Processes and predictions in plant ecological models: logic and causality

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Abstract

To make credible ecological predictions for terrestrial ecosystems in a changing environment and increase our understanding of ecological processes, we need plant ecological models that can be fit to spatial and temporal ecological data. Such models need to be based on sufficient understanding of ecological processes to be robust enough to make dependable predictions and account for the different sources of uncertainty. Here, I argue (1) for the use of structural equation models in a hierarchical framework with latent variables and (2) to specify whether our current knowledge of relationships among state variables may be categorized primarily as logical (empirical) or causal. Such models will help us to make continuous progress in our understanding of and ability to predict the dynamics of terrestrial ecosystems, and provide us with local ecological predictions with a known degree of uncertainty that are useful for generating adaptive management plans. Such hierarchical models are analogous to epistemological models of how knowledge is obtained.

Keywords: structural equation model; hierarchical model; ecological prediction;

Introduction

The climate and environment are changing and the effects of these changes on ecosystems and biodiversity are well documented (IPBES 2019). It is becoming increasingly important to develop credible ecological predictions, but what the limits of such a predictive approach is an open question. To what extent is it possible to predict the future of ecosystems in a changing environment? What ecological processes are most likely to dominate future ecosystem changes? How fast will ecosystem changes occur? Here, I focus on the vegetation component of the ecosystem as a dynamic system that is influenced by climate, interactions among organisms and disturbances as an example of attempts to develop predictive ecological models in general.

The conceptual framework and study methods of plant ecology, and therefore of plant ecological models, are embedded in concepts of time and space. One of the few generalizations that we can make about vegetation is that it is spatially heterogeneous, and the spatial patterns of the vegetation depend mainly on the environment and historical legacies (Greig-Smith 1979; Ricklefs 2004; Svenning and Skov 2004; von Humboldt and Bonpland 1805). Even in a homogenous environment, plant species are aggregated at large and small spatial scales. At a larger scale, plant species are aggregated among sites due to random extinction events and limited possibilities for colonization (Cordonnier et al. 2006; Leibold et al. 2004; MacArthur and Wilson 1967; Rees et al. 2001). Within sites, plants may be aggregated due to clonal growth, limited seed dispersal, and size-asymmetric competition (Herben et al. 2000; Pacala and Levin 1997; Stoll and Weiner 2000). The dominant plant species affect the soil, which leads to important feedback mechanisms, so the vegetation and soil may be described as a dynamic system in time and space, where different phases of the vegetation simultaneously co-occur in different patches (Watt 1947), or the ecosystem can develop in a successional pattern.

Moreover, it is a truism that ecological processes occur in time, and they are best studied when temporal dynamics are taken into account (Damgaard 2019a; Damgaard and Weiner 2017; Kratz et al. 2003; Pickett 1989). Generally, environments are non-stationary, and spatial and temporal variability in ecological systems have been demonstrated to be fundamentally important to ecosystem dynamics (Chesson 2000b; Cushman 2010; Huston 1979). For example, the successional changes in tree-dominated ecosystems are expected to be highly erratic and unpredictable at the local scale due to variable factors such as herbivore abundance (Schippers et al. 2014), while often being predictable at a larger scale. Temporal changes in the water level of Atlantic wetlands have been shown to affect both the nature of interspecific competitive relationships and the overall importance of competition for regulating population growth (Merlin et al. 2015).

When studying ecological processes, the ecosystem is a useful conceptual entity that focuses attention on important system properties (Tansley 1935). For example, Lenton et al. (2021) argue that self-perpetuating feedback cycles involving biotic as well as abiotic components may be critical for the stability and long-time success of ecosystems, and Tansley (1935) proposed that stable ecosystems will outlast unstable ecosystems. Furthermore, when ecosystems are situated near other ecosystems in a landscape, another level of emergent properties may arise among the ecosystems at the landscape level (Leibold et al. 2004). For example, environmental variation within a landscape may lead to a storage effect with coexistence of species that would otherwise not coexist (Chesson 2000a; Chesson and Warner 1981).

The goal of basic ecological research is to understand the underlying causes of observed patterns, which would enable us to make credible ecological predictions. However, an observed ecological pattern may be caused by several different processes and involve several important contingencies (Damgaard 2019a; Simberloff 2004; Vellend 2010), and the relationship between process and pattern may be influenced by time lags of unknown duration (Svenning and Sandel 2013). Consequently, although there is some level of generality, the quantitative importance of different ecological processes are generally unknown and expected to differ among sites. The resulting variation in vegetation dynamics among seemingly comparable sites leads to a level of complexity that limits our ability to generalize our understanding of the ecological mechanisms underlying observed patterns. While historical contingencies and variation among apparently similar sites preclude the generalization of ecological findings, careful local studies of the mechanisms conducted at the relevant spatial and temporal scales do provide causal information of the factors that determine important community dynamic features (Simberloff 2004; Weiner 1995).

There is increasing awareness of the limitations of classical community ecological models, e.g. Lotka-Volterra-type competition models, to predict ecosystem effects of a changing environment (Clark et al. 2020; Damgaard and Weiner 2021; Eigentler 2021; Martyn et al. 2020; Mayfield and Stouffer 2017; Neill et al. 2009; Vellend 2010). For example, it is widely appreciated that frequency-dependent species interactions, in which relatively rare species are favored over more common species, may play an important role in plant species co-existence and community dynamics in plant communities (Chisholm and Fung 2020; Connell et al. 1984). Species-specific soil-plant interactions have received increasing interest as a potentially important and general mechanism for regulating plant populations by hindering local establishment and growth of conspecific plant species in the next generation (Heinen et al. 2020; Mazzoleni et al. 2015a; Mazzoleni et al. 2015b; van der Putten et al. 2013). In an attempt to cope with the ecological complexity, Vellend (2010) suggested partitioning all ecological processes into a logically complete set of disjunct categories: selection, drift, dispersal and speciation (the nomenclature of these categories may be discussed in an ecological context, but the important characteristic is that they are logically disjunct and complete). Historically, such a classification scheme has been successful in evolutionary biology, and Vellend (2010) argued that the reason this approach has not been used more in ecology is due to universal familiarity with ecological patterns. For example, since prehistoric time it has been common knowledge that plant growth is reduced when plants grow close together, and it therefore seems natural to focus on the effects of competitive interactions rather than focusing on a logically complete set of possible processes in community ecology.

The quantitative scientific exploration of the underlying mechanisms that lead to observed ecological patterns among ecological state variables in time and space relies on statistical analyses, but often the investigation meets the obstacle summarized in the well-known phrase "correlation does not imply causality". More precisely and in the language of Jaynes (2003), the outcome of a statistical analysis is a *logical* statement of association rather than a test of different *causal* mechanisms. He argues that probability theory in a Bayesian setting may be thought of as an extended form of scientific logic, which enables us to quantify our belief in a hypothesis by modelling the different sources of uncertainty. The term "logical" *sensu* Jaynes (2003) highlights the assumed relationship between state variables and corresponds to the terms "statistical" or "empirical", which are commonly used in ecology.

The distinction between logical and causal dependencies is subtle and not always clear, but important nonetheless. Logical dependencies are investigated using probability theory by calculating the plausibility of different hypotheses when knowledge is limited (Jaynes 2003), and even though it is assumed that the calculated probabilities are determined by causal dependencies, the calculation of such probabilities is usually decoupled from causal dependencies. For example, if we want to know if a plant experienced competition from a neighboring plant at day t, when we know that the plant experienced competition at a later day $t + \tau$, then we may calculate the probability P (competition at day t | competition at day $t + \tau$). Such probability calculations allow us to make ecological predictions, even though the estimated relationship is not a causal dependence, since the outcome at a later day cannot influence the outcome at an earlier day. It can also be shown that the accumulation of new causally independent data may lead to logical dependencies when investigating the plausibility of multiple hypotheses (Jaynes 2003).

Logical and causal dependencies are not distinct entities but form a continuum from almost pure logical (statistical) relationships to primarily causal relationships, and the distinction is further complicated by unmeasured confounding factors that affect observed independent variables. These confounding factors may lead to "spurious correlations" or omitted variable bias (Gelman and Hill 2007). The effect of the confounding factors could potentially be teased out in an analysis of instrument variables or using structural equation models (Grace 2021; Rinella et al. 2020), and causal independence may be inferred from experimental manipulations and the use of the logical do-operator introduced by Pearl (2009). However, many important ecological processes operate at such large spatial and temporal scales that controlled experimental manipulations are impossible, although it may be possible in some cases to combine the information from manipulated experiments and large-scale observational studies (Benedetti-Cecchi et al. 2018).

The combined effect of both logical and causal dependencies among state variables at the ecosystem level is most effectively modelled using structural equations (Grace et al. 2010). However, it is important to note that structural equation models investigate the observed logical associations within a hypothesized causal network of measured ecological variables, where the associations are typically assumed to be linear functions. This means that structural equation models normally do not compare the likelihood of different functional forms of the association among the observed state variables - the nature of the ecological processes that link the observed variables is not investigated. For example, in a typical structural equation model of the possible association between the observed growth of two plant species, it is not addressed whether the growth data may be adequately explained by Lotka-Volterra type of interspecific competition or whether it is relevant to assume some additional form of frequency-dependency (e.g. Clark et al. 2020; Damgaard and Weiner 2021). This insensitivity to the underlying processes that link the measured ecological state variables in the hypothesized causal network may be critical for the ecological predictions that are made using a fitted structural equation model. For example, if frequency-dependency plays a role in interspecific competitive interactions, then more species can coexist (Chisholm and Fung 2020).

Consequently, when specifying structural equation models it is important to model the underlying ecological mechanisms in more detail than is usually done and to apply hypothesized mechanistic functional relationships among state variables, e.g., by assuming that plant growth decrease with the relative frequency of the plant species in a non-linear way (Damgaard and Weiner 2021). In this way, dependencies that are mainly logical can be replaced by dependencies of a more causal nature in structural equation models. The mathematical dependencies in a structural equation model will not be either strictly logically or strictly causal, but there is a continuum from simple linear logical dependencies to more causal mechanistic dependencies, such as a sigmoid growth functions, which capture known population ecological mechanisms at a sufficiently high level of aggregation to allow statistical treatment of available ecological data in a structural equation model. It is possible to use prior ecological insight to compare the statistical fit of different ecological processes in generating an observed ecological pattern (e.g. Clark et al. 2020; Damgaard and Weiner 2021). Clark et al. (2020) warn against the use of process models of relatively high complexity due to the risk of overfitting, but if frequency-dependency or feedback cycles are important ecosystem features, then such level of model complexity is needed in order to make credible ecological predictions.

Often, there is sizeable variation in the measured independent variables due to measurement and sampling errors in ecological studies (Muff et al. 2015; Yanai et al. 2018). Such measurement errors are typically not taken into account in ecological and environmental modelling, where measured independent variables are treated as if they were constant entities. This is unfortunate, since it has been shown that even normally distributed sampling and measurement errors may lead to important model and prediction bias, a phenomenon known as "regression dilution" (Carroll et al. 2006; Damgaard 2020b; Damgaard and Weiner 2021; Detto et al. 2019). Another typical problem in the analysis of ecological experiments is the use of the language of the experimental design, e.g. “control” and “treatment”, as orthogonal fixed independent factors, although there is often large variation and covariation among the variables that are manipulated in the experiment, e.g. soil humidity and temperature, which are the real independent variables of interest in the study and the ones that are being inferred and concluded upon (Damgaard et al. 2018).

How can we best improve the empirical modelling of plant ecological processes in space and time in order to make credible ecological predictions? Following the suggestion by Clark (2005; 2007) and several others, I argue for combining structural equation models with the flexibility of hierarchical models with latent variables in a Bayesian setting for investigating logical and causal plant ecological dependencies in a coherent way and at the same time model the different sources of uncertainty.

Hierarchical models

In ecosystem models, it is often relevant to use structural equations for modelling the effects of different factors on an ecological response (Grace et al. 2010; Pearl 2009). Importantly, structural equation models may also be formulated in a hierarchical setting, where the structural uncertainty is quantified by the residual error for each of the modelled processes (Clark 2007; Damgaard 2019b).

The use of hierarchical models with latent variables allows us to partition and model the different sources of uncertainty (Clark 2005; 2007; Wikle 2003). For example, in an empirical study of competitive plant growth there may be i) sampling and measurement errors when determining the size of plants at different times using non-destructive measuring methods. ii) structural uncertainty in the form of the competitive interactions, e.g. whether frequency-dependent competitive effects play a role or not, and iii) the possible confounding effects of unmeasured variables on individual plant performance at both an early and later growth stage, due to spatial variation in soil nutrients, pathogens and other factors (Fig. 1).

The effect of sampling and measurement uncertainty is accounted for in hierarchical models by introducing latent variables that model the true, but unknown, value of different variables (Clark 2007; Gelman and Hill 2007). The logical link between the latent variables and the corresponding observed data depends on the type of data and the measurement method. For example, in a study where plant biomass is measured destructively and it is known that the variance increases with the mean, then it may be appropriate to model the observed biomass by a gamma distribution with latent variables as mean parameters and a common scale parameter expressing the relationship between the mean and the variance. In a multi-species study of pin-point plant cover data, it may be appropriate to model the observed number of pin-point hits by a reparametrized Dirichlet-multinomial distribution, in which the latent variables are the mean cover of the different species and where the expected inter-specific spatial aggregation at the plot level is modelled by a parameter (Damgaard 2015; 2018).

When fitting fine-grained ecological data, it is relevant to examine how well different process models are supported by the data (e.g. Clark et al. 2020; Damgaard and Weiner 2021) by estimating the expected out-of-sample prediction error of the different functional models using the Watanabe-Akaike or other information criterion (Gelman et al. 2014b). In the absence of prior knowledge when modelling spatial and temporal vegetation data on relatively large scales, it may be a useful strategy to keep it simple and model changes using the logically complete set of ecological process categories such as those suggested by Vellend (2010), of which selection at the community level is the most important category. In more complicated ecological models, it is important to specify whether the hypothesized ecological dependencies among the state variables may be categorized as primarily logical or causal. In any case, when using relatively simple models it becomes increasingly important to quantify the uncertainties and restrain from making predictions outside the spatial and temporal domain of the data. For example, in a spatial and temporal comprehensive, but coarse-grained, study of vegetation changes in wet heathlands and how these changes were affected by the environment, changes in cover of selected species were modelled by simple linear models, thus ignoring any higher-order community dynamic effects (Damgaard 2019b). Instead, care was taken to partition spatial and temporal effects and different sources of uncertainty in a hierarchical model, which enabled short-term ecological predictions that are useful for generating local adaptive management plans (Damgaard 2020a). In this particular case, spatial and temporal effects were separated by assuming that the state of plant communities in the first year of sampled time series was controlled by spatial processes, which included the effects of the environment, as well as historical legacies, contingencies, and succession history at the site level prior to initiating sampling. The temporal processes were then modelled in a state-space model based on the observed yearly changes in vegetation cover during the sampling period (Fig. 2). In ecological systems with significant among-site dispersal, it may be relevant to model the effect of the dispersal in spatial and temporal diffusion models (e.g. Wikle 2003). The fitting of hierarchical models, which is most naturally done in a Bayesian setting using numerical methods, has received considerable attention (e.g. Gelman et al. 2014a).

Ideally, the possible confounding effects of unmeasured variables should be investigated using an instrument variable analysis (Gelman and Hill 2007; Rinella et al. 2020). However, this is often not possible and instead it has been suggested that we can account for possible confounding effects of unmeasured variables by modeling the unexplained covariance between the observed variables (Rinella et al. 2020), such as the unexplained covariance between early and later growth stages (Fig. 1).

From an epistemological point of view, it is noteworthy that the structure of hierarchical models with latent variables reflects well-known theoretical philosophical models of how knowledge of the world is obtained. Kant (1781) suggested that there is a fundamental division between a world of phenomena ("Das ding an sich") and an observer, and when an observer senses a certain phenomenon (the object), a representation of the object transcends into the mind of observer, and in this process the representation of the object is merged with several sources of relevant *a priori* knowledge, such as concepts of space and time, for the object to make sense for the observer (*a posteriori* knowledge). In a hierarchical model, the data are like Kant's phenomena and the latent variable may be thought of as being similar to the transcended representation of the object in the mind of the observer. Similarly, Wittgenstein (1922) described how we make mental pictures of objects and how these pictures are models of reality. He suggested that the relationship among the different picture elements corresponds to the relationship among the objects, and thus gives a representation of the structure of the reality. This notion is similar to how latent variables in a hierarchical model are linked by a structural equation model. It is encouraging that the treatment of measurement errors and causal dependencies in structural equation models in a hierarchical setting mimics these well-known general epistemological models and, consequently, provides a recipe for how to link models with data and causal hypotheses into a mathematical framework.

Discussion

I have argued that it is important to partition and model the different types of observed variance, and that hierarchical models are often the best tool for this purpose. For example, in a relatively fine-grained study of plant competitive growth of *Festuca ovina* and *Agrostis capillaris* it was concluded that the inclusion of frequency-dependence and measurement error improved model performance greatly, but taking possible unmeasured variables into account did not. Furthermore, when sampling and measurement errors were taken into account, the resulting ecological prediction differed qualitatively from the corresponding non-hierarchical models without latent variables (Damgaard and Weiner 2021). Moreover, in a study of tree fecundity Clark et al. (2004) found that random variation among individual trees and among years dominated the variation in tree fecundity. If this random variation was omitted from the analysis, parameter estimates would have been biased and led to qualitatively erroneous conclusions. They also found that estimated random variation could partly explain the observed pattern of coexistence among the tree species.

The current poor performance of ecological predictions is probably due to the relatively low quantity and quality of spatial and temporal ecological data. The increasing use of advanced technology in ecological monitoring, such as drones and satellites, may allow us to make better predictions. As fine-grained plant growth data at large spatial scales become increasingly available, it may be feasible to fit structural equation models in which different hypothesized species interaction processes are compared statistically. By increasing the resolution of spatial and temporal ecological data, it should become possible to increase the performance of the predictions. At the limit of better and better data and increasingly detailed understanding of the ecological processes, the increase in predictive performance may reach a boundary. If the intrinsic boundary of ecological predictive performance is low, due to historical or other contingencies, it may be necessary to rethink our current strategy of adaptive management of ecosystems based on ecological predictions in nature conservation.

For some simple ecosystems that operate on relatively small spatial scales and relatively short time scale, such as microbial decomposer systems, it may be possible to perform manipulative experiments that allow us to test and validate complete causal hypotheses of the system dynamics. However, the relevant temporal and spatial scales of most ecosystems are so large that a purely experimental approach is not feasible, so in our modelling of ecosystem processes we must recognize that our current ecosystem knowledge is incomplete and not be overconfident in hypothesized causal mechanisms. Consequently, ecological models with both causal and logical dependencies will be needed in the attempt to make credible ecological predictions. The goal of ecology as a science, however, is to increase our mechanistic understanding of the different processes and thereby enable us to convert assumed logical dependencies into more causal dependencies among state variables in our structural equation models. The current state of structural equation models in plant ecology, where many dependencies are strictly based on logical and statistical arguments will act as a guide into where knowledge is missing and suggest future research agendas. It is important to capture the causal mechanisms at a sufficiently high aggregation level to allow statistical treatment of available ecological data in a structural equation model. It is not necessary or even desirable to model all the known mechanistic details, such as modelling every single birth and death event using individual based models.

It is important to quantify the uncertainty of generated ecological predictions. In my opinion, the public notion of plant ecology as a “soft” science, which plays a disproportionally small role in real politics, hinges on our failure as a community to make credible predictions. Currently, the majority of plant ecological predictions, from local management plans of natural habitats to global assessments of biodiversity, are broad verbal statements without any attempts to quantify the uncertainty of the predictions. To communicate credibility of the verbal predictions, a common practice is to call on the consensus of experts. For example, in a report from IPBES (2019) 150 selected experts extracted the content of more than 15,000 scientific publications to make a global assessment of biodiversity and the obtained conclusions, including the recommended actions, were approved at a plenary meeting. How is such a process even possible and what is the role of the ecological data in the 15,000 scientific publications in reaching a consensus for the recommended actions? But no body of even distinguished experts can grasp the complexity of ecosystem dynamics in a changing environment and fairly assess the wealth of relevant spatial and temporal data in round-table and panel discussions. In the cases where good data are available it would be more appropriate to apply a quantitative modelling approach, where the uncertainty of the effects of the recommended actions may be assessed in a systematic way, and the results of the quantitative analyses can then be interpreted by experts for decision makers.

Acknowledgements

Thanks to Jacob Weiner for valuable discussions and suggestions in preparing this paper

Figures

Fig. 1. : Hierarchical model of competitive plant growth from plants at an early and later growth stage. The true, but unknown, plant size at the early and later growth stage is modelled by latent variables (squares) and denoted X, Y, respectively. The latent variables are logically linked to the observed data (circles), which are denoted x, y, respectively, with the corresponding latent variables as the mean value. The sampling and measurement uncertainty are modelled with σ_x and σ_y, respectively. The competitive growth process is modelled by the function, F, which depends on X and possibly on some measured environmental variables z_m. The effect of unmeasured variables affecting both earlier and later growth stages is modelled by σ_{xy} as the part of the covariance between the early and later growth stages that is not explained by the independent factors in the process model.

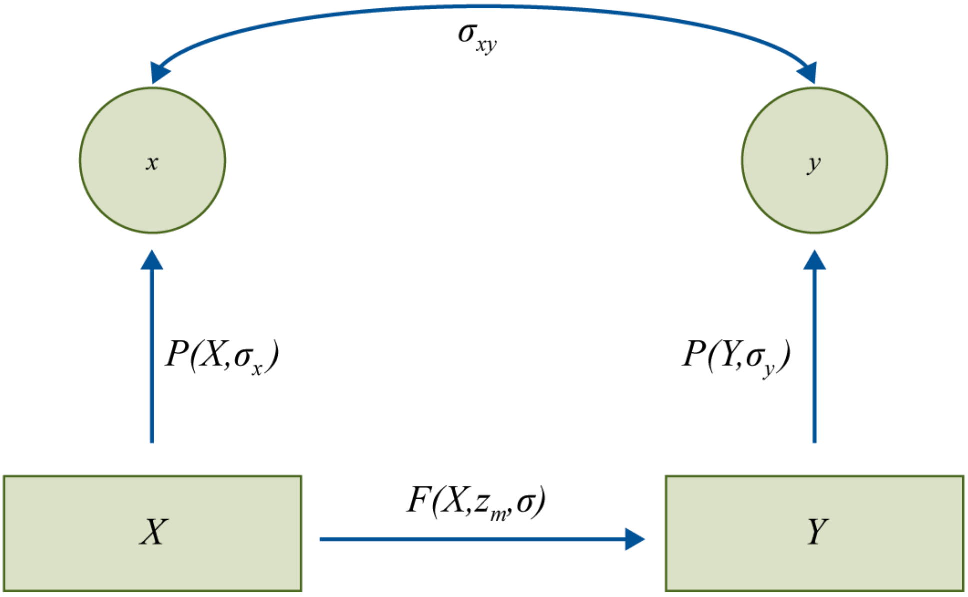
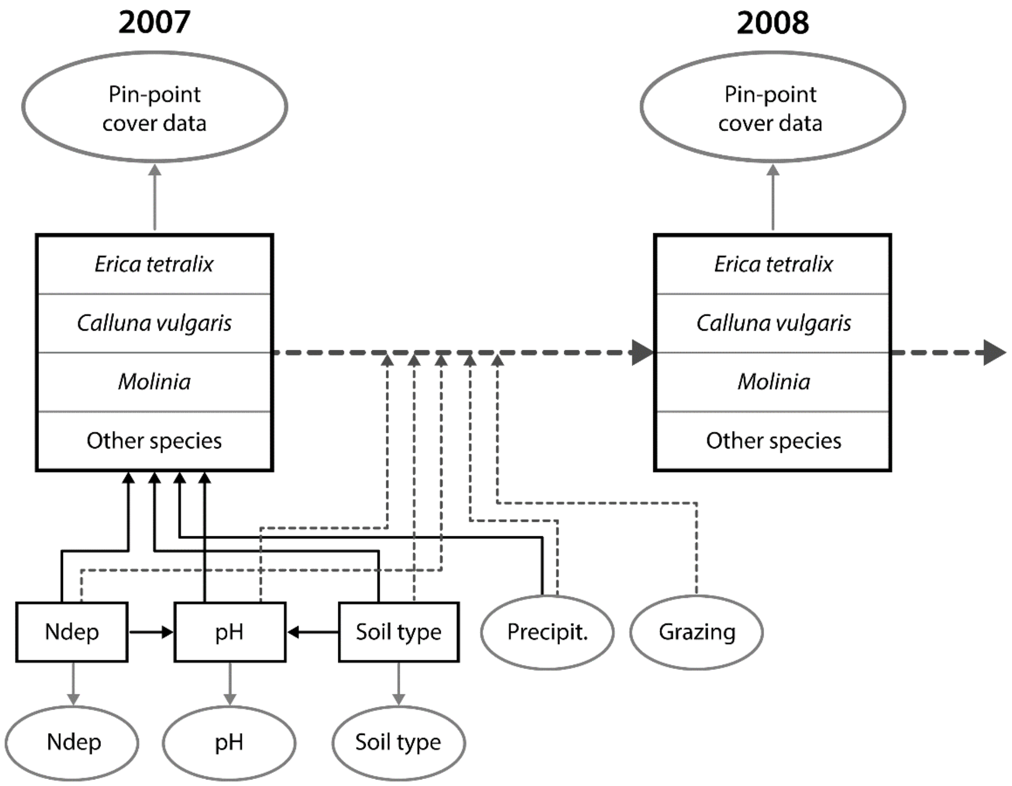


Fig. 2. Outline of a structural equation model where the spatial and temporal processes are separated. The spatial variation in vegetation cover in 2007 is modelled by nitrogen deposition (Ndep), soil pH (pH), soil type and precipitation (Precipit.). The yearly change in vegetation cover from 2007 to 2014 (only a single yearly change is shown in the figure) is modelled by all the former variables as well as grazing. The square boxes are latent variables and the oval boxes are data. The full black arrows denote spatial processes, the dotted black arrows denote temporal processes, and the grey arrows denote the logical modelling of sampling and measurement error (Damgaard 2019b).



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