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ORIGINAL RESEARCH

# Embedding and customizing templates in cross-disciplinary modeling

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## Abstract

In this paper, I develop a template-based analysis to include several elements of *processes* through which templates are transferred between fields of inquiry. The analysis builds on Justin Price's identification of the importance of a "landing zone" in the recipient domain, from which "conceptual pressure" may be created. I will argue that conceptual pressure is a characteristic feature of the process of template transfer; that this means that there are costs to the process of transfer as well as benefits; and that it would be reasonable if modelers try to mitigate these costs. I will discuss two such mitigation strategies: 'conceptual embedding' and 'customization'. I illustrate the claims, focusing on the mitigation strategies, with a case study: that of pioneering applications of reaction–diffusion equations in mathematical ecology.

**Keywords** Template transfer · Transdisciplinary modeling · Reaction–diffusion models · Customization · Conceptual embedding

Some scientific models and modeling techniques have a remarkable capacity for migrating between disciplines. Even in fields that, at first glance, deal with fundamentally different types of systems and that consequently conceptualize these systems differently, one finds usage of what, again at first glance, appear to be the same models. Thus, we see applications of Lotka–Volterra models in population ecology as well as studies of technology diffusion; or transfer of the ideal gas law from physics to population genetics.[1]

The notion of 'template', as introduced by Paul Humphreys (2002, 2004) proves useful for analyzing these episodes of cross-disciplinary modelling. A template-based analysis allows identification of what is the same in, e.g., Lotka–Volterra modeling of

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[1] These cases of cross-disciplinary modeling are discussed in detail in Houkes and Zwart (2019) and Price (2020) respectively.

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competing species and those of diffusing technologies—namely, the template—and what is different—namely, the models developed on the basis of this template. Importantly, it does so without reducing templates to mere formalisms or computational structures: it can be explicated how "model templates" (Knuuttila & Loettgers, 2014) have "non-detachable" (Humphreys, 2004, Chapter 3) or "thin" interpretations (Houkes & Zwart, 2019); in this, they can be distinguished from—but form the basis for—models. This gives templates a built-in flexibility that affords cross-disciplinary application.

In this paper, I supplement this perspective on cross-disciplinary modeling by analyzing the process through which templates are transferred between fields of inquiry. This goes beyond specifying identity and difference criteria for the objects involved in modelling episodes (roughly, 'what' is transferred) to studying processual aspects, such as characteristic stages of and conditions for transfer ('how' and 'why' a template is transferred). In two recent papers, Justin Price (2019, 2020) has highlighted some of these aspects: transferring templates in cross-disciplinary modeling requires a "landing zone" in the recipient domain, from which "conceptual pressure" may be created in the domain. Building on these insights, I will argue, first of all, that conceptual pressure is a characteristic feature of the process of template transfer; that, second, this means that template transfer carries a cost as well as bringing benefits; and that, third and finally, it would be reasonable if modelers try to mitigate these costs. I will discuss and illustrate, with a case study, two mitigation strategies: 'conceptual embedding' and 'customization'.

The paper proceeds as follows. Section 1 presents a brief review of template-based analysis of cross-disciplinary modeling, focusing on several basic concepts (template; model template; interpretation; types of transfer; landing zone; conceptual pressure) and setting the stage for a processual analysis. In Sect. 2, I argue for my central claims concerning the costs of template transfer and strategies for mitigation. In Sect. 3, I illustrate the claims, focusing on the mitigation strategies, with a case study: that of pioneering applications of reaction–diffusion equations in mathematical ecology. Section 4 concludes.

## 1 Templates: a state of the art

In this section, I outline how episodes of cross-disciplinary modeling may be analyzed as transfer of a template. I focus on basic concepts that are employed in a template-based analysis, using the application of Lotka–Volterra models in studies of technology diffusion as a running example. This prepares the grounds for later sections, so I will gloss over details, as well as some differences between template-based analyses in the literature.

Consider the Lotka–Volterra (LV) equations, which are coupled non-linear differential equations with the general form:

$$dx_i/dt = x_i\left(b_i + \sum_{j=1}^{m} a_{ij}x_j\right), \quad i = 1, 2, \ldots, m \tag{LV}$$

These equations are a staple of mathematical models in population biology, where in the established interpretation, the $x_i$ are the numbers or densities of $m$ populations or species; the $b_i$ are intrinsic growth or decay rates of these populations; and the 'interaction parameters' $a_{ij}$ "describe the effect of the $j$-th upon the $i$-th population, which is positive if it enhances and negative if it inhibits the growth" (Hofbauer & Sigmund, 1998, pp. 42). For the competitive Lotka–Volterra (LVC) equations for two populations, the interaction parameters $a_{12}$ and $a_{21}$ are both negative, i.e., the populations negatively affect each other's densities $x_1$ and $x_2$.

Since the late 1980s, an increasing number of studies of technology diffusion also uses the LV—or often, more specifically, the LVC—equations.[2] Typically, this is motivated by likening the diffusion process to population growth—where growth may be affected by 'interaction' with other technologies, like the growth of a biological population is affected by that of other species. Since, in ecology, the effects of these mutual interactions are represented by the LV equations, these are then transferred to the context of technology diffusion. In the latter context, the parameters and variables in the equations are interpreted in terms of "technological populations", "growth rates", and "modes of interaction", notwithstanding well-known differences between biological and technological systems. This line of inquiry is also often presented as explanatory: it seeks to go beyond merely predicting rates of diffusion, for which highly accurate phenomenological models are available.[3]

A template-based analysis of this ongoing process of cross-disciplinary modeling can be given as follows. First and foremost, we see usage of the same formal structure in both a source field and a recipient field; here, the LV equations, population ecology, and innovation studies respectively. Yet, importantly, similarities are not limited to the formal structure—systems in both fields are also understood in terms of the same basic concepts; here, "populations" undergoing "growth" and "interacting" with each other. A *model template* comprises both the formal structure and an interpretation. Here a model template is "a mathematical structure that is coupled with a general conceptual idea that is capable of taking on various kinds of interpretations in view of empirically observed patterns in materially different systems" (Knuuttila & Loettgers, 2016, pp. 396). The *interpretation* of a template can be distinguished from that of a model in terms of intensional versus analytical interpretations (Houkes & Zwart, 2019) or, more straightforwardly, in terms of levels of abstraction (Humphreys, 2019). In the running example, templates may be interpreted in terms of 'growing and interacting populations', models in terms of 'insect colonies competing for the same food source' or 'spillover and lock-in effects between automotive powertrain systems'.

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[2] See, e.g., Bhargava 1989 for one pioneering application; and Zhang et al., 2017 and Mirzadeh Pirouzabadi et al., 2020 for two recent examples.

[3] Both the basic narrative and the explanatory aim in this episode of cross-disciplinary modeling are illustrated in this passage: "Forecasting technological substitution requires a model that generates intuitive understanding of the factors affecting substitution, but that also has good predictive ability. (…) The Lotka-Volterra competition (LVC) equations, a set of coupled logistic differential equations, model the interaction of biological species competing for the same resources and can also model parasitic and symbiotic relations. The LVC equations model both the emerging and declining competitors, allowing intuitive understanding of the factors driving substitution." (Morris and Pratt 2003, p. 103).

In either field of application, templates are valued for their mathematical or computational tractability: they allow development of models from which solutions (closed-form, attainable with reasonable computational resources, etc.) may be derived. Crucially, they do so in combination with various assumptions and idealizations, which constitute the *construction assumptions* and *correction set* (Humphreys, 2004, Chapter 3). These are by default transferred together with the formalism. Here, the construction assumptions include the idealizations and abstractions involved in the original or entrenched[4] construction of the template; and the correction set indicates how a template could be adjusted to account for empirical data, e.g., through relaxing some of the construction assumptions. The need for tractability is a prime driver for modelers to transfer a template rather than construct a model from scratch (Humphreys, 1995). This benefit is easiest to obtain if similar solutions would be of use in the recipient field, so that models developed on the basis of the template use the same construction assumptions, stay within the correction set *and* are inspected for similar behavior. This reveals an analytically useful contrast between *conformist transfer* and *creative transfer*, in which a template and its interpretation are transferred, but different behaviors of the developed models are of interest to the recipient field (Houkes & Zwart, 2019, Sect. 4). Indeed, in the technology-forecasting case, some papers emphasize that the LV template offers various familiar, tractable solutions, e.g., for oscillating population densities;[5]others use the template to study behavior that is not particularly meaningful in the source field, e.g., systems exhibiting changing 'modes' of interaction.

This shows how template-based analysis identifies what remains the same in cross-disciplinary modeling (namely, the model template and, in conformist transfer, some of the model behavior) and what is different (namely, the models developed on the basis of the template and, in creative transfer, some of the model behavior). It was also highlighted, in passing, how it captures some aspects of the transfer *process*. In particular, template-based analyses show how cross-disciplinary modeling amounts to a package deal: in transferring a template from a source field, modelers in a recipient field adopt not just a tractable formal structure, but also its interpretation—at a suitable level of abstraction—and a suite of idealizations and other assumptions. The willingness to accept such package deals stresses how, also in template transfer, modeling is an outcome-oriented practice (Knuuttila 2009): modelers deliberately develop template-based models for familiar behavior and/or tractable solutions.

Several other processual aspects have been brought out in recent work. One concerns the point of origin of the process. Contrary to what was suggested above, not all templates get transferred from modeling practices in specific 'source' domains of application.[6] Some are constructed *as* templates, i.e., mathematical objects with

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[4] Although most case studies focus on a domain in which a template may be taken to have originated, I want to leave open the possibility that very widely used templates are constructed in ways that are disengaged from their original context of application. Even when so constructed, templates will come with an interpretation.

[5] E.g. "The L-V equations can produce the solution sets of a variety of standard mathematical forecasting functions used in the field of powertrains", Mirzadeh Pirouzabadi et al. (2020, p. 4).

[6] Lin (2022) identifies cases of 'spillover' in which application of the template in one domain is strictly prior to that in another.

relatively abstract, thin interpretations, and only then see application in specific modeling practices. One case in point is the NK template developed in complexity science (Kaufmann 1987); another is the LV template as developed by Lotka, in an interesting contrast to Volterra's development of it (Knuuttila & Loettgers, 2017).

A second processual aspect, analyzed by Justin Price (2019, 2020), concerns the initial deployment of the template in the recipient domain. In Price's terms, this requires that modelers identify a *landing zone*: "a target system that functions to make possible the application of a model template to a new domain" (Price, 2020, p. 45). A model template should be able to represent some set of items, features and behavior in the recipient domain: showing this minimal ontological compatibility is a precondition for being of any use in this domain. Thus, in early applications of the LV template in innovation studies, we find statements that are straightforwardly interpretable as identifying such a landing zone, e.g.: "Periodic behaviors are commonly found in natural populations and they can be successfully modeled using the Lotka–Volterra equations. Oscillatory behaviors have been observed … *in car and transportation systems in Europe* … These growths often show a logistic start followed by an overshoot and then oscillation around a supposed limit …" (Porter et al., 1991, p. 196; emphasis added).

Third and finally, Price points out that transfer of a template to a new domain might create what he calls *conceptual pressure*: identifying the landing zone for transfer of a template to a domain "may require conceiving of phenomena in tension with entrenched modelling practices [in that domain]" (Price, 2020, p. 45). This pressure reflects how template transfer is a package deal: in transferring a template (e.g., the Lotka–Volterra template), modelers need to represent the landing-zone system (e.g., powertrains) in terms of the thin interpretation (e.g., of interacting populations), which might be at odds with established ontologies (e.g., of every interaction between technologies being mediated by human agency). Furthermore, tractability of a template may require a set of construction assumptions (e.g., that the interaction parameters must be constant over time) which might likewise be at odds with the established understanding of phenomena in the new domain. Conceptual pressure, at least in the sentence just quoted, is an *optional* feature of template transfer and—more importantly—a potential *benefit* to the new domain. The re-conception of the landing zone may be a source of conceptual progress, introducing new concepts into a domain that may prove widely applicable to the phenomena that it studies. Thus, templates might bring computational benefits, based on their tractability, as well as conceptual benefits, based on their interpretation and construction assumptions.

## 2 The costs of template transfer and how to mitigate them

The previous section outlined how the notion of template has been used to clarify the units of analysis in cross-disciplinary modelling, and to give some insight into features of the process of transferring models from one disciplinary context to another. In this section, I build on earlier work in the latter, processual vein and argue for three consecutive claims: (i) that conceptual pressure is a characteristic feature of cross-disciplinary modelling[7]; (ii) that this pressure means that there are costs as well as benefits to template transfer, complicating the incentive structure for modelers; (iii) that the costs may be reduced through mitigation strategies, including ‘conceptual embedding’ and ‘customization’.

First, conceptual pressure is not a contingent feature of template transfer. Rather, it is a direct consequence of the basic characterization of templates as *interpreted* mathematical structures rather than mere formalisms. Thus, if modelers transfer a template from a source domain, they go beyond applying a tractable set of equations or computational technique: they also by definition carry over some set of associated concepts. If the formalism does not come with some conceptual baggage, it is not a template. To put it differently: one can take conceptual pressure as a tell-tale sign of (model-)template transfer rather than of, say, ‘mere’ extension of the scope of a computational technique (or computational-template transfer) such as multivariate regression analysis.[8] When transferring a model template, conceptual pressure can only be avoided if the interpretation is already fully compatible with the established understanding of phenomena in the recipient domain. Of course, it is an open empirical question how often cross-disciplinary modelling is restricted to extending formal techniques; features compatible templates; or comes with conceptual pressure. Yet if we accept Humphreys’ arguments for the ubiquity of templates (rather than formal techniques) in scientific practice and we assume some minimal conceptual diversity between domains, or acknowledge the ever-growing diversity *within* domains,[9] it follows that conceptual pressure is a widespread, characteristic feature of cross- and trans-disciplinary modelling.

This claim needs two qualifications. First, conceptual pressure strictly speaking only arises from interpretation of the *template*, and not from any models developed on its basis in other domains. Thus, application of the LV template by default only requires conceiving of technologies as consisting of interacting populations; not as full-fledged ecological systems, let alone as rabbits and foxes. Second and relatedly, the interpretation of a template may not be detachable (i.e., it never becomes a mere formalism), but it *is* negotiable. Application in a new domain may lead modelers to interpret the template in a different way. In Humphreys’ (2021) terms, template transfer requires a suitable abstraction step,[10] but this may not be specified beforehand—(re-)interpretation of the shared template might follow on its successful deployment in a new domain. This creates options for reducing conceptual pressure, dividing burdens of conceptual adjustment over the recipient domain and the template (and thus, indirectly, domains in which the template saw earlier use).

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[7] I would like to thank an anonymous reviewer for prompting me to clarify this point.

[8] Application of computational techniques might also require re-conceiving phenomena, e.g., because of strong linearity assumptions. This re-conception does not, however, result from any interpretation of the formal structure. It would be interesting, but beyond the scope of this paper, to see whether the costs of transferring computational templates are managed differently.

[9] See, e.g., Milojevič, 2015 for empirical evidence for this diversity claim, using lexical diversity as a proxy.

[10] This process of negotiating the interpretation of a template in a new domain of application also underlines the central role of those who Herfeld and Doehne (2019) have called ‘translators’.

A second claim, which follows directly from the first, is that template transfer does not only bring benefits to a new domain. If conceptual pressure is a characteristic feature of the process of template transfer, it may be a drawback or *cost* of transfer rather than a benefit. Instead of bringing progress, in the form of prompting productive conceptual change, it could also provoke resistance. As Price pointed out, a template might be at odds with entrenched modelling practices in a domain, so that its successful application in a landing zone might endanger vested interests in solving domain-specific problems in particular ways. A template-based analysis of such episodes of resistance might go beyond merely reformulating insights on disciplinary change: it locates the source of tension in modeling practices and their underlying ontologies. As such, it brings out at least one *cost* of engaging in cross-disciplinary modelling, namely one of managing—and potentially failing to overcome—*conceptual resistance*. It does so in addition to specifying benefits: templates offer computationally or analytically tractable solutions, as well as some interpretive flexibility. That there are costs to transfer and not merely benefits might explain why templates are not ubiquitous rather than very widespread, and why modelers still engage in designing models from scratch despite the availability of ever more tried-and-true templates: the cost of conceptual resistance provides at least some incentive for pursuing other options. This also means that template transfer is a *strategic* choice in modelling practice: it carries a risk of not being acceptable to a new domain.

This leads to the third claim: if conceptual pressure makes template transfer into an inherently risky process, modelers who engage in transfer would do well to mitigate these risks. Put more strongly, we may expect modelers who are aware of this risk to deploy mitigation strategies. Apart from demonstrating the benefits—in terms of applicability and tractability of the template in their domain—they might seek to decrease the associated costs, in order to manage the incentive structure for choosing modelling techniques in favor of the template. Without attempting to be comprehensive, I will here discuss two possible mitigation strategies: one, *conceptual embedding*, which focuses directly on the interpretation of the template in the new domain; and *customization*, which focuses on the construction assumptions and correction set. Both strategies aim at minimizing the conflict between the template and entrenched domain knowledge. They channel conceptual pressure into further opportunities to apply the template in a new domain, rather than risking persistent controversy or rejection of the template.

The first mitigation strategy, *conceptual embedding*, involves deliberately minimizing the semantic distance between the (interpretation of the) template and entrenched conceptions of the phenomena in the recipient domain. A modeler may, in transferring a template to a landing zone, acknowledge an apparent incompatibility, and proceed to explain how it is only apparent; how the template aligns with—and only requires—suitably abstracted existing conceptions of the phenomena (e.g., in terms of interactions rather than some specific mechanism); or how models developed on the basis of the template could be interpreted fully in line with existing conceptions—to name but a few options. This embedding strategy is especially needed if the source domain(s) in which the template has previously been successfully applied are conceptually far removed from the recipient domain. Then, a minimal, ‘negative’ form of embedding would be to point out that only a (highly) *abstract* interpretation is required, rather than the specific interpretations of models. There is, of course, no guarantee that implementing this embedding strategy will prevent conceptual resistance or fundamental debates over the ontology of the recipient domain. However, the strategy might prevent misunderstanding of the template, or unnecessary antagonism.

A second strategy is *customization* of the template to the new domain. Customization may be implemented in addition to conceptual embedding, because it focuses on the construction assumptions and correction set of a template rather than (only) on its interpretation. To motivate this strategy, it is useful to realize that application of a template to a landing zone may be necessary, but it is seldom sufficient to convince researchers in a recipient domain of the longer-term impact; indeed, if a template would only see use in the landing zone, it would for all practical purposes be equivalent to the model developed of that phenomenon on its basis. A more convincing and comprehensive case can be made for a template if it is demonstrated how it could be developed in a family of models that may be used for a variety of (related) phenomena in the new domain. This demonstration would go beyond the proof of concept that is offered in the landing-zone phenomenon; it would amount to a proof of customizability, leveraging the flexibility of the template. This proof of customizability provides evidence for the longer-term usefulness of the template in two ways. First, it may show how the template can, within its current correction set or a modified one that does not compromise its tractability, be used to accommodate phenomena in or features of the recipient domain that have been the focus on entrenched modeling practices—thus making plausible that the template can at least match their performance. Second, demonstrating customizability makes it more difficult to dismiss application of the template to the landing zone as a mere ‘toy model’ for lack of various well-represented features of characteristic systems in the domain; more generally, customizability might reveal the real potential of the template in further applications. Customization of a template is compatible with both conformist and creative transfer, i.e., model behavior familiar from a source domain may be replicated in the recipient domain or different model behavior might be explored.

The next section will illustrate these processual features with brief highlights from a case study. Before turning to this specific example, one general remark is in order. Although both conceptual embedding and customization may be implemented as mitigation strategies in any episode of template transfer, the need for such mitigation depends in part on characteristics of the recipient domain. If it is highly pluralistic, especially in terms of modeling techniques, conceptual diversity is likely to be high as well. Consequently, resistance to the transferred template may be small—but the same goes for the conceptual pressure that it creates: application of the template may show that phenomena can be re-conceived, but without large effects on entrenched modeling practices. In highly monistic domains, by contrast, transfer of a template would appear to require mitigation.

## 3 Reaction–diffusion models in ecology

In this section, the processual aspects discussed in the previous section—conceptual pressure; the costs associated with it; and conceptual embedding and conceptualization as possible mitigation strategies—will be illustrated with applications of reaction–diffusion models in population ecology. I will focus on mitigation strategies in one pioneering paper (Skellam, 1951), as well as in the family of so-called 'KiSS' models presented in this paper and another (Kierstead & Slobodkin, 1953).

Reaction–diffusion equations have the following general form (Grindrod, 1996, p. 5):

$$u_t = d\Delta u + f(u, \boldsymbol{x}, t) \tag{RD}$$

with $u$ the density or concentration of some entity at time t and position $x$ (in $\mathbb{R}^n$); $\Delta u$ the so-called 'diffusion term' (with $\Delta$ the Laplacian); $d$ the diffusion rate; and $f$ the 'reaction term'.[11] Few reaction–diffusion equations have closed-form solutions, but many have solvability conditions or known generic solutions, so that at least some of the behavior can be predicted. Various (sub-)domains, including physics and theoretical chemistry, are credited with their origin. Yet in principle, they can be used to represent any diffusive or dispersive process in which certain general balance laws obtain (Grindrod, 1996, Sect. 1.2). Current applications are as diverse as electrical activity in cardiac tissues, transport of chemicals through porous media, and formation of crime hotspots.

Given the above, we may speak of a reaction–diffusion *template* (rather than mere 'equations' or specific 'models'): there is a formal structure with an established 'thin' interpretation in terms of diffusion and reaction processes, broad and flexible applicability, as well as some measure of tractability. This highly general template comprises various structures that can be differentiated by the form of the reaction term *f*. These may themselves be regarded as templates, i.e., flexibly applicable formal structures with a thin interpretation. One example that is of particular interest here is:

$$u_t = d\Delta u + ru \tag{GD}$$

which specifies the reaction term as growth with rate $r$. Below, I will refer to (GD) as the 'growth-diffusion' equation or template, to distinguish it from the more general reaction–diffusion template.

Reaction–diffusion equations at present have a wide range of applications in mathematical ecology, where they are used to develop spatial models of population dynamics. A paper by J.G. Skellam (1951) is broadly acknowledged as the pioneering effort in this transfer episode.[12] In the paper, Skellam presents various reaction–diffusion equations, on the one hand clearly demonstrating their capacity for solving ecological problems, on the other hand acknowledging and partly addressing the conceptual pressure created by this successful application. Central elements of the paper can be straightforwardly reconstructed as implementing the embedding and customization strategies.

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[11] The reaction term is sometimes expressed as $f(u, \nabla u, \boldsymbol{x}, t)$, with $\nabla u$ the first derivative of $u$. For present purposes, the narrower form suffices.

[12] E.g., Cantrell and Cosner (2003, p. xi). Many, including Skellam himself, give credit for a first application to Fisher's (1937) model of the spread of genetic differences in a one-dimensional 'linear' habitat.

A first feature is that Skellam introduces the template in several stages. He starts with random-walk models, which are applied to solving a numerical problem regarding the dispersal of oak trees in post-glacial Britain (introduced at the very start of the paper).[13] Then, he turns to diffusion models, which are illustrated with the spread of muskrats in Central Europe and only in a third stage discusses various types of reaction–diffusion models, which add a reaction or ‘growth’ term for favorable and unfavorable bounded habitats (called “zones of multiplication” and “zones of extinction” respectively)—first for ‘logistic’ populations that are continuous in time, and then for discrete reproductive populations. This presentation, which is often imitated in mathematical-ecology textbooks (e.g., Kot, 2001, Ch.15; Cantrell & Cosner, 2003, Sect. 1.5), not only serves to introduce gradually the computational complexities of the equations, but also to show how they represent different processes in ecological target systems. Steps between each of these stages are thus motivated by fidelity-to-domain characteristics: by adding a growth term to the diffusion term, the representational power of the equations *vis à vis* ecological systems is enhanced, while—as Skellam shows—they remain computationally tractable. The full equations are no longer illustrated with specific cases or open problems; instead, Skellam demonstrates how numerical solutions may be derived for a variety of more abstract scenarios.

One set of scenarios is that of “Malthusian populations in two-dimensional habitats” (Skellam, 1951, Sect. 3.5). The spatial dynamics of such populations are governed by the growth-diffusion template. For purposes of tractability, Skellam focuses primarily on radially symmetric, homogeneous habitats, but not without interpreting this assumption in terms of natural habitats, such as islands, hilltops or woodland patches (similarly, linear habitats are, as in Fisher’s, 1937 population-genetic model, presented as narrow riverbeds). Several arrangements are studied, such as a circular ‘zone of multiplication’ surrounded by an ‘absolute’ or more gradual ‘zone of extinction’. Using reaction–diffusion equations, Skellam then derives the critical radius of the zone of multiplication: intuitively, if the zone is too small, diffusion into the zone of extinction will outweigh growth in the zone of multiplication, and the population will steadily decline.

As mentioned, Skellam does not relate this so-called ‘critical patch size’ result explicitly to any ecological phenomenon. Yet independently, in a virtually equivalent application of the reaction–diffusion equation, Kierstead and Slobodkin (1953; see in particular Eq. 3) derive the same result specifically for plankton blooms.[14] Like Skellam, they imagine a zone (here, a long and narrow or a cylindrical body of water) of constant diffusion that is “bounded on all sides by physiologically unsuitable water” (ibid., 145). In mathematical ecology, the combination of simple diffusion with linear growth is often called the KiSS model, acknowledging the contributions of Kierstead, Slobodkin and Skellam as well as referring to the common acronym recommending the use of simple models (“Keep It Simple Stupid!”). In the past decades, in which critical sizes of habitats have become an ever more pressing problem in ecosystems, the original model has generated countless variations and follow-up studies, which

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[13] In particular, Skellam argues that random-walk models support the hypothesis that the oak population must have regenerated from several remaining pockets, scattered over Britain.

[14] This closely resembles the different routes through which Lotka and Volterra independently arrived at their eponymous equations (Knuuttila & Loettgers, 2017).

for instance relax assumptions (e.g., allowing non-random, ‘biased’ movement or heterogeneous habitats), model systems with multiple species or multiple patches, or study under which boundary conditions the equations can be solved analytically (for reviews, see e.g., Kot, 2001, Chs.15–16; Cantrell & Cosner, 2003, Chs.2–3; Okubo & Levin, 2001, Ch.9).

Returning to Skellam’s paper, in the “Biological Discussion” (Sect. 5), it explicitly addresses—among other things—a central assumption of this entire family of reaction–diffusion models. This passage is worth quoting almost in full:

> “The analytical model developed here assumes that dispersal is effectively at random. This is at least approximately true for large numbers of terrestrial plants and animals. The behaviour patterns of certain animals may be such, however, as to tend to lead them to more favourable conditions. (…) Nevertheless, in most instances the range of an animal’s perception is small compared with its powers of dispersal, and even the more intelligent may not discriminate between two parts of a habitat differing considerably in their effect on survival. Local irregularities in the character of the environment act as stimuli initiating repeated tactic displacements, the ultimate cumulative effect of which is scarcely distinguishable from a blind randomness” (Skellam, 1951, p. 216)

This passage may be interpreted as a response to the conceptual pressure created by application of the reaction–diffusion template to ecology: the assumption that migration can be modelled on the basis of random diffusion is ontologically incompatible with the entrenched understanding of many species. This might lead those who favor this understanding to regard any modelling success as at best phenomenologically accurate while being fundamentally misleading or incomplete: they could, in other words, acknowledge that the template provides tractable results, but deny that these results have any explanatory value.

The quoted passage illustrates the conceptual-embedding strategy. It responds to conceptual pressure by presenting a *local*, field-specific justification of the randomness assumption. It not only motivates why the randomness assumption may be reasonably applied, but does so by explicating it in field-specific terms (referring to powers of perception and locomotion and their respective ranges; stimuli and intelligence). Thereby, in presenting the applicability of the template, Skellam performs *interpretive labor*, to borrow a concept from social epistemology (e.g., Fricker, 2006): rather than merely demonstrating the utility of the reaction–diffusion template through highlighting tractability or predictive power, he shows how central concepts or assumptions can be interpreted meaningfully in the new context of application. This embedding aligns the template as much as possible with established conceptualizations while still leveraging its added value to modelling efforts. In particular, Skellam points out that even for most animals with considerable cognitive capacities, their dispersive or locomotive powers outstrip their powers of perception or deliberation; that is, the latter set of abilities is not adequate to the task of determining whether the environment to which the former set of abilities leads them will be favorable or not. This local justification for applying the reaction–diffusion template is echoed in other texts in mathematical ecology (e.g., Aronson, 1985; Okubo & Levin, 2001, pp. 2–3). This shows that the conceptual pressure created by the template needs persistent attention, i.e., the template has not led to conceptual ‘progress’ (Price, 2019) in the sense of overturning the entrenched understanding of organisms. Yet it also shows a persistent deployment of conceptual embedding to justify application of the template.

By contrast, Kierstead and Slobodkin (1953) do not deploy conceptual embedding in their application of the growth-diffusion equation to plankton blooms. For this particular target system, however, the assumption of random dispersal arguably does not create conceptual pressure. Still, we see how the KiSS model is—by all authors presenting it—embedded by conceptualizing the population’s environment in terms of favorable and unfavorable zones. This, even more than Skellam’s justification of the random-dispersal assumption, has become an integral part of textbook presentations of the KiSS model and other solutions to the critical-patch-size problem; these are standardly interpreted in terms of ‘bounded isolated habitats’ such as islands or oases, surrounded by a ‘death region’ (e.g., Artiles et al., 2008; Cantrell & Cosner, 2003). Here, as in the cited passage from Skellam’s paper, the template is conceptually embedded by providing a field-specific interpretation over and above the thin or abstract interpretation of the template itself: those introducing the template to a new field perform additional interpretive labor.

Skellam’s paper also illustrates how the risks of template transfer may be mitigated by deploying the customization strategy. The reaction–diffusion template is presented through a stagewise development of increasingly complicated (albeit still relatively generic) models, from pure diffusion through reaction-term to coupled equations. This shows applicability beyond the first set of problems or target systems that constitute its landing zone. Here, customization involves more than demonstrating that basic assumptions can be relaxed or terms may be added without loss of tractability, although this is definitely part of the purpose. Rather, in line with a template’s nature as an interpreted structure and in many cases its conceptual embedding, customization includes additional field-specific interpretation or adjustment of the template’s correction set: any relaxation or addition reflects an effort to show how the template can be developed into a family of models that progressively represent more relevant features of target phenomena, or that represent them more accurately, than the first application in the landing zone. Thus, we see Skellam motivate each further stage of deployment through a need to represent features such as population growth and discrete, localized reproduction. Interestingly, these developments of the template are grounded in an ecological context, and some of its behavior is presented and again related to target phenomena (e.g., referring to travelling waves of invading species); but the performance of the models (e.g., in terms of fit to empirical data or accuracy of numerical predictions) is not compared to alternatives. This may be partly an artifact of the lack of entrenched modeling practices in population ecology in the 1950s, which Skellam notices at the outset of the paper. Yet it may also show how customization may be deployed as a mitigation strategy without discussing *comparative* merits; or, conversely, how conceptual pressure may result not from any conflict with entrenched modelling practices but from a mismatch with some more encompassing ‘folk’ ontology in the recipient domain.[15]

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[15] As a fictional example, consider the conceptual pressure generated by application to physical systems of a template applied primarily to animate objects (e.g., the Prisoner’s Dilemma).

The customization strategy is as entrenched in textbook presentations as the embedding strategy (e.g., Kot, 2001, Chs. 15–16; Okubo & Levin, 2001, Ch. 6; Cantrell & Cosner, 2003, Ch. 2). Thus, the KiSS model is often similarly presented in stages: first, showing how a population in a bounded habitat surrounded by a death region inevitably goes extinct if it disperses without growth; then demonstrating how growth may lead to an equilibrium in patches of critical size; and subsequently relaxing assumptions and otherwise de-idealizing by considering biased rather than random movement, spatial heterogeneity (i.e., zones of extinction and multiplication that vary in their (in)hospitability), or the effects of fragmenting larger contiguous zones.

## 4 Conclusion

The notion of template has been proposed and developed to provide a basis for specifying identity and difference criteria for the objects involved in cross- and trans-disciplinary modeling practices. Such practices can be analyzed as involving the transfer of computational as well as model templates, i.e., interpreted formal structures that are partly valued for their computational tractability. In this paper, I extended template-based analyses to encompass *processual* aspects of this transfer, focusing on how and why cross- and trans-disciplinary modeling practices arise in addition to what they involve. In particular, building on Price's ideas of a landing zone and conceptual pressure, I have argued that modelers try to mitigate some of the costs incurred by template transfer through strategies of conceptual embedding and customization of the template. Both strategies hinge on a template's nature as an interpreted rather than merely formal structure. One illustration of these strategies is provided by applications of the reaction–diffusion template in mathematical ecology, from Skellam's (1951) pioneering efforts onwards.

This paper showcases the possibility of including processual aspects in a template-based analysis, and thus providing insight into conditions for successful cross-disciplinary modeling. Conceptual pressure and its associated risks and mitigation strategies are, as I have argued, characteristic features of template transfer—but they are unlikely to be the only ones. Similarly, conceptual embedding and customization are sample mitigation strategies, which are unlikely to exhaust the repertoire of modelers. To make further headway into understanding processes of template transfer, the scope of the present analysis needs to be expanded in at least three ways.

First, most obviously, a wide range of other cases needs to be studied in order to identify additional associated costs and mitigating strategies, as well as corroborate the aspects and strategies discussed here. Given Humphreys' (1995, 2004) seminal insight that a relatively small set of templates is applied in a broad range of research activities, focusing a template-based analysis to one or two cases at a time is unnecessarily restrictive. It would be illuminating to compare various applications of the same template (e.g., the reaction–diffusion template) in a number of different fields (e.g., chemistry, geology, epidemiology, and ecology), in order to study which adjustments are made to local circumstances and what might be the same across disciplinary contexts (apart from formal structure and 'thin' interpretation). In particular, one might contrast cases in which the template is constructed 'from scratch', or from highly abstract principles, such as in theoretical chemistry, with cases in which it is explicitly *transferred* from another disciplinary context.

Second, current template-based analyses have, by and large, focused on a handful of highly successful efforts, which does serve to identify suitable units of analysis (as detailed in Sect. 1 of this paper), but is less appropriate for identifying success conditions. For that, we would also need to study cases of *failed* or at least *less successful* transfer. Clearly, even if it would turn out that in successful cases, like Skellam's transfer of the reaction–diffusion template, modelers seek to mitigate risks through embedding and customization, it cannot be said that this reliably contributes to success if the very same strategies are found in cases of *unsuccessful* transfer. Prior to this contrastive exercise, and perhaps partly in parallel with it, it needs to be specified what even constitutes (limited) success or failure—which is a non-trivial task in its own right.

Third, many analyses focus primarily on the initial deployment of a template in a new disciplinary context. There is, however, much more to the process than a study of pioneering efforts could reveal. For instance, successful transfer might require that after a first demonstration of customizability, a template is developed into a variety of models that address particular discipline-specific problems. There may well be cases in which transfer might stall, i.e., a template is never established beyond its landing zone. More longitudinal studies that do not suffer from 'pioneering bias', i.e., an exclusive focus on neatly circumscribed efforts (reflected in textbook cases or highly cited trailblazing papers) could expand the scope of template-based analyses in this respect and thus increase their historical depth.

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