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FE SPOTLIGHT

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Can we predict the long-term impact of earthworms on plant successions?

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The impact of earthworms on plants has been described in many studies (Brown, Edwards, & Brussaard, 2004; Scheu, 2003) and these studies largely announced the still developing field of below-ground–above-ground interactions (Hooper et al., 2000; Wardle et al., 2004). The mechanisms by which earthworms impact plant growth have mostly been identified (Brown et al., 2004; Scheu, 2003): (1) they improve soil structure, (2) increase mineralization, (3) help controlling herbivores and pathogens (Bertrand et al., 2015; Blouin et al., 2005), (4) trigger the release of plant growth regulating molecules (Puga-Freitas, Barot, Taconnat, Renou, & Blouin, 2012). However, the standard experiment is a short-term experiment, typically done in pots, so that the long-term effects of earthworms on plant growth in more complex ecosystems are still poorly understood. All combinations of earthworm species, plant species and soil type should be tested unless a general theory allowing to predict the outcome of these combinations on plant growth is developed. Such a theory is still in its infancy.

In this issue, Mudrák and Frouz (2018) throw new light on the old issue of earthworm impacts on plants. They compare the impact of earthworms on different late and early successional species, and when late and early successional species are competing in the same pots or when they are growing in separate pots. Such an approach is not fully new because some studies have already shown that earthworms impact plant competition (Laossi et al., 2009; Wurst, Langel, & Scheu, 2005). However, the fact that an a priori hypothesis, i.e. difference of behaviour between late and early successional species, was tested is particularly interesting. Their results confirmed this hypothesis by demonstrating that earthworms promote the growth of late successional species. The likely explanation for this difference is that (1) late successional species have been selected to grow well despite intense competition, i.e. when plant overall biomass is high, and that (2) earthworms increase the overall plant biomass so that they disfavour early successional species and that late successional species benefit more from the improved soil conditions in the presence of earthworms. Another original part of the study consists of comparing the impact of earthworms in two soils differing in their age of installation on post-mining sites. Again, though experiments already compared earthworm impacts in different soils (Laossi, Ginot, Noguera, Blouin, & Barot, 2010; Noguera et al., 2010), Mudrák and Frouz test a new a priori hypothesis, that earthworms should be more favourable to plant growth in the young soil than in the old soil. This hypothesis was verified in the sense that the relative increase in plant biomass was higher in the young soil. This was attributed to the legacy, in old soil, of former earthworm activities that improve soil structure and the storage of organic matter and mineral nutrients inside earthworm-created soil aggregates.

The authors conclude by proposing the general hypothesis that earthworms increase the speed of plant successions and that their positive impact on plant growth decreases along these successions. This general hypothesis is consistent with their current results and a diversity of other results accumulated on the same study system (Frouz, Pižl, & Tajovský, 2007; Frouz et al., 2008). However, the generality of their results, and thus the validity of their hypothesis, requires further testing. Several steps are still needed: (1) Mudrák and Frouz evaluated a small number of plant species (three early and three late successional species); it is necessary to compare additional early and late successional plant species, from diverse types of communities, to test the robustness and generality of their conclusions. (2) Similarly, the study was limited to just two earthworm species; robustness of the results towards the identity of earthworm species should be tested. (3) The impact of earthworms on plant communities depends on their impacts on plant growth but also on their impact on plant demography, i.e. survival from seed to adult plants and fecundity. Such demographical effects have rarely been studied but have been shown to be strong and may reverse the competitive hierarchy predicted by the impact of earthworms measured in terms of biomass accumulation (Laossi, Noguera & Barot 2010; Laossi et al., 2009). The authors mention that earthworm predation on seeds can explain a part of their results, and it has already been shown that earthworm predation on seeds may favour late successional plants (Clause, Barot, & Forey, 2016). However, it is important to also document earthworm impacts on fecundity and survival after germination. (4) The precise mechanisms and soil characteristics explaining the differences in earthworm impacts between young and old soils should be identified. (5) Maintaining the same type of experiment for several years, e.g.

in mesocosms, is necessary to test whether earthworm impacts on plants persist in the medium term.

To go further three approaches could be particularly useful: Meta-analyses are very useful to test hypotheses using a compilation of published data (van Groenigen et al., 2014). Testing the influence of plant traits on plant responses to earthworms, possibly in combination with meta-analyses, would be an efficient way to determine how different plant types react to earthworms (Lavorel & Garnier, 2002). Conversely, using earthworm traits to predict their impact on plants would help develop a general model for the role of earthworms in mediating plant successions (Pey et al., 2014). It has been suggested that more modelling efforts should be made in soil ecology (Barot et al. 2007) and, clearly, modelling could help testing Mudrak and Frouz's predictions and disentangling the underlying mechanisms. In particular, modelling can be very efficient at predicting long-term dynamics that are difficult to observe experimentally. Here, simulations should compare the short-, medium- and long-term impacts of earthworms on plant communities that, respectively, depend on earthworm impact on plant growth, plant demography, and soil properties.

To conclude, Mudrak and Frouz's study is particularly valuable for two reasons. First, it asks "when" questions. In ecology, many mechanisms, and links between these mechanisms and patterns, have been identified so that "why" questions have often been answered. Nevertheless, laws are generally contingent in ecology (Lawton, 1999). Here, earthworms are known to generally increase plant growth through various identified mechanisms. It is now necessary to identify rules predicting when (which plant species, which earthworm species, which soils) earthworms strongly favour plant growth and when they do not. Second, the authors ask a "how long" question, i.e. whether earthworm positive effects on plant growth are transient or sustainable. A model already suggested that the stimulation of mineralization by earthworms is sufficient to explain short-term increases in plant growth, but that an increase in the recycling efficiency of mineral nutrients is required for sustainable earthworm effects (Barot, Ugolini & Bekkal Brikci 2007). This model and Mudrak and Frouz's study should inspire new research on the long-term impacts of earthworms. This type of question is important because we all tend to quickly extrapolate results of short-term experiments to predict long-term dynamics or to build rationale that mix arguments that are only valid for transient states of ecological systems with arguments that are only valid for their equilibrium states. Finally, while Mudrak and Frouz's study addresses earthworm impacts on plant successions, all the arguments developed here should be valid for most soil organisms and especially other ecosystem engineers; e.g. termites. This suggests that research is still needed to develop general rules predicting the short- and long-term impacts of these organisms on plant communities and successions.

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