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Citation Classic commentary

A tale of two theories: a chronosequence and a bioindicator of soil quality

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ABSTRACT

In this Citation Classics commentary, we reflect upon a paper that we published in *Soil Biology & Biochemistry* in 1995 and that provided a critical assessment of the use of the microbial metabolic quotient (qCO_2 , or the ratio of microbial respiration to biomass) as a bioindicator of soil quality. This quotient is based on Eugene Odum's 'Theory of Ecosystem Succession' published in 1969 and has been widely used in soil ecology for over 30 years; a higher qCO_2 value is reflective of greater energetic inefficiency of the soil microbial biomass. At the time of our study a strong demand was emerging for easily measured soil quality bioindicators and qCO_2 was an obvious candidate. In our paper we drew on the plant ecological strategy theory of J. Philip Grime by highlighting that, in addition to the two major types of ecosystem identified in Odum's theory ('disturbed' and 'developed'), there is a third type, 'stressed' that is characterized by persistently harsh conditions (e.g., nutrient poor, cold, dry). We measured qCO_2 for soils collected from along the Franz Josef Glacier chronosequence in New Zealand that spans 120,000 years and which includes all three types of ecosystems, going from disturbed to developed to stressed. We found that qCO_2 was least for the developed stage and was similarly high for the disturbed and stressed stages; it was not possible to discriminate between early successional stages characterized by high disturbance and high quality resource inputs from late successional stages characterized by substantial nutrient limitation and poor quality resource inputs. We further reanalyzed data from several publications from which qCO_2 could be calculated and these reinforced our empirical findings. Upon reflecting on our earlier work, we conclude that highly contrasting types of ecosystems that vary in their disturbance regime and stress cannot be arranged to any satisfaction along a unidimensional axis, and that no simple, unidimensional bioindicator (including qCO_2) is capable of adequately summarizing variation of soil quality among ecosystems. However, we also emphasize that despite its limitations as a bioindicator of soil quality,

the qCO_2 concept has proven to be highly useful for advancing conceptual understanding of the functioning of the soil microbial community and its contribution to ecosystem processes.

1. Introduction

Over the past three decades there has been much focus on understanding ecosystem ‘health’, and a key element of this has been an emphasis on the construction of easily measured bioindicators of ‘soil quality’. This has been of particular interest in agricultural systems which are focused on maintaining soil fertility and agricultural production (Kibblewhite et al., 2008, Ghani et al. 2013), and in ecological restoration activities which are aimed at the recovery of communities and ecosystem processes impacted by human activities (Kardol and Wardle, 2010). There has been considerable discussion on the value of bioindicators of soil quality, and several commentaries over the past four decades have strongly endorsed the concept (e.g., Sims et al. 1977; Doran and Zeiss, 2000; Karlen et al., 2003; Ritz et al., 2009; Stone et al., 2016). Furthermore, there has been a recent resurgence of interest in soil quality indicators as governments and policy makers have become more aware of the need to manage soil sustainably and counter soil degradation (FAO, 2015). However, the use of soil quality indicators has also attracted scrutiny (Bastida et al., 2008) and even some significant criticism (Sojka and Upchurch 1999), on the grounds that many bioindicators are too simplistic to represent the complexity of real ecosystems, and because the link between the bioindicator and the performance of the system (e.g., in terms of soil fertility, sustainable production, or community and ecosystem functioning) is often not apparent.

A landmark advance in understanding soil functioning occurred around 40 years ago through the development of an approach by Jenkinson and Powlson (1976) for the rapid and easy measurement of microbial biomass in soils. This (and other related) methodology has now been used in many

thousands of studies for illuminating how microbial processes relate to the functioning of terrestrial ecosystems worldwide (Jenkinson and Ladd, 1981; Wardle, 1992; Tate et al., 2017). While the microbial biomass *per se* has its limitations as a bioindicator (because biomass by itself does not inform on dynamics, turnover or functioning), it has formed the basis of two bioindicators that have enjoyed wide usage. First, the ratio of microbial biomass carbon (C) to organic C gives a measure of the quality of soil organic matter; when quality is higher a greater proportion of C is present in the microbial biomass (Insam and Domsch, 1988; Wardle, 1992). Second, the ratio of soil basal respiration to microbial biomass (hereafter ‘metabolic quotient’ or ‘ qCO_2 ’) indicates the inefficiency of the microbial biomass; when the microflora is less efficient a larger proportion of the C that it metabolizes is respired and lost as CO_2 as opposed to taken up by the biomass for tissue maintenance and growth (Anderson and Domsch 1985).

In this *Soil Biology & Biochemistry* ‘Citation Classic’ commentary, we focus on the second of these indicators, the qCO_2 , with particular reference to our publication on this topic from 23 years ago (Wardle and Ghani, 1995). Specifically, we discuss the theoretical construct for that paper, then describe its development and relevance for understanding the potential of qCO_2 as a bioindicator of soil quality, and finally outline the research directions that have since developed and the broader implications of the work.

2. Theoretical constructs

In our study (Wardle and Ghani 1995) we drew on two theoretical constructs developed in community and ecosystem ecology. The first of these has its roots in the classic Odum’s Theory of Ecosystem Development (Odum, 1969; 1985). In this theory, succession is regarded not just as a shift in plant community composition over time (which was the prevailing view of succession) but also as a process

that involves major shifts in the structure and function of the system, including community energetics, cycling of materials and overall homeostasis. A key element of this theory was the proposition that as succession proceeds and ecosystem development occurs, the ecosystem becomes more energy-efficient and the proportion of C metabolized by organisms that is respired (and thus lost from the ecosystem) should decline. This rationale was applied to soil microbial communities by Anderson and Domsch (1985; 2010), who used the ratio of soil basal respiration to microbial biomass as a measure of microbial efficiency; a microbial community that is less efficient should have a higher rate of respiration per unit biomass. This ratio (i.e., qCO_2) was shown empirically by Insam and Haselwandter (1989) to decline during primary succession over 200 years following glacial retreat in each of two chronosequences, as well as during revegetation, in line with the predictions from Odum's theory.

Odum's theory, and the interpretation of qCO_2 based on that theory, recognizes two types of widely contrasting ecosystems: (i) developmental or recently disturbed ecosystem that occur early in succession; and (ii) developed or mature ecosystems that occur later in succession. In our study we drew on a second theoretical construct, which suggests there are actually three broadly contrasting types of ecosystems, based on the plant strategy theory developed for plant ecology by Grime (1977, 1979). Grime's theory proposed that there are three major plant strategies: (i) 'ruderal' (i.e., plants adapted for recently disturbed ecosystems); (ii) 'competitive' (i.e., plants adapted for developed ecosystems); and (iii) 'stress-tolerant' (i.e., plants adapted for stressed ecosystems, such as nutrient poor, cold, or dry). As such, Grime's theory is suggestive of three broadly distinct ecosystems, not just two. While unidimensional bioindicators such as qCO_2 can distinguish between disturbed and developed ecosystems, there are serious challenges in using a unidimensional variable to distinguish between three distinct types of ecosystems, especially when they are equally dissimilar. The questions which therefore emerge (and which interested us) are whether and how unidimensional bioindicators

can distinguish among the three types of ecosystems to any level of satisfaction and whether these indicators are useful measures of soil quality and ecosystem performance.

3. Research background and thinking

The research underpinning our study was conducted in the early 1990s when we were both junior research scientists at AgResearch, a New Zealand government research institute that is focused on pastoral agricultural research. Our study was not part of the main research programs that we were funded to work within, but we thought it addressed an interesting topic that merited attention, especially given the growing interest at that time in using easily measured microbial variables as bioindicators of soil quality. Because the study was not expensive or particularly time-consuming to perform, we managed to fit it all around the edges of our core assigned research tasks.

We were interested in how qCO_2 varied across the three types of ecosystems and this required a study system in which these three types were represented. Most chronosequences that had been characterized at the time of our study were comparatively short term (a few hundred years) and therefore contained only the ‘disturbed’ and ‘developed’ stages. However, Odum (1969) noted the possibility of a third stage and asked: *‘The intriguing question is, do mature ecosystems age, as organisms do? In other words, after a long period of relative stability.....do ecosystems again develop unbalanced metabolism....?’*. We both knew through our training in the Department of Soil Science at Lincoln University in New Zealand in the 1980s (DAW took his undergraduate soil science course while at Canterbury University, and AG completed his PhD there) about work by the legendary Professor T. W. (Tom) Walker and his colleagues from that department on a very long term chronosequence that resulted from the progressive retreat of the Franz Josef Glacier (located in the south-west of the South Island of New Zealand) and that spans >100,000 years (Stevens and Walker

1970; Walker and Syers, 1976) (Fig. 1). This chronosequence runs for long enough to include not just the 'disturbed' and 'developed' phases, but also a long subsequent decline or 'stressed' phase, in line with the third stage that Odum proposed. This long term decline results from increasing nutrient limitation over millennial timescales due to significant loss of soil phosphorus through weathering and leaching, as well as conversion of the remaining soil phosphorus to increasingly unavailable forms (Walker and Syers, 1976).

We collected soil samples from along this gradient and measured microbial biomass, the ratio of microbial C to total C, and qCO_2 (Fig. 1). We found that the microbial biomass peaked at the intermediate ('developed') stages of the chronosequence in parallel with vegetation biomass, while the ratio of microbial C to total C generally declined across the chronosequence, indicative of poorer quality organic matter (and presumably poorer quality litter inputs) as the chronosequence proceeded. Meanwhile, qCO_2 was least for the intermediate ('developed') stages and much greater for both the early 'disturbed' and late 'stressed' stages, and qCO_2 was unable to distinguish between the disturbed and stressed stages (Fig. 1). We concluded that this creates a significant problem with regard to the use of qCO_2 as a bioindicator because similarly high values were obtained for two vastly different types of ecosystems: (i) very early successional ones characterized by heavy disturbance and with high quality resource inputs; and (ii) very late successional ones that have not been subjected to major disturbances for thousands of years and are characterized by substantial nutrient limitation and poor quality litter inputs. This means that, disturbed and stressed conditions promote similar levels of inefficiency of C use by the microbial biomass, but for very different reasons.

The question remained as to whether the results we found were specific to the Franz Josef chronosequence or if were they more generalizable. To test this, we analysed data presented in three previously published papers to show that qCO_2 does not predictably decline during succession, and performed analyses for each of 24 published papers to show that qCO_2 often increases in tandem with

soil abiotic properties that are indicative of inherent ‘stress’ (e.g., low nutrients, low pH) rather than ‘disturbance’. We further showed through analyses of 16 published papers that some disturbances, such as following fertilizer and lime addition, are able to either increase or decrease qCO_2 values depending on whether the disturbance alleviates stress (reducing qCO_2) or is more severe than the stress it alleviates (promoting qCO_2). These analyses of literature data reinforced what we found for the Franz Josef chronosequence data, which is that qCO_2 is unable to discriminate between ecosystems that are disturbed and those that are stressed.

4. Subsequent directions and broader implications

Our study was conducted at a period which there was a strong and often uncritical advocacy for the use of simple unidimensional bioindicators of soil quality (e.g., Doran and Parkin; 1994; Karlen et al., 1997; Sims et al., 1997; but see Sojka and Upchurch, 1999), especially in agriculture. The microbial metabolic quotient (qCO_2) has been described as the ‘most straight-forward’ (Bastida et al. 2008) and ‘perhaps the most popular’ (Gil-Sotres et al. 2005) of these indicators, but as we have shown and has since been recognized by others (Gil-Sotres et al. 2005), there are significant limitations to its usefulness for this purpose. Firstly, it is difficult, and probably impossible, for any single unidimensional index to adequately discriminate among vastly different types of ecosystems (such as among stressed versus disturbed systems) because a group of widely contrasting ecosystems cannot be satisfactorily placed along a unidimensional axis (Fig. 2). Secondly, unidimensional bioindicators usually do not serve as good predictors of measures of ecosystem performance or sustainability, despite this being a supposedly key goal for indicators of soil quality. For example, it is impossible without additional information to predict whether an ecosystem that has a high qCO_2 will or will not be more productive, have a greater rate of nutrient supply from the soil, sustain high crop or livestock

yields over a longer period, or will be closer to some final goal of ecosystem restoration, when compared with an ecosystem with a low qCO_2 . The same is probably true for all unidimensional bioindicators of soil quality. We therefore posit that there is no ‘silver bullet’ for assessing soil quality based on a single and simple biological measure, and suggest that the best way forward in the quest to develop meaningful bioindicators is to adopt a multidimensional approach that includes the assessment of a spectrum of functionally important soil properties that collectively contribute to sustaining ecosystem functioning and performance (Bastida et al., 2008).

We emphasize at this point that despite querying its indiscriminate use as a bioindicator, we absolutely do not eschew the use of qCO_2 for addressing appropriate ecological questions, and maintain that there are several instances in which it has yielded useful and interesting insights about the functioning of microbial communities and terrestrial ecosystems. As such, many hundreds of studies have now used qCO_2 for addressing a range of scientific questions. For example, some recent studies have used qCO_2 to reveal strong links between microbial metabolism and the stoichiometry of both plant litter (Spohn, 2015) and the microbes themselves (Hartman and Richardson, 2013). Others have used qCO_2 to inform on how the types of plant species growing in a community may influence the energy use efficiency of the soil microbial community, both in the soil itself (Strecker et al., 2016) and in decomposing leaf litter (Makita and Fujii, 2015). Further, measures of qCO_2 in conjunction with other measures have been used to understand how microbial functioning may be impacted by global change phenomena such as CO_2 enrichment and climate warming (e.g., Luan et al. 2014). As such, despite its limitations as a bioindicator, there are many examples of where measures of qCO_2 has been successfully employed, often in conjunction with other variables, to advance our conceptual understanding of how microbial metabolism and microbially driven processes link to the functioning of terrestrial ecosystems.

The work that we conducted on the Franz Josef chronosequence represents one of the early studies on ‘retrogressive’ chronosequences, i.e., chronosequences that span at least several thousand years and that extend long enough to include not just a build-up (disturbed) and maximal biomass (developed) phase but also a ‘retrogressive’ (decline or stressed) phase (Fig. 1). This retrogressive phase is caused by the long-term decline in nutrient (notably phosphorus) availability and thus plant biomass and largely as a consequence of pedogenic processes. Our understanding of ecosystem retrogression has grown considerably over the 23 years since we published our study, and a number of such chronosequences, that extend long enough for retrogression to occur have now been identified globally, including in boreal (Sweden, Alaska), temperate (Arizona, New Zealand), subtropical (Hawaii, northeast Australia) and Mediterranean (western Australia) regions (Vitousek, 2004; Wardle et al., 2004; Peltzer et al., 2010; Laliberté et al., 2012, 2017). These are all characterized by a strong decline in vegetation biomass and stature that takes place after a few thousand years as nutrient availability diminishes (Fig. 1). Despite these chronosequences experiencing highly contrasting climates and parent materials, we now know that many commonalities occur across them as retrogression proceeds for a variety of aboveground and belowground variables, which include the structure, functioning and metabolic efficiencies of soil microbial communities (Wardle et al., 2004; Peltzer et al., 2010; Laliberté et al., 2017).

We make one final observation about this Citation Classic. As we note above, the underpinning research for this paper was not part of our ‘core’ work at the time, and we had no formal funding associated with it. Yet it has been cited >1.5 times more than any research publication that either of us has produced directly from a formally funded project grant or contract. This, along with many other examples, highlights that the research that is likely to have the greatest impact and applicability is frequently not that which is highly rated and specifically targeted for funding by government research councils or foundations, or by administrators, but is that which the investigators themselves genuinely

believe is interesting and worthy of pursuit. This is in line with recent calls, unfortunately seldom recognized at the decision-making level in many countries, that the delivery of the most important and useful science is most likely to result through funding people, rather than by funding projects through competitive grants schemes (Ioannidis, 2011; Germain, 2015).

5. Conclusions

We identify three important messages from our original study and what it set out to achieve. Firstly, the body of theory developed in the general area of ecology has a tremendous amount to offer to our understanding of soil organisms and processes (Wardle and Giller, 1996). As such, the qCO_2 concept as proposed by Anderson and Domsch (1985) draws heavily of Odum's Theory of Ecosystem Succession (Odum, 1969), and we have been able to further develop on its interpretation though drawing on the ecological strategy theory developed by Grime (1977, 1979). Secondly, highly contrasting types of ecosystems that vary in their disturbance regime and stress cannot be arranged along an unidimensional axis, and we conclude that no simple, unidimensional bioindicator is capable of adequately summarizing variation of soil quality or ecosystem health among ecosystems (Fig. 2). Thirdly, despite its limitations as a bioindicator, the qCO_2 concept has proven to be a very useful measure that has stood the test of time for advancing conceptual understanding of the functioning of the soil microbial community and its contribution to ecosystem functioning.

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Figure legends

Figure 1. (A) Stages along the Franz Josef Glacier chronosequence caused by retreat of the glacier over a millennial timescale, representing ‘disturbed’, ‘developed’ and ‘stressed’ stages. (B) Changes in tree biomass and nutrients across the sequence. (C) Changes in soil microbial properties across the sequence; note that the microbial metabolic quotient (qCO_2) is equivalent in the ‘disturbed’ and ‘stressed’ stages despite large ecological differences between them. C, N, P = carbon, nitrogen, phosphorus.

Figure 2. Why unidimensional bioindicators of soil quality have limitations for comparing ecosystems. The triangle, which is based on the triangular model of Grime (1977, 1979) recognizes that ecosystems (represented by crosses) vary in the degree that they are disturbed, stressed and developed (as represented by the three corners of the triangle). Because ecosystems are arranged in this scheme in more than one dimension and because the three corners of the triangle are equidistant from one another, no single unidimensional bioindicator can discriminate adequately between all three ecosystem types. As such, qCO_2 is equally maximized in both highly disturbed and highly stressed ecosystems (as indicated by the arrows), despite vast functional differences between the two types of ecosystems.

Figure 1.

Figure 2.