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From known to unknown unknowns through pattern-oriented modelling: Driving research towards the Medawar zone

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ABSTRACT

The metaphor of the Medawar zone describes the relationship between the difficulty of a scientific problem and the potential payoff of solving it. This zone represents the realm where questions offer high benefits relative to the effort required to address them. By harnessing the power of mechanistic modelling, scientists can navigate towards this zone, moving beyond known unknowns to discover unknown unknowns. This requires models to be realistic and reliable. Model usefulness, impact, and predictive power can be enhanced by achieving intermediate model complexity, where the trade-off between the realism and tractability of a model is optimised. To achieve these goals, we use the pattern-oriented modelling strategy (POM) to direct research into the Medawar zone by steering model structure towards intermediate complexity. We illustrate this strategy with a detailed conceptual process. Using example models from agri-ecological systems, we demonstrate how intermediate complexity can be attained through POM, and how pattern-oriented models of intermediate complexity that reproduce multiple patterns can uncover both known unknowns and unknown unknowns, which ultimately advances our understanding of complex systems and facilitates groundbreaking discoveries. In addition, we discuss the multidimensionality of the Medawar zone in the context of modelling philosophy and highlight the challenges and imperatives for achieving coherence in the modelling discipline. We emphasize the need for collaboration between end-users and modellers and the adoption of systematic modelling strategies such as POM.

1. Introduction

In his book ‘The Art of the Soluble’, Sir Peter Medawar (1967) describes the hump-shaped relationship between the degree of difficulty of a scientific problem and the payoff that can be achieved by solving it (Fig. 1). Solving an easy problem involves little or no risk. The necessary concepts and tools are readily available, and the processes are well understood, but solving such a problem is usually associated with a low-impact outcome, often being a piece of the jigsaw puzzle rather than the big picture, and rarely a breakthrough in itself. On the other hand, solving difficult problems can be expected to have a high impact, but the concepts, tools, and understanding required to solve the problem often are not yet available or fully developed. Attempting to solve such a problem carries a high risk of failure and therefore no payoff.

By considering this trade-off between difficulty and expected payoff, scientists can thus ask the ‘right questions’ that offer the highest benefit per unit of effort. These questions are located within a zone in Medawar’s diagram (Fig. 1), where solving them can lead to the maximum payoff. About two decades later, Loehle (1990) referred to this zone as the ‘Medawar zone’ in his seminal article about creativity in science. Innovative and productive scientists are supposed to ask questions that lead into the Medawar zone. However, a pertinent question arises: where exactly is the maximum of the Medawar zone, and is it possible to shift it to the right, towards more difficult and challenging problems? Loehle (1990) suggests choosing questions that reach beyond the mundane, because these tend to have a high impact. He sees true

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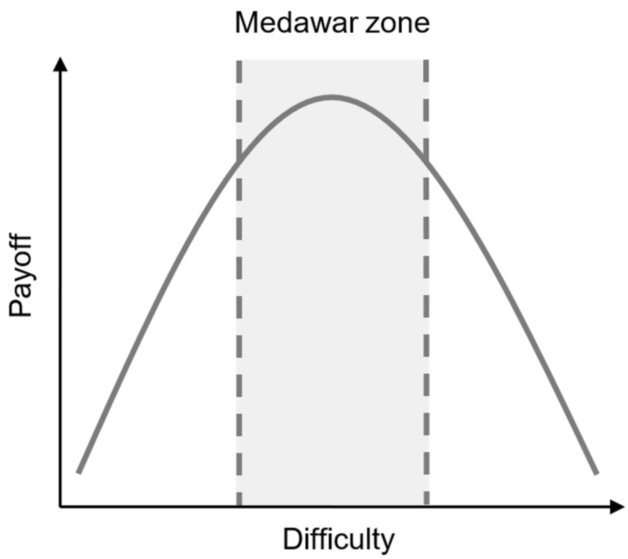

Fig. 1. The difficulty of a scientific problem vs. the payoff for solving the problem in terms of its impact and recognition. The 'Medawar zone', as depicted by Loehle (1990), refers to the zone of problems or questions where the highest benefit per unit of effort is achieved, striking a balance between difficulty and payoff.

innovation as the ability to recognize such problems when others do not even realise they exist.

It thus appears that the quest for the Medawar zone is related to the fundamental challenge in science to move on from known unknowns to unknown unknowns. Such hidden problems (unknown unknowns) are likely to be a pathway to breakthroughs in science. They can hide truths or outcomes that have potentially high impacts. Scientists, being human, however, tend to intuitively rely on known concepts when addressing complex problems. In linguistics, this phenomenon is termed 'hypocognition', referring to the inability to perceive a problem or phenomenon due to the lack of a word or concept for it (Wu and Dunning, 2018).

The only pathway towards unknown unknowns seems to be undirected, serendipitous or so-called blue-sky research, but with no certainty of success or contained timeframe. But what if we did not have to wait around for these unknown unknowns to become exposed accidentally? Here, modelling holds great potential as it allows us to play with ideas in a rigorous way, thereby leading to new insights into phenomena or problems that cannot at present be observed or otherwise explained (Mankin et al., 1975).

A model is a purposeful, simplified representation of a real system (Starfield et al., 1990), and modelling is the process of finding such a representation that allows us to answer a specific question or solve a specific problem (Grimm and Railsback, 2005). Therefore, by itself, modelling usually is a tool to discover known unknowns.

While early scientific models, in particular in physics, used the language of mathematics, computational models, also known as simulation models, have gained popularity in recent decades, due to the increasing availability of computing power. These models are computer programs that simulate hypothesised mechanisms or processes dynamically by the use of algorithms, equations, and probabilistic rules (Cabral et al., 2017). The advantage is that they allow key features of real systems to be fully considered, such as space, heterogeneity, and stochasticity, which are ignored in simple mathematical models (Evans et al., 2013). Therefore, computational models can serve as virtual experimental systems that can be manipulated more rapidly than their real counterparts (Peck, 2004).

Now, if a model is rich enough in structure and mechanisms (DeAngelis and Mooij, 2003), it may not only be able to reproduce known patterns, but also be able to predict patterns, also referred to as stylised facts, regularities, or signals, that were not considered, or not even known, while the model was being constructed. There is thus no risk that the model was adjusted via tuning of parameters and submodels to look right. While such secondary or independent predictions of models have been considered the 'gold standard' for model validation (Augusiak et al., 2014; Grimm et al., 2005), they are, in fact, much more.

When a simulation model produces patterns or phenomena that have not yet been observed or studied in the real world, these can be verified through experimentation or new data exploration, and lead to what can be called 'emergent unknown questions'. Importantly, these questions can direct new ventures in field or laboratory studies that have a greater likelihood of success and a high payoff. In this way, models can be used to guide researchers to identify deeper scientific research questions, shifting the maximum of the Medawar zone to the right, i.e., to reveal unknown unknowns and transition them to known unknowns.

However, to generate unknown patterns or phenomena that can be empirically confirmed, models need to be realistic enough to capture the key mechanisms underlying the internal organisation of a system. Realism, however, poses a double-edged sword for models: increasing realism enriches models with intricate structures and mechanisms (DeAngelis and Mooij, 2003), thereby offering more opportunities to compare model outputs with empirical data, but increased realism also comes with considerable or even prohibitive costs in terms of increased model complexity, which limits parameterisation, testing, and understanding.

In the following sections, we first emphasise the importance of achieving intermediate model complexity as the basis for optimal model performance, i.e., optimal model payoffs such as usefulness, predictive power, and impact. Next, we present a conceptualisation of the pattern-oriented modelling (POM) strategy (Grimm et al., 1996, 2005; Grimm and Railsback, 2012; Wang et al., 2018; Wiegand et al., 2003) that helps guide research into the Medawar zone by steering model structure towards intermediate complexity. Then, we demonstrate how intermediate complexity can be attained through POM, using several example models from agri-ecological systems. Using two of these example models with mid-level complexity, we further showcase the value of POM in maximising the chances of investigating known unknowns, discovering unknown unknowns, and transitioning from newly discovered unknown unknowns to known unknowns. By following this conceptualisation of the POM strategy, scientists can achieve high payoffs from their research. Next, we describe the multidimensionality of the Medawar zone in the context of modelling philosophy. Lastly, we discuss the challenges and imperatives for achieving coherence in the modelling discipline from the perspectives of both end-users and modellers.

2. Attainment of optimal model performance

Well-validated simulation models (Augusiak et al., 2014) with the appropriate level of detail are likely to provide useful insights and to make valuable predictions (Brooks and Tobias, 1996; Fulton et al., 2003; Getz et al., 2018; Grimm and Railsback, 2012; Grimm et al., 2005; Lawrie and Hearne, 2007; Van Nes and Scheffer, 2005), often with practical applications. Yet, despite the broad use of simulation models in many fields, there is an ongoing discussion regarding the appropriate level of detail required for modelling studied systems (Bolliger et al., 2005; Chwif et al., 2000; Evans et al., 2013; Hong et al., 2017; Kimmins et al., 2008; Larsen et al., 2016; Paola and Leeder, 2011; Paudel and Jawitz, 2012; Schwartz et al., 2017; Sivapalan, 2003; Sun et al., 2016). This discussion is important because the answer impacts the 'structural realism' of models, i.e., the likelihood that a model reproduces empirical observations for the right reasons (Grimm and Railsback, 2012; Grimm et al., 2005; Wiegand et al., 2003). Structural realism is achieved by reproducing observable patterns, as seen in the natural system, through selecting key factors, i.e., those which are the most significant drivers in the system's structure and dynamics. This selection is informed both by data and by the development and testing of hypotheses related to the research questions and systems under study (i.e., model purpose).

In terms of outcomes, modellers addressing real-world problems should look for useful and testable predictions. For example, improvements in pest management in agri-ecological systems largely rely on the predictive power of models. Realistic model outputs can enable stakeholders to make informed management decisions (Busi et al., 2020; Koralewski et al., 2020; Parry et al., 2017; Wang et al., 2019; Wang et al., 2021a, Wang et al., 2021b). However, realistic computational models tend to be relatively complex (Evans et al., 2013; Grimm, 1999; Janssen and Ostrom, 2006; Lorscheid and Meyer, 2016; Rounsevell et al., 2012; Sun et al., 2016; Thiele and Grimm, 2015). When model structure (entities, state variables, scales, and processes) becomes unnecessarily complex for model purpose, then not only model construction but also model performance can suffer in terms of usefulness and predictive power.

Grimm et al. (2005) therefore suggest that models should be neither too simple nor too complex, which corresponds to both the trade-off described in Fig. 1 and Einstein's famous quote that 'everything should be made as simple as possible, but not simpler'. If a model is too simple, it runs the risk of excluding essential elements of a real system, resulting in unreliable predictions and a lack of insight into relevant research questions. By contrast, an overly complex model will be difficult to parameterise and test, thereby suffering from reduced usability and predictive power. Its analysis will become unmanageable due to excessive unnecessary detail. For example, increased complexity in model structure requires more information (e.g., new parameters and submodels) that cannot often be determined from the currently available data sets. This leads instead to increased uncertainty and noise in model outputs.

In addition, higher-complexity models are often designed to closely mimic real-world systems, frequently relying on detailed imposed data when the necessary data are unavailable or when mechanistic understanding is lacking. These models might overly restrict the studied system's potential behaviours to only those previously observed or understood. As a result, these models could become 'blind' to unusual events or unexpected shifts in behaviour that could occur in real-world systems. In such cases, these higher-complexity models will be especially difficult to interrogate for unknowns, due to the mismatch between model outputs and experimental observations. Therefore, this limits the model's usefulness and impact in guiding decision-making and advancing scientific understanding.

The relationship between model complexity and model payoff can be understood in the context of the Medawar zone (Fig. 1) by relabelling the x-axis to represent model complexity and the y-axis to represent model payoff (e.g., model usefulness and predictive power, and model impact) (Fig. 2). There is a trade-off between 'realism' and 'tractability' of a model versus its complexity. To optimise this trade-off, systematic modelling strategies such as POM are needed.

3. A conceptualisation of POM leading to the Medawar zone

POM has been proposed to optimise the trade-off between realism and tractability by finding the appropriate level of complexity for model structure, targeting intermediate complexity, or as we are labelling it, the Medawar zone in modelling (Fig. 2). POM is described as using multiple patterns observed at different scales and organisational levels of a real system to design, select, and parameterise models of complex systems, thereby identifying the appropriate level of complexity and capturing the mechanisms underlying the dynamics of the studied system (Grimm and Railsback, 2012). POM is not a particular technique or invention; rather, it encapsulates the collective experience from models developed with consideration of multiple observed patterns. Although many experienced modellers have employed this approach, they often have done so implicitly. Thus, POM was established as an explicit, coherent, and effective strategy for creating structurally realistic models that strike a balance between being overly simple and overly complex.

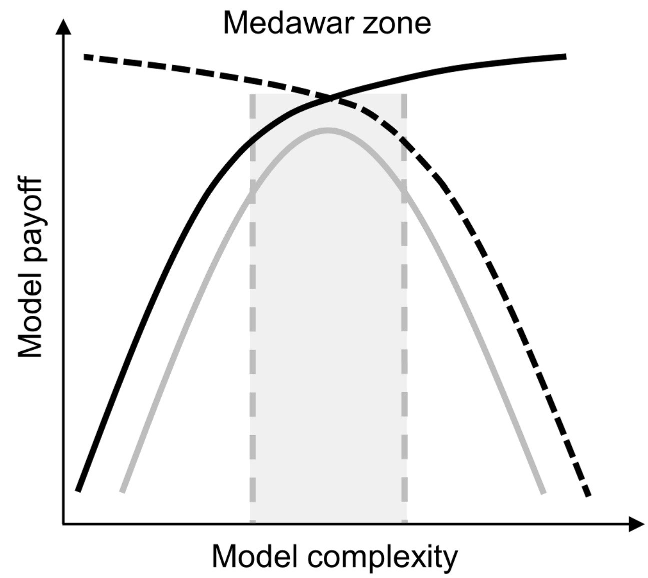

Fig. 2. The 'Medawar zone' in the context of modelling philosophy adapted from Grimm et al. (2005) and Wiegand (2017): the trade-off between realism (black solid curve) and tractability (black dash curve) of a model versus its complexity determines payoff of the model (light grey curve). An increase in model complexity leads to greater realism but reduced tractability. The light grey shaded area is the zone of intermediate complexity, i.e., the area where realism and tractability are balanced and hence the payoff is optimised.

Consequently, we propose a conceptualisation of POM that illustrates how it can shape model structure towards mid-level complexity and guide research into the Medawar zone (Fig. 3).

In this conceptualisation, there are two key elements: (1) POM leads to mid-level model complexity, and (2) the resultant models with intermediate complexity generate reliable and robust multi-scale model outputs, facilitating the exploration of known unknowns and the discovery of unknown unknowns. As illustrated in Fig. 3, pattern-oriented models are constructed to address specific questions and use a set of multiple patterns at various scales as filters to quantify and select model structure during the processes of model design, development, and refinement (including verification and parameterisation). As a result, these models tend to include the most essential entities, processes, and scales for representing the systems being modelled with regard to the specific questions, which typically leads to mid-level model complexity.

Following the scheme in Fig. 3, a model is first designed, developed, and refined to reproduce the patterns that are intended to be reproduced (Patterns 1 – n, Fig. 3), and is then analysed with sensitivity and robustness analysis. After this 'model output verification' (Grimm et al., 2014), further exploration of model outputs aims to identify additional patterns (Patterns $\alpha - \omega$, Fig. 3), which were not used for model design, development, or refinement, and ideally were not even known (to the modellers) beforehand. If these independent or secondary predictions are subsequently confirmed by data or observations, this is often referred to as 'validation'. However, since this term is ambiguous, Augusiak et al. (2014) and Grimm et al. (2014) suggested calling it 'model output corroboration'.

As an example of independent model predictions that matched patterns subsequently confirmed by existing data or observations, we focus on the beech forest model (BEFORE). BEFORE predicted that in natural beech forests, the age difference between neighbouring canopy trees is on average 60 years (Rademacher et al., 2001); this pattern was confirmed by data from surveys carried out decades earlier. This is an example of patterns that had been previously observed but not perceived as containing important information, and hence not fully understood. Thus, these patterns were known unknowns. In this case, the model had the potential to disentangle mechanisms underlying these patterns

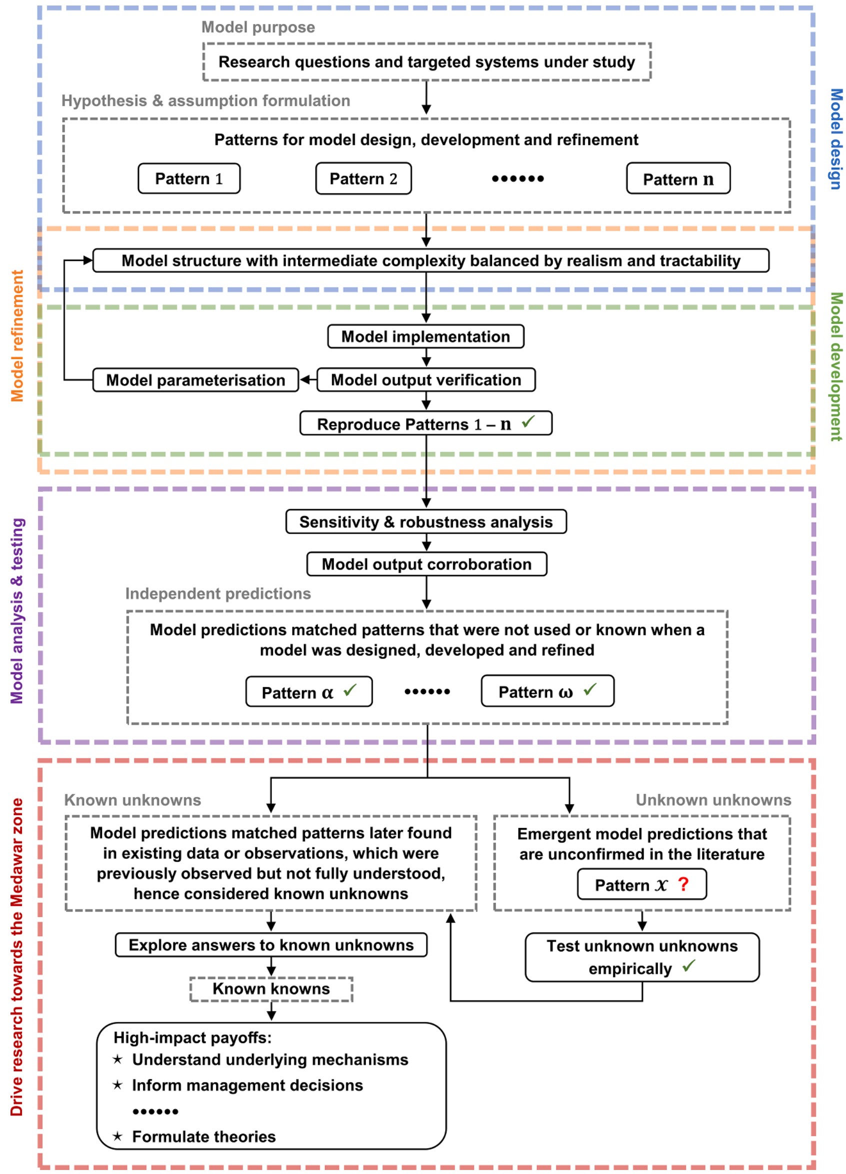

Fig. 3. A conceptualisation of pattern-oriented modelling (POM) illustrating how it can drive research into the Medawar zone. The terms 'model output verification' and 'model output corroboration' are adopted from the TRACE document (Ayllón et al., 2021; Grimm et al., 2014; Schmolke et al., 2010). Model output verification involves comparing model outputs to the patterns and data that a model was meant to reproduce. In contrast, model output corroboration refers to the identification of patterns in the model that were not used during model design, development, or refinement (including verification and parameterisation); these patterns are thus considered independent predictions. Corroboration of these patterns with existing or new data or experiments indicates a high level of realism and trustworthiness of the model.

(known unknowns) observed in the real world and then turn them into known knowns, as in Rademacher et al. (2001).

In contrast, it may be that the patterns identified as independent predictions in model outputs cannot yet be confirmed by data or observations in the literature (e.g., Pattern χ, Fig. 3). Such new patterns can be considered candidates for being unknown unknowns, which can potentially be tested and confirmed empirically. This allows for the allocation of time and resources to experiments and data exploration to reveal unknown but potentially important mechanisms. These unknown unknowns can thus subsequently be transformed into known unknowns for further exploration.

Attaining mid-level complexity in model structure is essential for generating reliable and robust model outputs. By exploring these model outputs, it is likely to address known unknowns and discover emergent unknown unknowns. Therefore, POM facilitates higher payoffs in research by driving it towards the Medawar zone.

4. POM steering model structure towards intermediate complexity: demonstrations with example models

To demonstrate the POM process, we first look at how POM directs model structure towards the Medawar zone, i.e., towards intermediate complexity, in terms of realism and tractability, using models of agri-ecological systems (Table 1).

4.1. Modelling development of branching architecture in horticulture tree crops

Growing avocado (*Persea americana*, cv. Hass) has global economic significance (Bost et al., 2013). The growth of avocado trees has, therefore, been studied in great detail (Thorp and Sedgley, 1993), which provides the basis for constructing models aimed at understanding and predicting the branching architecture of the trees and the determinants

Table 1
The description of the example models from agri-ecological systems in terms of realism, tractability and complexity.

Model name	Description	Realism	Tractability	Complexity	Reference
Avocado-S	The model was constructed in L-studio to simulate the dynamic development of avocado branching architecture. Physiological parameters like thermal time (average degree days in a day), phyllochron and the size of leaves or internodes were selected solely for visualisation, and the growth rate of inflorescences, leaves and internodes was assumed to be linear. To reproduce multiple observed patterns (e.g., the number of nodes for leaves and leaf bracts, and the number of sylleptic and proleptic shoots) at various scales for model output verification, several parameters were inversely determined through model parameterisation. After model output corroboration, the model could only reproduce the architecture patterns such as the number of nodes for leaves and leaf bracts and the proportions of sylleptic and proleptic growth units, the occurrence of third-order growth axes, but it was not capable of predicting the growth patterns such as shoot length and leaf area.	Low	High	Simple	Wang et al. (2016b)
Avocado-M	The model was constructed in L-studio to simulate the dynamic development of avocado branching architecture, incorporating photosynthesis and adaptive carbon allocation at the organ level. Carbon allocation was modelled as being dependant on current organ biomass and the sink strength of each organ type. For model output verification, the model was parameterised using a set of observed patterns, such as the number of sylleptic and proleptic shoots and growth units. For model output corroboration, independent model predictions were compared with a different set of empirical patterns from various field studies that were not used for parameterisation and verification. These model predictions, such as the length of growth flushes, leaf area, and vegetative flush durations, were consistent with the observed patterns in the real world. The model successfully predicted these patterns for model output corroboration. Therefore, the model reproduced and predicted not only the architecture but also growth patterns that were observed empirically at various scales.	Medium	Medium	Intermediate	Wang et al. (2018)
Qfly-S	The model was constructed in 3D NetLogo to simulate Qfly movement and distribution on host plants, based on hypothesised behavioural rules associated with insect movement choices. The spatial unit in the model is based on 'vegetation cubes', which are relatively coarse. The model was used to assess whether such coarse resolution is appropriate for simulating Qfly movement and distribution on host plants, and to investigate which other types of research questions it is best suited to address. The model predicted the observed patterns (i.e., Qflies visited more in the mid to upper canopy), which is consistent with the published literature. The model can be better used to investigate research questions such as insect spatial population distribution on plant canopies and how different tree architectures affect their behaviour.	Low	High	Simple	Wang et al. (2015)
Qfly-M	The model was constructed in 3D NetLogo to simulate movement patterns and spatial distributions (e.g., across canopy regions and trees) of Qfly visits on foliage and fruits within fruiting plant canopies with different architectures. The model incorporated insect movement decisions underlying host fruit-seeking behaviour. Both qualitative and quantitative observed patterns, such as most visits occurring in the inner part of the tree, most Qflies leaving the tree within 15 min, and the number of visits per Qfly on tree foliage, were used for model output verification. After model parameterisation and output verification, the model was used to run simulation experiments for model output corroboration. The model successfully generated independent predictions related to the behavioural ecology of Qflies in plant canopies (e.g., fewer Qflies found in the lower canopy compared with the middle and upper canopy in closed-canopy trees, and significant differences in movement patterns of Qflies among different types of tree architecture: closed-canopy vs. vase-shaped), which matched the observations from the literature. In addition, it predicted unknown patterns (e.g., Qflies visiting host fruit in total more in vase-shaped canopies than in closed-canopies) that were later tested and confirmed in the field. Such independent or secondary and testable predictions are strong indicators that the model is structurally realistic for the system being studied.	Medium	Medium	Intermediate	Wang et al. (2016a)
Qfly-C	The model was constructed in L-studio to simulate Qfly movement and distribution on host plants, based on hypothesised behavioural rules associated with insect movement choices. The model featured detailed plant architecture, with individual leaves and stem segments. It was used to assess whether such fine resolution is appropriate for simulating Qfly movement and distribution on host plants, and to investigate which other types of research questions it is best suited to address. The model predicted the observed patterns (i.e., Qflies visited more in the mid to upper canopy), which is consistent with the published literature. However, the predictions were not superior to those of Qfly-S. The model is better suited for examining how foliage density and foliage position affect Qfly behaviour and for simulating landscape scales, such as orchards with multiple trees. This is due to the fine resolution as well as the enhanced computational capability and efficiency of L-studio.	High	Low	Complex	Wang et al. (2015)

of fruiting and yield. Incorporating key features such as space, heterogeneity, and stochasticity into mathematical or statistical models is challenging due to the complex interactions between plant architecture and the physical and biological processes driving plant growth at different spatial and temporal scales. Therefore, two computational models (i.e., functional-structural plant models: Avocado-S and Avocado-M; Table 1) of the branching architecture of avocado (Wang et al., 2016b, 2018) were constructed using POM to attempt to capture the dynamic development of this branching architecture under changing environmental conditions. These models were programmed with the L+C modelling language (Karwowski and Prusinkiewicz, 2003; Prusinkiewicz et al., 2007b) in L-studio (Karwowski and Prusinkiewicz, 2004; Prusinkiewicz et al., 2000) using L-systems (Lindenmayer, 1968a, b; Prusinkiewicz et al., 1997) to create a 3D 'virtual plant' representation (Hanan, 1997; Room et al., 1996) of this branching architecture.

The two models have different levels of complexity in the submodel that represents the process of carbon allocation for plant growth. Avocado-S (Wang et al., 2016b) had a simple submodel where the growth rates of organ components were assumed to be linear. This model could reproduce the architecture patterns, but was not capable of predicting the growth patterns such as shoot length and leaf area, which were crucial for addressing the research questions. In contrast, to describe carbon allocation in plants, Avocado-M (Wang et al., 2018) incorporated the sink regulation approach (Marcelis and Heuvelink, 2007), which was selected because it was less complex than a transport resistance approach (Prusinkiewicz et al., 2007a). The latter requires many difficult-to-measure parameters (Lacointe, 2000; Reynolds and Thornley, 1982) for avocado trees, as well as significant time and resources for data collection and implementation within the L+C modelling language.

Avocado-M can hence be considered a mid-level complexity model. It successfully reproduced and predicted both the architecture and growth patterns that were observed empirically at various scales. Thus, instead of using the transport resistance approach, the sink regulation approach did not make the model structure unnecessarily complex, and made it more computationally tractable for the research questions being studied. Specifically, it did not increase the number of parameters by including unnecessarily difficult-to-measure ones. This helped avoid adding significant uncertainty to the model, which could lead to unreliable model predictions.

4.2. Modelling movement patterns of pest insects in canopies of horticulture tree crops

To maximise fruit yield, sound management practices require not only a better understanding of tree growth but also knowledge of how to reduce the occurrence of pest insects such as the Queensland fruit fly (Qfly), *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae) (Balagawi et al., 2012; Clarke et al., 2011; Senior et al., 2017). Qfly is a major pest that infests many varieties of commercial fruit and vegetable crops, including avocado (Hancock et al., 2000, p. 39). This insect pest relies on movement patterns to find fruit in which to lay eggs and successfully reproduce, thereby ruining the fruit. To address this, three 3D spatially explicit individual-based models (Qfly-S, Qfly-M, and Qfly-C; Table 1) with different levels of detail and complexity have been developed using POM to simulate Qfly behaviour and movement patterns on host plants.

The first two models, Qfly-S and Qfly-C, were built on different software implementation platforms (Wang et al., 2015). Qfly-S was built using NetLogo (Wilensky, 1999), where vegetation was represented as cubes, while Qfly-C was built in L-studio using the L+C modelling language and L-systems, which provided more detailed plant architecture with individual leaves and stem segments. Qfly-S and Qfly-C were then compared to determine the appropriate level of detail required for modelling such a targeted system (Wang et al., 2015). In addition, Qfly-S and Qfly-C used completely different submodels for representing the hop behaviour of Qflies. Qfly-S used NetLogo's built-in functions as simple insect behavioural rules for this process, whereas a complex method aiming for the better outcomes (i.e., a ray tracing algorithm from computer science), was applied in Qfly-C to represent the sensory aspect of Qfly hop behaviour.

Comparison of Qfly-S and Qfly-C showed that they had the same output patterns regarding the spatial population distribution in the plant canopy, indicating that neither is superior in terms of the model outputs. Qfly-C, the more structurally complex model (i.e., more detailed plant architecture with a complex submodel and additional parameters) did not result in better alignment with the observed patterns when contrasted with the simple Qfly-S. In addition, the NetLogo model (Qfly-S) was relatively easy to build with many built-in functions and user-friendly graphical interfaces, which increased its computational tractability. In contrast, the L-studio model (Qfly-C) required a higher level of computer science knowledge, especially computer graphics and programming languages.

Therefore, Qfly-S was chosen to be further developed into a model (Qfly-M) with a more detailed submodel representing host fruit-seeking behaviour (Wang et al., 2016a). This makes the model moderately complex, compared to the simple NetLogo model (Qfly-S), but less complex than the L-studio model (Qfly-C).

5. POM directing research into the Medawar zone: demonstrations with example models

The mid-level complexity models (Avocado-M and Qfly-M; Table 1) produced reliable and robust outputs and demonstrated strong predictive power (Wang et al., 2016a, 2018). This provided answers to known unknowns and uncovered unknown unknowns, thereby driving research towards the Medawar zone by shifting the maximum payoff to the right through the use of intermediate complexity models to address high-impact questions (Fig. 1).

5.1. Exploration of answers to known unknowns

The competition for carbon between developing fruitlets and developing leaves on indeterminate floral shoots in avocado trees is a key determinant of final fruit yields (Finazzo et al., 1994; Salazar-García et al., 2013; Whiley, 1990). For this competition, a key point is the so-called leaf sink–source transition, where the leaf ceases to be a consumer and becomes a generator of resources. Understanding the timing of this transition during a growing season allows the exploration of methods for identifying horticultural practices that maximise fruit yield. For example, if orchardists can remove leaves still acting as carbon sinks and thus drawing resources away from fruit at some time during the period of early fruit set, then final fruit yield should increase. Avocado-M: the functional-structural plant model with intermediate complexity (Wang et al., 2018), was used to investigate this known unknown. Avocado-M was capable of predicting the timing of the leaf sink–source transition successfully under changing environmental conditions, which occurred at around 25 % leaf expansion. Hence, computational modelling provided a suitable tool to move a significant problem into the Medawar zone; in other words, to solve for a known unknown.

A similar example addressed the widely used practice of orchardists to prune tree canopies into different shapes to increase fruit yield and reduce the occurrence of pests and diseases (Campbell et al., 1996; Costes et al., 2013; Simon et al., 2007). Here too, a complex interaction needs to be explored to compensate for limited knowledge regarding how different types of tree architecture affect the movement patterns of Qflies. To investigate how the flies find fruit and what can be done to minimise their success, Qfly-M was used (Wang et al., 2016a). As an output, this mid-level complexity model successfully predicted the movement patterns of Qflies within plant canopies of different shapes. So here again, a computational model served as a tool to move problems into the Medawar zone and solve for known unknowns.

5.2. Discovery of emergence of unknown unknowns

A computer model that is sufficiently realistic can be considered a 'virtual laboratory', which can be manipulated via simulation experiments more easily and quickly than experiments in the real world. Therefore, previously unobserved interactions may be revealed, providing researchers with important new directions for exploration: towards unknown unknowns. While this potential of simulation models is not new, in particular for discovering previously unknown Black Swan events (Berner et al., 2017), the quest for unknown unknowns can be conceptualised more explicitly, based on POM (Fig. 3). This allows us to focus more directly on the two axes of achievability and significant outcomes (Figs. 1 and 2).

For example, the results generated from Qfly-M, led to outcomes that refocused research within the discipline. Comparing different canopy shapes, it turned out that female flies would spend more time on host fruit in vase-shaped canopies. Then, for validation purposes, a field study was designed and conducted as reported in Wang et al. (2016a), and indeed, the observations from the field experiment were consistent with the model predictions. The discovery that plant architecture plays a significant role for insect behaviour in an insect for which most research has concentrated on the olfactory and visual sensory systems, driven by an intermediate level of complexity in the model, led to a significant departure from the conventional research that aims at informing pest management.

Once there was confidence in the ability of the model to uncover such unknown unknowns, further predictive simulations were carried out. The model predictions indicated that Qflies spend more time on host fruit in the peripheral region of a closed-canopy, in contrast to those in the central region; again, a finding related to an unknown unknown within the discipline and a result that has the capacity to impact practices in horticulture.

For example, a potential outcome for orchardists from exploring a high-density planting system for avocado orchards is to increase plant yield, while at the same time reducing fruit loss from Qfly infestation. Indeed, Menzel and Le Lagadec (2014), who reviewed decades of research on the effects of orchard configurations on avocado yield, note that despite the focus on the effect of light interception in different canopy shapes, which is important for yield, orchard configuration is not yet well enough understood for field-based recommendations to be made, but that the use of high-density dwarf trees or flattened canopies (espalier technique) looks promising.

An important feature of models developed following the POM strategy (Fig. 3) is that they can be modified with limited effort to answer related questions, or even be combined with other models. For example, the beech forest model (BEFORE) did not keep track of dead wood, but this was easily implemented with a few additional assumptions and parameters (Rademacher and Winter, 2003). In turn, this new model version was used to explore how large and how frequently available unmanaged 'deadwood islands' in managed forests would have to be to ensure continuous availability of woody debris, which provides habitat for a wide range of species (Jakoby et al., 2010).

For the models discussed here, Avocado-M could be modified to explore light interception through manipulation of architecture (canopy factors) and resultant yield in such configurations. In combination with Qfly-M, a recommendation would be possible with regard to orchard architecture. Since fruit flies prefer host plants with dense foliage that provides them with resting sites and protection (Dalby-Ball and Meats, 2000, 2002; Hendrichs and Hendrichs, 1990; Kaspi and Yuval, 1999; Raghu et al., 2004), an espalier (trellised) architecture canopy can be hypothesised as reducing Qfly infestation. Such a flattened canopy has the added benefit of removing the protection from winged predators, which is afforded to fruit flies by the dense foliage of rounded canopies. Such combined exploration of the effects of changing plant architecture points toward recommendations for experimentation that should allow confirmation by horticulturalists in the near future.

Qfly-M also suggests a new research focus regarding sensory behaviour in pest management. Simulating the searching behaviour of fruit flies involves specifying their detection radius (i.e., how close a fly needs to be to a host fruit to respond to it). The importance of this parameter was highlighted via this model, despite a lack of focus on this topic for several decades of research. The model analysis also indicated that the detection radius for fruit flies in plant canopies with the same foliage density but different heights may vary significantly and is largely associated with tree size. This agrees with the finding that animals tend to optimise their movement strategies during foraging (Pyke, 1984). This discovery shifts focus within the research discipline from a previously unknown unknown to a now known unknown. As a result, future research efforts should be able to achieve more rapid progress in the theory of optimal foraging behaviour for pest fruit flies.

6. Multidimensionality of the Medawar zone in modelling

The shape and the location of the Medawar zone in the context of modelling philosophy (Fig. 2) are bound by both realism and tractability. However, these two factors are not absolute, and consequently, neither is the Medawar zone in modelling. The realism of a model needs to be seen through comparison with the real world, and hence with what we currently know about our system of interest and how precisely and accurately we can describe it. Similarly, the tractability may vary with the availability of resources. Therefore, the conceptual representation of the Medawar zone (Fig. 2) can be expanded in various contextual dimensions to reflect the relative nature of the relationship between model complexity and model payoff.

For example, a problem that was virtually intractable at the dawn of the computer era may presently be trivial due to technological advances. Thus, both the shape and the location of the Medawar zone in modelling would differ between then and now. In addition to temporal aspects, other dimensions could reflect crucial modelling considerations such as model purposes, scales, spatial resolutions, computational time, and real and model domains. One could represent the Medawar zone in a three- (or higher-) dimensional coordinate system as a more complex 'optimality landscape' with optimal peaks and suboptimal valleys (Fig. 4). The multidimensionality of the Medawar zone in modelling suggests a need for additional context-dependant optimality considerations.

7. Challenges and imperatives for coherence in the modelling discipline

Modelling faces fundamental challenges in two main areas in terms of disciplinary coherence. First, modelling provides services, so it must ensure that models are capable of producing reliable outcomes for end-users (Hamilton et al., 2022). For example, modelling enables biologists

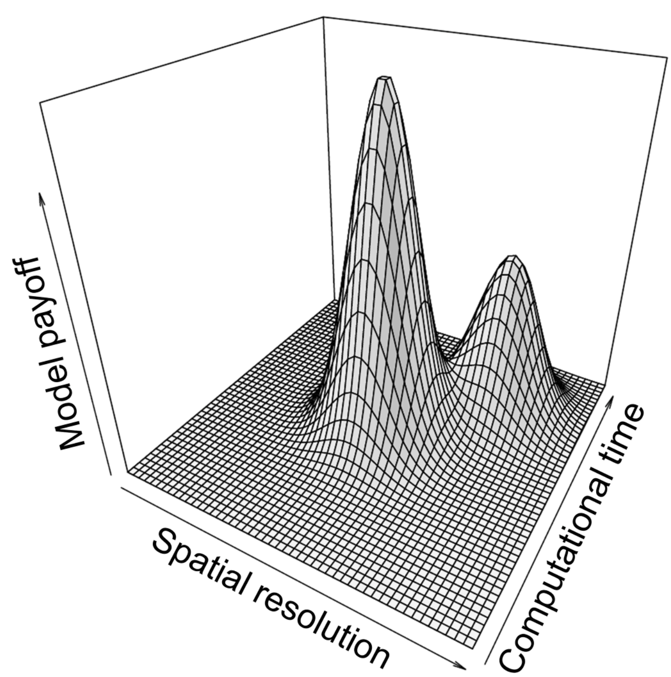

Fig. 4. An example of a three-dimensional representation of the Medawar zone in the context of modelling philosophy. The model payoff is determined by the spatial resolution and the computational time. In this case, the Medawar zone in modelling (i.e., the ideal mid-level complexity) refers to the two optimal peaks.

to interact with their studied systems, generating insights and predictions that bring their research questions into the achievable (Medawar) zone (Loehle, 1990). This makes models more attractive as a tool. However, only models with the right level of detail are likely to provide answers to unusual research questions (known unknowns) or discover unknown unknowns. Before model construction, the responsibility of gathering suitable data often, for instance, lies with empirical researchers in agri-ecological systems, which can result in the collection of unnecessary data for modelling. With a clear understanding of the required level of detail for model structure, modellers can guide empirical researchers to gather targeted data, thereby avoiding wasted time and effort. This can be facilitated by applying modelling strategies such as POM for the formulation of assumptions and hypotheses on model structure to refine the targeted data that need to be collected. This highlights the importance of collaboration between end-users and modellers in building reliable models and achieving disciplinary coherence.

Second, just like any other discipline, modelling should function as a coherent and unified whole, transcending individual practices. This requires the adoption of a common or standard approach to modelling, i.e., a systematic modelling strategy that modellers can rely on and that allows modellers to gain confidence in their techniques and their ability to develop reliable models (Jakeman et al., in press). In the long term, such coherence helps move the discipline beyond the practice of 'siloed modelling' (Grimm, 2023) and should facilitate the future development of modelling strategies such as POM, which assists in finding model structure with ideal mid-level complexity (Grimm and Railsback, 2012; Grimm et al., 2005; Wiegand et al., 2003). This ideal mid-level complexity offers the greatest likelihood of success in investigating known unknowns and discovering unknown unknowns.

8. Conclusions

POM is a systematic modelling strategy that enables modellers to identify the mechanisms underlying a studied system and thus determine the right level of complexity for model structure. When POM is used for model design, development, and refinement, the resulting model structure tends to be located in the Medawar zone in modelling. This limitation of complexity associated with realism and tractability is achieved through the use of multiple observed patterns at different scales as filters (Grimm and Railsback, 2012; Wang et al., 2020). By doing so, modelling can facilitate the investigation of known unknowns and the discovery of unknown unknowns, ultimately transitioning them to known unknowns. Therefore, such modelling holds significant potential to drive research towards the Medawar zone in science, which empowers researchers to make groundbreaking discoveries.

CRediT authorship contribution statement

Ming Wang: Writing – review & editing, Writing – original draft, Visualization, Investigation, Funding acquisition, Conceptualization. **Hsiao-Hsuan Wang:** Writing – review & editing, Writing – original draft, Investigation, Conceptualization. **Tomasz E. Koralewski:** Writing – review & editing, Writing – original draft, Investigation, Conceptualization. **William E. Grant:** Writing – review & editing, Writing – original draft, Investigation, Conceptualization. **Neil White:** Writing – review & editing, Writing – original draft, Investigation, Conceptualization. **Jim Hanan:** Writing – review & editing, Writing – original draft, Supervision, Investigation, Funding acquisition, Conceptualization. **Volker Grimm:** Writing – review & editing, Writing – original draft, Supervision, Investigation, Conceptualization.

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.

Data availability

No data was used for the research described in the article.

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