# Philosophy of science in practice in ecological model building

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**Abstract**: This article addresses the contributions of the literature on the new mechanistic philosophy of science for the scientific practice of model building in ecology. This is reflected in a one-to-one interdisciplinary collaboration between an ecologist and a philosopher of science during science-in-the-making. We argue that the identification, reconstruction and understanding of mechanisms is context-sensitive, and for this case study mechanistic modeling did not present a normative role but a heuristic one. We expect our study to provides useful epistemic tools for the improvement of empirically-riven work in the debates about mechanistic explanation of ecological phenomena.

Keywords: scientific practice, interdisciplinarity, mechanistic modeling, heuristics, ecology.

## 1. Introduction

The new mechanistic philosophy of science (NMP) has been very successful in accounting for how mechanistic explanation (ME) is used in several scientific areas. Even though mechanisms have been increasingly investigated in ecology since the 1980s, there are relatively few philosophical works devoted to elucidate how mechanisms are described and depicted in ecology (see Matthewson and Calcott 2011; Pâslaru 2009, 2015; Raerinne 2011). One of the putative reasons, we believe, lies in the fact that ecological systems are influenced by multiple drivers at different spatial and time scales (Nelson et al. 2006). Many of these drivers interact in a complex and non-linear way, increasing the challenge of modeling ecological systems and processes in mechanistic terms, which may have suggested that it would be harder to advance in understanding mechanistic models though considering ecology.

Currently, the new mechanistic perspective deals with multilevel systems, and with complex features like hierarchical organization and nonlinearities (see Wimsatt 1994; Bechtel and Richardson [1993]2010; Glennan 1996, 2002; Craver 2001, 2007; Bechtel 2015), which seems likely to suggest that ME conceived according to this perspective can be helpful in the process of building and explaining ecological models[1] for dealing with complex and non-linear phenomena. This raises an interest in applying the NMP to foster modeling practices in ecology but also to verify whether the NMP can be helpful for scientists making science as it is helpful

[1] Without neglecting the polysemy of the term "model", we conceive models here as constructs created by the scientific community in order to represent relevant aspects of experience, for instance, phenomena and processes/mechanisms that can explain and/or predict them.

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for philosophers wanting to understand science. Thus, this paper provides an analysis of mechanism modeling in ecological research and, at the same time, show that interdisciplinary collaboration between philosophy and ecology is valuable to produce both philosophical and scientific knowledge.

This article uses philosophy of science in practice through an empirical (collaborative and interdisciplinary) case study of model building in ecology to advance the understanding of how mechanisms can be elucidated in this science. We used an action-research approach (Tripp 2005) to investigate the collaborative and interdisciplinary work of a philosopher of science (the first author of this paper) and an ecologist (the second author). We show that, even though a mechanistic model was developed, it was nonetheless substituted for a broader theoretical model that fitted best the ecological system, suggesting that mechanistic explanation and mechanistic models presented limitations to explain the ecological system at stake. Besides, our results also show that part of the ideas derived from the NMP could not be applied to the ecological phenomenon. As our in-depth study of an ecological mechanism was forced to depart from the strategies for mechanism discovery as proposed by Craver and Darden (2013), Bechtel and Richardson (2010), and others; which suggests that mechanism modeling in complex ecological systems needs not follow all the steps usually proposed for reconstructing mechanistic modeling in past work in NMP. This means that such strategies are maybe not universally applicable nor a necessary condition for mechanism reconstruction, suggesting a heuristic role rather than normative role for the NMP in mechanism modeling in ecology.

## 2. Methods overview

This article addresses the contributions of the literature on the new mechanistic philosophy of science for the scientific activity of building models in ecology. It portrays an interdisciplinary collaboration between *an ecologist and a philosopher of science in a one-to-one interaction* to create a heuristic set to guide model building.

We apply a notion of interdisciplinarity expounded by Tress, Tress and Fry (2005), according to which interdisciplinary research integrates knowledge from different disciplinary fields in order to build a new body of knowledge to tackle a common research goal or solve a real-world problem. In interdisciplinary research, disciplinary knowledge from all the fields (in this case philosophy and ecology) contributing to the interdisciplinary project is recontextualized in relation to interdisciplinary goals. In our case, the new body of knowledge produced is a *heuristic set* constructed according to the new mechanistic philosophy of science and ecology, and this heuristic set is pivotal as it will guide the ecologist's modeling activity.

The 'heuristic set' gathers the instruments that guide scientists' actions in model building but also works as a display for philosophical assessment (see Poliseli 2020). The general conception of the heuristic set was developed based on the philosophical literature on mechanistic explanation, which was adapted to features of the ecological phenomenon. It is importantly to highlight that although philosophers do no typically describe the characterization of a phenomenon as a heuristic strategy, we have called the stages for mechanistic building as 'heuristic' because in our case study, the heuristic set was problem-specific fallible strategies that helped the ecologist to cope with model building about the phenomenon of interest. By 'heuristics' we mean then, a rule of thumb for model building and other epistemic actions used to grasp a phenomenon and the processes generating it. Going beyond some sort of algorithmic application of modeling steps, the heuristics were used in this research as epistemic instruments for the modeler to grasp the ecological phenomenon at stake and the components and causes interacting to produce it.

The dynamics of the heuristic set construction and application is illustrated in Figure 1. Through monthly meetings, the general conception of each heuristics was elaborated by the philosopher and the ecologist together. Concomitantly with this elaboration, the ecologist applied the heuristics to model the ecological phenomenon. Whenever the heuristics were applied, it also worked as feedback for their theoretical improvement. Thus, the heuristics influenced the scientist's practice but the scientist's practice also influenced the heuristics' theoretical framework. It is important to clarify each participant's task. The construction of the heuristics' general conception was a collaborative work of both, the elaboration of the theoretical framework was a task of the philosopher, while the process of application to the ecological phenomenon was a task of the ecologist.

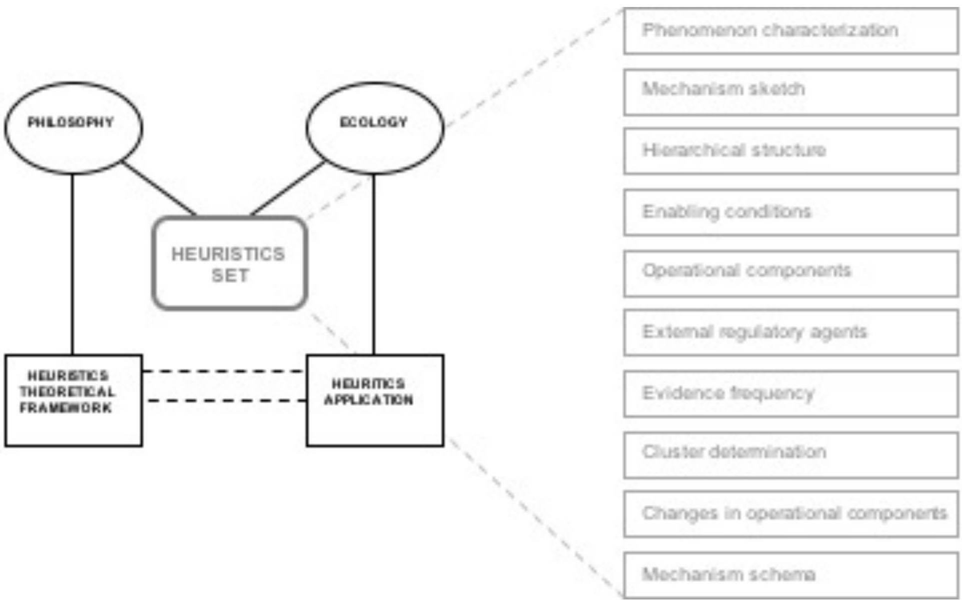


Figure 1: Dynamics of the collaboration between the philosopher and the ecologist for building the heuristic set (for a full caption of the heuristics see supplementary material). *Circles* represent the philosopher and ecologist. *Square boxes bellow*, the tasks developed by each participant. *Central box*, the heuristic set developed by them, with the heuristics themselves shown in the *right rectangles*. Source: adapted from Poliseli 2020.

This was a continuous four-year project, and accordingly, the information resulting from the applications of the heuristic was continuously revised and modified. Even though we took the NMP as a starting point, the heuristic construction and application showed that part of the ideas derived from this literature could not be applied to the phenomenon investigated in the case study. This is in accordance with recent literature that shows that mechanistic explanation possesses limitations concerning explanatory demarcation, explanatory normativity, ecological generalizations, and so on (see Raerinne 2011; Halina 2017).

The assessment of this scientific process as well as the collaboration between the philosopher and the ecologist was guided by action-research methods (see Tripp 2005), and the data regarding the heuristics application and model building was gathered through open interviews, questionnaires and personal communications during >45 meetings, which took place over a four-year period. This methodological approach was used to identify explanatory patterns and variations which were used as evidence of scientific practices that were under way. This paper presents, therefore, the outcomes of an action-research approach to the study of this collaboration, from which we derived a philosophical interpretation. Thus, what is addressed here is not only the prospect of applying ME to ecology, but also whether heuristics developed from the philosophy of science can indeed contribute to science-in-the-making, more specifically, to ongoing scientific practice in ecology. This is in accordance with prior suggestions in the literature that both philosophy can contribute to science, and science can be relevant to the reassessment of philosophical stances (*e.g.*, Chang 1999, 2014; Ankeny et al 2011; Kosolosky 2012; Boumans and Leonelli 2013; Boon 2017; Mallaterre et al. 2019; Poliseli 2020; Pradeu et al. 2021).

## 3. Mechanistic modeling in the new mechanistic philosophy of science

The philosophy of mechanisms can be considered a mature subfield within philosophy of sicence. The literature is rich, with numerous accounts developed over the years (see Bechtel and Richardson [1993]2010, Machamer et al. 2000, Darden 2002, 2006, Craver and Becthel 2006, Craver 2002, 2007, etc.). A more recent systematization is found in the *Routledge Handbook of Mechanisms and Mechanical Philosophy* (Glennan and Illari 2018), which highlights the historical, philosophical and practical significance of the philosophy of mechanisms. We adopt here the 'minimal definition' of mechanism proposed by Glennan and Illari (2018, p. 120) as a useful stating point, that somehow captures the most important commonalities of the available accounts: "a mechanism for a phenomenon consists of entities and activities organized in such a way that they are responsible for the phenomenon". Hence, to discover a mechanism one needs to discover the entities and involved and how they are organized such that the phenomenon of interest is produced. The organization and the dynamics of the entities and activities establish the path through which the phenomenon is produced. Thus, entities must be specifically situated, structured, and oriented while the activities in which they participate must be coordinated temporally, involving order, rate, and duration (Machamer et al. 2000, p. 2).

Although ME have played a pivotal role for our understanding of explanatory practices in biology in the last three decades, this debate is still incipient in relation to ecology. Moreover, as Halina (2017), Pâslaru (2009, 2015), Raerinne (2011) and others have pointed out, one can identify several limitations of NMP for the understanding of ecological practices. For instance, Matthewson and Calcott (2011) draws attention to the general fact that the entities and activities considered in ME are well-defined, being the models built with localizable parts that interact in distinctive ways, while models such as those built in population ecology include parts and interactions that are neither local nor discrete. This might be a reason why many ecological mechanisms are not well known and ME in ecology is often undetermined due to lack of sufficient data (Raerinne 2011).

According to Raerinne (2011) when ecology is contrasted with other biological disciplines, such as genetics, molecular biology, and neurobiology, in which the mechanistic aspects of explanations seem to be more prominent, ecological causal explanations appear to be "phenomenological" invariant generalizations whose mechanistic aspects remain to be discovered. In ecology it is often the case – as we will see in the ecological models discussed in this paper – that there will be a lot of interest in identifying target explananda, which will be explained later in the research agenda. This has to do, on the one hand, with a pragmatic orientation commonly found in ecological practice, namely, that of looking for effective points to intervene on an ecological system to fulfill some purpose, say, to improve the sustainability of productive practices or to support a better choice of conservation strategies. But it also has to do, on the other hand, with the fact that in ecological research we are times in a situation where the explananda themselves are not sufficiently clear and, thus, ecological research naturally targets such explananda in their modeling practices. Another aspect discussed by Raerinne (2011) that us relevant to the models discussed in this paper lies in the fact that many explanations in ecology are simple causal claims in the sense that there are no known or confirmed mechanistic explanations for how the causes involved produce their effects. There is, however, controversy in this respect. Pâslaru (2009, 2015), for instance, defends that components and activities can be identified in ecological mechanisms. However, he agrees that NMP possess limitations as it does not capture the full expectations of what an ecological explanation aims for in his view, namely, realism and prediction. To mitigate these limitations, he suggests ME should be integrated with other approaches such as Woodward's manipulability theory of causation because it would allow recognizing invariant and insensitive features of the system.

Finally, Matthewson and Calcott (2011, p.738) point out that "it is sometimes difficult to see where the analysis of mechanisms in the world finishes and where (or if) a discussion of their representation begins". According to them, mechanisms and models should have a flexible interaction with their targets, for instance, even when there is a mismatch between the target phenomenon and its model, a mechanistic explanation and mechanistic representation are still possible. This is feasible because models can be explanatory even when its properties diverge from what they represent. Thus, the demarcation between model and mechanisms may not be that clear in ecological contexts which justifies the usage of a "mechanism talk" in these occasions (see ibid., Darden 2013).

## 4. The case study: bee functional diversity in agroecosystems

Most examples in debates about mechanistic explanation are elaborated from cases in neurobiology and molecular biology. Moreover, past cases of mechanistic explanation are typically addressed. In this inquiry we take a different approach, using insights from the new mechanistic philosophy of science to engage with ongoing scientific practice in ecological research investigating the functional diversity of native bees in agroecosystems. To understand this case study, let us first introduce some of its background.

Bees are the most important organisms providing pollination services in most regions of the world (Klein et al. 2007). They are responsible for the pollination of approximately 70% of the crops around the world and of more than 80% of the angiosperms (Potts 2010). Bees are, accordingly, of key importance in agroecosystems. Agroecosystems are defined as communities of plants and animals interacting with their physical and chemical environments that have been modified by people to produce food, fibre, fuel and other products for human consumption and processing (Vandermeer, 1995). They show an intricate set of ecological and non-ecological characteristics that defines their dynamics. Agroecosystems can have significant impacts on landscape management, biodiversity patterns, and other ecological features. For instance, decisions on landscape management that aim at suppressing native vegetation to implement agroecosystems may affect negatively several groups of animal species through habitat loss (Pardini et al. 2010; Ferreira et al. 2015). In particular, these decisions affect distinct groups of bees that are usually involved directly or indirectly in different ecosystem services, such as water depuration, soil nutrient cycling, biological pest control, and pollination (Gurr et al. 2003, Wratten et al. 2012). All these services are intimately connected with food supply for human societies and other species (Gallai et al. 2009; Garibaldi et al. 2014). However, bees do not respond evenly to intensive land use by agriculture (Coutinho et al. 2018). Because they have different functional traits, the impact of environmental changes affects species differently (Oliver et al. 2015).

By investigating functional diversity in community ecology one can describe biological diversity in terms of the identification of morphological, anatomical and behavioral attributes of species that show important relationships with ecosystem functions or services or that help to explain the presence of certain species in an environmental context (Cadotte et al. 2011). Because species are a mosaic of functional traits, there are intricate relationships of trade-offs and complementarity between these attributes (Williams et al. 2010), requiring an effort to establish a hierarchy of relevance linked to the ecological questions we ask. For example, large-bodied species may be trophic generalists or specialists, nest above-ground or below-ground, and be solitary or social. Each of these traits can generate a different response to an ecological driver and the importance of this trait will be context-dependent. In a meta-analysis carried out by Williams et al. (2010), it was detected that although larger and more mobile species responded less to habitat isolation, larger species tended to nest above ground and more mobile species were more affected by isolation. Thus, understanding the complementarity or trade-offs between these traits is essential to indicate the relationship of ecological predictors with functional responses of the community. Considering bees, this hierarchy of relevance is important to tackle questions such as: which functional traits best explain the presence of a group of bee species in an agroecosystem? Which functional traits best explain the success of the pollination service in agroecosystems? To answer these questions about functional traits, we need a deep understanding of the system, the species involved, and the ecological processes at stake. For years, ecologists have been looking for ways to establish less subjective criteria for hierarchizing the relevance of functional traits (Oliver et al. 2015). Mechanistic and hierarchical modeling provides a promising way to highlight the more relevant ecological processes, functions, and traits, and, thus, provide objective grounds to ascertain those criteria.

The conservation of ecosystem services requires that functional diversity be maintained, as such diversity allows the maintenance of the magnitude or stability of ecological functions related to ecosystem services (Oliver et al. 2015; Coutinho *et al.,* 2018). From current scientific knowledge we can predict that intensive land use is not consistent with medium- and long-term stability of agroecosystems in time and space (Garibaldi et al. 2011), partly because of functional diversity loss (Oliver et al. 2015; Woodcock et al. 2019). To maintain stability, it is necessary to restructure land use so as to be compatible with biodiversity conservation and ecosystem services (Garibaldi et al. 2014). Detailed understanding of how the structure of a pollinator community affects the pollination service is a key goal in pollination ecology (Gagic et al. 2015; Oliver et al. 2015). This understanding is crucial to promote agroecosystems compatible with maintaining the diversity of functional traits in order to increase the probability of maintaining pollination stability over time and space (Bartomeus et al. 2017; Woodcock et al. 2019). For this reason, the ecological research project that offered the context for the case study reported in this paper dealt with changes in the functional composition of native bee communities in agroecosystems as the ecological phenomenon.

The ecologist aimed to address the most relevant ecological processes to explain changes in the functional diversity of bees in agroecosystems. In particular, the ecological study used a complex systems perspective alongside with the theoretical-methodological framework provided by philosophical approaches to mechanistic explanation in order to tackle its main research goal, namely, to create a mechanistic model to explain the functional composition of autochthonous bee communities in agroecosystems, which may allow the creation of predictive scenarios for the conservation and stability of the pollination ecosystem services. To derive a theoretical-methodological framework from mechanistic philosophy, a heuristic set was developed in order to guide the model-building activity. In the next sections, we will describe in detail the application of the heuristics along the case study and the series of mechanistic models built to explain the ecological phenomenon at stake.

Figure 2 shows the mechanism built by the ecologist. On the right side, one can see the main spatial scales influencing pollination services: regional, landscape, patch, and flower scales.

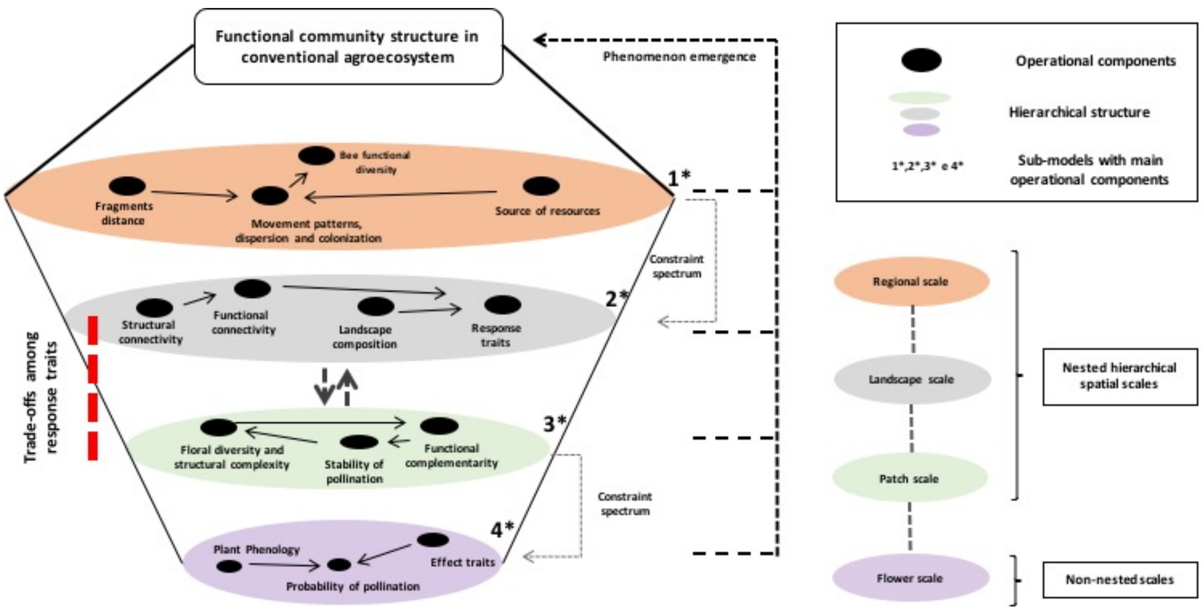

Figure 2: General hierarchical mechanistic model indicating the main spatial scales influencing the pollination ecosystem service with the respective operational components. Constraint spectrum is a set of restrictions exerted by a hierarchical level above, that influences the dynamic of ecological processes at the level below. Nested scales indicate a set of spatial scales where interrelated ecological processes occur in that system. Non-nested scale indicates a specific spatial scale where the phenomenon analyzed occurs.

On the left side of Figure 2, the operational components are depicted at each level: 1* indicates ecological components and processes at a regional scale, which provides the regional pool of species that operate at the smaller spatial scales; 2* includes aspects of the structure of the landscape that influence bee functional composition through the interaction with certain response traits, which are the traits that condition the response in richness and abundance of bees species at the patch level to such landscape spatial aspects; 3* contains structural characteristics of habitat patches that influence the probability of more or less complementarity of traits at this scale, influencing the spatiotemporal stability of the pollination service; 4*, the smallest scale in this model, indicates that pollination success will ultimately depend on plant phenological attributes (supply of resources compatible with the needs of bee communities, for example) and effect traits (bee traits related to the successful transfer of pollen grains) (for a zoom-in at each system level see supplementary material).

## 5. Heuristic set and model building

In this section we explain how the theoretical framework related to each heuristic was applied and modified according to the scientific practice. Thus, we will mainly discuss how the heuristics were applied in the case study and will not deal with examples from a general heuristic practice extracted from the literature. For reasons of space, some but not all of the heuristics used for the modeling practice will be presented. For each heuristic, we will provide a brief description of its theoretical grounds and application. Although the process of developing the heuristics and carrying out the ecological modeling may appear to be a series of sequential steps, this is not how it occurred. Most of the time, the heuristics were developed and applied simultaneously. For example, drawing the phenomenon structure occurred at the same time as developing a table of enabling conditions. Every time a different structure was elaborated, it also impacted the phenomenon characterization, and so on. The heuristics presented here are those perceived to be the most important ones during the modeling process and explanation construction, according to the philosophers' eye. In other words, what will be explained below is a rational reconstruction of the way the inquiry proceeded because although it can be reconstructed into sequential steps, the reality of its application was less structured and systematic. For reasons of space, some but not all of the heuristics used for the modeling practice will be presented.

We will begin by considering the phenomenon characterization. Then, we will discuss the mechanism sketches that allow one to ponder about the components and causal connections that enable the phenomenon to exist. By examining the hierarchical structure provided through these sketches, we will tackle the scales at which the causal connections take place. The enabling conditions for the phenomenon to happen will receive attention next, followed by the distinction of the operational components in the mechanism. The frequency of the causal connections among the components as supported by the scientific literature will be considered afterwards. The next aspect will be to address the exploration of alternative scenarios. The last heuristic we will discuss is the final mechanism schema. Although it is a hard task to identify these heuristics in the scientific practice, as they are often deployed together in different combinations, for intelligibility it is important to present them individually, so that we can understand the role each of them had in model building and the process of understanding the phenomenon and its causation.

It might seem that the heuristics described below are too fine-grained to be heuristics of causal modeling in general, being rather tied down to the details of the study analyzed in the paper. However, the heuristics are not related just to the particular case we modeled. For instance, when we refer to hierarchical levels, changes of components in a scenario and their repercussions, elaboration of sketches, characterization of a phenomenon, all of them can be applied to a very large set of ecological phenomena. If we think about biological pest control in agroecosystems, eutrophication processes in a lake, litter decomposition in a forest, all these phenomena and many others are likely to be modeled using the heuristics discussed in the paper, as there will be some specific level of generalization that can be applied to the components of these systems and the ecological processes in which they participate. It is important, thus, to be attentive below about the general meaning of each heuristics per se and their particular applications to the case in point.

## 5.1 Phenomenon characterization

A common claim in the literature on mechanisms is that the phenomenon is a product that emerges from mechanisms (Craver and Darden 2013). Therefore, a characterization of the phenomenon is needed to unravel the underlying mechanisms. Such description will aid in the identification of the mechanism's actions and boundaries, which will then be framed according to the requirements for explaining the phenomenon. At a first impression, this may sound tautological, but it is important to be clear that "to describe a phenomenon is to characterize it in the language of a given field and to implicitly call up the host of explanatory concepts" (Craver and Darden 2013, pp. 52). One implication is that components, activities, and functions will only be included in the description of a mechanism if they are relevant to the phenomenon itself, *i.e.*, if they, once organized in a certain way, directly or indirectly enable the phenomenon (Craver and Bechtel 2006).

The heuristic 'phenomenon characterization' is formulated here in terms of a description of the *explanans* and *explanandum* in a given study. The modeling of a mechanism usually involves several phenomenon characterizations as data become available (Craver and Darden 2013). Bee functional diversity and pollination services are embedded into complex systems. Thus, the characterization of the phenomenon through the description of every single element that enables it is not feasible. Nonetheless, acknowledging that it is not always necessary (or possible) to have a full explanation in order to characterize the phenomenon, the strategy of this heuristic became to develop several characterizations throughout the modeling practice.

In our case study, the phenomenon was first characterized as the "diversity patterns of insect pollinators in agroecosystems". A second characterization strived for narrowing down the phenomenon by selecting a category of pollinator and a specific type of diversity: "functional composition of autochthonous bee communities in agriculture systems". The third characterization focused on a specific agricultural model and ecosystem service: "the functional structure of an autochthonous bee community, as well as the maintenance of its pollination services in an agroecosystem."

As the *explanandum* changed along the successive phenomenon characterizations, what was doing the explaining (the *explanans*) changed accordingly. In the third definition above, the aim became to model the mechanisms related to soil use in intensive agricultural practices and establish a link between these mechanisms and bee functional diversity, appraising response and effect traits. Response traits are attributes that influence the persistence of individuals of a species in the face of environmental changes (Oliver et al. 2015). Effect traits are attributes of the individuals of a species that underlie their impacts on ecosystem functions and services (Diaz et al. 2013). Taken together, these traits provide ways to understand how changes in the environment influence an ecosystem function (Wood et al. 2015). No matter which heuristics was applied, it was possible to perceive a clear feedback onto the phenomenon characterization.

### 5.2 Hierarchical structure

This heuristic identifies the levels in which the mechanism is organized. This enables the visualization of interactions among different spatial and temporal scales, which are typically involved in the generation of ecological patterns. Our strategy to build mechanism sketches considering hierarchical levels combines contributions from Salthe (1985), Craver (2001) and Filotas et al. (2014).

Usually, definitions of 'mechanism' are bounded to a certain notion of organization, *i.e.*, the component and activities composing a mechanism are displayed under at least a minimal organization. For the case study, it was previously assumed that the agricultural system is a complex system organized hierarchically, more specifically, in a nested way (Filotas et al. 2014). In hierarchically structured systems, a hierarchy of entities existing at different levels of organization is assumed, such that, as highlighted by Salthe (1985), things exist as wholes with their parts. Each part or whole is modeled as belonging to a level, or as the level *per se*. In a system with several levels, each level may influence one another or not. The components at one level interact with other components at the same level and produce a phenomenon at this level, or at different levels (Bechtel 2015). At different levels, the components may use or be favored by a product or phenomenon from another level, and, therefore, there may exist an interaction between different levels. Thus, hierarchical organization may facilitate the tractability and characterization of each system component (Bechtel and Richardson [1993] 2010).

To better grasp the hierarchical structure of the phenomenon at stake, we must understand that first, levels are organized. While spatial structure is important to understand the phenomenon and the causal processes underlying it, this organization must not be understood as something fixed and stationary. The spatial localization itself will not be as important as the activity it allows if and only if the location is not crucial to the very activity. Thus, to realize that levels are organized is to realize that they enable something to happen, while sometimes the components possess rigid spatial locations, sometimes not.

Second, levels are organized and interact consistently within a timescale. For example, it is mandatory in our case study that there is synchronism between flower and animal in order for the pollination service to take place. This example is interesting because it works with interacting levels to produce an outcome: the pollination itself. It is crucial to notice that the ecological phenomenon also exhibits evolutionary aspects that cannot be ignored. Therefore, it involves distinct timescales (Maron 2010).

Furthermore, this heuristic is consistent with the idea that ecological systems exhibit a multilevel network structure (Filotas et al. 2014). After all, the patterns of species distribution, abundance and interaction, which constitute the domain of community ecology, "… occur at different spatial scales and can vary with the scale of observation, suggesting that different principles might apply at different scales" (Leibold et al. 2004, pp. 601).

In our case study, this heuristic allowed the identification of three spatial scales in the first phenomenon characterization (Figure 3). In a top-down view, the larger scale includes the metacommunity dynamics, which is in the domain of landscape theories. One of the components that enable the higher level to work as a mechanism is the patch, the second level in this hierarchical model. In an agricultural system, a landscape may possess several heterogeneous patches, from native to secondary vegetation to agricultural field. Each of these patches will possess different internal dynamics and different impacts on the pollination system. This uniqueness in the dynamics allows us to recognize the bee-flower interaction as the lowest level. Even though this sketch clearly identifies a three-level mechanism, note that neither the components nor the activities are still established, which only occurred with the assistance of the heuristic 'enabling conditions' and 'operational component distinction'.

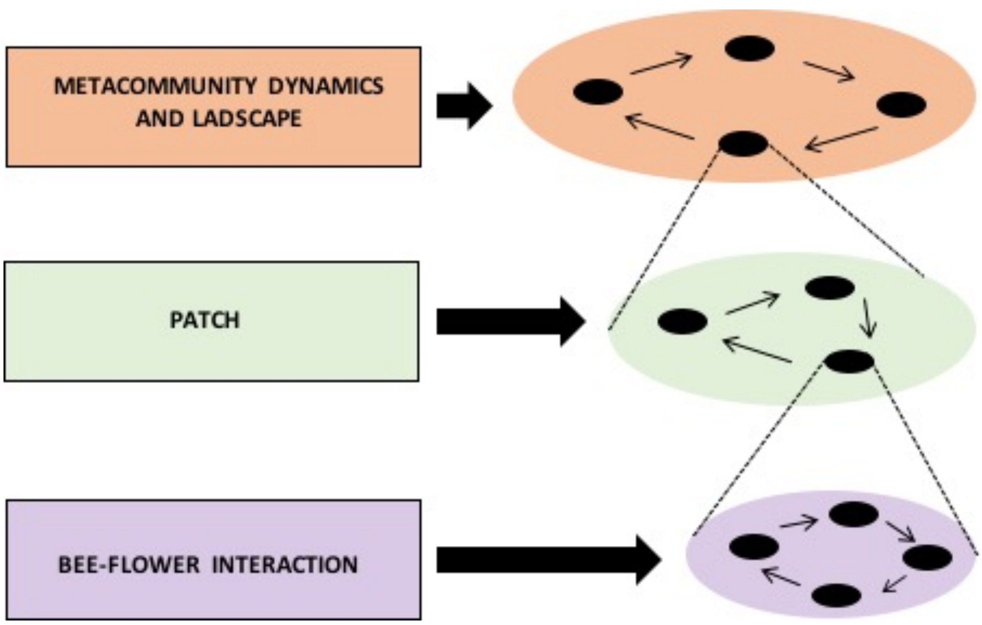


Figure 3: Mechanism sketch showing three spatial scales in the characterization of the phenomenon of interest in our case study.

### 5.3 Mechanism sketch

A mechanism sketch is a draft, a simple diagram containing gaps, black and grey boxes, which will be discarded when no longer useful (Machamer et al. 2000). This heuristic allows putting pieces together whenever they seem to be related, for instance, the causal relations underlying a phenomenon. One strategy to build a model of a mechanism is to treat its parts as placeholders (Holyoak and Thagard 1995). By doing this, it is possible to arrange the steps of the mechanism operation, *i.e.*, to ascribe to the entities a number of activities that functionally contribute to the working of the mechanism. There is no strict rule or better path to follow. It is possible that in one moment the easier way is to identify the activities and then the components. In another moment it may be easier to recognize the components and then the activities. And perhaps in another situation to identify modules or clusters could provide the easiest way to unravel the components and activities of the mechanism (Darden 2006).

This heuristic suggests that it is possible to start by drawing a mechanism sketch that is closely related to a conceptual map. This is a starting point to derive the components and activities of the mechanistic model. In this sense, conceptual maps can serve, just as the mechanism sketches constructed using them, as instruments to organize and structure knowledge about a mechanism. This is shown, for instance, in one of the several mechanistic sketches elaborated in the case study (Figure 4).

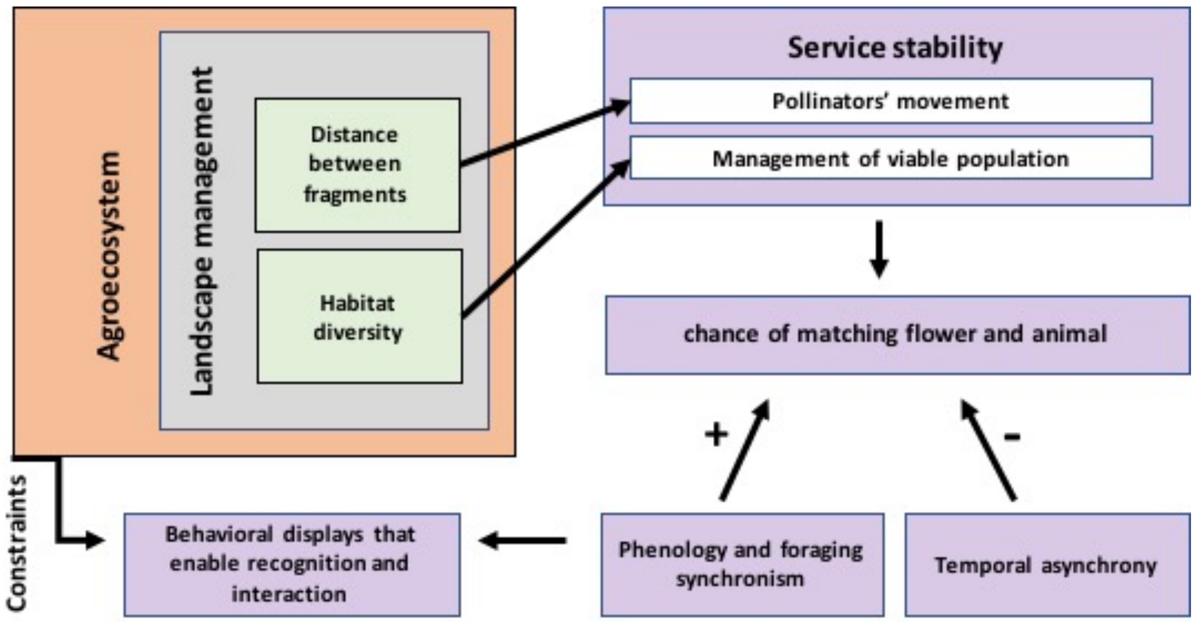


Figure 4: One of the mechanistic sketches built in the case study, showing similarities to a conceptual map and illustrating the most important interactions concerning pollination in agricultural systems.

The sketch shown in Figure 4 represents an agricultural system associated with a certain kind of landscape management, which shows features influencing the phenomenon at stake. Examples include fragment distance and habitat diversity. Fragment distance influences pollinators' movement: the smaller the distance between the fragments the larger the dispersion of the pollinators in the landscape. Therefore, it can be assumed that it is likely that there is a viable population of pollinators and, consequently, the ecosystem service they provide exhibits stability. The management of this population also needs a synchronism between plant flowering and animal presence. For pollen gathering there must be synchronism between phenology and foraging; otherwise, there is no possibility of gathering. If the synchronism is positive, then the encounter between flower and pollinator happens, involving behavioral displays and structural features that enable recognition and interactions.

Sometimes, some boxes in the sketch will be incomplete due to unsolved problems or unavailable data (Bechtel and Richardson [1993]2010). Other times this will be due to the need to use abstraction while building the model. Black and grey boxes may be filled in gradually. The gaps are initially shown in black boxes, where neither the components nor the functions are known. Along the construction of the model, the intention is to transform black into grey boxes, where either the components or functions are known. And, finally, it is intended that the grey boxes be transformed into glass boxes, where every component and activity are known (Darden 2006; Craver and Darden 2013).

In sum, the mechanism sketch functions as a draft that can always be discarded or improved. The continuous failure to fill in its parts may lead to an abandonment of the sketch in favor of another one (Darden 2006). For instance, in our case study the sketch shown in Figure 4 was relinquished. Other sketches will be introduced whenever they are best incorporated in the discussion of a heuristic. The important thing to keep in mind is that in our case study these sketches worked as epistemic instruments to organize and structure the knowledge about the phenomenon and how to explain it.

### 5.4 Enabling conditions

In classical discussions of mechanistic explanation, enabling conditions are usually characterized as those factors or conditions that are sufficient to bring about the phenomenon. In such cases, the parts with properties of a mechanism are entities that trigger the phenomenon. In the case of ecological phenomena, two aspects should be stressed: there may be no triggers that bring about the phenomenon, and the parts of a mechanisms are not necessarily real entities but features of objects and states of affairs or even more abstract things, e.g. functional connectivity, population stability, functional diversity, distance between fragments, etc. To accommodate the diverse nature of enabling conditions in ecological mechanisms, we can understand them - in rather general terms - as variables involved in activities in the mechanism under investigation that are relevant to the production of the phenomenon at stake. The goal of this heuristics is, thus, to identify the most relevant variables related to the phenomenon of interest, that is, the enabling conditions.

The information about the enabling conditions for the phenomenon investigated in the case study was extracted from major ecological theories and published literature specifically tackling that phenomenon. One interesting aspect is that at the beginning of model building this heuristic mainly concerned the explicit systematization of this information. However, the more elaborated the sketch became the more information was aggregated, and vice versa, allowing a refinement of the phenomenon characterization and, therefore, the *explanans* and *explanandum*. Ultimately, this refinement changed the application of the heuristic ‘enabling conditions" from simple systematization to analysis and representation of information through graphs and mathematical indices (Figure 5).

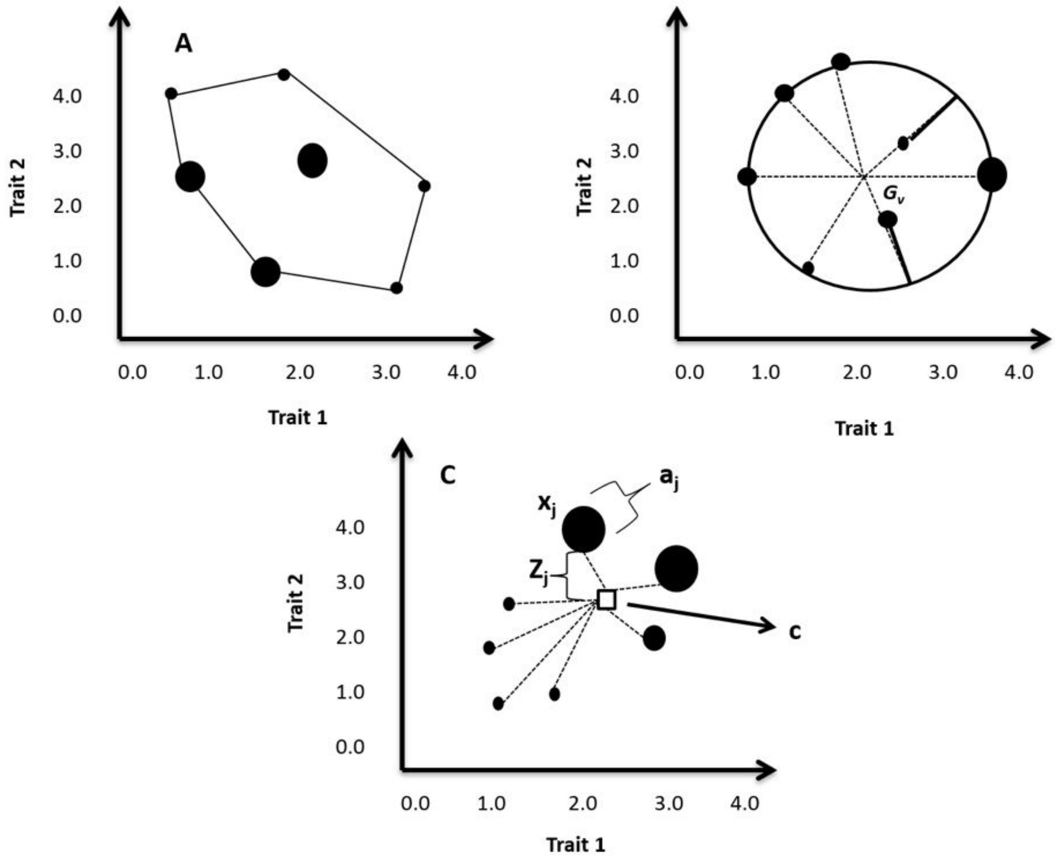


Figure 5: Three different indices that reflect distinct properties of functional diversity. (A) Functional richness; (B) functional divergence; (C) functional dispersion; (Gv)functional space; (Xj) position of species j; (Zj) distance from species j to centroid c; ($a_j$) species abundance; (c) centroid of the species present in the community. The size of the circles represents the distinct abundances of species in the community. Source: Author et al. (forthcoming).

The examples in Figure 5 illustrate how this heuristic was used in our case study. These three graphs represent distinct and complementary aspects of functional diversity, constituting important steps in understanding the connection between biodiversity and ecosystem functions, as well as in elucidating the influence of environmental predictors on functional diversity (Villéger et al. 2008; Laliberté and Legendre 2010). Functional richness (A) is understood as the volume occupied by the species of a community in a space formed by multiple functional traits (Villéger et al. 2008). Functional divergence (B) reflects how much the species of a community diverge in their distances from the center of gravity of the functional space, considering also the abundance of those species (Mason et al. 2005). Functional divergence will be low if the most abundant species are close to the center of this multi-trait space, while it will be high when the most abundant species occupy extremes of the space (Villéger et al. 2008). Finally, functional dispersion (C) indicates the average distance of individual species to the centroid of all species (Laliberté and Legendre 2010). Understanding how these properties may vary in a certain environmental context (say, an agricultural system) was critical to build the final framework developed in the case study.

5.5 Operational components distinction

Through this heuristic, the components, activities, functions and relations linked to the enabling conditions are identified. Usually, it is suggested that the key for developing a mechanistic explanation is to determine the components of a system and their functions by applying the strategies of decomposition and localization (Bechtel and Richardson [1993]2010), as well as the strategies of forwarding and backward chaining (Darden 2002, 2006). Despite the recommendation to use these strategies, some mechanism's parts will be easily identified without the need of those efforts. Nevertheless, there will be moments where only a component or a function will be identified, but not both. Sometimes the activity may be identified without the recognition of the components. Sometimes the component may be identified without discovering the exact activity it realizes. When there are such uncertainties, we refer to an "operational component" and a grey box is included in the mechanistic sketch.

We need to consider that not every system can be subjected to manipulation, *i.e.*, it is not always possible to physically isolate the components of the system in order to determine their functions. In cases like this the strategies proposed by Darden (2002, 2006) and Bechtel and Richardson ([1993]2010) may not be completely suitable. Despite their effectiveness to recognize components, it is important to highlight that not every pattern reveals useful information. Even though the enabling conditions are variables that provides information about the mechanism, this structure is not exclusively provided by those variables. There will exist some features delimited by some constraints of the systems. Thus, how is it possible to differentiate patterns that reveal information from patterns that do not? Considering the case study, Figure 6 shows a strategy that was used to identify effect and response traits, as well as properties of functional diversity more relevant to the phenomenon. Effect traits are used to illustrate the strategy.

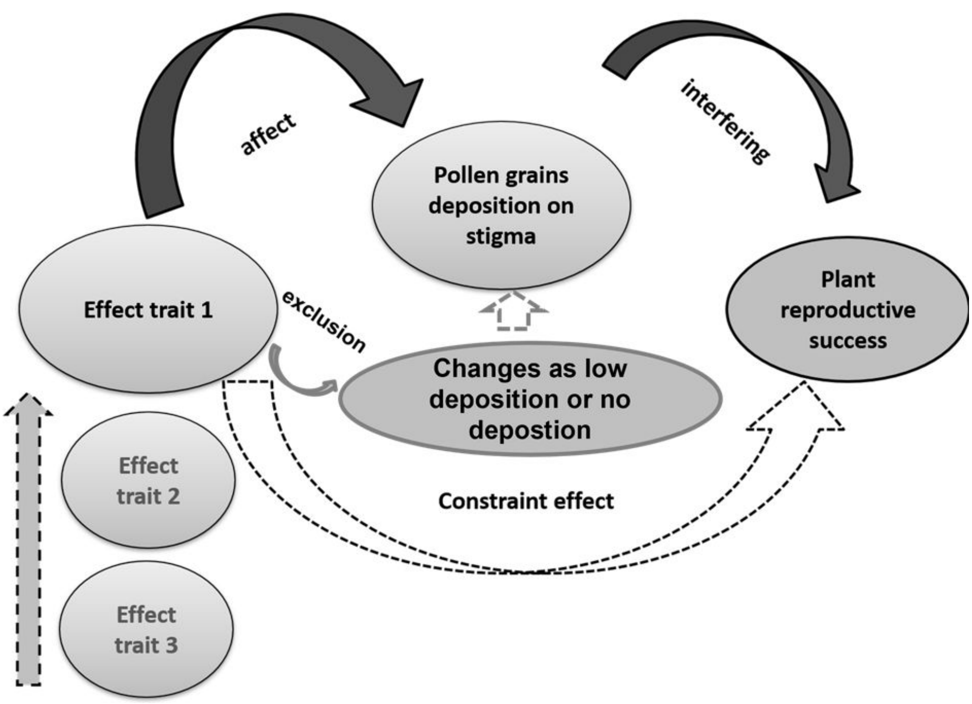

Figure 6: Diagram indicating the steps for the recognition of relevant effect traits related to pollination in a system. In this approach, experimental designs should pay attention to each effect trait separately, in order to understand the relative role of each one in the efficiency of the pollination process. This design can include, for example: foraging rate, foraging duration, the incidence of nectar versus pollen visits, and whether or not the bee made contact with the stigma, as suggested by Martins et al. (2015).

As shown in Figure 6, an effect trait (1, 2, 3) will be relevant if, and only if, its exclusion implicates changes in the deposition of pollen grains on the stigma. This will consequently reduce the amount of fruits and/or seeds of the target plant species, which will deviate from its maximum potential. This constraining influence of the effect trait on the reproductive success of the plant should guide the selection of relevant traits for model building.

One interesting aspect that also changed with the process of *explanans* and *explanandum* refinement in the case study was the use of mathematical indices, as addressed in the previous heuristic. In the heuristic 'enabling conditions' the response traits were initially considered individually, but with the use of these indices, the set of traits came to be approached from a multidimensional perspective. The most used index was functional dispersion. As we saw above, this metric quantifies the average distance of each species of the community toward the centroid of a multivariate space previously defined (Laliberté and Legendre 2010). In the case study, this index represented a feature of the community. For instance, the extent to which a species occupies a volume formed by a set of functional traits indicates how much functional complementarity occurs in a given community and, also, the complementarity consequences for the pollination service. Despite the fact that this multivariate perspective is not often used to analyze bee communities, this approach may be interesting to compare communities over a spatial gradient. This may also be an initial step to discuss features that are part of the structuring processes of these communities.

### 5.6 Evidence frequency

This heuristic indicates the frequency of dependency relations between enabling conditions, which is given according to probabilistic and mechanistic information available in the scientific literature or gathered through the previous heuristics. The expectation is that this heuristic helps systematizing the variables by indicating dependency relations between the enabling conditions. The chart showing evidence frequency is similar to the evidence hierarchy in the biomedical sciences (see Oxford Center for Evidence-Based Medicine 2011; Canadian Task Force 1979). Presumably, this chart is equivalent or similar to the enabling conditions set, but with the addition of a weight to the evidence, according to its frequency in the explanation of certain relations. In this sense, the weight (and thus the hierarchy) of evidence indicates how often the enabling conditions were shown to depend on each other. In other words, this weight is assumed to inform the frequency in which a relation between ecological processes takes place, at least as indicated by currently available knowledge.

This heuristic is related to the evidence-based medicine literature and, in particular, appeals to the *epistemic theory of causality* proposed by Russo and Williamson (2007, 2011). According to the Russo-Williamson Thesis (RWT), in the biomedical sciences evidence is indicated not only by mechanisms and statistics, but also made through inference. According to RWT, to establish a causal claim we typically need to establish a mechanistic claim and a correlation claim. Therefore, it is important to describe and grade evidence for both. Once graded, they will serve as complementary tools. For instance, the evidence for mechanism will allow evaluating whether statistical studies have been appropriately interpreted, while the evidence for correlation will determine the net effect of a mechanism and whether there may be other mechanisms concealed (Clarke et al. 2014).

In the case study, this heuristic played a major role as it considered the complementarity of distinct sorts of evidence. This allowed, for example, its application to change the delimitation of the *explanans* and *explanandum* along the investigation. Instead of constructing charts, the information regarding causality and probability was gathered through graphs, such as the one shown in Figure 7.

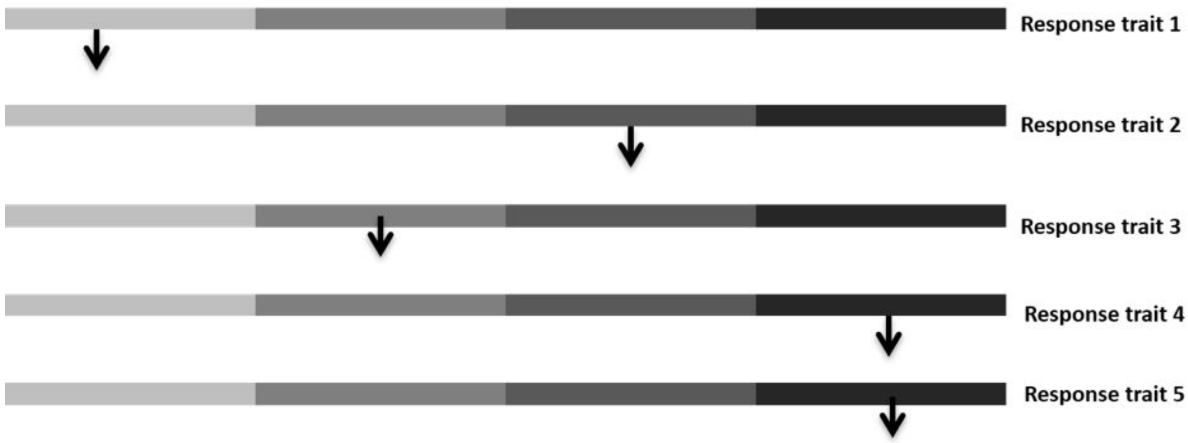


Figure 7: Graph used to classify species according to their response traits in relation to the responsiveness of the multiple states of each trait. Bars represent five hypothetical response traits and the shading indicate the degree of responsiveness to an environmental driver (light gray is the most sensitive and black the more resistant state to the driver). The location of the arrow indicates the position of our hypothetical species at this responsiveness scale for each trait represented here (for further explanation, *vide* text). Source: Author et al. forthcoming)

In Figure 7 the weight of the evidence indicates how strong are the dependency relations (expressed as responsiveness) between the driver and the response traits. The bars represent five hypothetical response traits and the shading, the degree of responsiveness to an ecological driver. In the case study, 'response traits' were conceived as traits that clearly influence the presence of a given item of biodiversity, while this item (which may be one species or a group of species) must contribute precisely to a constraining action on the flow of matter and energy in order for a function to be ascribed to it, according to the organization theory of ecological functions (Nunes-Neto et al. 2014). The location of the arrow indicates the position of the hypothetical species at this responsiveness scale for each trait.

To have a better picture of how this heuristic worked in the study case, suppose, for instance, that response traits 1, 2, 3, 4, and 5 are body size, gloss size, nesting habits, sociality, and life cycle, respectively. If response trait 1 is the bee body size then the different shades of grey will correspond to distinct size classes. This is an important response trait for bees. When environmental drivers such as the suppression of natural vegetation and landscape fragmentation are added to this scenario, for example, it will be possible to see how they will influence bee mobility and dispersion between the patches (Krewenka et al. 2011; Aranda and Graciolli 2015). In this example, the hypothetical bee possesses a small size. The body size is a highly important feature with regard to the mobility between patches in a fragmented landscape (Greenleaf et al. 2007; Warzecha et al. 2016). Bees with larger body size show larger mobility, which is important in relation to the occupation of wide areas that suffered reduction of native vegetation and are composed, therefore, by relatively isolated patches (Warzecha et al. 2016). The expectation is that the probability of reduction of this bee population would be lower than in the case of another species in the opposite extreme (*i.e.*, with small body size, such as the one in our example). If you consider the other response traits shown, we can conclude that one needs to evaluate each of these traits with regard to the probability of the occurrence of the bee species in the landscape. For instance, the fact that they are social animals with a multi-vital cycle may reduce the negative effect of their small body size, because they possess a larger amount of individuals in the hive with frequent reproductive events throughout the year (De Palma et al. 2015). This may increase its capacity of persisting in the landscape despite its small mobility. Therefore, some response traits constrain the effects of other response traits, depending on how much they are able to guarantee the maintenance of individuals of a given species in the agricultural landscape (Coutinho et al. 2018).

5.7 Changes in operational components

This heuristic explores alternative scenarios and predicts possible paths of the system under investigation. In the case study, this was achieved by modifying elements from the enabling conditions chart to produce distinct scenarios for the ecological patterns included in the model. Therefore, this heuristic gives the chance to alter some system attributes in order to consider other ecological frameworks and reflect on a diversity of scenarios (see Poliseli 2018, 2020).

## 6. Mechanistic modeling in ecological research

The mechanistic model in Figure 2 (for details, see supplementary material) expresses features of mechanistic explanations such as components and activities, productive continuity, spatial and temporal organization, hierarchical structure, and others. Although this model includes mechanistic submodels that are ontologically diverse (departing from the classical notion of mechanism with entities and activities) they still display relationships of causal dependency between well-defined variables despite not being discovered through classical strategies such as decomposition and localization, forward/backward chaining, and other. As these standard strategies were identified based on the practices of particular sciences, they account for investigations on a specific set of relatively well-behaved mechanisms, as portrayed in Craver and Darden's claim that in order to characterize a mechanism "there must be some experimental means of determining whether or not the phenomenon in question is present or absent at a given time" (2003, p. 57).

It is important to recall that the heuristics application in the case study was not only shaped by theoretical foundations but also by pragmatic limitations. That is, the heuristics proposed from a philosophical and theoretical perspective had to be recurrently modified according to the empirical context of our case study. Such modifications occurred on the account of background ecological knowledge and the level of complexity the phenomenon and the underlying mechanisms exhibited. To give an example, it was expected that several mechanism sketches would be developed and abandoned along the modeling process, up to the point where a more stable mechanism schema would be reached. However, the mechanism schema shown in Figure 8 was, at a subsequent moment in the scientific process, also discarded. While this happened more promptly than expected, it does not comes as a full surprise, since scientific research is a self-correcting process striving to deepen understanding. History and sociology of science has already showed us that progress in the scientific endeavor is not only a matter of successful linear experiments. A successful science engages with scientific practices and methods in a non-linear fashion. For instance, models can also be successfully explanatory even when the properties of the model and what it represents diverge - confusions arising from such ambiguities sows the gap between models and what they represent, which may lead to a valuable and useful set of model-target relations that can help clarify how scientists investigate the world (Matthewson and Calcott 2011). In our case, the mechanistic model was not discarded for lacking some expected cognitive value, such as, say, explanatory power, but for a broader reason, namely, that the very goal of developing a mechanistic model for the pollination service in agricultural systems was no longer suitable to the ecologist's understanding of the complex features involved in the phenomenon. The scientist decided, thus, that developing a more comprehensive conceptual framework embracing contributions from complex systems sciences, the new mechanistic philosophy of science, and metacommunity theories seemed more adequate at that point. Nevertheless, this decision was dependent on the previous developments in the project, while constructing a mechanistic model. Even though the schema shown in Figure 2 was no longer used, it was nonetheless an important step to grant intelligibility for further conceptual development. This was only possible because mechanistic representation and explanation can occur even when there is a mismatch between the mechanism of the model and what is being targeted (Matthewson and Calcott 2011). Such behavior of eliminating diagrams to best fit the ecological data is also portrayed by Pâslaru (2015) in a case study concerning ecological research on competition and pollination.

The integration of different assumptions from metacommunity models, mechanistic explanation, and complex systems science in a new ecological framework (Figure 8) was defended by the ecologist based on the argument that such integration help shedding light on some important relationships between ecological processes and bee functional diversity in agroecosystems that were not considered in the mechanism schema of Figure 2. This framework has as main characteristics the (i) functional diversity, which was presented in the mechanism schema in terms of complementarity, was reevaluated and decomposed into its three most relevant properties in the context of agroecosystems: functional richness, dispersion, and diversity; (ii) the relationships of these properties of functional diversity to environmental predictors within each spatial scale point to testable hypotheses in different agricultural landscape configurations, making the theoretical expectations clearer, which also represents an advance in relation to the previous mechanism schema; and (iii) based on the response traits of bee species, it is possible to propose from the conceptual framework response groups to certain environmental stressors, making the explanation of properties closer to a cause-and-effect relationship (in terms of the sensitivity of bee groups according to their response traits).

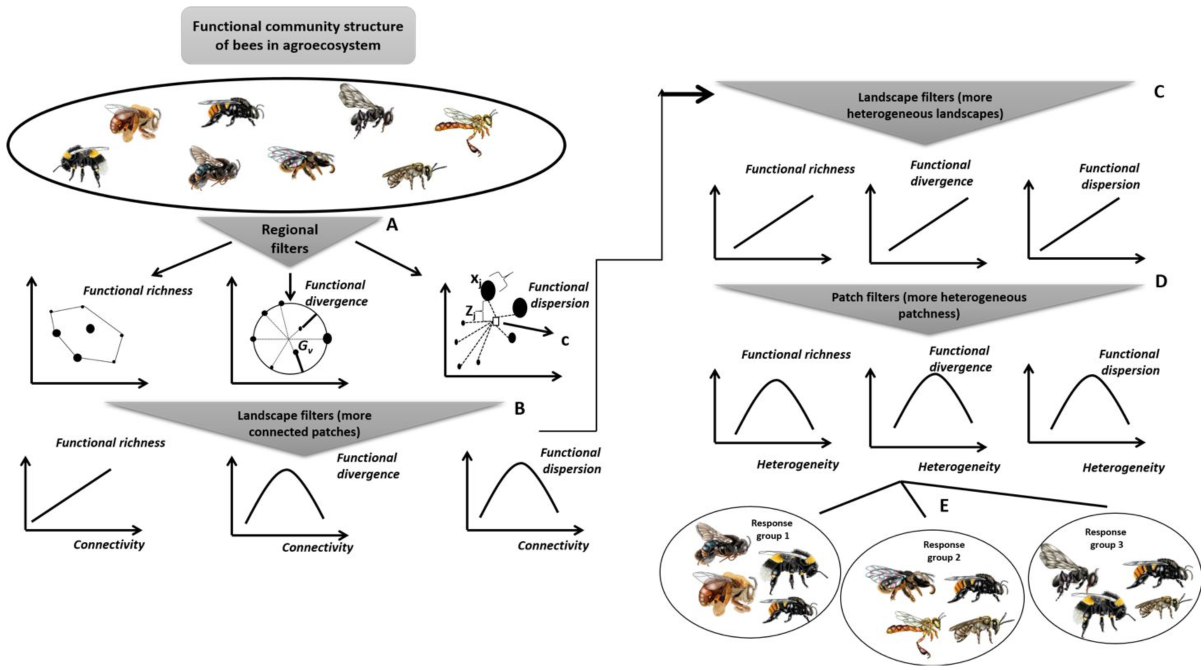


Figure 8: Conceptual framework indicating processes and scales in agroecosystems that are needed to explain three properties of bee functional diversity: functional richness, dispersion, and divergence (see explanation in the body of the text). A. Processes at the regional scale determine the pool of response and effect traits available in a given region, which constrains functional diversity in its three properties – functional richness, divergence, and dispersion. B. The landscape acts on these three properties in a different manner, being the functional connectivity of the landscape patches a factor increasing functional richness but showing an inversely proportional relation from certain values of connectivity to functional divergence and dispersion. C. More heterogeneous landscapes favor the increase of those three functional properties. D. At the patch level, the marked increase in heterogeneity shows an inversely proportional relation to the three functional properties. E. Different response groups present in the habitat patches differ in their competitive abilities according to their response traits. Source: Author et al. (forthcoming).

The framework resulting from the interdisciplinary effort to develop and apply the heuristic set in the case study indicates factors that regulate the functional diversity of bees in agricultural systems. Three complementary properties were distinguished in relation to functional diversity: richness (different types of functional traits in the community); divergence (degree of dissimilarity of the functional traits presented by different species); and dispersion (how much the most abundant species in the system differ in their functional traits). These three properties have important implications for the pollination service in agricultural systems. The conceptual framework proposes that the values assumed by these descriptors will depend on the degree of connectivity of the landscape patches and on landscape heterogeneity, since different species with different response traits will tend to respond differently. The form of the relationships is based on some assumptions from the ecological literature, but most still lack empirical investigation. Thus, this framework points to a core of testable hypotheses and a cycle of model revision will be triggered once the results of hypotheses tests become available, supporting changes in the framework that may make it more robust.

Our findings are consonant with Pâslaru's (2009, 2015) claim that ME is not enough to explain ecological phenomena. Ecological explanations seek to explain a system behavior while at the same time providing forecasts about it. However, to have prediction and realism in the same explanation, we need to integrate ME with other approaches. Although Pâslaru suggests Woodward's manipulationist approach, in our ecological phenomenon it ME was combined with metacommunity theories and complex systems science. This integration was necessary to recognize the invariant and insensitive features of the targeted system, as also suggested by Raerinne (2009).

The case study has shown how fruitful the interdisciplinary approach was for model building and sharpening of the theoretical knowledge available in the ecological literature, as well as for articulating theoretical pillars that had been previously treated separately, such as metacommunity theory and landscape ecology. The assumptions of metacommunity models were conceived from the perspective of landscape ecology, indicating underlying mechanisms that regulate bee functional diversity in agroecosystems. Through a more detailed analysis of the components of functional diversity, we were able to indicate factors that can influence each of these components in agricultural systems. This approach indicates important theoretical advances in the study of bee communities in agroecosystems. It also shows how an interplay of mechanistic and heuristic approaches was fruitful in model building and explanation construction.

## 7. Concluding remarks

We have shown that mechanistic modeling did not have a normative role for modeling the ecological system, but rather a heuristic one. Although philosophers do not typically describe the identification of mechanisms as a heuristic strategy, we have designated the mechanistic modeling stages as 'heuristics'. In other words, the heuristic set indeed contained problem-specific fallible strategies that helped the ecologist to cope with the construction of models and explanations about the phenomenon of interest. If the heuristics were not adjusted to the phenomenon in question, the mechanistic explanation *per se* would have not succeeded. This means that mechanistic modeling was a useful epistemic tool to explain the ecological complex system at stake. This allowed the elaboration of a conceptual framework that provided satisfactory explanation for the phenomenon, and also showed enough predictive power to generate a series of testable hypotheses for future scientific work. The contributions from the NMP helped in the analysis of the complex system through supporting the selection of components, activities, and properties that seemed most fundamental. In turn, the heuristics allowed to combine contributions from different fields to improve understanding, derive testable predictions, and generalize knowledge. We highlight, however, that this was only possible because of the interdisciplinary and collaborative effort in which philosophical and scientific expertise walked hand in hand. Thus, although we have assumed that ME in ecology shows limitations, we have also shown that it is possible to overcome such limitations by recognizing that mechanistic explanation is context-sensitive because it reflects a pragmatic orientation of a research agenda in ecology that aims to uncover practicable and efficient points of intervention on the environment.

While we have indicated that the NMP literature played a major role in scaffolding model building and explanation construction, we expect this case study to provide useful epistemic tools for the improvement of empirically-driven work in the debates about mechanistic explanation of ecological phenomena. We departed from the strategies usually suggested for mechanism discovery by arguing that the identification, reconstruction and understanding of mechanisms are context-sensitive, and in the case of complex ecological systems they also require the use of imagination and mental modeling when deciding which criteria should be considered to judge the explanatory status of ecological generalizations (Raerinne 2010; Poliseli 2018, 2020 connects imagination and mental modeling to the use of intuition. For more details, see Poliseli and El-Hani 2020, Poliseli 2020).

Lastly, it is expected that this investigation will help draw attention to the important role that both mechanistic reasoning and heuristics can play in modeling practices in ecology, especially if conceived under the light of contemporary discussions in the philosophy of science in practice. In particular, the meaning and use of mechanistic models and heuristics in ecology may hold important similarities with causal models in clinical practices (e.g. biopsychosocial models of diseases), which are oriented towards identifying a small number of risk factors that largely determine an outcome instead of focusing in the mechanistic details. However, we leave thorough comparisons across fields for future work. We also expect that it shows the potential fruitfulness of interdisciplinary collaboration between practicing scientists and philosophers of science in science-in-the-making.

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**Supplementary Material**

Section 2 of the manuscript introduces the methodological procedures and the heuristic set developed during the interdisciplinary collaboration. Below, we provide further material about the description of the heuristics in order to clarify their role for mechanistic modeling.

| **Heuristic** | **Brief definition** |
|---|---|
| *Phenomenon characterization* | Description of the *explanandum* and *explananda.* |
| *Mechanism sketch* | Development of diagrams (usually incomplete and disposable) that attempt to establish relations between the theoretical frameworks and the phenomenon. |
| *Hierarchical structure* | This heuristic enables visualizing the interaction between different spatial and temporal scales by creating a structure that identifies and locates the levels in which the mechanism (or mechanisms) are organized (and/or nested) in the phenomenon superstructure. |
| *Enabling conditions* | Usually characterized as factors and conditions sufficient to bring about a phenomenon. More generally speaking, variables involves in the activities of a mechanisms that are relevant to the production of the phenomenon. |
| *Operational components distinction* | Distinguishes the components and functions of the enabling conditions within the mechanism and specifies the relations and boundaries of these components. Whenever this distinction is not possible, the component/action is addressed as an operational component. If this information is not yet present in the literature, it is highly recommended that one carries out procedures of decomposition & localization, forward & backward chaining, and synthetic & analytic strategies to achieve this goal. |
| *Changes in operational components* | Allow the researcher to exploit alternative scenarios and predict possible courses of the system under investigation by modifying the operational components. |
| *External regulatory agents* | Identification of variables that are external to the phenomenon but nonetheless exert influences on it. Such influences may be related to boundaries delimitations. |
| *Evidence frequency* | Indicates causality between the enabling condition according to probabilistic and mechanistic information already available in the scientific literature or gathered through previous heuristics. |
| *Cluster determination* | Use of graph networks to grant robustness to the heuristics operational component distinction, enabling conditions and evidence frequency. |
| *Mechanism schema* | Mechanistic model obtained after the use of the heuristics above. |

Section 4 of the manuscript describes the ecological phenomenon. In order to provide more details about it, we present the submodels of the ecological mechanism below by zooming-in at each system level.

Figure A indicates the ecological processes that occur at the regional spatial scale. For instance, the distance between natural habitats and crop fields influences the patterns of movement of bee species in space. This generates consequences to the probability of colonization of the patches, which will influence the chances of maintaining viable populations of bees that promote pollinic flow over large territorial expanses. The effect on the network will be conditioned by the response traits that the bee communities exhibit in the area. Such predictions consider the assumptions derived from the patch dynamic model (from metacommunity theory), considering the probability of trade-off between colonization and competition in the different habitat areas (Leibold et al. 2004). In this schema the heuristic 'evidence frequency' is represented by the arrows. Even though there is no explicit information on how frequently each of these relations between the operational components occurs, the solid arrows show high evidence frequency and the dotted arrows, low evidence frequency in the literature.

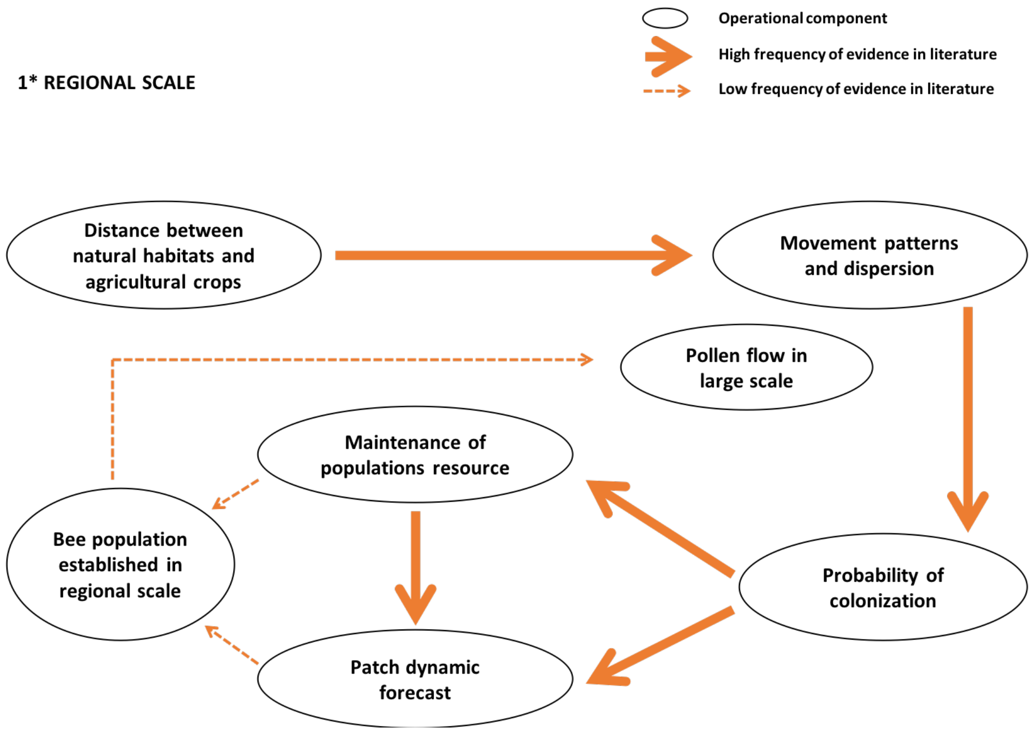


Figure A: Mechanistic sub-model at the larger scale included in the mechanism schema built in the case study and shown in Figure 8. Arrows indicate facilitating relationships between operational components.

At the landscape scale (Figure B), the mechanistic sub-model indicates ecological processes predominant under intense agricultural regime and low landscape diversity, which can lead to a simplification of the pool of bee response and effect traits that would contribute to the increase in landscape diversity (according to the species sorting model, see Whittaker 1962 and Leibold et al. 2004) via pollination process. Low functional diversity may lead, then, to a cyclical process that maintains the landscape structure with these characteristics. Landscape configuration affects the pattern of bee movement between the habitat patches of this agricultural landscape (according to the mass effect model, see Shmida and Wilson 1985). But regardless of the degree of complexity of this configuration (high or low) the system is driven to the same cycle, since functional diversity has been reduced below a critical level.

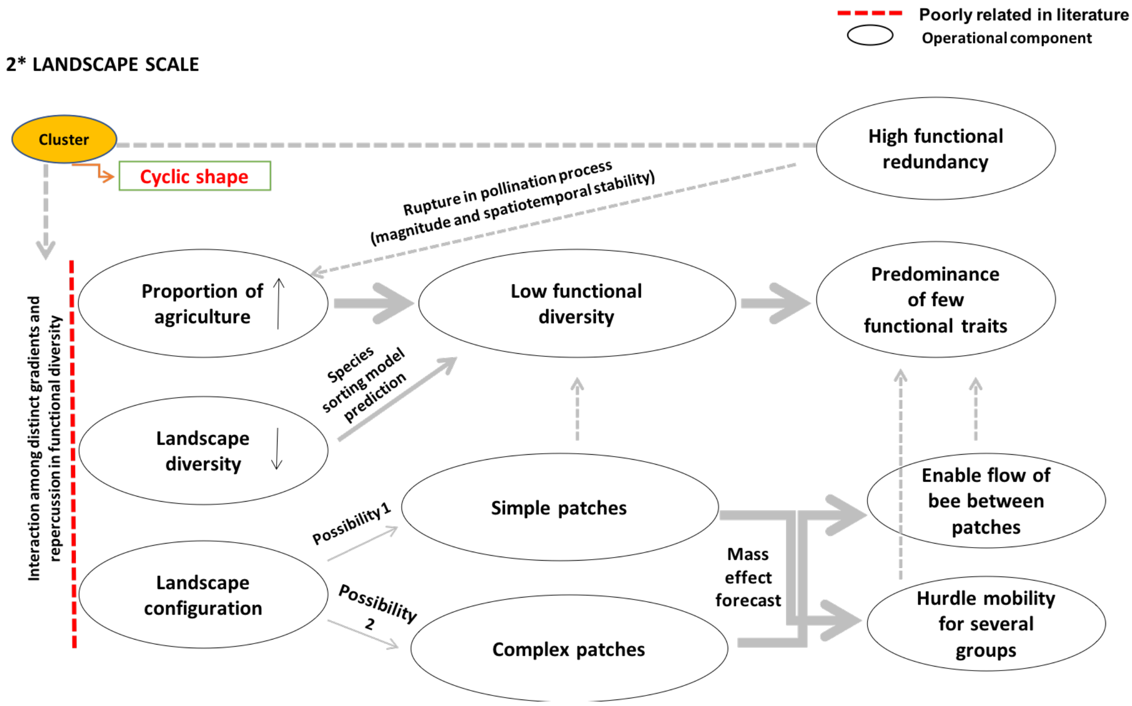


Figure B: Mechanistic sub-model at the landscape scale in the mechanism schema built in the case study and shown in Figure 8. Arrows indicate facilitating relationships between operational components.

Figure C represents the mechanistic sub-model at the third scale of the system, the habitat patches. According to the species sorting model, a high diversity of plants, floral resources and different types of soil cover may promote in the medium and long terms higher bee functional diversity in a patch (through complementarity of niches). Through positive feedback mechanisms, this system is cyclical and contributes to the increase of the stability of the pollination service at this scale. Issues that have not yet been reported in the empirical literature are related to the possible trade-offs that may exist between response and effect traits, and the potential impacts that such trade-offs may have on the maintenance of the system itself.

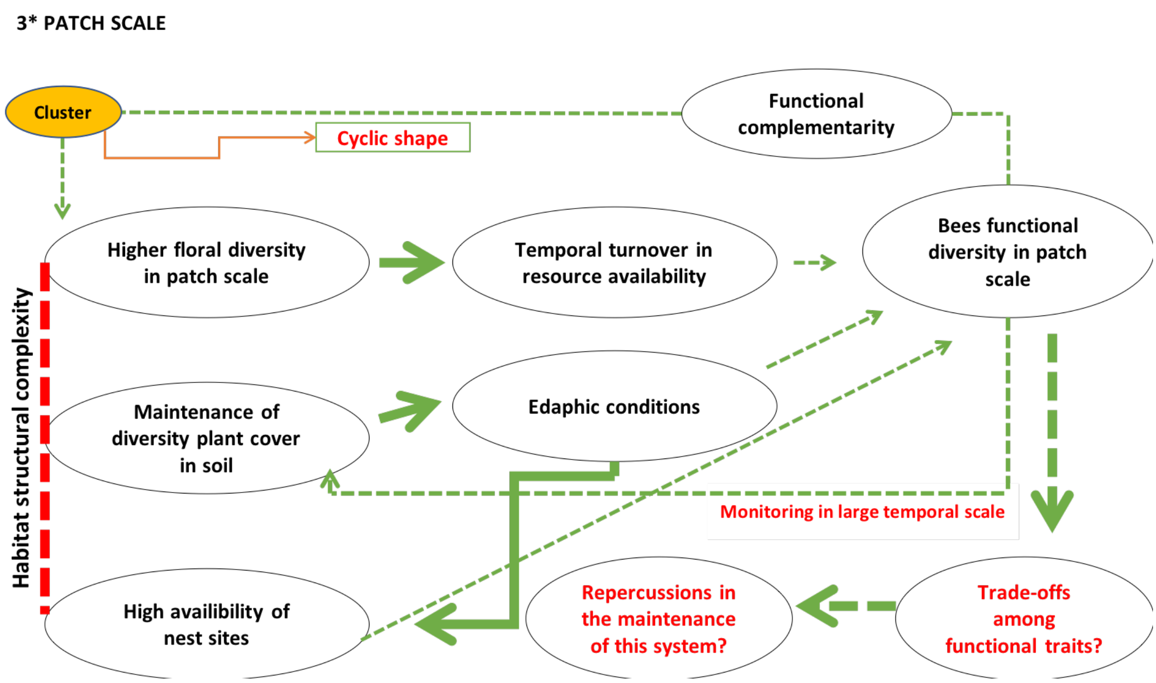


Figure C: Mechanistic sub-model indicating ecological processes that occur at the spatial scale of the habitat patch, as included in the mechanism schema built in the case study and shown in Figure 8. Dotted arrows indicate predictions with low empirical support. Arrows indicate facilitating relationships between operational components.

The mechanistic sub-model at the fourth and smallest scale included in the mechanism schema is shown in Figure D. The ecological processes at stake occur at the spatiotemporal scale of the interaction between the bee community and the plant community, focusing on their functional attributes. Different combinations of bee response and effect traits, associated with a high supply and diversity of resources along time, contribute to a cyclical process of maintenance of these communities. Interactions between bees and plants occur through the ecological processes of functional complementarity, facilitation, and sampling effects (Blüthgen and Klein 2011, Woodcock et al. 2019). The evaluation of specific combinations of traits and their influence on the successful pollination of native plants is a subject rarely explored in the empirical literature and, therefore, needs further investigation, as indicated by the model built in the case study.

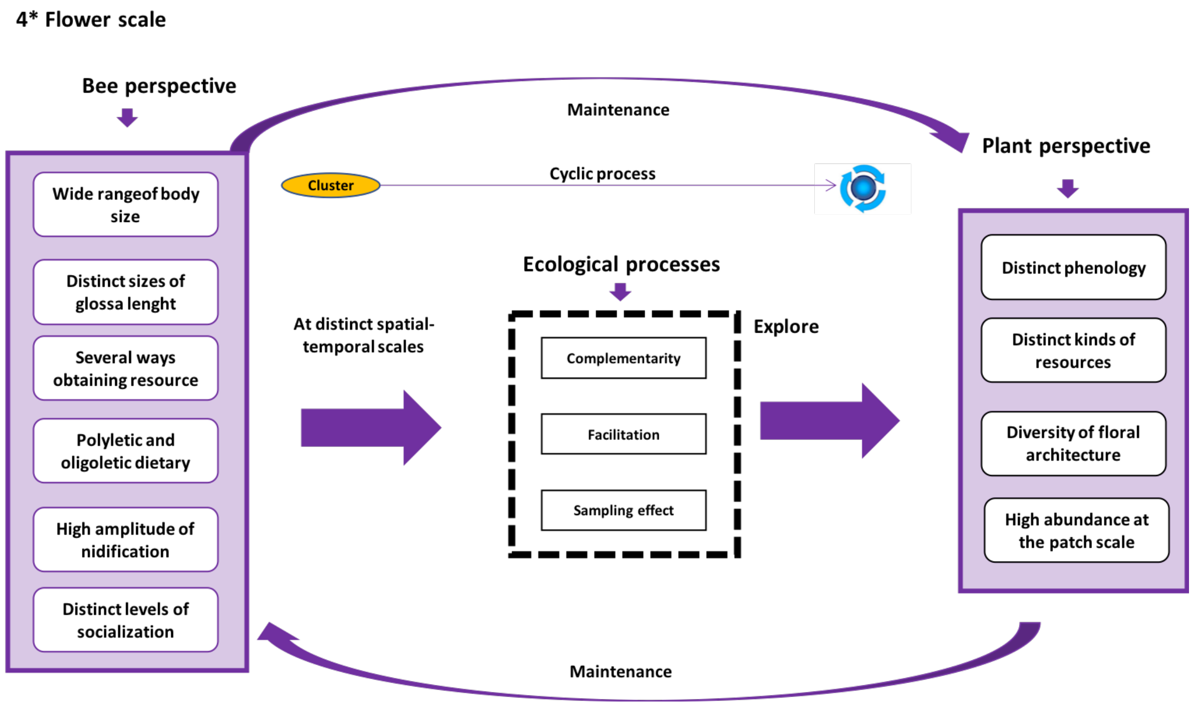


Figure D: Mechanistic sub-model indicating ecological processes that occur at the spatial scale of the interaction between the bee community and the plant community, as included in the mechanism schema built in the case study and shown in Figure 2.