Viewpoints

Mechanisms underpinning nonadditivity of global change factor effects in the plant–soil system

Summary

Plant–soil systems are key for understanding the effects of factors of global change. Recent work has highlighted the general importance of considering the simultaneous incidence of some factors or stressors. To help mechanistically dissect the possible interactions of such factors, we here propose three broad groups of mechanisms that may generally lead to nonadditivity of responses within a plant–soil system: direct factor interactions (that is one factor directly changing another), within-plant information processing and crosstalk, and effects of factors on groups of soil biota interacting with plants. Interactions are also possible within and across these groups. Factor interactions are very likely to be present in experiments, especially when dealing with an increasing number of factors. Identifying the nature of such interactions will be essential for understanding and predicting global change impacts on plants and soil.

Global change and nonadditivity of effects

Plants and their associated soil biota are key for understanding responses of ecosystems to global change (Heijden *et al.*, 2008; Wardle, 2013; Vries *et al.*, 2020). Global change is inherently a phenomenon that involves quite a range of different human-caused factors, including warming, drought, elevated atmospheric CO_2, nitrogen deposition, pesticides, microplastics, invasive species and many more (Rillig *et al.*, 2021); this means that terrestrial ecosystems are exposed to a wide range of simultaneously acting anthropogenic factors at any point in time (Côté *et al.*, 2016; Bowler *et al.*, 2020; Sage, 2020; Zhou *et al.*, 2020). This joint impact of many factors is a major research challenge, because when many factors act concurrently, this may lead to nonadditive responses or potentially unpredictable effects on plants and soils (Rillig *et al.*, 2019; Zandalinas *et al.*, 2021b).

When faced with the necessity to deal with a potentially large pool of human-caused factors, we need an in-depth understanding of how such nonadditive effects might arise in target systems. Here, we wish to address this issue, examining how effects of factors could

be modified by the presence of others, using the plant–soil system as a model. Such modifications could lead to nonadditivity of effect sizes; that is the effect size resulting from the combined action of factors cannot be obtained by simply adding up individual effect sizes.

Specifically, nonadditivity is the deviation from an additive null model of the combined effects of factors. Nonadditivity therefore causes the combined effect of factors to be either larger or smaller than the additive expectation, resulting in synergistic or antagonistic interactions, respectively (Folt *et al.*, 1999). However, these interactions between factors are more generally defined as deviations from any null model used to predict the combined effects of factors. Indeed, the multiplicative and dominance null models, as well as more complex models (typically originating in the field of ecotoxicology), can be superior predictive models when the underlying mechanisms of a specific system are understood (Schäfer & Piggott, 2018). Here, we take a more general approach – one that is a prerequisite for predictive models – by asking what types of mechanisms could generally lead to nonadditive effects of anthropogenic factors (depending on the research field, factors are also referred to as drivers or stressors; we consistently use 'factors' in this paper). Effects always have to be understood in relation to a particular response variable; in the plant–soil system being discussed here, this can be any parameter measured for plants, soil processes and properties and soil biota (e.g. decomposition, plant productivity or soil biodiversity). It is important to emphasise that nonadditivity might occur for one response variable, but not for another. Additionally, some null models may be more appropriate for some response variables than for others (e.g. if the response variable is bounded, such as mortality).

Three broad groups of mechanisms leading to nonadditivity in a plant–soil system

We distinguish three broad groups of mechanisms that may generally lead to nonadditivity within a plant–soil system (Fig. 1): direct factor interactions (i.e. one factor directly changing another), within-plant information processing and crosstalk, and effects on groups of soil biota interacting with plants. Even though in the following these groups of mechanisms are discussed separately, all of these mechanisms will be in operation concurrently and, therefore, the joint action of these mechanisms is another important aspect to consider.

Direct factor interactions

Direct factor interactions only consider the factors themselves, not the effects they may exert on any component within the plant–soil system (i.e. 'chain interactions'; Didham *et al.*, 2007). We offer five such interaction mechanisms, all soil borne, and involving
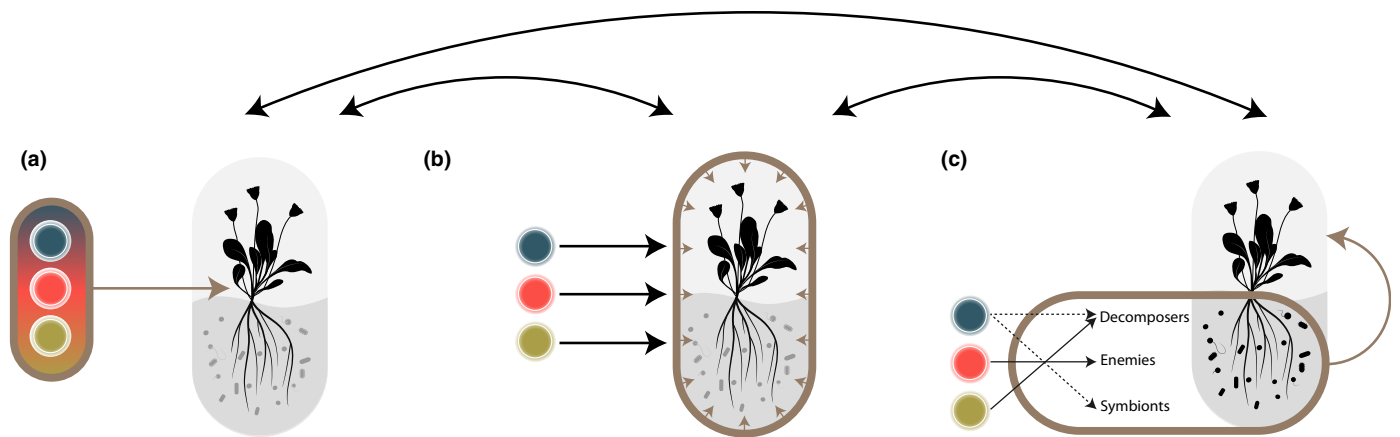
Fig. 1 Overview of the three groups of mechanisms that are potential sources of nonadditivity of factor effects in the plant–soil system. Three different coloured symbols represent three different factors (standing for a larger pool of factors) concurrently acting on the plant–soil system. The brown oval shape in each panel portrays the sphere of interaction of the factors. (a) Direct factor interaction; the factors themselves influence each other before they affect the target system. (b) Within-plant information processing and crosstalk; the integration of factors occurs within the plant. (c) Differential effects on soil biota that directly interact with the plant; factors differentially affect different functional groups of soil biota (decomposers, enemies, symbionts). The three groups of mechanisms can also interact with each other (arrows at the top of the figure), constituting an additional source of nonadditivity of responses. Responses can be any variable of interest in the plant–soil system; nonadditivity may be present for some but not all response variables.

chemical-based factors as one of the players. Several of these direct interactions could occur at the same time.

Concentration amplifiers Drought is probably the factor for which such direct interactions with other parameters are most widely appreciated (Vries *et al.*, 2020), as a decrease in water content can increase solute concentrations in the soil (causing osmotic stress), and potentially also render nutrients and other chemicals less available. It follows that drought can, therefore, at least increase the concentration of any dissolved chemical-based anthropogenic factors, such as organic pollutants.

Chemical/physical rate enhancer Temperature is a factor that pervasively acts on many chemical and physical process rates. As such, temperature can shift chemical reaction rates, chemical equilibria, solubility and almost all chemical processes. Physical processes can be affected by the temperature as well. For example, diffusion of chemicals inside microplastics is regulated mainly by the temperature, so temperature increase leads to a faster leaching of the additives or of nonintentionally added substances (Mercea *et al.*, 2018), therefore affecting chemical factors. An additional, closely related case could be the increase in temperature favouring the competitiveness of an invasive microbial species or invasive plant (in this case the favoured rate is one inside the invasive organism).

Solubility enhancer Surfactants are likely to be common in the environment (Kuhnt, 1993), especially in soils, as they are included in many formulations of chemicals, for example agrochemicals. Given their properties, they can increase solubility and transport of hydrophobic compounds (Haigh, 1996; Dollinger *et al.*, 2018). As half of the persistent organic pollutants of global concern listed in the Stockholm Convention are hydrophobic pesticides (Idowu *et al.*, 2013), surfactants can increase their solubility and transport through the soil.

Chemical modifier Different chemicals present in the soil solution at the same time could react with each other (European Chemicals Agency (EU body or agency), 2017), for example if they are acids and bases, or if they carry electrophilic and nucleophilic chemical groups; this could lead to the production of chemicals that are more or less toxic than the original substances. An additional form of interaction is that chemicals could compete for the same biochemical ligand (Kamo & Yokomizo, 2015). A further theoretical possibility is that an invasive microbe, representing a biotic global change component, could metabolise one of the chemical pollutants.

Concentration diluter Flooding can cause a range of effects, including decreasing oxygen availability and potentially an increased linking of microbial habitats within the soil, but it would also effectively dilute any chemical agent present in the soil.

Within-plant integration of factors

Plants integrate a range of external factors through different signal pathways, networks and hormones. This has been typically studied in pairs of environmental factors (Roeber *et al.*, 2021). The within-plant integration of a larger number of simultaneously acting factors (up to six) has recently been experimentally studied in the model plant *Arabidopsis thaliana* (Zandalinas *et al.*, 2021a,b), even though not all factors included in this experiment are related to global change. Whereas individual factors (high temperature, salt, high light, cadmium, acidity, and a herbicide) had only minimal effects, the combined application of several factors led to strong detrimental effects on plant performance and survival; that is the authors observed strong nonadditivity of effects.

Previous work on factor interactions revealed that the combination of stressors typically leads to unique transcripts, proteins or metabolites that only occur in the combination treatment. This was

also found in the multifactor interaction study, in which transcriptomic analyses showed that some of the responses caused by individual factors (including stress response pathways such as autophagy, osmoregulation or heat shock transcription factors) were not activated in the combined application of factors. By contrast, the number of transcripts specific to certain combinations of factors increased (Zandalinas *et al.*, 2021b). More work is necessary to mechanistically dissect the exact nature of factor integration when many factors act on a plant; but from this pioneering set of experiments it seems clear that plant internal integration of factors can be a major source of nonadditivity of responses in the plant–soil system.

Additional evidence for the existence of nonadditivity of factor effects in plants comes from the literature on resource limitation; several factors of global change are in fact changes of resources such as water, nitrogen, or carbon dioxide (Sage, 2020; Rillig *et al.*, 2021). Many studies have found co-limitation of plants by different such resources, leading to synergistic (i.e. nonadditive) effects with resource addition (Harpole *et al.*, 2011).

Soil biota-mediated effects

Soil is highly biodiversity-dense (Thakur *et al.*, 2020), and each organism will have an internal processing and reaction to global change factors and their combinations. However, for the sake of this discussion we divide organisms broadly by the kind of effect they have on the plant: mutualists, enemies and decomposers (Wardle, 2013; Putten *et al.*, 2016). Mutualists include mycorrhizal fungi, plant growth-promoting microbes, or nitrogen-fixing microbes; enemies include pathogens or root consumers; and decomposers encompass saprobes, whose collective effect on plants can be either positive (net mineralisation, i.e. making nutrients available to the plant) or negative (net immobilisation; that is nutrients are locked up in microbial biomass, and therefore not available to the plant).

Various factors will affect these microbial groups differently, in terms of overall abundance or community composition. An excellent example of guild-specific differences is the response of fungi to nitrogen and phosphorus inputs. Drawing on high-throughput sequencing results from 25 grasslands on four continents, using FUNGUILD to assign potential functions to fungal taxa (Nguyen *et al.*, 2016), it was found that fungal pathogens were consistently favoured by nutrient additions, mutualists (arbuscular mycorrhizal fungi) decreased, while relative abundance of decomposer fungi was not affected (Lekberg *et al.*, 2021). Similarly, the relative proportion of soil fungal plant pathogens is also expected to increase with increasing temperatures, as concluded from a global survey and experimental approach (Delgado-Baquerizo *et al.*, 2020). Therefore, factors such as these will lead to shifts within the three different soil biota groups and therefore overall differences in effects on plants (Marín & Kohout, 2021).

Another pathway towards shifts in the three functional groups is given by the possibility that invasive microbes, representing an important factor of global change, could belong to one of these functional groups, therefore directly affecting community composition, and potentially overall abundance and functioning. Data on microbial invasions in terrestrial ecosystems are heavily biased towards the observation of disease-causing fungi and bacteria (Thakur *et al.*, 2019) and, while saprobes and mutualists could also be invasive, much less information is available. Examples do exist from ectomycorrhizal fungi, in particular for those producing conspicuous fruiting bodies, for example *Amanita*, in which co-invasion of host and fungal mutualist is important (Wolfe *et al.*, 2010; Dickie *et al.*, 2016, 2017).

Integrating responses within and across the three levels

Having discussed these three broad mechanisms separately, it is important to emphasise that co-action is an additional important source of nonadditivity of responses within the plant–soil system.

Certainly, cross-reactions among mechanisms in the direct factor interaction category can occur. For example, as concentration plays a key role in surfactant action (solubility enhancers), concentration amplifiers such as drought can conceivably increase the effectiveness of surfactants as solubility enhancers. As another example, dilution can shift partition equilibria causing a faster release of the pollutants sorbed on particulates (Davis & Masten, 2021) such as soil (Smit *et al.*, 2008) or microplastic particles.

Similarly, as there is some overlap in resource use among the functional groups of soil biota, changes in one group could influence the community composition, abundance or functioning of another. One well known example is the 'Gadgil effect', an interguild fungal interaction between mycorrhizal fungi and decomposer fungi (Gadgil & Gadgil, 1971; Fernandez & Kennedy, 2016). Other examples are that members of one group (e.g. saprobes) favour processes conducted by another (e.g. mycorrhizal fungi), leading to increased plant performance such as nitrogen uptake (Hestrin *et al.*, 2019).

Crosstalk among the three levels, which we have separated here just for the purpose of structuring our discussion, are similarly highly plausible (Fig. 1). For example, direct factor interactions, having determined the level of available chemical stressors in the soil, for example, could then alter the plant internal processing to other factors affecting the plant, for example elevated atmospheric CO_2, UV radiation or the arrival of an invasive species competitor. Similarly, these direct (mostly) chemical-based factor interactions could also determine the level of a chemical stressor that affects the different functional groups of soil biota, in turn providing altered effects on the plant.

Conclusion and future perspectives

Our synthesis shows that there are indeed many possibilities for crosstalk among mechanisms and, therefore, for nonadditivity of responses to occur, even though we have certainly not captured all complexity within a plant–soil system. Therefore, it is unsurprising that factor interactions are often observed in experiments, especially when dealing with an increasing number of factors (Rillig *et al.*, 2019). However, it is possible that, in any given experiment, we may fail to observe nonadditivity because of a lack of statistical power. This can be brought about by high variability inherent to

soils (Ettema & Wardle, 2002) and low sample size, or also by small individual effect sizes of each factor, or a combination of these parameters. An additional important consideration is that the mechanisms leading to nonadditivity may cancel each other out partially or completely, resulting in a no net detectable factor interaction effect in experiments, unless the various mechanisms are included in the measurement campaign (hidden effects). This highlights how the practice of classifying results as either nonadditive or additive, or indeed as synergistic or antagonistic, and then comparing the frequencies of these classes (i.e. vote counting), does not enhance our mechanistic understanding of nonadditivity (Griffen *et al.*, 2016). Finally, system-internal buffering mechanisms through compensatory processes may lead to responses not being detectable at the system-level (Connell & Ghedini, 2015).

This approach of identifying the potential sources of nonadditivity has also been conducted for environmental factors in aquatic ecosystems. Analogous to the direct factor interactions occurring in the plant–soil system, the physicochemical interplay between environmental factors such as acidification and warming that occurs directly in the water before any biology is considered have been highlighted as key sources of nonadditivity (Boyd & Brown, 2015). Similarly, efforts have been made to outline the potential sources of nonadditivity between aquatic environmental drivers at different levels of biological organisation from individuals to ecosystems (Boyd & Brown, 2015; Kroeker *et al.*, 2017).

There are very few experiments addressing effects at very high factor dimensionality, with a systematic mapping of the literature revealing that over 98% of experimental studies addressing global change effects on soils deal with only one or two factors at a time (Rillig *et al.*, 2019). There are several reasons for this gap in knowledge (Rillig *et al.*, 2021), including fragmentation of the research area of global change (Orr *et al.*, 2020) and logistic challenges. Perhaps the most important reason is that the main tool to address such questions, the factorial experiment, fails to deliver because of the combinatorial explosion problem (Katzir *et al.*, 2019); this means that the number of treatment combinations rises rapidly with the number of factors considered. While our analysis here cannot solve this issue per se, it offers a way to better predict pairwise factor interactions based on an enhanced mechanistic understanding; this will eventually also be helpful in any approaches addressing the interplay of many simultaneously acting factors.

We carried out this analysis with individual plant–soil systems. Our hope is that future work will explicitly focus on mechanistically dissecting the various pathways leading to nonadditive responses to global change factors. Similar exercises should also be contemplated for other ecosystem types, and also for different scales, both spatial and temporal, and for different levels of ecological complexity (e.g. at the level of the plant community).

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Author contributions

MCR wrote the first draft of the manuscript, to which all coauthors added text and references. AL designed the figure.

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