Perspectives Paper

From patterns to causal understanding: Structural Equation Modeling (SEM) in soil ecology

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ABSTRACT

In this perspectives paper we highlight a heretofore underused statistical method in soil ecological research, structural equation modeling (SEM). SEM is commonly used in the general ecological literature to develop causal understanding from observational data, but has been more slowly adopted by soil ecologists. We provide some basic information on the many advantages and possibilities associated with using SEM and provide some examples of how SEM can be used by soil ecologists to shift focus from describing patterns to developing causal understanding and inspiring new types of experimental tests. SEM is a promising tool to aid the growth of soil ecology as a discipline, particularly by supporting research that is increasingly hypothesis-driven and interdisciplinary, thus shining light into the black box of interactions belowground.

Keywords

Aboveground-belowground interactions, path analysis, hypothesis testing, mechanistic understanding, soil processes

Introduction

The diversity and complexity of interactions among soil organisms, as well as their interactions with the environment, have fascinated and challenged soil ecologists for decades (Powell et al., 2014). While researchers strive to identify the factors that drive soil communities and the complexity of aboveground-belowground interactions, the soil still is often referred to as a “black box” of potentially interacting organisms (Wardle et al., 2004; Bardgett and van der Putten, 2014). Past studies have identified many of the drivers of belowground biological communities (e.g., Wu et al., 2011; Eisenhauer et al., 2013; Prober et al., 2014; Tedersoo et al., 2014) and processes (e.g., Wall et al., 2008; Handa et al., 2014). A next essential step in soil ecology is to disentangle the mechanistic links that connect soil chemical, physical, and biotic properties in what is a multivariate ecological system.

Soil scientists commonly formulate and present conceptual figures and multivariate hypotheses that include direct and indirect relationships, feedback effects, changes in communities, and responses of ecosystem processes, a framework that is remarkably similar to the models used in structural equation modeling (SEM) (see e.g., Fig. 2 in Wardle et al., 2004 and Fig. 2 in Bardgett and van der Putten, 2014). SEM can be defined as “the use of two or more structural [cause-effect] equations to model multivariate relationships” (Grace, 2006) and allows for an intuitive graphical representation of complex networks of relationships. Thus, SEM can be used to represent and test mediation and direct versus indirect relationships (Fig. 1A), the partial contributions of correlated explanatory variables (Fig. 1B), and alternative hypotheses (Fig. 1C). The methodology also allows for the inclusion of unobserved latent variables (Fig. 1D), and pooling effects of multiple variables into composite variables (Grace and Bollen, 2008). Further, it can be used to derive new hypotheses, inspiring targeted experimental work.

The statistical tools used by ecologists should be able to offer insights into systems of intercorrelated entities and events in studies in all ecological systems. Filling this role, structural equation modeling is increasingly being used either to test multivariate hypotheses or to explore several possible alternative hypotheses in ecological studies (e.g., Grace et al., 2010; de Mazancourt et al., 2013; Laliberté et al., 2014; Tedersoo et al., 2014) as it provides the multidimensional framework needed to capture the complexity of ecological networks and relationships (Grace et al., 2014). SEM is sometimes called a “second generation” multivariate method as it provides some advances beyond other, so-called “first generation” multivariate methods, such as canonical correspondence analysis (CCA), principal components analysis (PCA), nonmetric multidimensional scaling (NMS), multiple regression (Fornell, 1982; Grace, 2006). As detailed in Grace (2006), SEM exceeds the descriptive nature of first generation approaches by allowing confirmatory tests and testing of multivariate hypotheses. It is a highly flexible method that can be applied many situations, and is suitable to test networks of causal relationships. While often relying on correlative information, SEM brings researchers closer to causal understanding (as used by Shipley, 2002) by fitting data to models representing causal hypotheses and by determining goodness-of-fit as well as comparing fit among models representing alternative, mechanistic hypotheses.

Even when causality is relatively well-known in a system, SEM has another great strength: the ability to partition direct and indirect effects, and make distinct the multiple pathways by which one entity can influence another. The strength of these various pathways can then be estimated and compared. For example it was well-known that grasses, digging by rabbits, and biological soil crusts could influence water infiltration rates in soil (Eldridge et al., 2010). An SEM analysis revealed that rabbit digging activity did not *directly* influence infiltration in an appreciable way, but rather *indirectly* affected infiltration through the reduction of biological

crust cover (Eldridge et al., 2010). SEM is uniquely suited among multivariate modeling techniques for making such discoveries.

It is generally recommended that SEM be used following a hypothesis-driven approach, with clearly defined initial models and a thorough description of their rationale and alternatives based on the published literature in the main text (e.g., Ebeling et al., 2014) or in an accompanying table (Fig. 2A; Chaudhary et al., 2009). Initial hypotheses can be supported and retained or rejected based on their correspondence with the available data. An *a priori* model supported in this way provides the strongest inference. If an initial model is rejected based on poor fit to the data, it is common to consider alternatives until a satisfactory degree of support is attained. Ultimately, modified models should be confirmed in later work before receiving full confidence.

As an illustration of the SEM process, the study by Pérès et al. (2013) follows this *a priori* approach and, via partitioning, demonstrates another exciting strength of SEM (redrawn in Fig. 2B). Although not given in the figures of that paper, the authors allowed alternative mechanisms to explain variation in the response variable “soil aggregate stability”, by not only having indirect paths from plant diversity/community properties through the hypothesized mediating variables (the endogenous variables root biomass, soil organic carbon concentrations, soil microbial biomass, and earthworm biomass), but by also having a direct path from plant diversity to soil aggregate stability. This potentially allows the discovery of new, unsuspected mechanisms, which could inspire future experimental work.

Most examples of SEM in the ecological literature utilize observational data. It is important to point out, however, that SEM can also be used with experimental data. In such cases, the experimenter imposes treatments and wishes not only to learn the net responses of individual variables, but rather, the way in which treatment effects cascade through the interconnected system. In one such study, Chen et al. (2013) performed a field experiment in grassland

communities applying seven levels of soil acidification. They found that associated declines in plant productivity and richness were explained by both direct effects of hydrogen and aluminum ions on plants, as well as altered nutrient levels resulting from changes in the soil biota. Classical approaches to the analysis of experimental data (e.g., ANOVA) do not permit such system-level insights to be discovered and can be profitably supported by SEM studies.

Our intention in this paper is to inspire soil ecologists to consider the advantages of SEM when analyzing their data or, even better, in the early stages of their research when designing experiments. This is a high-level overview of the potential of SEM in soil ecological research in which we provide select examples of how SEM can be used; for a more comprehensive picture, please see Shipley (2002), Grace (2006), and a variety of other books and resources related to specific aspects of SEM (including available software).

Some practical considerations

Estimation and analysis options

SEM is best thought of as a quantitative modeling approach rather than a specific statistical technique. A fundamental premise of SEM is that abstracting systems as probabilistic networks provides scientists a practical and effective way to study cause-effect relationships. Thus, it is the overall motivation of evaluating causal network hypotheses that distinguishes SEM from most other statistical techniques. There are certain general steps and procedures that have developed in support of this motivation (Grace et al., 2010; Grace et al., 2012). In this section, we discuss some of the practical issues that accompany the great flexibility inherent in SEM.

Throughout its historical development, SEM practice has incorporated the latest advances in statistical specification and estimation. Beginning in the early 1970s, specialized software was developed that greatly facilitated the application of SEM. We wish to point out, however, that individual software packages do not fully represent the potential applications of SEM. The great majority of SEM analyses rely on matrix methods designed for obtaining global solutions, typically determined using maximum likelihood procedures. Commonly used software packages based on these estimation methods include Amos (Arbuckle, 2014), Mplus (Muthén and Muthén, 1998-2014; Byrne, 2012) and the R packages lavaan (Rosseel, 2012) and sem (Fox, 2006). These packages support a wide range of models and applications. In certain cases, SEM practitioners may choose a more specialized approach, typically involving local (equation-by-equation) estimation methods. Locally estimated solutions can incorporate more complex specifications (e.g., nonlinear or hierarchical equations) and estimation methods (including full-Bayesian estimation), though they are more limited in terms of the kinds of models that can be evaluated. Further discussion of the strengths and limitations of the various options can be found in Grace et al. (2015).

Design considerations

Many of the conceptual figures presented in (soil) ecology studies are very similar in form to an *a priori* structural equation model. Such hypothetical frameworks can be directly tested if studies are designed in the right way. SEM, like most multivariate methods, is most powerful when using large sample sizes. The recommendations by SEM experts range between 50 and 200 samples as the minimum requirement to analyze complex models (Grace, 2006), although sample size needs are strongly dependent on the degree of model complexity and the strengths of relationships. A common rule of thumb is to have 5 to 10 samples per parameter in the

model. While small-sample situations are indeed challenging, strategies are available that can maximize the opportunity for using SEM (Grace et al., 2012).

There are other major study design considerations and these may interact with software choices. Ease of modeling is facilitated when studies are simple in design and avoid complex subsampling schemes. When samples are clustered, various approaches may be considered. These include multi-group modeling (discussed below), which can be performed using all standard software, but also hierarchical modeling techniques, which are only found in a subset of the packages. Similarly, when response (endogenous) variables are continuous or semi-continuous and relationships are linear, modeling is straightforward, as are the interpretations of model coefficients. Various approaches can be used to model nonlinear relationships and non-normal errors. These include simple, approximate methods, such as the use of polynomials (for nonlinear relationships) and bootstrapping (for non-normal, but continuous errors), which are accommodated in nearly all software packages. When models include categorical responses, assumptions become more complex, though again most software provides some assistance with modeling this type of complexity. Individual studies will vary in their abilities to conform to standard simplifying assumptions. The use of SEM is not limited by specification complexities, but the choices of software one can use might be.

Model fit and selection

A key and somewhat unique feature of SEM is the ability to test network structure. Unlike classical statistical models, which do not represent indirect pathways, it is possible in SEM to determine that important linkages (and therefore important processes) are omitted from a model. It is this feature of SEM that allows for the discovery of new unsuspected processes, which is a compelling part of the SEM experience, as we mention elsewhere. Statistical

programs for SEM generally provide several indicators of model fit, leaving it up to the user to interpret these indicators. This can be an intimidating prospect for beginners, but certain indicators are used more commonly in practice.

One method of testing models is the evaluation of *absolute fit*, i.e., determining if the model structure is plausible in light of the data. Discrepancies between observed covariances and those implied by the model are summarized as model likelihoods. The likelihood of a model, compared to a model with perfect fit, follows a chi-square distribution. Classically, the respective P-values associated with the model chi-square are used to judge the fit between model and data. Unlike null hypothesis methods, in SEM the theory-based models are supported when fit is close (and P values are high). The historical tradition in SEM has been to use an alpha, such as P *greater than* .05, to determine whether or not to accept a model, though this practice is not universal. Other common measures of model fit include the Root Mean Square Error of Approximation (RMSEA; Steiger, 1990) and the Comparative Fit Index (CFI; Bentler, 1990), which both provide means to test the absolute fit of a model to the data (compared to a null model). It is often recommended that multiple measures of model fit be used; particular combinations of model fit measures are often recommended based on sample size and model complexity (Hu and Bentler, 1999). Recent methodological investigations (Bollen et al., 2014) suggest that various information-theoretic methods can be used to judge absolute fit (in addition to their use for comparative fit).

A complement to the evaluation of absolute fit is testing *comparative fit*, i.e., answering the question which of a set of *a priori* models is the most plausible. Increasingly, Akaike's Information Criterion (AIC; Akaike, 1974) is used to compare competing models fit to the same data, although there are several other approaches. Ultimately, model selection is a scientific decision problem and in causal modeling both measures of data-model fit as well as expert judgment are to be relied on.

Latent and composite variables

SEM allows for testing and comparing different, alternative general hypotheses and broad ecological concepts, e.g., by using latent variables. Latent variable analysis is a significant strength of structural equation modeling, setting it apart from ‘simpler’ forms of SEM (e.g., modern path analysis). Latent variables are constructs that represent drivers of responses and are extremely valuable for testing general concepts but are not variables that are, in themselves, measured directly. Instead, they are informed by one or more variables that are indicators or proxies of the driver. For instance, in a study investigating microbial process rates as affected by an experimental treatment, different, highly correlated soil microbial activity measures could inform the latent variable to explain observed differences in process rates. These activity measures either represent the outcomes of biological processes (e.g., respiration, microbial biomass) or may only be measured *ex situ* under specific environmental conditions (e.g., enzyme assays, denitrification potential); the processes themselves cannot be measured. However, the process as a concept can be assigned a value through the construction of a latent variable informed by these activity measures. This is analogous to approaches used for partitioning variation to classes of variables representing spatial or environmental drivers of multivariate responses (Legendre et al., 2005). However, variation in the response that is shared among classes cannot be explored further nor subjected to statistical tests using variation partitioning, while SEM provides an opportunity to disentangle these relationships via the inclusion of paths representing causal relationships or covariances between variables among classes.

Composite variables, on the other hand, represent the collective effect of a group of variables and are completely defined by their causes in most cases (Grace, 2006). Composite variables are not yet commonly used in ecological studies, but because they can integrate information

from a collection of influences they may be of greater value than their current usage suggests. One of the few examples, where composite variables have been used in a study on aboveground-belowground interactions, is the study by Antoninka et al. (2011). In that study collective effects of four different plant biomass variables informed the composite variable ‘plant community structure’, whose effect was then tested on target and weed plant biomass as well as on arbuscular mycorrhizal fungal richness and biovolume. Chaudhary et al. (2009) grouped arbuscular mycorrhiza variables as well as soil and climatic variables to the composite variables ‘AM fungal abundance’ and ‘soil/climate region’, respectively, to observe the combined effects of conceptually linked variables on soil aggregate stability. In order for a composite variable to effectively represent a construct (e.g., plant community structure), sufficient effort must be made to measure the main aspects of the construct that are important for the variable(s) that it is predicting.

While latent variables thus can be regarded as conceptual constructs of highly correlated variables, composite variables represent groups of variables, which do not have to be closely correlated but are conceptually related, such as in the case of different abiotic drivers (e.g., soil pH, soil temperature, soil moisture). Thus, a latent variable is analogous to a factor analysis embedded in a model, whereas a composite is comparable to a multiple regression nested in the model. Notably, while latent variables and composite variables represent powerful tools in some cases, they are more advanced approaches, and there is no inherent need to include those in SEM if there is no role for them to play.

Feedback loops

Unidirectional flow effects are a simplified and sometimes misleading representation of natural systems. Feedback loops form the basis of many functionally important aboveground-

belowground interactions (Wardle et al., 2004; Bardgett and van der Putten, 2014). These can most easily be modeled using temporal data, e.g., through the study of cross-lag effects ($x_1 \rightarrow y_2$ while $y_1 \rightarrow x_2$). However, it is also possible under certain circumstances to evaluate models with feedback loops (so called "nonrecursive" models) using single-sample data. Following the example on aboveground-belowground interactions, feedback loops necessarily involve a temporal component, and the outcomes of temporal dynamics are then given as a static representation of a feedback effect (Grace, 2006). For instance, global change can alter the composition and functioning of communities in soil, which can then have feedback effects on global change, e.g., by influencing greenhouse gas emissions (see Fig. 2 in Bardgett and van der Putten, 2014). Another example is plant-soil feedback effects where plant communities shape specific communities of soil organisms, which in turn influence the composition and performance of the plant community (Bever et al., 2010). As detailed in Grace (2006), estimating such nonrecursive models poses some complications (e.g., correlations of arrows of reciprocal interactions and correlated errors), and problems can arise with model identification. For instance, one important prerequisite for identified models is that each variable must have sufficient independence in its predictors so that it contains unique information (Grace, 2006).

Multi-group modeling

A different approach to SEM may be applied when data belong to different groups, such as different study sites, observations of the same entities at different points in time, or different treatments. Rather than being focused on the plausibility of a single causal hypothesis for all groups, a common causal structure is initially assumed for all groups and the emphasis is on determining which model parameters differ among groups. In one of only a few examples existing in soil ecology, de Vries et al. (2012) modeled the shifting influence of different

attributes of the soil decomposer community on N losses from soils, in the same set of samples through time. The analysis revealed several dynamics, such as an early dominant influence of microbial activity that became eclipsed by microfaunal activity, and a waxing and waning influence of fungal dominance on total soil respiration.

Structural Equation Modeling in Soil Ecology vs. General Ecology

To compare the frequency of structural equation modeling in the soil ecology literature and the general ecological literature, we performed an online literature search (via ISI Web of Knowledge, Thomson Reuters, August 2014) using the terms "structural equation model*" OR "path analys*". This was done for two categories of journals: we identified eight scientific journals associated with the general field of ecology (Ecology, Ecology Letters, Ecological Monographs, Functional Ecology, Journal of Applied Ecology, Journal of Ecology, Oecologia, and Oikos). Accordingly, we selected eight journals more specifically associated with soil ecology (Soil Biology and Biochemistry, Soil Tillage Research, European Journal of Soil Biology, Geoderma, Plant and Soil, Soil Science Society of America Journal, Biology and Fertility of Soils, and Applied Soil Ecology). The literature search was restricted to the last 30 years (1984 – 2013). To determine whether, in each journal category, there was a comparable proportion of studies addressing the drivers of ecological patterns, we also scanned the same set of journals using the search term "effect*" or without search term.

In general, the number of papers published in these subsets of ecology journals and soil ecology journals was similar, with 60,306 and 70,312 papers, respectively, without research term and 28,166 and 32,341 papers, respectively, with "effect*" as a search term. However, the number of papers identified as applying structural equation modeling or path analysis in the subset of soil ecology journals was less than one fifth (46 papers) of that in the subset of

general ecological journals (259 papers; Fig. 3). In both journal categories, the number of papers using structural equation modeling or path analysis increased exponentially during the last 30 years, with those in general ecological journals appearing earlier and in higher numbers (Fig. 3). Performing the same search within articles published in *Pedobiologia* between 1984 and 2013 revealed that not a single paper was identified as applying structural equation modeling or path analysis.

The results of the literature search show that structural equation modeling and path analysis appear in only a small fraction of publications from the ecological literature, regardless of whether those journals are focused on soil ecology or ecology more generally. Even so, SEM was applied much more often in the general ecological literature than in the soil ecological literature in the 1990s and this continues to be the case, even though the method increased in popularity among soil ecologists around the start of the 2010s (Fig. 3a). Why is this the case? There is no reason to think that soil ecological studies are less suitable for SEM. One possibility is that soil ecologists may be more reluctant to adopt novel statistical techniques. That said, other multivariate methods, particularly ordination, are widespread in the soil ecology literature. Another aspect that discounts this view is that soil ecologists have exhibited the qualities of pioneers for other types of methodologies; for example, soil microbiologists were quick to adopt and adapt the DNA-based methods that have largely replaced culture-based approaches in environmental microbiology. An alternative explanation could be that studies by soil ecologists using SEM reflected a more mechanistic and hypothesis-driven approach that was more likely to be published in general ecological journals; this was certainly the case for some of our own papers (Sikes et al., 2010; Eisenhauer et al., 2012; Delgado-Baquerizo et al., 2013). However, scanning the 259 papers in general ecological journals (checking titles and abstracts, if necessary) revealed that the

fraction of soil ecological studies was small with 19 papers in total (Fig. 3b), suggesting that SEM is still underused in soil ecology.

Outlook and conclusions

We have demonstrated that SEM is an underused approach in soil ecology and present a case that it could be used to generate mechanistic, and potentially transformational, insight into the drivers of ecological interactions and processes in soils. However, before these insights can be gained, we must develop (or rediscover) concepts and theory that paint a picture of terrestrial ecosystems in a way that links aboveground-belowground interactions, different environmental factors, populations, and process rates. Bardgett and van der Putten (2014) recently highlighted that the conceptual integration of soil ecological data is urgently needed and that theory has lagged behind experimental work in soil ecology. They claimed that new theoretical models have to be developed to comprehend the drivers of the composition of belowground communities as well as their manifold impacts on ecosystem processes and aboveground communities. We argue that SEM is particularly suited to provide the statistical framework to pave that path, both by testing statistical hypotheses representing predictions of mechanistic hypotheses, as well as by generating new hypotheses that could be tested following the development of innovative experimental methods.

In addition, to do so, more multidisciplinary and integrative research in soil ecology is needed to characterize and comprehend these complex networks of ecological interactions (Powell et al., 2014). To develop comprehensive SEMs that measure essential aspects of ecological systems in soils may require collaboration between researchers from different disciplines such as, for instance, plant biologists and biogeochemists. A few examples of these approaches exist. For instance, Pérès et al. (2013) used SEM to investigate the underlying mechanisms

determining how plant community properties influence soil aggregate stability by considering variation in soil organic carbon content, soil microbial biomass, root biomass, and earthworm biomass; this endeavor required collaboration between plant ecologists, soil ecologists, soil microbiologists, and soil chemists. Chaudhary et al. (2009) collaborated in a similar way to study the vertical distribution of soil stability in semi-arid shrublands, characterizing the contributions of climate, soil properties, vegetation, biological soil crusts, and arbuscular mycorrhizal fungi to surface and subsurface soil stability.

We also see great potential for SEM to generate a more mechanistic understanding of how soil food webs are structured and how energy flows through these food webs. SEM may allow for testing the interplay between bottom-up and top-down effects (Sandom et al., 2013) and the identification of key groups of soil organisms controlling ecosystem process rates (Eisenhauer et al., 2013), and elucidation of how these change through time (de Vries et al. 2012). Further, SEM can be used to relate density and diversity data from multiple trophic levels to process rates, such as done in the frame of a grassland biodiversity experiment to explain plant diversity effects on herbivory and decomposition rates via shifts in the herbivore and decomposer communities (Ebeling et al., 2014). Ultimately, however, experiments are needed wherever possible to test the hypotheses generated by SEM conducted on observational data to sort out alternative explanations (Veen et al., 2010). Pairing SEM-based analyses with manipulative experiments may be an especially powerful way forward, and SEM offers some new flexibilities for traditional challenges to study designs, such as incomplete control and non-independent covariates.

SEM may provide a new perspective on aboveground–belowground interactions by considering the interwovenness but also the relative importance of different, often correlated variables (e.g., Scherber et al., 2010; Eisenhauer et al., 2013). However, this has yet to be extended to the study of feedback loops that are an implicit component of aboveground-

belowground interactions. There is a rich literature on the relevance of plant-soil feedback effects for plant community dynamics (Bever et al., 2010; van der Putten et al., 2013), and SEM may be particularly well suited to test and illustrate the underlying feedback loops. However, as described above, the respective experiments have to be carefully designed to consider the complications of nonrecursive models (Grace, 2006). Moreover, broad ecological questions can be addressed, such as comparing the effect strength of abiotic versus biotic determinants of soil communities and processes (e.g., Wu et al., 2011). Thereby, biotic and abiotic drivers could be represented by composite and/or latent variables. Another example would be the test of the relative significance of aboveground versus belowground plant inputs in driving soil communities and processes (Pollierer et al., 2007; Eisenhauer and Reich, 2012).

Researchers studying microbial interactions in soil, as well as the interactions between symbiotic microorganisms and roots, particularly struggle to generate mechanistic insight into these interactions in the natural environment. This is due to the difficulties associated with manipulating only a single component of the microbial system without affecting other biotic or abiotic components that are also likely to affect ecosystem processes. As a result, researchers studying these interactions under ecologically relevant conditions rely on natural or manipulated environmental gradients and use correlations among microbial groups and environment properties to infer the contributions of microorganisms to those processes (Torsvik and Øvreås, 2002). It is very common in the microbial ecology literature for researchers to measure many structural and functional responses of microbial communities and several edaphic properties of systems exposed to some environmental manipulation (e.g., addition of mineral fertilizer or organic amendment) and then interpret significant correlations between individual response variables as important causative links in the biogeochemistry of the system. Such interpretations may not be necessarily correct as those correlations may

simply arise as a result of common responses to changes in the environment and be independent of each other. However, researchers could approach these valuable datasets in a different way: SEM informed by well developed, *a priori* causal hypotheses can be used to evaluate whether the evidence supports these inferences and to estimate the potential contribution of particular microorganisms or microbial communities in ecosystem responses to manipulation. This can be valuable, for example, to identify new microbial groups (Jones et al., 2014) or to estimate the relative importance of microbial diversity and abundance compared with edaphic properties (Powell et al., 2015) during denitrification.

To summarize, SEM is a promising but underused tool that we think can greatly aid the growth of soil ecology as a discipline, particularly by supporting research that is increasingly hypothesis-driven and interdisciplinary, thus shining light into the black box of interactions belowground. Notably, however, structural equation modeling and path analysis have some unique limitations and risks for misuse (see Chapter 11 in Grace, 2006), and caution must be taken when applying those methods. We provided some basic information on the many advantages and possibilities associated with using SEM, as well as some prime examples of how SEM can be used by soil ecologists to shift focus from describing patterns to getting an improved mechanistic understanding. However, careful consideration is required, all the way back to the planning stages of a study, to utilize this tool to the fullest; planning experiments and observational studies with an *a priori* SEM in mind will facilitate the identification of key variables needed to test different effects pathways and competing hypotheses. Finally, we view SEM as more than another tool, rather it is an alternative way of conducting science. In our personal experience, the practice of thinking about our systems in their entirety, and articulating and testing complex hypotheses about how the systems work has been transformational to the way in which we approach ecology.

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Figure legends

Figure 1. Some examples of how structural equation modeling can be used to test soil ecological theory in a multivariate context. Rectangles represent observed variables, while ovals represent unobserved influences. Depicted are tests of direct versus indirect relationships (A), the partial effects of correlated explanatory variables (B), hypotheses about alternative mediating mechanisms (C), and latent variables (D). Error= unexplained variance. The term “exogenous” refers to a predictor variable that is not influenced by any other variable in the model. The term “endogenous” is applied to any variable that responds to influence from another variable in the model.

Figure 2. (A) Depiction of how an *a priori* conceptual structural equation model of hypothesized causal relationships between exogenous and endogenous variables could be shown in a figure and an accompanying table. Error: unexplained variance. (B) Conceptual model tested in Pérès et al. (2013) (redrawn and simplified; in the original version the presence of grasses and legumes in the plant community were also tested as exogenous variables) to compare alternative hypotheses how plant diversity increases soil aggregate stability. Based on previously published work, it was assumed that plant diversity effects can be mediated by changes in root biomass, soil organic carbon concentrations, soil microbial biomass, and earthworm biomass. In addition, a direct path from plant diversity to soil aggregate stability was considered to allow for alternative explanations not captured by the four potentially explanatory, endogenous variables. For illustration purposes errors are not shown although all endogenous variables do have unexplained variance.

Figure 3. (A) Number of papers published per year in selected soil ecological (Soil Biology and Biochemistry, Soil Tillage Research, European Journal of Soil Biology, Geoderma, Plant and Soil, Soil Science Society of America Journal, Biology and Fertility of Soils, and Applied Soil Ecology) and general ecological journals (Ecology, Ecology Letters, Ecological Monographs, Functional Ecology, Journal of Applied Ecology, Journal of Ecology, Oecologia, and Oikos) between 1984 and 2013 using the keywords "structural equation model*" OR "path analys*" based on an online literature search via ISI Web of Knowledge, Thomson Reuters in August 2014. (B) Number of papers published per year in selected general ecological journals (as defined in A) with soil ecological studies highlighted in blue.

Figure

Figure

Table X. Pathways and expected processes associated with an *a priori* conceptual model of hypothesized causal relationships between [...] depicted in Figure Y.

Pathway	Code	Interpretation	Mechanistic examples	References
Exo → Endo#1	A	...	...	...
Exo → Endo#2	B	...	...	...
Endo#1 → Endo#3	C	...	...	...
Endo#2 → Endo#3	D	...	...	...

Figure

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