Trade-offs in soil microbial functions and soil health in agroecosystems

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Opinion

Trade-offs in soil microbial functions and soil health in agroecosystems

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Soil microbial communities play pivotal roles in maintaining soil health in agroecosystems. However, how the delivery of multiple microbial functions in agroecosystems is maintained remains poorly understood. This may put us at risk of incurring unexpected trade-offs between soil functions. We elucidate how interactions between soil microbes can lead to trade-offs in the functioning of agricultural soils. Interactions within soil microbial communities can result in not only positive but also neutral and negative relationships among soil functions. Altering soil conditions through soil health-improving agricultural management can alleviate these functional trade-offs by promoting the diversity and interrelationships of soil microbes, which can help to achieve more productive and sustainable agroecosystems.

Highlights

Trade-offs between soil functions hamper maximizing soil multifunctionality in agroecosystems.

Taking soil microbial functional trade-offs into consideration in agricultural management is crucial for optimizing the impacts of changes in soil microbial communities on soil health in agroecosystems.

Interactions within soil microbial communities influence functional trade-offs.

Manipulating soil microbial diversity and interactions through soil health-improving management can alleviate functional trade-offs and improve soil health and agricultural sustainability.

Better mechanistic understanding of the interdependencies between soil-induced functions is essential to improve soil health and agricultural sustainability.

Soil health

Soil is a vital component of the Earth's biosphere because it provides myriad ecosystem functions that are essential for supporting life. Soil also forms the basis of agriculture and provides a multitude of services that benefit society. Increasing agricultural productivity on existing land is among the top-priority goals in agroecosystems [1]. However, maintaining soil health has long been ignored, and has only recently received broader consideration when facing major issues such as global food security, climate change, carbon (C) neutrality, and environmental degradation [2].

In this Opinion we define soil health as the continued capacity of soil to perform multiple functions that sustain crop productivity, mitigate environmental issues, improve nutrient cycling, and promote plant, animal, and human health [3,4]. A comprehensive understanding of how to maintain soil health, and at the same time optimize agricultural productivity and other essential functions, is of great importance for sustainable agriculture [2]. However, the mechanisms behind the maintenance of multiple functions for soil health in agroecosystems remain poorly understood. This lack of knowledge hinders our ability to accurately assess the multifunctionality of soil and our ability to manage agroecosystems in a sustainable way.

Soil microbes and soil health-related functions

A wealth of studies have demonstrated that soil microbes play a fundamental role in maintaining the multiple soil functions (e.g., nutrient cycling, primary productivity, decomposition of plant input, and climate regulation) that are closely related to soil health [4,5]. In the field of soil health, advancing soil multifunctionality by promoting soil microbial diversity has become a primary goal [6,7]. So far, most efforts have been made towards understanding the relationship between soil microbial diversity and ecosystem functions [8,9], but often overlook the fact that soil microbial functions [e.g., plant growth, nitrogen (N) fixation, and C sequestration] are interrelated in

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complex ways. Such relationships can fundamentally influence the delivery of multifunctionality and even threaten the stability of entire agroecosystems [10,11]. Therefore, maximum soil microbial multifunctionality is often not achieved in agroecosystems. A lack of understanding of the mechanisms behind the intricate relationships between soil microbes and their associated functions hampers our capacity to steer microbial communities towards optimizing multiple ecosystem functions simultaneously.

Trade-offs between soil microbial functions

Soils harbor a remarkable taxonomic and functional diversity of interacting microbes, including fungi, bacteria, and protozoa [12]. Together these contribute to a broad spectrum of ecological functions, including nutrient cycling, organic matter decomposition, as well as symbiotic and pathogenic interactions with plants [13]. Given that microbes are drivers of multiple key ecosystem functions, their interactions can also affect these functions [14]. The provision of multiple functions depends not only on the abundance and composition of the soil microbial communities but also on the interactions between soil microbes [13,14]. Soil microbial communities can form complex interconnected microbial networks [15,16] in which microbes can engage in a range of interactions such as competition, facilitation, predation and parasitism (Table S1 in the supplemental information online). To comprehensively understand the involvement of soil microbes in multiple functions, it is therefore important not only to consider when soil microbes are linked to a specific function but also to investigate how the multitude of interactions between these microbes collectively drive multiple functions simultaneously (Figure 1).

Interactions between soil microbes are manifold. An example of such interactions involves the competition between soil-borne pathogens and other microbes. Several microbes (e.g., *Pseudomonas*, *Trichoderma*) exhibit antagonistic activity against fungal pathogens via the production of antimicrobial compounds [17,18], thereby promoting crop growth. In addition, **arbuscular mycorrhizal (AM) fungi** (see Glossary) can impede the activity of microbial decomposers by competing for soil nutrients, including C, or by producing secondary metabolites [19,20], thus decreasing the rate of litter decomposition. Interestingly, from a human perspective, this negative interaction between AM fungi and decomposers leads to a positive relationship between two soil-derived functions – plant production and soil organic carbon (SOC) sequestration (Figure 1).

There is also substantial evidence of facilitative interactions between soil microbes, such as those between AM fungi and **mycorrhizal helper bacteria (MHB)** (e.g., *Bacillus* and *Pseudomonas*), as well as with N-fixing bacteria such as *Rhizobium*. For instance, MHB can support AM fungal establishment and functioning by (i) promoting AM fungi spore germination, (ii) modifying root architecture to facilitate fungal entry into the host root, and (iii) enhancing AM hyphal growth by solubilizing phosphorus (P) [21,22]. These facilitative interactions can thereby improve the utilization of resources by the host plant (e.g., the availability of soil P) and ultimately promote the growth of the host [23]. However, on the other hand, such facilitative interactions can also enhance the decomposition of organic C in the soil, which then results in a negative relationship between plant production and SOC sequestration [24].

Although recent studies have shown that it is possible for a soil to deliver a range of functions simultaneously [7], we argue that the pervasive existence of functional trade-offs (where the increase in one or more functions is coupled to an unexpected or undesirable decline in another function) in the soil (Table S2 in the supplemental information online) presents a significant challenge for maximizing soil multifunctionality [10,25] (Figure 1).

Glossary

Arbuscular mycorrhizal fungi (AM fungi): a key group of root-associated mutualists that establish relationships with >80% of terrestrial plant species. AM fungi penetrate the cortical cells of the roots of a vascular plant to form arbuscules. This is essentially a nutritional symbiotic relationship where nutrients [phosphorus (P) and others] are exchanged with plant hosts for plant-assimilated carbon (C; i.e., sugar and lipids). AM fungi play crucial roles within ecosystems, encompassing nutrient cycling, modifying the soil environment, and influencing interactions between plants and other soil biota.

Cover crop: the vegetation most commonly grown between periods of regular productions of the main crop plantings with the purpose of protecting the soil from erosion, improving soil productivity, health, and quality, and to some extent reducing weeds and pests.

Greenhouse gas (GHG) emissions: the release of gases (e.g., CO_2, CH_4, N_2O) into the Earth's atmosphere that have the capacity to trap heat, leading to the greenhouse effect and contributing to global warming and climate change. This phenomenon has profound effects on the Earth's climate, including more frequent and severe heatwaves, altered precipitation patterns, and disruptions to ecosystems.

Mycorrhizal helper bacteria (MHB): a group of microbes that establish symbiotic relationships with mycorrhizal fungi and play a crucial role in supporting the formation, function, and effectiveness of mycorrhizal associations between fungi and plant roots. These bacteria contribute to the mutualistic relationship by aiding nutrient cycling, enhancing plant growth and health, and promoting the establishment of mycorrhizal colonization.

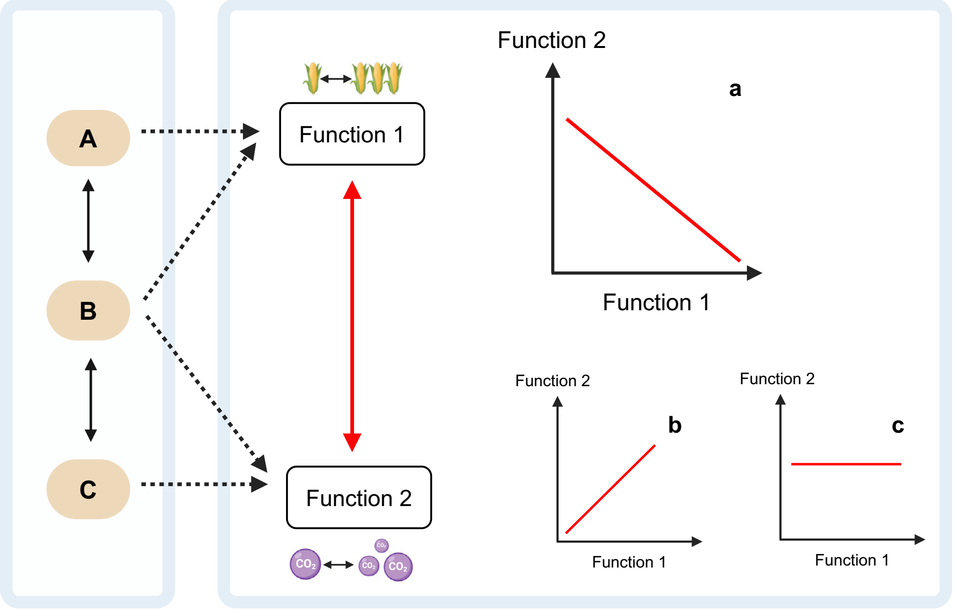

Figure 1. The intricate interplay between soil microbes influences multiple relationships between various soil microbial functions. Some ecosystem functions are provided by specific microbial functional groups, in the figure denoted as groups A and B, and function 1. For example, arbuscular mycorrhizal (AM) fungi (group B) and nitrogen (N)-fixing rhizobia bacteria (group A) complement each other in providing the plant with limiting nutrients [phosphorus (P) and N, respectively], thus supporting plant productivity. Microbial groups (group B in this example) also influence another function, here denoted as function 2 – soil organic carbon (SOC) sequestration. For instance, AM fungi (group B) can contribute to the stabilization of soil organic matter, while saprotrophic fungi (group C) can break down organic matter. Because several microbial groups influence multiple functions, changes in the interactions between these groups, in this case AM fungi and saprotrophic fungi, can lead to alterations in the relationships between soil microbial functions, including (a) negative relationships/trade-offs, (b) positive relationships/synergy, and (c) neutral relationships/ independence. A trade-off synergy refers to the increase in one soil function and simultaneous decline/rise of another function. Functions 1 and 2 represent distinct soil microbial functions. The black arrows indicate the interactions between different soil microbial groups. The black broken lines indicate the interactions between soil microbes and soil functions. The red unbroken line connecting the two soil functions represents the relationship. The three types of relationships are shown in the bivariate plots on the right. Figure created with BioRender.

Conventional agricultural practices and functional trade-offs

Traditionally, conventional agricultural practices such as inorganic fertilization, intensive soil tillage, and the application of pesticides are generously applied to meet the goal to increase plant productivity in agroecosystems. However, this frequently impacts on the diversity and functions of the soil microbial community [26–28]. Shifts in the diversity, structure, and activity of soil microbial communities as a result of changes in agricultural practices can result in a reduction in functioning or even the loss of an entire function. For instance, fertilization is an important management practice for maximizing plant productivity in agroecosystems. However, it can reduce the diversity and abundance of particular groups of soil microbes (e.g., AM fungi, N-fixing bacteria, and nitrifying bacteria), and this in turn strongly impedes soil microbial enzyme activities and a range of biogeochemical processes in the soil that are closely linked to functions, such as C storage, N retention, and regulation of P availability [29–32]. Several studies have also demonstrated that conventional tillage leads to a reduction in soil microbial alpha diversity and induces consistent shifts in composition (e.g., loss of keystone taxa which correlates with SOC accumulation rate) [26,33,34] which can consequently lead to a reduction in SOC stocks and increasing **greenhouse gas (GHG) emissions** [35].

In addition to these well-known impacts on soil microbial diversity, conventional agricultural practices can also change soil microbial co-occurrence networks [36]. Although soil microbial networks give limited insights into microbial interactions, they can be a valuable tool for providing complementary insights into community structure and assembly mechanisms, and can increase our understanding of the complexity of microbial communities [37,38]. Changes in soil microbial networks can alter the functions delivered by soil microbes, which can result in trade-offs between crop yield and the functions provided by soil microbes (e.g., N retention and SOC sequestration) or in the exacerbation of these trade-offs (paths I and III in Box 1). For example, in a

Box 1. Soil microbial interactions and soil functional trade-offs

We illustrate the different ways in which agricultural management-induced changes in soil microbial interactions can affect functional trade-offs supported with real examples. Figure I shows possible relationships between two functions, function 1 and function 2. The black unbroken line shows the initial relationship between the two functions. The starting status is point A. The arrows indicate the direction of changes in functional trade-offs. The red broken line illustrates the status of an exacerbated trade-off, whereas the green broken line illustrates the status of a reduced trade-off.

Path I

A change in soil microbial composition does not affect the functional trade-off but does affect the extent of trade-off. The implementation of particular agricultural practices improves soil microbial function 1 but impairs function 2. As a result, the extent of the trade-off changes from A to B, but the relationship itself does not change. For example, the application of pesticides improves crop yield by killing pathogenetic microbes, but impairs soil N cycling by eliminating nitrifiers [28].

Path II

The functional trade-off diminishes. The implementation of particular agricultural practices improves soil microbial function 1 and has a less negative or actually even a positive impact on function 2. As a result, the extent of the trade-off changes from A to C, thereby minimizing the functional trade-off (indicated by the green broken line). For example, introduction of a beneficial soil inoculum (e.g., AM fungi or N-fixing bacteria) improves plant productivity by enhancing plant N/P uptake, but also reduces nutrient loss, such as by nitrate leaching [63].

Path III

The functional trade-off increases. The implementation of some agricultural practices improves function 1 but impairs function 2, resulting in a stronger functional trade-off (indicated by the red broken line). As a result, the extent of the trade-off changes from A to D. This pattern is more common under intense soil management. For example, excess N fertilization can significantly improve plant productivity but strongly inhibits the role of soil microbes in nutrient cycling by reducing their abundance and network complexity, which ultimately results in reduced N mineralization [30].

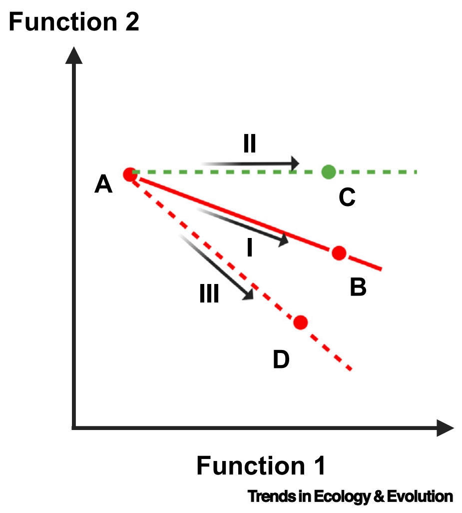

Figure I. Conceptual illustration of agricultural management-induced changes in soil microbial interactions that affect functional trade-offs. Figure created with BioRender.

mesocosm study, the application of synthetic pesticides decreased the complexity of the soil microbial network and the restructured community favored taxa that were less efficient at degrading organic compounds [39]. Long-term addition of excess N fertilizer can also simplify co-occurrence networks including bacteria and fungi by decreasing the number of connections between fungal and bacterial nodes, which in turn can affect processes of nutrient cycling and result in decreasing N retention [40]. Collectively, these studies suggest that conventional management-induced changes in soil microbial networks indeed can lead to functional trade-offs or exacerbate existing functional trade-offs (e.g., GHG emissions and N_2 fixation) (paths I and III in Box 1). Moreover, the conventional management-induced shift in soil microbial networks through changes in a multitude of soil microbial interactions can impede long-term functional resilience and exacerbate soil health in agroecosystems. Hence, there is a need for sustainable agricultural practices that, on the one hand, fulfill the increasing demand for plant productivity while on the other hand maintaining or even optimizing soil microbial functions to mitigate environmental impacts.

Minimizing the trade-offs between soil microbial functions in agroecosystems

To achieve healthy soils, agricultural practices that accomplish a balance between multiple ecosystem functions, in particular between yield and other functions, are urgently required. A growing number of studies have suggested that implementation of soil health-improving agricultural practices holds significant potential to maintain or even enhance plant production without reducing soil fertility, thus simultaneously improving soil health and ensuring environmental sustainability [7,31,41]. This can ultimately minimize the functional trade-offs and result in win–win outcomes [7,41] (Table 1).

Recent research has demonstrated that soil health-improving agricultural practices can optimize the diversity and activity of beneficial functional guilds in the soil and/or suppress microbes that have a detrimental effect on a particular function, ultimately promoting particular functions (Table 1). For instance, crop diversification, such as crop rotation or intercropping, can be a promising approach to enhance plant productivity while positively impacting on soil microbial communities [42]. An increase in the abundance of soil microbes, particularly beneficial microbes such as AM fungi and bacteria

Table 1. Examples of soil health-improving agricultural practices influencing soil microbial community structure, composition, and related functions

Agricultural practices	Effects on soil microbes	Potential mechanisms of affecting functional trade-offs	Refs
Bio-inoculants	Directly influence the structure and diversity of soil microbes by adding specific soil microbial guilds	Improve soil functional diversity by promoting targeted soil functions	[63,64]
Organic amendments	Increase soil microbial biomass Modify soil microbial composition Change soil nutrient cycling Reduce soil-borne diseases	Improve functional redundancy by promoting soil microbial diversity Enhance soil functions by promoting soil microbial abundance	[30,31]
Crop diversification	Changes soil microbial community structure Reduces the build-up of pathogens in soil Indirectly influences soil microbial community composition via changes in soil nutrient availability, soil structure, and water-holding capacity	Improves functional redundancy by promoting soil microbial diversity Enhances soil functions by promoting beneficial microbes	[41,65,66]
Conservation tillage	Promotes soil biodiversity by creating a more stable and supportive environment for soil microbes Modifies soil microbial activity by retaining more C in the soil	Improves functional redundancy by promoting soil microbial diversity and activity	[67,68].

associated with litter degradation, can contribute to enhancing SOC sequestration and reducing N leaching [43]. In addition, organic amendments can not only increase productivity but also at the same time benefit the abundance and activity of groups of soil organisms such as diazotrophs, which can result in enhanced biological N fixation, reduce N leaching, and increase N use [44]. Amendments may also enhance GHG emissions, depending on the type or quality of the organic amendment [45]. Optimizing the quality of organic amendments can therefore control CO_2 emissions while enhancing plant productivity via beneficial soil microbes [45].

While these examples demonstrate that soil health-improving agricultural practices can positively influence the diversity and activity of soil microbes and their associated functions, they do not evaluate how interactions between soil microbes are affected. Existing trade-offs between soil microbial functions need to be minimized to maximize multifunctionality (e.g., by enhancing plant productivity and increasing SOC sequestration simultaneously) (path II in Box 1). Soil health-improving agricultural practices may achieve this by either mitigating the negative interactions between soil microbes, thus positively promoting specific soil microbial groups while having minor or positive effects on other groups, or by promoting the stability in the soil microbial network as a whole. The latter component has been partly tested by recent studies that explored the impacts of soil health-improving agricultural practices on the properties of soil microbial networks. For example, crop diversification can increase the strengths of soil microbial networks and promote a more elaborate network structure by modifying antagonistic and facilitative trophic interactions between different microbes [46,47]. In addition, recent studies have shown that the link between soil biodiversity and ecosystem functioning is highly dependent on the associations between soil microbes [9,48,49]. However, compared to the well-known impacts of soil health-improving agricultural practices on soil microbial diversity and activity, the underlying mechanisms of these practices in regulating the interactions between soil microbes and ultimately on achieving multifunctionality in agroecosystems remain elusive.

Beyond eliminating some of the trade-offs between individual functions, some of the aforementioned practices can also stimulate functional redundancy [50,51]. Soil health-improving management practices can promote the functional redundancy of soil microbial communities not only by promoting soil biodiversity but also by enhancing microbial co-occurrence network complexity (Table 1). For example, a recent study conducted in a vegetable field showed that organic fertilization with partial substitutions (25–50%) of chemical N fertilizer enhanced soil bacterial and fungal diversity and interactions, which in turn promoted enzyme activities involved in C, N, and P cycling [51]. This will likely improve the stability and resilience of agroecosystems. Nevertheless, increasing soil biodiversity via agricultural practices can lead to unexpected changes in the functional structure of soil microbial communities. For instance, a recent study demonstrated that anthropogenic perturbation reduces the relative abundance of beneficial soil microbes while increasing the prevalence of potential fungal pathogens, and consequently did not necessarily promote ecosystem functioning [52]. It is therefore important to focus on functions of soil microbial communities and their functional trade-offs rather than merely striving to increase soil microbial diversity. Taken together, implementing soil health-improving practices can be a promising approach to alleviate functional trade-offs, achieve multifunctionality, and attain higher resilience in agroecosystems.

Concluding remarks and future perspectives

The past years have witnessed a surge of interest related to the enormous potential of soil microbes and their importance for plant productivity and sustainability in agroecosystems. However, the complex interactions between soil microbes and our limited knowledge of the mechanisms that enable the simultaneous provision of multiple soil functions constrain the

Outstanding questions

What are the elusive mechanisms governing the intricate interactions between soil microbial communities?

To what extent can soil health-improving management alleviate functional trade-offs and improve the interconnectivity of the soil microbial community?

How is the relationship between the soil microbial community and ecosystem functions altered by agricultural practices?

Can we optimize agricultural management practices to promote a multifunctional agroecosystem?

How do trade-offs between soil microbial functions vary over time in response to agricultural practices?

How do changes in interactions between soil microbes and invertebrates caused by changes in agricultural practices affect soil multifunctionality and soil health?

practical application of soil microbes in sustainable agriculture. Taking soil microbial functional trade-offs into consideration in agricultural management is crucial for optimizing the impacts of soil microbes on soil health in agroecosystems. Optimizing current agricultural management practices, such as the use of organic amendments and **cover crops**, can be helpful to minimize the trade-offs by promoting the diversity and associations of soil microbes. This opens up exciting possibilities for the development of more productive and sustainable agroecosystems.

We propose six themes for future research on mediating functional trade-offs and optimizing the effects of soil microbes on soil health in agroecosystems. First, there is an urgent need to better understand the elusive mechanisms governing the intricate interactions between soil microbial communities. Extensive studies have focused on pairwise interactions between microbes or microbial groups under controlled conditions, but the multiple interactions that occur simultaneously in microbial communities in real ecosystems remain greatly understudied [14,17]. Such knowledge, however, can greatly contribute to the development of a holistic understanding of microbial functions in complex environments and will provide a scientific basis for predicting and managing the multifunctionality of soil microbes [13,53].

Second, a systematic and quantitative assessment of how agricultural management influences the relationships between soil microbial functions is largely missing and we lack a broader understanding of when agricultural practices are capable of sustaining multiple soil functions and crop yield simultaneously [7,54].

Third, microbiome management through soil health-improving agricultural practices can have negative effects on functional trade-offs [55]. For example, the use of AM fungal inoculation can enhance plant growth and reduce nutrient loss, but alien AM fungi can negatively affect native AM fungi [56]. The addition of organic amendments can promote soil CH_4 emissions while simultaneously reducing soil N_2O emissions [57]. Therefore, the consequences of soil health-improving agricultural practices need to be carefully examined, particularly in long-term experiments.

Fourth, attaining win–wins for crop productivity and soil health via switching from conventional to soil health-improving management can be hampered by shifts in soil microbial activity in the face of a changing climate [58]. Understanding how management decisions influence the activity of the soil community and the associated changes in ecosystem functioning in a changing climate with extreme events such as droughts and flooding will be crucial to identify suitable practices and develop 'climate-smart' management [59].

Fifth, achieving a more sustainable development pathway that involves managing trade-offs in a multitude of functions is also promising for tackling the major challenges in agriculture, such as GHG emissions, water pollution, and biodiversity loss [56,60].

Last but not least, the functional trade-offs discussed here occur in current soil and climate conditions. It remains unknown how functional trade-offs will vary in response to anthropogenic disturbances, climatic changes, and over longer time-periods. Considering the rapid turnover rates of soil microbial communities [61] and the importance of long-term land-use information in interpreting soil biodiversity data [62], investigating changes in functional trade-offs over extended periods will yield important insights for the sustainable management of agroecosystems.

Overall, we argue that a deeper mechanistic understanding of trade-offs between soil microbial functions in agroecosystems will be an important advance for soil microbial ecology and for its application to sustainable agriculture (see Outstanding questions).

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Declaration of interests

The authors declare no conflicts of interests.

Supplemental information

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