Spatial and temporal models in plant ecology: logic and causality

Christian Damgaard, Ecoscience, Aarhus University

Abstract

It is argued that in order to make credible ecological predictions for terrestrial ecosystems in a changing environment, we need empirical plant ecological models that are fitted to spatial and temporal ecological data. Such models need to include sufficient ecological process understanding in order to make correct predictions and at the same time account for the different sources of uncertainty. Here, it is advocated to use structural equation models in a hierarchical framework with latent variables and be careful to specify whether our current process knowledge may be categorized as either logical or causal dependencies among state variables. Such models will provide us with local ecological predictions with a known degree of uncertainty that are useful for generating adaptive management plans and lead to a general progress in our understanding of the causes underlying a possible predictive limit of terrestrial ecosystems. Furthermore, it is an advantage that the proposed hierarchical models are analogous to well-known theoretical epistemological models of how knowledge is obtained.

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

Introduction

The climate and environment are changing and general effects on ecosystems and biodiversity are well documented (IPBES 2019). In order to meet societal needs, it is becoming increasingly important to develop credible ecological prediction, however, it is an open question what the boundaries of such a predictive approach are. To what extend 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? In the attempt to develop predictive ecological models for terrestrial ecosystems and as a consequence of the green world hypothesis (Hairston et al. 1960), it seems relevant to focus attention on the vegetation component of the ecosystem as a dynamic system that is influenced by climate, herbivores and other disturbances.

The notion and study methods of plant ecology, and therefore of plant ecological models, are embedded in the 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). However, even in a homogenous environment plant species are aggregated both at large and small spatial scales. At the large scale, among-sites plant species are aggregated due to random extinction events and limited possibility of 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). Dominant plant species may also affect the soil, which, again, may lead to important feedback mechanisms, i.e. 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).

Moreover, it is a truism that ecological processes occur in time, and they are best studied when the effect of time is 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 herbivore abundance (Schippers et al. 2014). Likewise, temporal changes in the water level of Atlantic grasslands have been shown to affect both the nature of the 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) already proposed that stable ecosystems 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 ultimate goal of an ecological investigation is to understand the detailed underlying causes of an observed pattern, 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 are some levels of generality, the quantitative importance of ecological processes are generally unknown and expected to differ among sites. The resulting variation in succession history among otherwise comparable sites leads to a level of complexity, which hinders our ability to generalize our understanding of the ecological mechanisms underlying observed patterns. However, while historical contingencies and variation in succession history among otherwise similar sites preclude the generalization of ecological findings, careful local studies of the ecological mechanisms conducted at the relevant spatial and temporal scales do provide causal information of the factors that determine important community dynamic features (Simberloff 2004).

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). Especially, 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 to partition all ecological processes into a logically complete set of ecological process categories: selection, drift, dispersal and speciation. Historically, a similar classification scheme has been successful in evolutionary biology, and Vellend (2010) convincingly argues 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 dynamics.

The quantitative scientific exploration of the underlying mechanisms that lead to observed ecological patterns 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. More generally, Jaynes (2003) 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 our uncertainty. The distinction between logical and causal dependencies is subtle, but important. Logical dependencies are investigated using probability theory by calculating the plausibility of different hypotheses when knowledge is incomplete (Jaynes 2003), and even though it is assumed that the calculated probabilities are determined by causal dependencies, the actual calculation of logical dependencies may de 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 studied 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).

The distinction between causal and logical dependencies is also complicated by possible unmeasured confounding factors that affect observed independent variables. These confounding factors may lead to a spurious correlation 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 almost 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).

Moreover, it is important to note that structural equation models investigate the logical associations within a hypothesized causal network of measured ecological variables, where the associations typically are 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 variables, i.e. 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 investigated 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 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 relatively more species will be expected to coexist (Chisholm and Fung 2020).

Consequently, it is important to investigate the underlying ecological mechanisms in more detail than is usually done in structural equation models, and 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) generally warn against using process models of relatively high complexity due to the risk of overfitting, but, on the other hand, if e.g. 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 a 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 highly 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 to use the codes of the experimental design, e.g. “control” and “treatment”, as orthogonal fixed independent factors, although there often is 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).

The aim of this paper is to discuss 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, it is advocated to apply the flexibility of hierarchical models with latent variables in a Bayesian setting for investigating logical and causal plant ecological dependencies in a coherent way by modelling the different sources of uncertainty.

Hierarchical models

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, e.g. spatial variation in soil nutrients or pathogens (Fig. 1).

The effect of sampling and measurement uncertainty may be accounted for in a hierarchical model 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 data type and 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 that models 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, where 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).

The structural uncertainty is quantified by the residual error of the structural or process model, which is typically assumed to be normally distributed due to the central limit theorem. When fitting fine-grained ecological data, it may be relevant to examine how well different process models are supported by the data (e.g. Clark et al. 2020; Damgaard and Weiner 2021), e.g. by estimating the expected out-of-sample prediction error of the different models using the Watanabe-Akaike information criterion (Gelman et al. 2014b). In causal models at the ecosystem level, it is often relevant to use structural equation models for modelling the effects of different factors on the ecological response (Grace et al. 2010; Pearl 2009). Such 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).

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

In the absence of prior knowledge and 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 suggested by Vellend (2010), of which selection is the most important category. In more complicated ecological models, it is important to specify whether the hypothesized ecological process knowledge may most likely be categorized as either logical or causal dependencies among the state variables. 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, the cover changes 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 to be made at a local site where the level of uncertainty was quantified that are immediately useful for generating adaptive management plans (Damgaard 2020a). In this particular case, spatial and temporal effects were separated by assuming that the state of the 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 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). However, in ecological systems with significant among-site dispersal, it may be relevant to model the effect of the dispersal in spatio-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). Generally, the most simple and robust numerical methods are MCMC iterations, either using Metropolis-Hastings methods, such as the Gibbs sampler, or using the Hamiltonian gradient descent algorithm (Stan Development Team 2017). However, for models with large datasets and many latent variables, these methods may be too slow and it may be necessary to estimate at least some of the variables by the Laplace approximation (e.g. Gómez-Rubio and Rue 2018).

From an epistemological point of view, it is interesting 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, e.g. concepts of space and time, in order 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. Likewise, Wittgenstein (1922) described how we make mental pictures of objects and how these pictures are models of reality. Furthermore, he suggested that the relationship of 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 intellectually satisfying that the treatment of measurement errors and causal dependencies in structural equation models in a hierarchical model setting in this way mimic these well-known general epistemological models and, consequently, provide a recipe for how to link epistemological models with data and causal hypotheses into a mathematical framework.

Discussion

It has been demonstrated that it is important to partition and model the different types of observed variance, and that this partition of the variance very effectively is done using hierarchical models (Clark 2007). 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 be biased and have lead to qualitatively erroneous conclusions. Furthermore, it was found that estimated random variation could partly explain the observed pattern of species coexistence among the tree species.

Currently, it is an open question what the limiting factors for the performance of ecological predictions are; is it mainly the quality of ecological data or our knowledge of the underlying processes? If the current boundary for the performance of the ecological predictions is due to a relatively low quality of the spatial and temporal data, then there may be potential advantages in increasing the use of technology, e.g. drones and satellites, in ecological monitoring. Conversely, if the inherent boundary of the predictive performance is low, then it may be necessary to rethink our current strategy for e.g. adaptive management of ecosystems.

In the near future, when fine-grained plant growth data at large spatial scales are expected to become increasingly available, e.g. due to the use of drones, then it may be feasible to fit structural equation models where different species interaction process models are compared statistically. A working hypothesis may be that by increasing both the resolution of spatial and temporal ecological data and the level of understanding of the underlying ecological processes, it will become possible to increase the performance of the predictions. However, at the limit of better and better data and increasingly detailed understanding of the ecological processes, the increase in predictive performance may reach a maximum. It will be interesting to examine what factors control this possible maximum in the predictive performance of ecological systems.

For some simple ecosystems that operate on relatively small spatial scales and a relatively fast time scale, e.g. microbial decomposer systems, it may be possible to make manipulated 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, and 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.

Generally and to ensure credibility, it is important to quantify the uncertainty of the 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. In an attempt 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? In my opinion, it is self-evident that 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. Instead, it is essential to apply a quantitative modelling approach, where the uncertainty of the effects of the recommended actions may be assessed in a systematic way.

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.

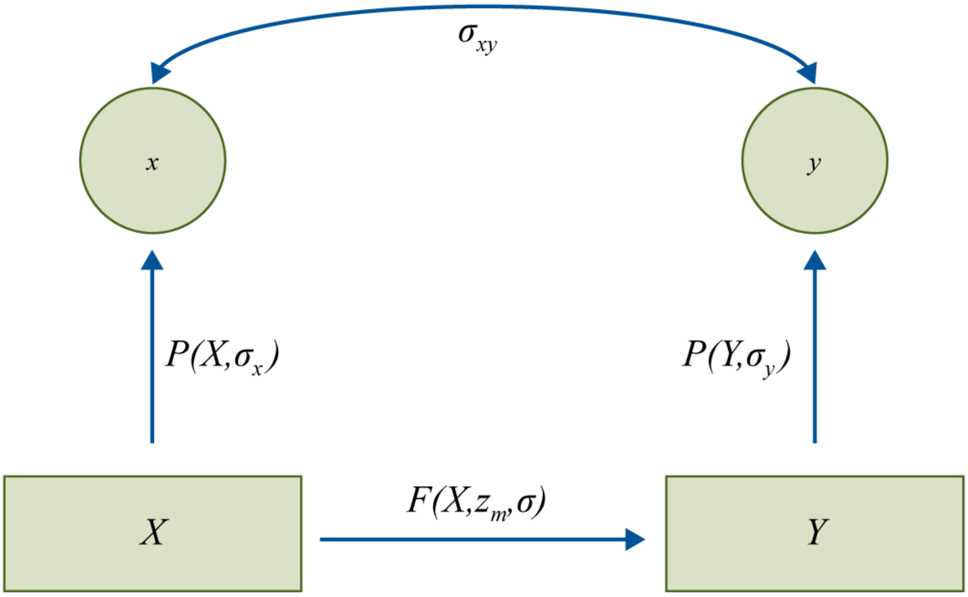
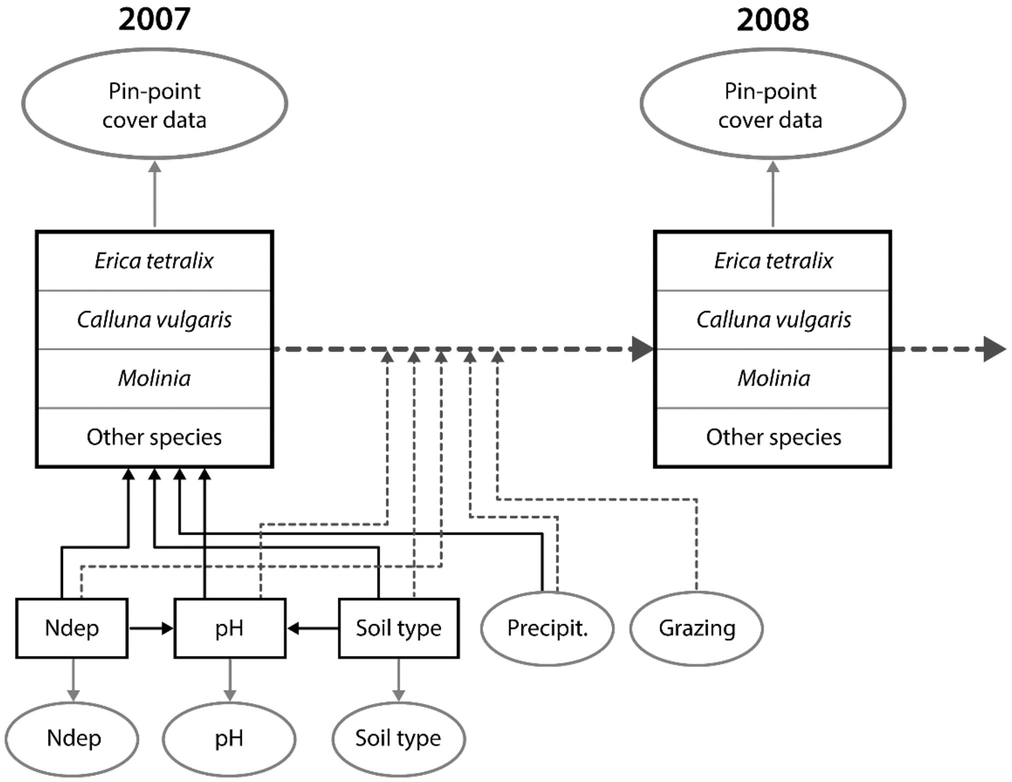


Fig. 2. Outline of a structural equation model where the spatial and temporal processes are separated. The spatial variation in vegetation cover in 2007 is modelled by nitrogen deposition (Ndep), soil pH (pH), soil type and precipitation (Precipit.). The yearly change in vegetation cover from 2007 to 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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