrowly defined agroecosystems, whereas general theoretical models can only represent systems with a limited level of realism. The few general and relatively realistic conceptual models cannot produce quantitative testable predictions. Furthermore, model complexity can be both a strength and a weakness, and has to be adjusted to the diverse socioecological settings of planned model applications, along with the availability of knowledge and data. Agroecosystems in developing regions of the world are disproportionately afflicted by this methodological challenge. Research output per unit financial investment is increasing in these regions, but financial restrictions for ecological research are likely to persist in the near future (Holmgren and Schnitzer, 2004). Consequently, specific models of natural pest control for major agroecosystems worldwide may not be available soon, with no alternative, due to the lack of existing general and realistic predictive frameworks. Finally, predictions linked directly to agricultural applications are generally lacking, as model output primarily comprises ecological components of natural pest control and to a limited extent its agronomic and economic benefits, such as crop yield or net returns. This lack reflects the difficulty of obtaining accurate yield data across agroecosystems (Holland et al., 2017), especially in the context of interdisciplinary agricultural research (Beckmann et al., 2019).

Approaches to mechanistic modelling of natural pest control that are positioned between the extremes currently occupied by specific and

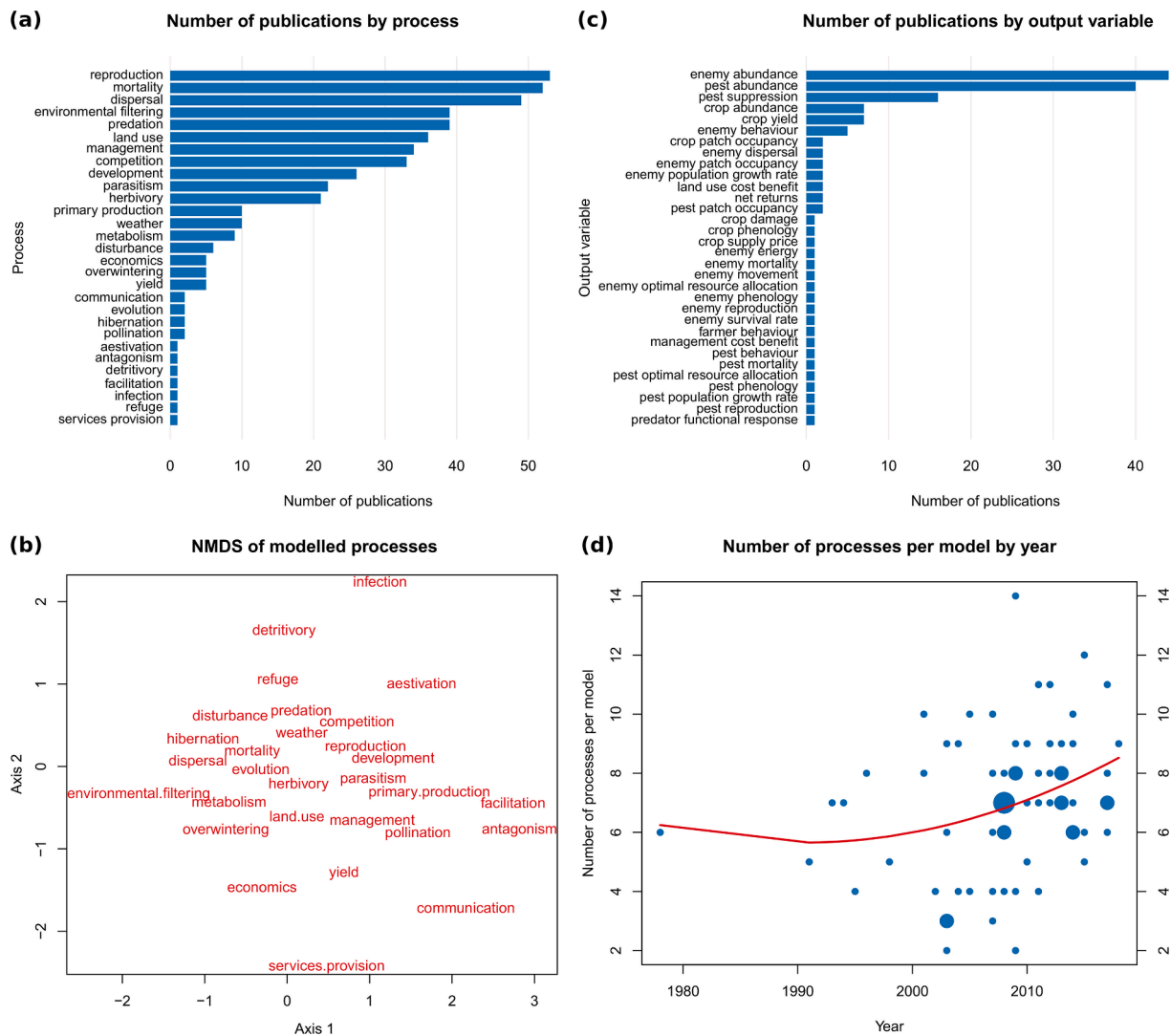


Fig. 3. (a) Number of reviewed publications representing each listed process in their mechanistic models. Single models may represent several processes. (b) Nonmetric multidimensional scaling (NMDS) showing the associations of processes represented among reviewed mechanistic models (stress = 0.2). The closer the processes are, the more often they are represented together (Barbosa, 2015; Oksanen et al., 2019). (c) Number of reviewed publications having each listed variable as the main output of their mechanistic models. Single models may have several variables as their main output. Note that a represented process in one model may be an output variable in another. (d) 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 line was fitted to the data with least-squares second-degree polynomial regression. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

theoretical models are almost completely unexplored. Our review indicates promising directions towards bridging this gap (Fig. 4a). For instance, models of specific agroecosystems identify at least one of the crops, pests or natural enemies, but the rest of the organisms are often modelled without being specified. Such general representation of functional roles instead of specific organisms suggests some potential for models that may apply to more than one agroecosystem. Typical attributes of specific models, such as stochasticity or spatial explicitness, reduce a model's analytical tractability, and may therefore need to be disregarded initially. Alternatively, theoretical models can be used as departure points. Sacrificing a substantial degree of a theoretical model's generality can achieve the minimum level of realism required to represent the defining properties of a smaller group of agroecosystems. Existing theoretical models of natural pest control can provide both a methodological and a theoretical basis for such an approach. Should either direction or a combination of the two be followed, model development will require that focal organisms share key functional roles (e.g., dispersal or diet attributes), and that the respective systems respond similarly to environmental change (e.g., landscape composition or

configuration) as a result. Large-scale studies of natural pest control point to such similarities in causal relationships (e.g., Martin et al., 2019; Tamburini et al., 2020). Based on these observations, agroecosystems across the world can be separated into groups that share not only their response to change, but also the underlying mechanisms.

The resulting contextually bound generalizations can achieve a useful compromise between generality and realism (Fig. 4b), similar to the way middle-range theories provide explanations that are valid in more than one case, but within a narrower range of conditions than grand theories (Meyfroidt et al., 2018). Each model would then resemble a "minimum realistic model", which in managed marine ecosystems aims to include only key variables and interactions (Punt and Butterworth, 1995), or the "dominant processes" concept in hydrology, which identifies and models the most determinant hydrological processes (Grayson and Blöschl, 2001). Applying such an approach to a broad collection of agroecosystems would not only facilitate model development for specific systems, but also help to uncover and model fundamental ecological principles or mechanisms across systems. Emerging differences between system groups can thus lead to a more complex,

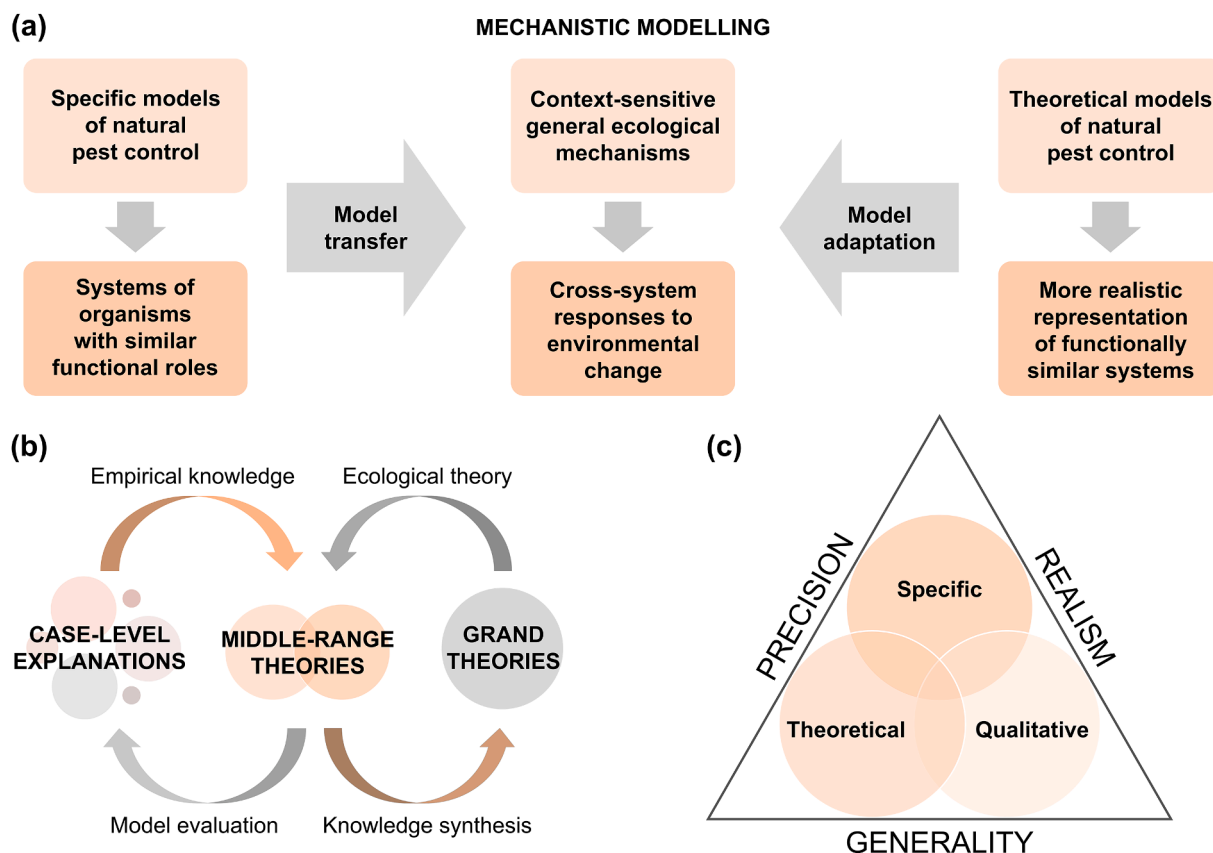


Fig. 4. Promising directions towards general predictive models of natural pest control. (a) Transfer of specific models to systems of organisms that play similar functional roles, or adaptation of theoretical models to a more realistic representation of fewer functionally similar systems. The resulting mechanistic models should represent general ecological mechanisms within bounded agroecological contexts, and be able to predict the responses of natural pest control to environmental change across the respective agroecosystems. (b) The result should resemble middle-range theories (Meyfroidt et al., 2018), by incorporating empirical knowledge from specific cases and general ecological theory, hence being positioned between these extremes in terms of generality and realism of system representations. The validity of the ensuing models should be tested against case-level empirical evidence, while emerging differences between models can lead to a more complex and general understanding of natural pest control. (c) Common predictions (overlapping disks) of independently developed qualitative and quantitative (theoretical and specific) mechanistic models, with different combinations of the desired properties of generality, precision and realism (Levins, 1966) would account for uncertainties in model formulation and increase predictive robustness.

nuanced and, for that matter, consistent theory of natural pest control (Levins, 2005). Ultimately, the success of this approach will depend on its ability to predict benefits beyond the ecological components of natural pest control, such as avoided pesticide sprays and yield stability, which are crucial for the promotion of synergies in multifunctional landscapes and the management of risk by farmers. Although the inclusion of more variables may exacerbate existing methodological challenges, such model output will promote mainstreaming natural pest control in agriculture (Chaplin-Kramer et al., 2019), as well as its inclusion in promising frameworks that bridge ecology and agro-economics (Seppelt et al., 2020).

An adequately general and realistic approach to models of natural pest control will have to consider the link between model complexity and predictive performance (Myung, 2000; Raick et al., 2006). Solving this difficult challenge can be facilitated by a strategy that constrains the many uncertainties behind predictive error. Conceptual models face fewer uncertainties than quantitative modelling techniques, but they cannot generate predictions at high quantitative detail (Justus, 2006). In the field of classical biological control this challenge has been partly addressed through qualitative mathematical modelling for the study of key issues, such as the role of environmental variability (Levins, 1969) and the mechanisms behind predator – prey correlation patterns (Levins and Schultz, 1996). The strengths of this approach include facilitation of participatory model development and inclusion of socioeconomic factors in models of ecological systems (Fulton et al., 2015). Qualitative

modelling can therefore leverage available knowledge of experts and local stakeholders in poorly studied agroecosystems worldwide. Furthermore, qualitative analyses are increasingly generating quantitative information about environmental change (Dambacher et al., 2003; Alexandridis et al., 2021), while retaining the strengths of conceptual models. Still, patterns such as non-linearities or transient dynamics are best investigated through quantitative techniques (Justus, 2006). Qualitative models can then be used to address structural uncertainty, before the development of quantitative models, where the study of potential system structures is often computationally impractical (Levins, 1998). Alternatively, qualitative and quantitative models of a system can be developed independently, based on the same ecological assumptions, towards the simplest form of multimodel inference, i.e., considering only predictions in which the two approaches agree (Fig. 4c). Qualitative and quantitative models typically require very different secondary assumptions, making common predictions relatively free of these side effects of model formulation and more robust to the associated uncertainties (Levins, 1966).

6. Conclusions

A practical trade-off between generality and realism among strategies of ecological modelling appears to prevent the development of predictive models of natural pest control that can be applied across agroecosystems. The potential to bridge this gap, with existing models of

specific systems or general theoretical models as the departure point, has not been adequately explored. Trait-mediated and context-sensitive similarities in causal relationships across the world can guide the grouping of diverse agroecosystems and the development of models that represent general ecological mechanisms under the respective agroecological settings. A combination of qualitative and quantitative techniques can constrain model uncertainty and broaden the exploitable ecological knowledge. More effort is required to develop, demonstrate and test such an integrated framework, while further empirical and modelling research would greatly benefit world regions that are underrepresented in our review results. We contend that a systematic framework of contextually bound generalizations would catalyze this much needed progress, by facilitating the transfer of available understanding and its synthesis into consistent theory of natural pest control. Future model development can thus be, at least partly, channeled towards a concerted effort to better understand and predict natural pest control around the world, promoting broadly the agricultural changes that are necessary to achieve sustainable development.

CRediT authorship contribution statement

Nikolaos Alexandridis: Conceptualization, Data curation, Formal analysis, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Glenn Marion:** Conceptualization, Formal analysis, Methodology, Visualization, Writing – review & editing. **Rebecca Chaplin-Kramer:** Conceptualization, Writing – review & editing. **Matteo Dainese:** Conceptualization, Writing – review & editing. **Johan Ekroos:** Conceptualization, Writing – review & editing. **Heather Grab:** Conceptualization, Writing – review & editing. **Mattias Jonsson:** Conceptualization, Writing – review & editing. **Daniel S. Karp:** Conceptualization, Writing – review & editing. **Carsten Meyer:** Conceptualization, Writing – review & editing. **Megan E. O'Rourke:** Conceptualization, Writing – review & editing. **Mikael Pontarp:** Conceptualization, Writing – review & editing. **Katja Poveda:** Conceptualization, Writing – review & editing. **Ralf Seppelt:** Conceptualization, Writing – review & editing. **Henrik G. Smith:** Conceptualization, Writing – review & editing. **Emily A. Martin:** Conceptualization, Formal analysis, Methodology, Visualization, Funding acquisition, Writing – review & editing. **Yann Clough:** Conceptualization, Formal analysis, Methodology, Visualization, Funding acquisition, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Scott C. Merrill and an anonymous reviewer for critically reading the manuscript and suggesting substantial improvements. N.A. was supported by the 2013–2014 BiodivERSA/FACCE-JPI joint call for research proposals (project ECODEAL), with the national funders ANR, BMBF, FORMAS, FWF, MINECO, NWO and PT-DLR. The work was supported by two workshops at Lund University funded by the strategic research area Biodiversity and Ecosystem services in a Changing Climate (BECC) and a workshop funded and hosted by UFZ. G.M. is supported by the Scottish Government's Rural and Environment Science and Analytical Services Division (RESAS). M.J. acknowledges support from SLU Centre for Biological Control. C.M. acknowledges funding by the Volkswagen Foundation through a Freigeist Fellowship (A118199), and additional support by iDiv, funded by the German Research Foundation (DFG–FZT 118, 202548816).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocontrol.2021.104761>.

References

- Alexandridis, N., Bacher, C., Jean, F., Dambacher, J.M., 2021. Revealing perturbation responses with limited observations of biological communities. *Ecol. Indic.* 128, 107840 <https://doi.org/10.1016/j.ecolind.2021.107840>.
- Allaire, J.J., Gandrud, C., Russell, K., Yetman, C.J., 2017. networkD3: D3 JavaScript Network Graphs from R.
- Arel-Bundock, V., Enevoldsen, N., Yetman, C., 2018. countrycode: An R package to convert country names and country codes. *J. Open Source Softw.* 3, 848. [10.21105/joss.00848](https://doi.org/10.21105/joss.00848).
- Axelsen, J.A., 2009. Simulation studies of Senegalese Grasshopper ecosystem interactions I: the ecosystem model. *Int. J. Pest Manag.* 55, 85–97. <https://doi.org/10.1080/09670870802601084>.
- Banks, J.E., Yasenak, C.L., 2003. Effects of plot vegetation diversity and spatial scale on *Coccinella septempunctata* movement in the absence of prey. *Entomol. Exp. Appl.* 108, 197–204. <https://doi.org/10.1046/j.1570-7458.2003.00083.x>.
- Barbosa, A.M., 2015. fuzzySim: applying fuzzy logic to binary similarity indices in ecology. *Methods Ecol. Evol.* 6, 853–858. <https://doi.org/10.1111/2041-210X.12372>.
- Beckmann, M., Gerstner, K., Akin-Fajiyi, M., Ceaușu, S., Kambach, S., Kinlock, N.L., Phillips, H.R.P., Verhagen, W., Gurevitch, J., Klotz, S., Newbold, T., Verburg, P.H., Winter, M., Seppelt, R., 2019. Conventional land-use intensification reduces species richness and increases production: A global meta-analysis. *Glob. Change Biol.* 25, 1941–1956. <https://doi.org/10.1111/gcb.14606>.
- Bianchi, F.J.J.A., Booi, C.J.H., Tschamtké, T., 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proc. R. Soc. Lond. B Biol. Sci.* 273, 1715–1727. <https://doi.org/10.1098/rspb.2006.3530>.
- Bianchi, F.J.J.A., Schellhorn, N.A., van der Werf, W., 2009. Predicting the time to colonization of the parasitoid *Diadegma semiclausum*: The importance of the shape of spatial dispersal kernels for biological control. *Biol. Control* 50, 267–274. <https://doi.org/10.1016/j.biocontrol.2009.04.014>.
- Bommarco, R., Wetterlind, S., Sigvald, R., 2007. Cereal aphid populations in non-crop habitats show strong density dependence. *J. Appl. Ecol.* 44, 1013–1022. <https://doi.org/10.1046/j.0021-8901.2007.01332.x>.
- Ceccarelli, S., Balsalobre, A., Susevich, M.L., Echeverria, M.G., Gorla, D.E., Marti, G.A., 2015. Modelling the potential geographic distribution of triatomines infected by *Triatoma virus* in the southern cone of South America. *Parasit. Vectors* 8, 153. <https://doi.org/10.1186/s13071-015-0761-1>.
- Chaplin-Kramer, R., O'Rourke, M., Schellhorn, N., Zhang, W., Robinson, B.E., Gratton, C., Rosenheim, J.A., Tschamtké, T., Karp, D.S., 2019. Measuring What Matters: Actionable Information for Conservation Biocontrol in Multifunctional Landscapes. *Front. Sustain. Food Syst.* 3 <https://doi.org/10.3389/fsufs.2019.00060>.
- 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. *Ecol. Lett.* 14, 922–932. <https://doi.org/10.1111/j.1461-0248.2011.01642.x>.
- Chatterjee, S., Isaia, M., Venturino, E., 2009. Spiders as biological controllers in the agroecosystem. *Spec. Issue Math. Biointeractions* 258, 352–362. <https://doi.org/10.1016/j.jtbi.2008.11.029>.
- Clough, Y., Kruess, A., Kleijn, D., Tschamtké, T., 2005. Spider diversity in cereal fields: comparing factors at local, landscape and regional scales. *J. Biogeogr.* 32, 2007–2014. <https://doi.org/10.1111/j.1365-2699.2005.01367.x>.
- Cotes, B., Gonzalez, M., Benitez, E., De Mas, E., Clemente-Orta, G., Campos, M., Rodriguez, E., 2018. Spider Communities and Biological Control in Native Habitats Surrounding Greenhouses. *Insects* 9, 33. <https://doi.org/10.3390/insects9010033>.
- Cuddington, K., Fortin, M.-J., Gerber, L.R., Hastings, A., Liebhold, A., O'Connor, M., Ray, C., 2013. Process-based models are required to manage ecological systems in a changing world. *Ecosphere* 4, art20. <https://doi.org/10.1890/ES12-00178.1>.
- Dambacher, J.M., Li, H.W., Rossignol, P.A., 2003. Qualitative predictions in model ecosystems. *Ecol. Model.* 161, 79–93. [https://doi.org/10.1016/S0304-3800\(02\)00295-8](https://doi.org/10.1016/S0304-3800(02)00295-8).
- DeAngelis, D.L., Mooij, W.M., 2005. Individual-based modeling of ecological and evolutionary processes. *Annu. Rev. Ecol. Evol. S.* 36, 147–168. <https://doi.org/10.1146/annurev.ecolsys.36.102003.152644>.
- 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, 916–919. <https://doi.org/10.1126/science.aat3466>.
- Diekötter, T., Haynes, K.J., Mazeffa, D., Crist, T.O., 2007. Direct and indirect effects of habitat area and matrix composition on species interactions among flower-visiting insects. *Oikos* 116, 1588–1598. <https://doi.org/10.1111/j.0030-1299.2007.15963.x>.
- Dong, Z., Ouyang, F., Lu, F., Ge, F., 2015. Shelterbelts in agricultural landscapes enhance ladybeetle abundance in spillover from cropland to adjacent habitats. *Biocontrol* 60, 351–361. <https://doi.org/10.1007/s10526-015-9648-5>.
- Dormann, C.F., 2007. Promising the future? Global change projections of species distributions. *Basic Appl. Ecol.* 8, 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. *J. Biogeogr.* 39, 2119–2131. <https://doi.org/10.1111/j.1365-2699.2011.02659.x>.
- Downie, I.S., Wilson, W.L., Abernethy, V.J., McCracken, D.I., Foster, G.N., Ribera, I., Murphy, K.J., Waterhouse, A., 1999. The Impact of Different Agricultural Land-uses on Epigeal Spider Diversity in Scotland. *J. Insect Conserv.* 3, 273–286. <https://doi.org/10.1023/A:1009649222102>.
- Dwyer, G., Dushoff, J., Yee, S.H., 2004. The combined effects of pathogens and predators on insect outbreaks. *Nature* 430, 341.
- Egerer, M.H., Liere, H., Bichier, P., Philpott, S.M., 2018. Cityscape quality and resource manipulation affect natural enemy biodiversity in and fidelity to urban agroecosystems. *Landsc. Ecol.* 33, 985–998. <https://doi.org/10.1007/s10980-018-0645-9>.
- Ekroos, J., Olsson, O., Rundlöf, M., Wätzold, F., Smith, H.G., 2014. Optimizing agri-environment schemes for biodiversity, ecosystem services or both? *Biol. Conserv.* 172, 65–71. <https://doi.org/10.1016/j.biocon.2014.02.013>.
- Englund, O., Berndes, G., Cederberg, C., 2017. How to analyse ecosystem services in landscapes—A systematic review. *Ecol. Indic.* 73, 492–504. <https://doi.org/10.1016/j.ecolind.2016.10.009>.
- Fordham, D.A., Bertelsmeier, C., Brook, B.W., Early, R., Neto, D., Brown, S.C., Ollier, S., Araújo, M.B., 2018. How complex should models be? Comparing correlative and mechanistic range dynamics models. *Glob. Change Biol.* 24, 1357–1370. <https://doi.org/10.1111/gcb.13935>.
- Fulton, E.A., Boschetti, F., Sporic, M., Jones, T., Little, L.R., Dambacher, J.M., Gray, R., Scott, R., Gorton, R., 2015. A multi-model approach to engaging stakeholder and modellers in complex environmental problems. *Environ. Sci. Policy* 48, 44–56. <https://doi.org/10.1016/j.envsci.2014.12.006>.
- Glaum, P., 2017. A theoretical basis for the study of predatory syrphid fly ecology. *Theor. Ecol.* 10, 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., Webb, C.O., Willig, M.R., 2009. Patterns and causes of species richness: a general simulation model for macroecology. *Ecol. Lett.* 12, 873–886. <https://doi.org/10.1111/j.1461-0248.2009.01353.x>.
- Grayson, R., Blöschl, G., 2001. Spatial patterns in catchment hydrology: observations and modelling. CUP Archive.
- Hagen, O., Flück, B., Fopp, F., Cabral, J.S., Hartig, F., Pontarp, M., Rangel, T.F., Pellissier, L., 2021. gen3sis: A general engine for eco-evolutionary simulations of the processes that shape Earth's biodiversity. *PLOS Biol.* 19, e3001340. <https://doi.org/10.1371/journal.pbio.3001340>.
- Halley, J.M., Thomas, C.F.G., Jepson, P.C., 1996. A Model for the Spatial Dynamics of Linyphiid Spiders in Farmland. *J. Appl. Ecol.* 33, 471–492. <https://doi.org/10.2307/2404978>.
- Hambäck, P.A., Vogt, M., Tschamtké, T., Thies, C., Englund, G., 2007. Top-down and bottom-up effects on the spatiotemporal dynamics of cereal aphids: testing scaling theory for local density. *Oikos* 116, 1995–2006. <https://doi.org/10.1111/j.2007.0030-1299.15800.x>.
- 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. *Agron. Sustain. Dev.* 37, 31. <https://doi.org/10.1007/s13593-017-0434-x>.
- Holmgren, M., Schnitzer, S.A., 2004. Science on the Rise in Developing Countries. *PLOS Biol.* 2, e1. <https://doi.org/10.1371/journal.pbio.0020001>.
- 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. *J. Anim. Ecol.* 78, 253–269. <https://doi.org/10.1111/j.1365-2656.2008.01460.x>.
- Iuliano, B., Gratton, C., 2020. Temporal Resource (Dis)continuity for Conservation Biological Control: From Field to Landscape Scales. *Front. Sustain. Food Syst.* 4. <https://doi.org/10.3389/fsufs.2020.00127>.
- Justus, J., 2006. Loop analysis and qualitative modeling: limitations and merits. *Biol. Philos.* 21, 647–666. <https://doi.org/10.1007/s10539-006-9050-x>.
- 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., Tschamtké, T., Wratten, S.D., Zhang, W., Iverson, A.L., Adler, L.S., Albrecht, M., Alignier, A., Angelella, G.M., Anjum, M.Z., Avelino, J., Batáry, P., Baveco, J.M., Bianchi, F.J.J.A., Birkhofer, K., Bohnenblust, E.W., Bommarco, R., Brewer, M.J., Caballero-López, B., Carrière, Y., Carvalheiro, L.G., Cayuela, L., Centrella, M., Četković, A., Henri, D.C., Chabert, A., Costamagna, A.C., la Mora, A.D., de Kraker, J., Desneux, N., Diehl, E., Diekötter, T., Dormann, C.F., Eckberg, J.O., Entling, M.H., Fiedler, D., Frank, P., van Veen, F.J.F., Frank, T., Gagic, V., Garratt, M.P.D., Getachew, A., Gonthier, D.J., Goodell, P.B., Graziosi, I., Groves, R.L., Gurr, G.M., Hajian-Porooshani, Z., Heimpel, G.E., Herrmann, J.D., Huseuth, A.S., Inclán, D.J., Ingraio, A.J., Iv, P., Jacot, K., Johnson, G.A., Jones, L., Kaiser, M., Kaser, J.M., Keasar, T., Kim, T.N., Kishinevsky, M., Landis, D.A., Lavandero, B., Lavigne, C., Ralec, A.L., Lemessa, D., Letourneau, D.K., Liere, H., Lu, Y., Lubin, Y., Luttermoser, T., Maas, B., Mace, K., Madeira, F., Mader, V., Cortesero, A.M., Marini, L., Martinez, E., Martinson, H.M., Menozzi, P., Mitchell, M.G.E., Miyashita, T., Molina, G.A.R., Molina-Montenegro, M.A., O'Neal, M.E., Opatovskiy, I., Ortiz-Martinez, S., Nash, M., Östman, Ö., Ouin, A., Pak, D., Paredes, D., Parsa, S., Parry, H., Perez-Alvarez, R., Perović, D.J., Peterson, J.A., Petit, S., Philpott, S.M., Plantegenest, M., Plečáček, M., Pluess, T., Pons, X., Potts, S.G., Pywell, R.F., Ragsdale, D.W., Rand, T.A., Raymond, L., Ricci, B., Sargent, C., Sarthou, J.-P., Saulais, J., Schäckermann, J., Schmidt, N.P., Schneider, G., Schüepp, C., Sivakoff, F.S., Smith, H.G., Whitney, K.S., Stutz, S., Szendrei, Z., Takada, M.B., Taki, H., Tamburini, G., Thomson, L.J., Tricault, Y., Tsafack, N., Tschumi, M., Valantin-Morison, M., Trinh, M.V., van der Werf, W., Vierling, K.T., Werling, B.P., Wickens, J.B., Wickens, V.J., Woodcock, B.A., Wyckhuys, K., Xiao, H., Yasuda, M., Yoshioka, A., Zou, Y., 2018. Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. *Proc. Natl. Acad. Sci.* 201800042. <https://doi.org/10.1073/pnas.1800042115>.
- Kean, J.M., Barlow, N.D., 2001. A spatial model for the successful biological control of *Sitona discoideus* by *Microctonus aethiops*. *J. Appl. Ecol.* 38, 162–169. <https://doi.org/10.1046/j.1365-2664.2001.00579.x>.
- 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. *Philos. Trans. R. Soc. B Biol. Sci.* 369, 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 Ecol. Evol.* 34, 154–166. <https://doi.org/10.1016/j.tree.2018.11.002>.
- Kondoh, M., 2003. Habitat fragmentation resulting in overgrazing by herbivores. *J. Theor. Biol.* 225, 453–460. [https://doi.org/10.1016/S0022-5193\(03\)00279-0](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. *Annu. Rev. Entomol.* 45, 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. *Agron. Sustain. Dev.* 31, 515–524. <https://doi.org/10.1007/s13593-011-0007-3>.
- Lester, P.J., Yee, J.M., Yee, S., Haywood, J., Thistlewood, H.M., Harmsen, R., 2005. Does altering patch number and connectivity change the predatory functional response type? Experiments and simulations in an acarine predator–prey system. *Can. J. Zool.* 83, 797–806. <https://doi.org/10.1139/z05-072>.
- Levins, R., 2005. How Cuba is going ecological. *Capital. Nat. Social.* 16, 7–25. <https://doi.org/10.1080/10455750500208706>.
- Levins, R., 1998. Qualitative mathematics for understanding, prediction, and intervention in complex ecosystems. *Ecosyst. Health* 178–204.
- Levins, R., 1969. Some Demographic and Genetic Consequences of Environmental Heterogeneity for Biological Control. *Bull. Entomol. Soc. Am.* 15, 237–240. <https://doi.org/10.1093/besa/15.3.237>.
- Levins, R., 1966. The strategy of model building in population biology. *Am. Sci.* 54, 421–431.
- Levins, R., Schultz, B.B., 1996. Effects of Density Dependence, Feedback and Environmental Sensitivity on Correlations Among Predators, Prey and Plant Resources: Models and Practical Implications. *J. Anim. Ecol.* 65, 802–812. <https://doi.org/10.2307/5678>.
- Losey, J.E., Vaughan, M., 2006. The Economic Value of Ecological Services Provided by Insects. *BioScience* 56, 311–323. [https://doi.org/10.1641/0006-3568\(2006\)56\[311:TEVOES\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2006)56[311:TEVOES]2.0.CO;2).
- 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., Baños-Picón, D., Bartomeus, I., Batáry, P., Burel, F., Caballero-López, B., Concepción, E.D., Coudrain, V., Dänhardt, J., Diaz, M., Diekötter, T., Dormann, C.F., Duflot, R., Entling, M.H., Farwig, N., Fischer, C., Frank, T., Garibaldi, L.A., Herrmann, J., Herzog, F., Inclán, D., Jacot, K., Jauker, F., Jeanneret, P., Kaiser, M., Krauss, J., Féon, V.L., Marshall, J., Moonen, A.-C., Moreno, G., Riedinger, V., Rundlöf, M., Rusch, A., Scheper, J., Schneider, G., Schüepp, C., Stutz, S., Sutter, L., Tamburini, G., Thies, C., Tormos, J., Tschamtké, T., Tschumi, M., Uzman, D., Wagner, C., Zubair-Anjum, M., Steffan-Dewenter, I., 2019. The interplay of landscape composition and configuration: new pathways to manage functional biodiversity and agroecosystem services across Europe. *Ecol. Lett.* 22, 1083–1094. <https://doi.org/10.1111/ele.13265>.
- Meyer, K.M., Vos, M., Mooij, W.M., Hol, W.H.G., Termorshuizen, A.J., van der Putten, W.H., 2012. Testing the Paradox of Enrichment along a Land Use Gradient in a Multitrophic Aboveground and Belowground Community. *PLOS ONE* 7, e49034. <https://doi.org/10.1371/journal.pone.0049034>.
- Meyfroidt, Chowdhury, R., de Bremond, A., Ellis, E.C., Erb, K.-H., Filatova, T., Garrett, R. D., Grove, J.M., Heinemann, 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., Rodríguez García, V., Schlüter, M., Turner, B.L., Verburg, P.H., 2018. Middle-range theories of land system change. *Glob. Environ. Change* 53, 52–67. Doi: 10.1016/j.gloenvcha.2018.08.006.
- Milne, A.E., Bell, J.R., Hutchison, W.D., van den Bosch, F., Mitchell, P.D., Crowder, D., Parnell, S., Whitmore, A.P., 2015. The Effect of Farmers' Decisions on Pest Control with Bt Crops: A Billion Dollar Game of Strategy. *PLOS Comput. Biol.* 11, e1004483. <https://doi.org/10.1371/journal.pcbi.1004483>.
- Myung, I.J., 2000. The Importance of Complexity in Model Selection. *J. Math. Psychol.* 44, 190–204. <https://doi.org/10.1006/jmps.1999.1283>.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2019. *vegan: Community Ecology Package*.
- Palladino, P., 2013. *Entomology, Ecology and Agriculture: The Making of Science Careers in North America, 1885–1985*. Routledge.
- Pedigo, L.P., Rice, M.E., 2014. *Entomology and Pest Management, Sixth Ed.* Waveland Press.
- Pontarp, M., Brännström, Å., Petchey, O.L., 2019a. Inferring community assembly processes from macroscopic patterns using dynamic eco-evolutionary models and Approximate Bayesian Computation (ABC). *Methods Ecol. Evol.* 10, 450–460. <https://doi.org/10.1111/2041-210X.13129>.

- Pontarp, M., Bunnefeld, L., Cabral, J.S., Etienne, R.S., Fritz, S.A., Gillespie, R., Graham, C.H., Hagen, O., Hartig, F., Huang, S., Jansson, R., Maliet, O., Münkemüller, T., Pellissier, L., Rangel, T.F., Storch, D., Wiegand, T., Hurlbert, A.H., 2019b. The Latitudinal Diversity Gradient: Novel Understanding through Mechanistic Eco-evolutionary Models. *Trends Ecol. Evol.* 34, 211–223. <https://doi.org/10.1016/j.tree.2018.11.009>.
- Provencher, L., Riechert, S.E., 1994. Model and Field Test of Prey Control Effects by Spider Assemblages. *Environ. Entomol.* 23, 1–17. <https://doi.org/10.1093/ee/23.1.1>.
- 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 Afr. J. Mar. Sci.* 16, 255–285. <https://doi.org/10.2989/025776195784156494>.
- R Core Team, 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Raick, C., Soetaert, K., Grégoire, M., 2006. Model complexity and performance: How far can we simplify? *Prog. Oceanogr.* 70, 27–57. <https://doi.org/10.1016/j.pocean.2006.03.001>.
- 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. *Ecol. Indic.* 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, 1160–1170. <https://doi.org/10.1111/oik.01759>.
- Robertson, M.P., Peter, C.I., Villet, M.H., Ripley, B.S., 2003. Comparing models for predicting species' potential distributions: a case study using correlative and mechanistic predictive modelling techniques. *Ecol. Model.* 164, 153–167. [https://doi.org/10.1016/S0304-3800\(03\)00028-0](https://doi.org/10.1016/S0304-3800(03)00028-0).
- Root, R.B., 1973. Organization of a Plant-Arthropod Association in Simple and Diverse Habitats: The Fauna of Collards (Brassica Oleracea). *Ecol. Monogr.* 43, 95–124. <https://doi.org/10.2307/1942161>.
- Schellhorn, N.A., Gagic, V., Bommarco, R., 2015. Time will tell: resource continuity bolsters ecosystem services. *Trends Ecol. Evol.* 30, 524–530. <https://doi.org/10.1016/j.tree.2015.06.007>.
- Seppelt, R., Arndt, C., Beckmann, M., Martin, E.A., Hertel, T.W., 2020. Deciphering the Biodiversity–Production Mutualism in the Global Food Security Debate. *Trends Ecol. Evol.* 10.1016/j.tree.2020.06.012.
- 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. Nat. Cap. Proj. Stanf, CA USA.
- Soetaert, K., Herman, P.M.J., 2009. A Practical Guide to Ecological Modelling: Using R as a Simulation Platform. Springer Science & Business Media.
- Tamburini, G., Santoiemma, G., E. O'Rourke, M., Bommarco, R., Chaplin-Kramer, R., Dainese, M., Karp, D.S., Kim, T.N., Martin, E.A., Petersen, M., Marini, L., 2020. Species traits elucidate crop pest response to landscape composition: a global analysis. *Proc. R. Soc. B Biol. Sci.* 287, 20202116. Doi: 10.1098/rspb.2020.211.
- Thomas, C.F.G., Brain, P., Jepson, P.C., 2003. Aerial activity of linyphiid spiders: modelling dispersal distances from meteorology and behaviour. *J. Appl. Ecol.* 40, 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., Wratten, S., Zhang, W., 2016. When natural habitat fails to enhance biological pest control – Five hypotheses. *Biol. Conserv.* 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. *Ecol. Lett.* 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. *Proc. R. Soc. B Biol. Sci.* 282, 20151369. <https://doi.org/10.1098/rspb.2015.1369>.
- Urban, M.C., Bocedi, G., Hendry, A.P., Mihalob, J.-B., Pe'er, G., Singer, A., Bridle, J.R., Crozier, L.G., Meester, L.D., Godsoe, W., Gonzalez, A., Hellmann, J.J., Holt, R.D., Huth, A., Johst, K., Krug, C.B., Leadley, P.W., Palmer, S.C.F., Pantel, J.H., Schmitz, A., Zollner, P.A., Travis, J.M.J., 2016. Improving the forecast for biodiversity under climate change. *Science* 353, 10.1126/science.aad8466.
- 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, e38227. <https://doi.org/10.1371/journal.pone.0038227>.
- Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York.
- World Bank DataBank, 2018. World Development Indicators: GDP per capita, PPP (constant 2017 international \$). The World Bank Group, Washington, D.C.
- Yates, K.L., Bouchet, P.J., Caley, M.J., Mengersen, K., Randin, C.F., Parnell, S., Fielding, A.H., Bamford, A.J., Ban, S., Barbosa, A.M., Dormann, C.F., Elith, J., Embling, C.B., Ervin, G.N., Fisher, R., Gould, S., Graf, R.F., Gregr, E.J., Halpin, P.N., Heikkinen, R.K., Heinänen, S., Jones, A.R., Krishnakumar, P.K., Lauria, V., Lozano-Montes, H., Mannocci, L., Mellin, C., Mesgaran, M.B., Moreno-Amat, E., Mormede, S., Novaczek, E., Oppel, S., Ortuño Crespo, G., Peterson, A.T., Rapacciolo, G., Roberts, J.J., Ross, R.E., Scales, K.L., Schoeman, D., Snelgrove, P., Sundblad, G., Thuiller, W., Torres, L.G., Verbruggen, H., Wang, L., Wenger, S., Whittingham, M.J., Zharikov, Y., Zurell, D., Sequeira, A.M.M., 2018. Outstanding Challenges in the Transferability of Ecological Models. *Trends Ecol. Evol.* 33, 790–802. <https://doi.org/10.1016/j.tree.2018.08.001>.
- Zhang, W., Swinton, S.M., 2009. Incorporating natural enemies in an economic threshold for dynamically optimal pest management. *Ecol. Model.* 220, 1315–1324. <https://doi.org/10.1016/j.ecolmodel.2009.01.027>.