Soil respiration across scales: The importance of a model–data integration framework for data interpretation

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Abstract

Soil respiration represents the second largest CO₂ flux of the terrestrial biosphere and amounts 10 times higher than the current rate of fossil-fuel combustion. Thus, even a small change in soil respiration could significantly intensify—or mitigate—current atmospheric increases of CO₂, with potential feedbacks to climate change. Consequently, to understand future dynamics of the earth system, it is mandatory to precisely understand the response of soil respiration to changing environmental factors. Among those changing factors, temperature is the one with clearest and most certain future trend. The relationship of soil respiration to environmental factors and particular temperature has been tackled at a variety of scales—from laboratory via field scale to global, with each of the approaches having its particular problems, where results from different scales are sometimes contradictory. Here, we give an overview of modeling approaches to soil respiration, discuss the dependencies of soil respiration on various environmental factors, and summarize the most important pitfalls to consider when analyzing soil respiration at the respective scale. We then introduce a model–data synthesis framework that should be able to reconcile and finally integrate apparently contradictory results from the various scales.

Key words: soil respiration / modeling / upscaling / Bayesian / temperature dependence

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1 Introduction

With globally 68–120 Pg C y⁻¹ soil respiration represents the second largest C flux between ecosystems and the atmosphere (Schimel et al., 1996). This is more than 10 times the current rate of fossil-fuel combustion and indicates that each year approx. 10% of the atmosphere’s CO₂ cycles through the soil. Thus, even a small change in soil respiration could significantly intensify—or mitigate—current atmospheric increases of CO₂, with potential feedbacks to climate change. Despite this global significance as well as considerable scientific commitment to its study over the last decades, there is still limited understanding of the factors controlling temporal and across-ecosystem variability of soil respiration.

This understanding is largely hampered by the fact that studies are often conducted and compared at different temporal and spatial scales that are not compatible. Since particularly in large-scale studies factors influencing soil respiration often correlate with each other, responses of soil respiration to those factors are confounded by other factors, and only apparent relationships are obtained.

In this study, methods and problems analyzing soil-respiration data from different scales are reviewed and jointly interpreted with emphasis on the temperature and moisture dependence of soil respiration. The application of an ecosystem model–data integration framework which is developed in a cascade from fine scale to landscape scale, and parameterized by using observations across these scales, is proposed to provide additional insights into the factors controlling temporal and across-ecosystem variability of soil respiration and C content.

2 Environmental factors controlling soil respiration

2.1 Abiotic factors

Temperature is virtually influencing all biological and physico-chemical processes. This has been empirically observed in the 19th century (van’t Hoff, 1898) and later formalized by...
Arrhenius (1889). Not surprisingly, temperature has also been the most obvious and most often studied factor influencing soil respiration, one of the first studies dating back to the 1920s (Waksman and Gerretsen, 1931). All studies confirm a nonlinear positive direct relationship between temperature and soil respiration. A number of shapes have been proposed, but the most commonly used are reviewed by Kätterer et al. (1998), Kirschbaum (1995) and as well by Lloyd and Taylor (1994). The simplest, but theoretically not justified function is the so-called exponential Q10 relationship (Tab. 1), where the parameter Q10 is the factor by which soil respiration increases with a 10°C temperature increase. The Arrhenius function is theoretically justified from first physicochemical principles of the underlying biochemical reactions and predicts an increasing Q10 towards lower temperatures. However, the validity of a simple transfer from physicochemical reactions to complex processes controlling soil respiration has not been proved yet. Instead, more flexible exponential relationships have been derived from empirical field data, which imply an even stronger variation of the Q10 with temperature. Since enzymes act in a certain temperature interval, all biological processes exhibit optimum temperatures. Hence, the optimum function (Kirschbaum, 1995) may be considered as the most appropriate description. However, soil temperatures rarely reach such high values, so that within the normal range of temperatures, the monotonic exponential function may be as valid.

The effect of soil water status on soil respiration has been described empirically via absolute or relative measures of volumetric water content and soil water potential as reviewed by Rodrigo et al. (1997) (see examples in Tab. 2). It is usually assumed, that both very low and very high water contents reduce soil respiration, via direct inhibition of biological activity or inhibition of O2 diffusion, respectively. The relationship between soil water status and soil-respiratory processes is complex, since many individual processes vary with soil water content, in particular gas and solute diffusion, enzyme activities, and growth and mortality of microorganisms (Killham, 1994; Marshall and Holmes, 1988). Soil water potential

Table 1: Typical functions used for describing soil respiration in relation to temperature.

<table>
<thead>
<tr>
<th>Author</th>
<th>Function</th>
<th>Background</th>
<th>Properties</th>
<th>df</th>
</tr>
</thead>
<tbody>
<tr>
<td>van’t Hoff (1998)</td>
<td>( f(T) = a \cdot Q_{10}^{(T-T_{ref})/10} )</td>
<td>empirical</td>
<td>always above 0</td>
<td>2</td>
</tr>
<tr>
<td>Ratkowsky et al. (1982)</td>
<td>( f(T) = a \cdot (T - T_{min})^2 )</td>
<td>empirical studies on microbial growth</td>
<td>zero respiration at ( T = T_{min} )</td>
<td>2</td>
</tr>
<tr>
<td>Arrhenius (1989)</td>
<td>( f(T) = a \cdot e^{E_a/(R \cdot T)} )</td>
<td>physical chemistry</td>
<td>always &gt;0, very similar to ( Q_{10} )</td>
<td>2</td>
</tr>
<tr>
<td>Lloyd and Taylor (1994)</td>
<td>( f(T) = a \cdot e^{E_a/(T - T_{min})} )</td>
<td>Arrhenius + study on field respiration</td>
<td>zero respiration at ( T = T_{min} ), no optimum</td>
<td>3</td>
</tr>
<tr>
<td>O’Connell (1990); Kirschbaum (1995)</td>
<td>( f(T) = a \cdot e^{b \cdot T(1.057/T_{ref})} )</td>
<td>empirical studies on soil respiration in lab</td>
<td>optimum function</td>
<td>3</td>
</tr>
</tbody>
</table>

\( ^a \) degrees of freedom (i.e., number of free parameters)

Table 2: Typical model formulations used for soil-drought effects on soil respiration.

<table>
<thead>
<tr>
<th>Formulation(^a)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>( f(\theta) = a \cdot \theta + b ) (plain linear)</td>
<td>Stanford and Epstein (1974)</td>
</tr>
<tr>
<td>( f(\theta) = a \cdot e^{(\theta - \theta_0) / \theta_0} ) (scaled linear)</td>
<td>Myers et al. (1982)</td>
</tr>
<tr>
<td>( f(\theta) = \frac{\theta}{\theta + \theta_0} ) (hyperbolic)</td>
<td>Bunnell et al. (1977)</td>
</tr>
<tr>
<td>( f(\Psi) = m \cdot \log_{10}(-\Psi) + c )</td>
<td>Sommers et al. (1981); Orchard and Cook (1983); Andrén and Paustian (1987)</td>
</tr>
<tr>
<td>( f(\Psi) = \frac{\log_{10}(-\Psi) - \log_{10}(-\Psi_{\min})}{\log_{10}(-\Psi_{\text{opt}}) - \log_{10}(-\Psi_{\min})} ) (log-linear)</td>
<td></td>
</tr>
<tr>
<td>( f(\Psi) = a \cdot e^{b \cdot \Psi} ) (exponential)</td>
<td>Davidson et al. (1998)</td>
</tr>
<tr>
<td>( f(P) = g(a(P - P_{\text{opt}}) + b(P - P_{\text{ref}})^3) ) (exponential)</td>
<td>Howard and Howard (1993)</td>
</tr>
</tbody>
</table>

\( ^a \) symbols \( a, b, \theta_{\text{opt}}, \theta_0, a_1, m, c, \Psi_{\min}, \Psi_{\text{opt}}, P_{\text{ref}} \) are model parameters determining the shape and scale of the functions.
has often been considered the physiologically more appropriate predictor of activities in soil, because it expresses the actual availability of water independent of texture (Davidson et al., 1998; Miller and Johnson, 1964). However, plausible arguments for soil water content as a predictor have also been presented, based on the reasoning that the number and extent of microenvironments where microbial activity may take place is a function of the volume of the water in the soil (Fang and Moncrieff, 1999; Orchard and Cook, 1983). Furthermore, nutrient and $O_2$ diffusion seem to be better described as dependent on soil water content (Skopp et al., 1990). A practical advantage of water content as a predictor is that it is more readily measured in the field than water potential, but the criticism remains that water content is not comparable among different soil texture classes. A possible way to partly overcome this problem is to express soil water content as a proportion of water-holding (field) capacity or available water, because then the effect of texture on water availability is included to some extent.

Obviously, there are indirect effects of drought on soil respiration, e.g., the impact on soil macrofauna which may retreat into deep layers and/or fall dormant under drought. Although macrofauna assimilates <10% of C, it acts as important catalyst by cracking larger structures and increasing the reaction surface area. Also, rewetting events often increase soil respiration by large amounts, which can only be explained by remineralization of dead biomass or by desorption processes, which make labile substrate available to microbes (Orchard and Cook, 1983). While the temperature dependency of soil respiration has been analyzed for different compartments (roots, litter, mineral soil) with quite different observed responses (Anderson, 1991; Liski et al., 1999), no such efforts have been undertaken with respect to drought effects.

Other abiotic factors have been much less systematically studied than soil water availability and soil temperature, but include soil acidity, $O_2$ and nutrient availability. Oxygen can be a limiting factor of soil respiration in water-logged soils or in aggregates after rain events, that cause anaerobic conditions. The response of soil respiration to soil acidity is thought to be an optimum function, where bacteria operate optimally under neutral conditions while fungi prefer slightly acidic soil pH. A recent study has shown that such optimum curve can be found through analysis of field data of respiration (Reth et al., 2005), although confounding factors have to be considered.

Also in the temporal domain, processes from various timescales overlap and superimpose on the resulting soil biological activity and soil respiration (Fig. 1). Consequently, a currently observed soil respiration can be the result of processes that have occurred a long time ago. A typical example for this would be the unusually high and persisting soil respiration from crop fields that have been established on previous peatland by hydrological regulation and aeration. Another relevant example is the effect that after a long soil drying and subsequent rewetting, soil-respiration rates often exceed rates under well-watered conditions before the drying. This so-called Birch effect has been first observed in the laboratory and is usually explained by the rapid mineralization of microbes that died during the drying, a dynamic effect (Birch, 1958). Recently this effect has been found being of importance also for ecosystem C dynamics (Borken et al., 2003; Xu and Baldocchi, 2004). The scheme in Fig. 1 also elucidates that the type of model developed to describe soil respiration (i.e., the processes included) must be dependent on the temporal extent that needs to be covered by the application of the model.

2.2 Biotic factors

Given that soil respiration is by >90% a biological process, it is conceptually evident that biotic factors are important determinants of soil respiration. Roots as well as microorganisms eventually depend on the carbon supply that is assimilated by the green vegetation and enters the soil via phloem transport to the root, root exudation, and incorporation of dead plant material into the soil (litter fall). The proportion of root respiration has been shown to vary usually between 30% and 70%. Extreme values of 10% and 90% have been reported, but those numbers may be subject to extreme conditions and methodological problems. Global analysis of soil-respiration data sets has clearly shown, that soil respiration is strongly

Figure 1: Dominant temporal scales of factors and processes influencing soil respiration. (sSOM = stable soil organic matter).
correlated with net primary productivity (Janssens et al., 2001; Raich and Schlesinger, 1992; Raich and Tufekcioğlu, 2000).

Macrofauna cracks large structures, thereby making available substrate for microorganisms and increasing the surface area for biochemical reactions. Thus, macrofauna importantly acts as catalyst for the decomposition of soil organic material (SOM).

3 Modeling approaches

Soil respiration—defined as the CO₂ efflux from the soil surface—originates from the metabolic activity of roots (autotrophic respiration), microorganisms (bacteria, actinomycetes, fungi), and soil meso- and macrofauna (heterotrophic respiration). Only under certain circumstances (carbonate soils), significant amounts of CO₂ can abiotically evolve through weathering of carbonates (e.g., CaCO₃). While for modeling carbon assimilations by plants, the leaf is easily identified as the functional unit with clear boundaries and a well-known organization of tissues and a general biochemistry (Calvin-Cycle), soil processes occur very heterogeneously without a single functional unit. Instead, a number of organisms and enzymes are decomposing a large variety of chemical substances. Moreover, while virtually all higher plants are described as species and a large number of plant species of various functional types have been studied extensively, not even 10% of soil microbes are described at all. Consequently, for modeling plant productivity, species-oriented and reductionistic approaches have been successful, while soil respiration is often modeled as a whole (holistic approach), and soil processes are more related to the substances that are decomposed rather than to the function of decomposing species.

Despite the obvious importance of biological control of soil respiration, empirical models have often not included biotic factors but focused mainly on the abiotic controls. Even for global and interannual variation, models are developed that predict soil respiration solely from climate variables (Raich and Potter, 1995; Raich et al., 2002). The hypothesis behind these climatically driven models is that vegetation productivity and climate are correlated and their effect on soil respiration cannot be disentangled. However, Reichstein et al. (2003a) showed that it is possible and necessary to separate climatic and biological effects on soil respiration, since their biologically driven model explained more than 6-fold more site-to-site variance of soil respiration data than a climate-driven model.

Mechanistic models generally rely on a few common paradigms when modeling soil respiration. Root respiration is assumed—as for other plant tissues—to be the sum of growth and maintenance respiration, according to the 30 year–old so-called Penning-de-Vries paradigm (Amthor, 2000). Heterotrophic respiration is usually modeled as the decomposition of 2–8 SOM pools with different turnover times. According to this approach, each pool decomposes with a first-order kinetic, analogue to nuclear decay:

\[ \frac{dC_i}{dt} = l_i - k_i C_i, \]

where \( l_i \) is the input to the pool \( l \), \( C_i \) is the pool size (e.g., kg m⁻²), and \( k_i \) is the first-order decomposition rate constant (cf., Fig. 2). Labile pools with high decomposition rates are sugar, alcohols, and starch, while cellulose, ligno-cellulose, waxes, and lignin are considered more stable components. Dependences of \( k_i \) on temperature (Tab. 1) and moisture (Tab. 2) are mostly assumed to be multiplicative although this must be questioned (Borken et al., 1999; Carlyle and Than, 1988; Reichstein et al., 2003a) since the relationship between soil water status and soil-respiratory processes is complex (see above). Humification is modeled as transition from a more labile to a more stable pool. This concept goes back to Jenny (1941) and Meentemeyer (1978).

The structure of current soil respiration models is oversimplified in several ways. First of all, biotic constraints on soil respiration, environmental effects on the population dynamics of macrofauna and microbes, remineralization of dead biomass, and drought−influenced seasonality of root-exudation and growth respiration are mostly neglected. In addition, the quite pronounced vertical differentiation in soils is largely neglected. For instance, the decomposition rate of SOM in different depths depends on the temperature and moisture in those depths (see below). The soil also is a horizontally very heterogeneous system, which is constantly modified and organized by organismic activity. This leads to a concentration of the activity into few areas. Hence, one has to consider that the environmental factors that prevail in those areas are important for the soil activity and respiration, and not necessarily average conditions in the soil. In current soil-respiration models, a number of processes (e.g., priming or microbial growth dynamics) are not explicitly considered, nor a direct link (other than litterfall) from assimilation to belowground processes. Recent girdling experiments seem to indicate that current models underestimate the importance of the interactions between aboveground and belowground processes. (Högberg et al., 2001; Subke et al., 2004). Biologically focused, food-web−based models of soil respiration have been developed, but did not achieve much general attention (Hunt, 1977; Hunt et al., 1977; Smith et al., 1998).
4 Extracting the response of soil respiration to environmental factors

While a general description of the response of soil respiration to environmental factors (see above) seems quite straightforward, there are a number of complications that occur when a formal modeling of soil respiration, e.g., in response to temperature, is sought. These complications arise mainly from misunderstandings about what “the response of soil respiration to temperature” actually is and from different interpretations at different scales. The largest misunderstanding may occur between field ecologists and mechanistic modelers of soil respiration. The former would define the response of soil respiration to temperature basically from the scatter between observed soil CO₂ efflux and measured temperature. The latter would say there is no such definition of “the response of soil respiration to temperature” as a whole, but defines how individual components—e.g., rate constants of decomposition, root maintenance, and growth respiration—depend on temperature. These two very different approaches can lead to very different results that are per se not comparable as will be outlined in the next sections.

4.1 Analyzing soil respiration at the laboratory scale

Measuring and modeling soil respiration in the laboratory has got the advantage that the influence of different factors can be analyzed under controlled conditions. Disadvantages of such method can be summarized under the notion of introducing artificial conditions that are not further discussed here. In the laboratory, usually only respiration stemming from the mineralization of SOM is observed, while roots are either sieved out or considered inactive, since they do not get any supply of photosynthates. Thus, with such experiments it should be possible to easily obtain the temperature dependence of SOM mineralization. However, even in this case the situation is not as “controlled” as it might appear, mainly due to the dynamic nature of the decomposition process (Fig. 3). At higher temperatures, the easily decomposable fraction will be mineralized more quickly than at lower temperatures. That implies that after a certain time, there will remain more easily decomposable matter in the low-temperature treatment than in the high-temperature one. The result is a relatively higher soil-respiration rate in the low-temperature treatment after a certain time, i.e., a decreasing Q₁₀ with incubation time. When the easily decomposable fraction also in the low-temperature treatment is nearly completely decayed, then the Q₁₀ rises again. So, the Q₁₀ dynamics is a result of the changing amount of decomposable matter in the different temperature treatments. In the literature, it is very often not reported when and how the Q₁₀ was derived, e.g., the decent scatter of Q₁₀s in the review by Kirschbaum (1995), may have been caused by these spurious changes in Q₁₀.

As a consequence, it is dangerous to derive the Q₁₀ of C mineralization from the respiration rates at only one arbitrary incubation time, because then the temperature effect is confused with the incubation-time effect. There are three ways to solve this problem: (1) to calculate the Q₁₀ values from only the respiration rates at the beginning of the incubation (e.g., Winkler et al., 1996), because the composition of the samples is still unaltered, (2) to use the respiration rates at a very late incubation time (e.g., Ross and Cairns, 1978), when the light fraction is (nearly) mineralized and respiration rates are nearly constant, (3) to fit a model of C mineralization combined with a temperature-response function of the rate constants to the mineralization curves. With approaches 1 and 2, only a small part of a long-term incubation is considered. Moreover, at the beginning of an incubation, soil respiration may still be influenced by disturbance, introduced by sample preparation (Bliet-Charaudeau et al., 1990; Schinner et al., 1993), while at the end of an incubation, inhibiting metabolites may have accumulated, which could adulterate the temperature dependence of C mineralization (Kirschbaum, 1995). Therefore, it is strongly recommended to fit a model of C mineralization combined with a temperature-response function of rate constants to the temperature-dependent mineralization curves (e.g., Kätterer et al., 1998; e.g., Updegraff et al., 1995). This approach provides the temperature dependence of decomposition rate constants, and, additionally, the model is compatible with current C balance models (e.g., Andrén and Kätterer, 1997; e.g., Parton et al., 1987), which also use temperature-dependent rate constants.

4.2 Analyzing soil respiration at the plot scale

The rapid development of soil respiration chambers with reliable infrared gas-analyzers has made possible diurnal as well as year-round observations of in situ soil respiration. These studies have also been used to derive the response of soil respiration to environmental factors, most often being soil temperature and water availability. However, the observed response can be easily confounded by other biotic or abiotic factors, so that care has to be taken when interpreting and extrapolating the results, e.g., in the context of global change. Here, the effect of seasonally varying factors and the effect of fluxes coming from different soil layers are discussed.

Figure 3: (A) Theoretical dynamics of the available SOM substrate during an incubation experiment at high (lower curve, dashed) and lower temperature (upper curve). (B) Resulting apparent Q₁₀ time series that would result from relating the instantaneous fluxes from the high- and the low-temperature treatment (see Reichstein et al., 2000, for details and real-data analysis). The Q₁₀ relationship was only used for simplicity; the principle holds true for any function.
When analyzing seasonal variation of soil respiration, the problem is that several factors co-vary (e.g., temperature, moisture, plant assimilation, root activity). When the variation is then attributed to one factor only, background correlations with other factors can confound the relationship. A typical situation is depicted with the temperature-soil respiration relationship in Fig. 4. In a summer-active ecosystem (e.g., a summer-green deciduous forest), the general higher biological activity in summer adds on to the “pure” or direct temperature response. In such an ecosystem, the true temperature sensitivity would be overestimated using seasonal data. The opposite effect occurs in summer-passive (e.g., summer-drought-affected ecosystems, cf., Fig. 4). One prominent example of such a misinterpretation of seasonal data is the study from a trenching experiment (Boone et al., 1998), where an (apparent) stronger temperature sensitivity of root respiration compared to the bulk soil respiration was found. In view of the fact that the actual temperature response of root respiration does not differ from soil respiration (Bååth and Wallander, 2003), this result can only be explained by a stronger seasonality of root respiration, hence a spurious result. Also it cannot be ruled out that strong decline of Q_{10} at higher temperatures in the review by Lloyd and Taylor (1994) is partly caused by interaction with soil moisture limitations, i.e., that the currently most commonly used function is a spurious or confounded one.

The relation between observed in situ respiration rates and soil temperature is also ill-defined since soil respiration is originating from different depth with each depth having its own temperature dynamics. Depending on which depth for soil temperature is used as a predictor in the regression with soil respiration, varying temperature sensitivities will result: the deeper the soil-temperature measurement, the smaller is the amplitude of temperature and consequently the larger will be the estimated temperature sensitivity, e.g., the Q_{10} (cf., Fig. 5). Theoretically to solve this problem, one would have to fit a multisource model to the respiration data, but experience shows that such a model is often overparameterized. One work-around is to use the temperature at that depth where the best correlation is obtained (in the example 5 cm). Nevertheless, temperature sensitivities obtained from different studies are only partly comparable, even if the depth is standardized, since thermal properties (insulation) differ between soils (and even seasonally within the same soil), as well as the depth of main respiratory fluxes. It should be clear after those examples that these empirical apparent Q_{10} values are not compatible to what is used in mechanistic models.

### 4.3 Analyzing soil respiration at larger scales

Analyzing soil respiration at larger scales brings the spatial dimension into play, where site-to-site variability needs to be modeled. From site to site all factors that were discussed above potentially (co-)vary by large magnitude. Thus, a direct link from empirical results obtained at this scale to mechanistic model parameters is even less possible than from results at the field scale because of the confounding effects. For example, a result showing that decomposition rates did not vary significantly with temperature along a continental gradient (Giardina and Ryan, 2000) does not invalidate the fundamental temperature dependence of decomposition rate constants that is used in C-balance models. Instead the correct interpretation is that there are other factors that override the temperature effect.

Similarly, there has been some controversy about biological and climatic controls of soil respiration stemming from different interpretation of large scale analysis. In several studies, Raich and coworkers have shown that large part of spatial-temporality variability of soil respiration can be statistically explained by monthly temperatures and precipitation, i.e., by purely climatic drivers (Raich and Potter, 1995; Raich et al., 2002). This apparently contrasts other findings that productivity (biological control) is the main determinant of soil respiration across continental scales (Janssens et al., 2001; Valentini et al., 2000). But again, these are only correlative relationships being obscured by the background correlation between productivity and climate. With a careful analysis, it may be possible, however, to statistically separate biological and climatic controls on soil respiration. Reichstein et al. (2003a) have done such analysis and showed that both categories are important for describing spatial and temporal variation of soil respiration, with a model that used temperature, precipitation, and leaf-area index as predictors. While this model is also statistical, it better accounts for variations caused by biotic and abiotic factors, e.g., with respect to interannual variations of soil respiration, that were very small according to the climate-driven model.

![Figure 4](image-url) Schematic representation of the confounding effects introduced into a temperature dependence of soil respiration derived from annual data. Triangles and squares are hypothetical data for summer-active and summer-passive ecosystems, respectively.
4.4 General strategies for linking observations and models across levels

We have discussed several instances where a direct transfer of empirical relationships, e.g., from the ecosystem level to the process level is misleading, as in a generalized way depicted also in Fig. 6. Instead of trying to directly establish fundamental relationships (like temperature dependence of decomposition rate constants) from large-scale pattern there are more fruitful approaches to analyze soil respiration and other ecosystem flux data (Fig. 6): In the forward approach, different C-balance models are tested if they are able to generate the spatial or temporal patterns (e.g., continental or environmental gradients) that are empirically observed. An important task in this approach is actually to define and identify the important general patterns in the data that needs to be reconstructed by a “good” model. In the inverse approach, model parameters at the process level are inferred from ecosystem-level observations, such that the model reaches a maximal consistency with the observation. Inferred para-
meters can then be confronted with theoretical expectations at the process level. Bayesian model-data synthesis to some extent mediates between these two approaches, in the sense that a model is constructed that obeys both the data and prior expectations about parameter at the process level (Knorr and Katge, 2005; Reichstein et al., 2003b; Tarantola, 1994). Regardless of the method applied, often the problem is underdetermined, i.e., the data is not sufficient to distinguish between model structures or parameterization. In these cases, it is crucial to define new observations that exert further constraints on the models (multipleconstraint approach). With respect to soil respiration, this implies that more attention should be drawn to collect not the flux data themselves but also information about system properties, like soil C fractions, soil microbial biomass, and their vertical distribution.

Figure 6: Scheme of inappropriate (crossed out) and alternative ways of linking model and observations across scales. Direct comparisons should only be performed at corresponding levels. In the forward approach, process-level observations ("system components", e.g., root biomass, soil organic-matter pools, temperature sensitivities of those) are put together in a model that predicts the behavior at the whole (eco-)system level. These predictions can then be compared to direct observations at the ecosystem level. In the inverse approach, model parameters at the process level are inferred from ecosystem-level observations, such that the model reaches a maximal consistency with the observation. Inferred parameters can then be confronted with theoretical expectations at the process level.

Table 3 summarizes ecosystem processes across scales which importantly contribute to the overall soil respiration. For being able to explain as much observed phenomena across scales as possible, we propose to build and constrain a landscape-scale model of soil C dynamics by using as much information as possible from observations at different scales (Fig. 7). Observations in clay aggregates in conjunction with rhizosphere studies will increase our understanding about temperature and moisture dependencies of dynamics of microbes, biochemical kinetics of C decomposition, and autotrophic root respiration. This leads to a first dynamic process model operating on spatial and temporal fine scales.

At the pedon scale, many of the required variables are not observable anymore. Instead, a scaling model has to predict the quantities emerging of reaction surface area, moisture, and temperature at which the underlying biochemical reactions take place. Since representation of environmental conditions, which occur at the aggregate level, is not known a priori at the pedon scale, parameters have to be re-estimated at this scale. Parameters for both scaling and condition representation can be obtained by inverse modeling (see above) of the enhanced process model against measurements of soil respiration and C profiles. At the same time, the temporal coverage of this scale might be higher, thus temporal variability from day-to-day to interannual are represented by such reparameterization. In addition to scaling the reaction area and representation of environmental conditions, there are processes at the pedon scale which are not observable at fine scale, e.g., cracking higher organic structures or spatial replacement of organic material (OM) by macrofauna (rain worms etc.). These processes might be represented separately in the pedon-scale model, and kinetic-related parameters have to be retrieved in a classical way. On the other hand, such processes could act as intermediate steps in the decomposition of products (OM) to educts (CO₂ and H₂O). This would either change the whole kinetics approach or just modifies the parameters derived at aggregate level. In the latter case, the Bayesian inference is preferred again for parameter retrieval. Effects of aboveground productivity on soil respiration mediated through root exudation could be also

Table 3: Processes, heterogeneity, and observables of soil respiration at different scales. Processes occurring at lower scales are also represented by observations at larger scales, also when not repeated in related table rows.

<table>
<thead>
<tr>
<th>Spatial scale</th>
<th>Temporal scale—affected organics compounds</th>
<th>Process</th>
<th>Represented heterogeneity</th>
<th>Observable</th>
</tr>
</thead>
<tbody>
<tr>
<td>Laboratory and partly sub-pedon (process level)</td>
<td>seconds to days—high labile organic matter</td>
<td>respiration of roots, bacteria, and fungi; population dynamics of microbes</td>
<td>no</td>
<td>Soil CO₂ efflux, [C] change</td>
</tr>
<tr>
<td>Pedon (ecosystem level)</td>
<td>days to years—medium labile compounds</td>
<td>root exudation, i.e., productivity effects, aboveground autotrophic respiration, catalytic effects of meso- and macrofauna and their respiration</td>
<td>vertical distribution of organic matter and abiotic factors</td>
<td>soil respiration, mean [C] change, C profile</td>
</tr>
<tr>
<td>Plot and landscape (ecosystem level)</td>
<td>years to millennia—ore stable compounds</td>
<td>turnover of less labile organic matter</td>
<td>horizontal distribution of organic matter, macrofauna, and environmental abiotic conditions</td>
<td>spatial details of C storage, humus forms</td>
</tr>
</tbody>
</table>
clarified at this scale if whole-ecosystem (e.g., eddy covariance) flux measurements were available.

Finally, pedon-scale conditions have not necessarily to be representative at landscape scale (between-site variability). In addition, environmental conditions like soil moisture and temperature vary even more than at the pedon scale and also with time because of variable soil properties and microrelief. Thus, parameters for the prediction of the product of surface area, moisture, and temperature, as well as process parameters should be re-estimated by using observations like spatial details of total C storage or humus forms, also via a Bayesian approach. The application of such ecosystem model representing dynamic vegetation and soil fauna at a landscape scale leads to spatial details of soil C content and dynamic ecosystem properties, that are to be evaluated by independent estimates from data-oriented upscaling. In doing so, different locations for model development and validation have to be chosen.

### 5 Conclusion

Soil respiration at ecosystem scale is the result of various processes occurring across orders of magnitudes in the spatiotemporal domain. Since most of the responsible species are not known, a holistic representation of metabolic activity of roots and microorganisms seems to be appropriate at the finest scale of clay aggregates. Careful experiments at this scale are pivotal to the parameterization of a dynamic process model of autotrophic and heterotrophic respiration. Observations at pedon scale (chamber measurements, C profile) and at landscape scale (C-storage maps) are important to include processes at larger scales and to account for scaling effects. In doing so, the information gained at lower scales is utilized at higher ones by applying the Bayesian approach.

### References


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