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Review

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Revisiting the 'Gadgil effect': do interguild fungal interactions control carbon cycling in forest soils?

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Summary

In forest ecosystems, ectomycorrhizal and saprotrophic fungi play a central role in the breakdown of soil organic matter (SOM). Competition between these two fungal guilds has long been hypothesized to lead to suppression of decomposition rates, a phenomenon known as the 'Gadgil effect'. In this review, we examine the documentation, generality, and potential mechanisms involved in the 'Gadgil effect'. We find that the influence of ectomycorrhizal fungi on litter and SOM decomposition is much more variable than previously recognized. To explain the inconsistency in size and direction of the 'Gadgil effect', we argue that a better understanding of underlying mechanisms is required. We discuss the strengths and weaknesses of each of the primary mechanisms proposed to date and how using different experimental methods (trenching, girdling, microcosms), as well as considering different temporal and spatial scales, could influence the conclusions drawn about this phenomenon. Finally, we suggest that combining new research tools such as high-throughput sequencing with experiments utilizing natural environmental gradients will significantly deepen our understanding of the 'Gadgil effect' and its consequences on forest soil carbon and nutrient cycling.

I. Introduction

Soil fungi are major drivers of terrestrial biogeochemical cycling through their roles in the breakdown and recycling of organic matter (Swift *et al.*, 1979) as well as the mediation of plant nutrition and production via mycorrhizal symbioses (Read & Perez-Moreno, 2003). Their communities are highly diverse, both taxonomically and functionally (Anderson & Cairney, 2004; Gessner *et al.*, 2010), and include a wide range of life-history strategies that allow these fungi to acquire resources from both detritus and/or symbiotic partnerships (Berbee & Taylor, 1993; Cairney, 2000; Hibbett *et al.*, 2000; Wilkinson, 2001; Bruns & Shefferson, 2004; James *et al.*, 2006; Powell *et al.*, 2009). Owing to the considerable diversity of many soil fungal communities, researchers studying

their ecology have frequently grouped individual members into guilds (i.e. groups of species that exploit the same resources in a similar manner (Root, 1967). This approach has provided important insights into the different roles that fungi play in ecosystems (Dighton, 2003), but it is often done by focusing only on individual guilds (e.g. ectomycorrhizal fungi, wood decomposer fungi, etc.) while knowingly ignoring others. Because members of specific fungal guilds frequently live in environments shared by other guilds, consideration of both intra- and interguild interactions is essential to fully understanding of the effects of fungi on ecosystem processes.

Ectomycorrhizal (EM) and saprotrophic fungi represent two of the major fungal guilds in forest soils and both are involved in the breakdown of soil organic matter (SOM) (Read, 1991; Dighton, 1995; Read & Perez-Moreno, 2003). Competition for limiting resources held in SOM between saprotrophic and mycorrhizal fungi has long been hypothesized to suppress decomposition rates, resulting in greater sequestration of carbon (C) in forest soils (Gadgil & Gadgil, 1971, 1975). This phenomenon, known as the 'Gadgil effect', has recently received renewed interest as concerns about rising atmospheric CO_2 concentration and associated shifts in climate have increased (Averill *et al.*, 2014). Because more C is held in SOM than the biotic and atmospheric pools combined (Lal, 2008), attaining mechanistic understanding of SOM C sequestration represents a central part of current research on global change (Schlesinger, 1999; Lal, 2004).

Since the last review of the 'Gadgil effect' (Cairney & Meharg, 2002), a number of new studies have emerged, providing further insights into the phenomenon. In this review, we begin by re-examining the cumulative literature on the 'Gadgil effect' to assess its frequency and magnitude in different forest ecosystems. We then discuss possible underlying mechanisms, many of which are not mutually exclusive. To help understand the observed variation with regard to the 'Gadgil effect' (see Section VI), we also identify potential factors leading to context-dependent results. Finally, we discuss strengths and weaknesses regarding different experimental and methodological approaches to better inform future research on this phenomenon.

II. Documenting the 'Gadgil effect'

While known as the 'Gadgil effect', it appears that Romell (1938) was actually the first to report shifts in fungal activity in response to the interruption of C allocation to roots and EM fungi in a boreal *Picea* forest in Sweden. This interruption of C was achieved by physically severing root connections to trees via trenching. In the trenched plot, Romell observed an increase in sporocarp production by saprotrophic fungi and a decline in the presence and abundance of EM fungal sporocarps. He postulated that this observation could be the result of the stimulation of saprotrophic growth through the generation of new root litter and EM fungal necromass caused by trenching or by releasing saprotrophic fungi from the competitively dominant EM fungi within the trenched plot.

Building on these observations, Gadgil & Gadgil (1971) explicitly set out to test the effect of EM roots on decomposition rates of litter in a *Pinus radiata* plantantion in New Zealand. Using a similar experimental approach, they observed much faster litter decomposition rates in trenched plots than in control plots and hypothesized that the effect was a consequence of relieving saprotrophic fungi from suppression caused by negative biotic interactions with EM fungi and associated host roots (Fig. 1a). Gadgil & Gadgil (1975) conducted a follow-up study in the same *P. radiata* stand, implementing additional treatments to help tease out possible mechanisms and artifacts associated with trenching. In addition to this second field experiment, they also ran a complementary microcosm experiment to control for environmental variables and more closely examine fungal–fungal interactions. The findings from both the field and microcosm experiments largely supported those found in the original study and the effect appeared not to be the result of experimental artifacts. Since these two studies, the suppression of saprotrophic fungi and litter or SOM decomposition by EM fungi has been generally referred to as the 'Gadgil effect', although exactly when the term was coined remains unclear.

III. Generality of the 'Gadgil effect'

Despite being a highly cited phenomenon throughout the fungal and soil ecology literature, the 'Gadgil effect' has received explicit

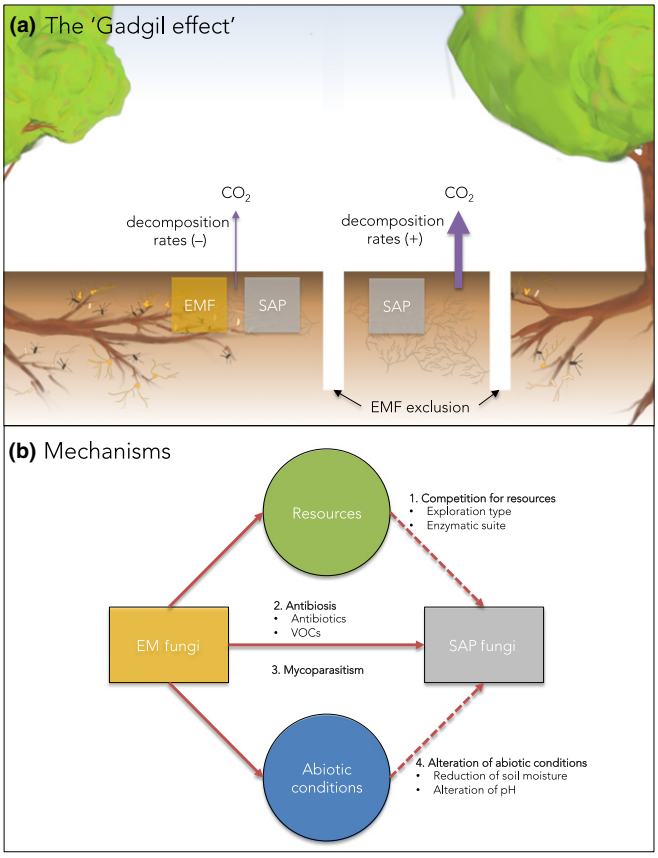

Fig. 1 Schematic representation of the response in litter and soil organic matter (SOM) decomposition to ectomycorrhizal fungal and root exclusion, that is the 'Gadgil effect' (a). Four hypothesized mechanisms responsible for the suppression of saprotrophic (SAP) fungal activity and organic matter decomposition by ectomycorrhizal fungi (EMF) (b). Arrows indicate direct (solid) and indirect (dashed) effects of ectomycorrhizal (EM) fungi on saprotrophic fungi and their activity. VOCs, volatile organic compounds.

a priori testing in only a handful of studies (Table 1). When looked at collectively, it is clear that the effect that EM fungi have on litter or SOM decomposition dynamics is inconsistent. This is true even when only considering the studies conducted in stands dominated by *Pinus* hosts at temperate latitudes. Strong negative effects of EM fungi on decomposition were found in a *P. radiata* plantation in New Zealand (Gadgil & Gadgil, 1971, 1975) and in a *Pinus resinosa* stand in Pennsylvania, USA (Koide & Wu, 2003), yet EM roots were found to stimulate the decomposition rates of litter in a *P. rigida* stand in New Jersey, USA (Zhu & Ehrenfeld, 1996). In temperate hardwood forests, the presence of EM fungi has been shown to have no effect on litter decomposition in Swedish *Fagus sylvatica* stands (Staaf, 1988), but to stimulate litter decomposition in *Quercus* spp. stands in Indiana, USA (Brzostek *et al.*, 2015). In tropical systems, Singer & Araujo (1979) found that saprotrophic fungal sporocarp production was notably higher in lowland Amazonian forests without EM fungi and suggested that biogeochemical cycling was much faster in nonEM forest soils than in EM-dominated forests. While both of those results are consistent with the 'Gadgil effect', both Mayor & Henkel (2006) and McGuire *et al.* (2010) explicitly examined EM fungal effects on litter decomposition in monodominant *Dicymbe corymbosa* EM lowland tropical forests and found no inhibition. Taken together, these studies suggest that the influence of EM fungi on litter and SOM decomposition is much more variable than previously recognized and that a better understanding of underlying mechanisms is probably required to explain the inconsistency of the size and direction of the 'Gadgil effect'.

IV. Mechanisms of the 'Gadgil effect'

Given the many methodological advances in fungal ecology since the 1970s, it is surprising that our basic understanding of the mechanism(s) responsible for the 'Gadgil effect' remains largely unknown. Over the years, a number of possible mechanisms have been suggested (Fig. 1b) and we discuss each of them as well as their empirical support. It should be stressed that the identified mechanisms are not necessarily mutually exclusive and that they do not represent an exhaustive list; other mechanisms may also be responsible for the 'Gadgil effect'.

1. Mechanism 1: nitrogen competition

As heterotrophic organisms, fungi are primarily limited by C but also limited by nitrogen (N) (Schimel & Weintraub, 2003), particularly in ecosystems where N is scarce (Kaye & Hart, 1997). Instead of acquiring C from litter and SOM, EM fungi rely on C allocated from their hosts in the form of simple sugars (Smith & Read, 2010). This alleviation of C limitation (relative to saprotrophic fungi) is thought to allow EM fungi to allocate more resources to finding and exploiting nutrient patches in the soil, particularly nitrogen (Smith & Read, 2010). The resultant activity of EM fungi would increase the C : N ratio of the substrate, which would limit saprotrophic growth as those fungi become increasingly N limited (Gadgil & Gadgil, 1971). The mining of SOM for N by EM fungi is thought to create a positive feedback loop, which ultimately results in the accumulation of C stored in SOM. Using a modeling approach, Orwin *et al.* (2011) indicated that organic N uptake by EM fungi increased the C : N ratio of SOM pools, which thereby suppressed the activity of saprotrophs and led to substantial increases in C storage. Further support for a N-related mechanism comes from Averill *et al.* (2014), who analyzed global datasets to examine the effects of dominant mycorrhizal type (EM and ericoid mycorrhizal vs arbuscular mycorrhizal) of ecosystems on the C and N content held in SOM. They found that ecosystems identified as EM- or ericoid-dominated held 70% more C per unit of N than AM ecosystems, which have less notable SOM decomposition capabilities (Read & Perez-Moreno, 2003; Hodge *et al.*, 2010).

While there is theoretical and correlative evidence for this mechanism driving C storage in forest SOM, there is currently little direct empirical support. The ability of EM fungi to decompose and acquire nutrients from SOM has been exhaustively demonstrated throughout the literature (Abuzinadah *et al.*, 1986; Entry *et al.*, 1991; Durall *et al.*, 1994; Bending & Read, 1996; Wu *et al.*, 2003), yet it remains unclear if these capabilities have a significant negative effect on saprotrophic activity. A primary issue with this mechanism is that these two fungal guilds typically occupy largely

Table 1 Studies in which the effect of ectomycorrhizal (EM) roots on the decomposition of litter and/or soil organic matter have been explicitly examined

References	Dominant host vegetation	Location	Latitude	Stand age (yr)	Treatment	EM effect on decomposition
Gadgil & Gadgil (1971)	*Pinus radiata*	New Zealand	Temperate	18	Trenching	−
Gadgil & Gadgil (1975)	*Pinus radiata*	New Zealand	Temperate	22	Trenching	−
Berg & Lindberg (1980)	*Pinus silvestris*	Sweden	Boreal	120	Trenching	−
Harmer & Alexander (1985)	*Picea sitchensis*	Scotland	Boreal	37	Trenching	0
Fisher & Gosz (1986)	Mixed conifer	New Mexico, USA	Temperate	NR	Trenching	−
Staaf (1988)	*Fagus sylvatica*	Sweden	Temperate	95–110	Trenching	0
Zhu & Ehrenfeld (1996)	*Pinus rigida*	New Jersey, USA	Temperate	NR	Trenching	+
Koide & Wu (2003)	*Pinus resinosus*	Pennsylvania, USA	Temperate	65	Correlative	−
Mayor & Henkel (2006)	*Dicymbe corymbosa*	Guyana	Tropical	Mature	Trenching	0
McGuire *et al.* (2010)	*Dicymbe corymbosa*	Guyana	Tropical	Mature	Trenching	0
Brzostek *et al.* (2015)	Mixed hardwood	Indiana, USA	Temperate	80	Girdling	0

The effect of EM fungi on decomposition rates of litter or soil organic matter is reported as a negative effect or suppression (−), no significant effect (0), or a positive effect or stimulation (+). NR, information not reported in the study.

different vertical positions in the soil profile (Lindahl *et al.*, 2007; Baldrian *et al.*, 2012; Clemmensen *et al.*, 2015). Saprotrophic fungi typically dominate litter layers, whereas EM fungi typically dominate humic and mineral layers present at lower depths. Although there are some cases where EM fungi occur higher in the soil profile (Goodman & Trofymow, 1998; Rosling *et al.*, 2003; Baier *et al.*, 2006), determining whether this spatial separation of fungal guilds is the result of EM competitive exclusion of saprotrophic fungi via decreased N availability or the result of niche differentiation remains a major outstanding question.

From the perspective of enzyme production, there seems to be more support for niche differentiation among EM and saprotrophic fungi than competitive exclusion (note that our use of saprotrophic fungi does not include those involved in wood decay, which share many of the same enzymatic abilities as EM fungi). In general, saprotrophic fungi favor hydrolytic enzyme production, while EM fungi favor nutrient-acquiring hydrolytic (e.g. proteases) and oxidative enzymes (Baldrian *et al.*, 2012; Talbot *et al.*, 2015). Litter layers generally have high C : N ratios but have high concentrations of labile substrates from fresh above-ground inputs, while deeper in the soil profile, SOM is depleted of labile substrates and enriched with recalcitrant substrates such as lignin and humic substances (Finzi *et al.*, 1998; Lindahl *et al.*, 2007). Considering substrate energetics, Baldrian (2009) argued that degradation lower in the soil profile would require more engergy from saprotrophic fungi to produce the enzymes than they would gain from degrading the available substrate. Furthermore, genomic studies are beginning to reveal that multiple EM fungal lineages have experienced convergent losses of genes coding for enzymes involved in plant cell wall degradation; however, many have retained genes coding for oxidative enzymes that are involved in lignocellulose degradation (Hibbett *et al.*, 2000; Kohler *et al.*, 2015). Mounting evidence suggests that many EM fungi utilize these oxidative enzymes in order to access nutrients, and not C found in relatively recalcitrant SOM (Rineau *et al.*, 2013; Talbot *et al.*, 2013, 2015; Phillips *et al.*, 2014; Lindahl & Tunlid, 2015). That said, lignocellulose decomposition capabilities have been shown to be quite variable among EM fungi (Hobbie *et al.*, 2013), which may be a consequence of the unique niche they occupy (Buée *et al.*, 2007).

While evidence for niche partitioning appears to be relatively strong, there have been numerous demonstrations of EM fungi competing with saprotrophic fungi for resources in pure culture or microcosm studies (Shaw *et al.*, 1995; Baar & Stanton, 2000; Lindahl *et al.*, 2001; Wu *et al.*, 2003). Fewer, however, have investigated the consequence of these interactions on decomposition rates of litter or SOM. Gadgil & Gadgil (1975) complemented their field study with a microcosm experiment involving saprotrophic fungi and both EM and nonEM colonized plants, which largely supported the competitive exclusion mechanism. Conversely, Dighton *et al.* (1987) found that EM fungi and roots actually stimulated the decomposition of organic substrates in a microcosm experiment. While the aforementioned findings are sometimes consistent with the competitive exclusion mechanism (but do not directly address a change in N availability), microcosm experiments frequently utilize pairwise combinations of fungal species that are not representative of interactions and consequences found *in situ*. For instance, microcosm studies using cord- and rhizomorph-forming EM fungi may be more aggressive colonizers compared with EM fungi that produce diffuse mycelia (Boddy, 1993), resulting in increased antagonistic interactions. Similarly, the saprotrophic fungi used in some studies are also cord-forming wood decay fungi (i.e. Lindahl *et al.*, 2001), which may not necessarily reflect the functional capabilities of litter-associated saprotrophic fungi.

2. Mechanism 2: chemical inhibition

Fungi, like plants, can produce and exude antagonistic secondary metabolites to suppress the activity of nearby competitors (Keller *et al.*, 2005). To date, there are *c.* 800 known fungal compounds with antibiotic properties (Keller *et al.*, 2005). EM fungi are no exception and have been found to produce a wide range of antagonistic antimicrobial compounds, including antifungals (Santoro & Casida, 1962; Krywolap & Casida, 1964; Krupa & Fries, 1971; Garrido *et al.*, 1982; Sylvia & Sinclair, 1983; Duchesne *et al.*, 1988; Kope & Fortin, 1990; Werner *et al.*, 2002). Because EM fungi are less limited by C than are saprotrophic fungi (as a result of direct C allocation from plant hosts), it has been speculated that they may produce these chemicals in greater quantities relative to free-living saprotrophic fungi, which could result in the retardation of saprotrophic activity (Marx, 1972). EM fungi also produce volatile organic compounds (VOCs) (Krupa & Fries, 1971), which might also reduce the effectiveness of decomposer organisms by directly inhibiting or controlling their growth near EM fungal mycelium (Splivallo *et al.*, 2011). For example, the mycelium of *Tuber* spp. produces large quantities of VOCs that reduce above-ground plant diversity by creating bare soil patches known as *brûlés* (meaning 'burnt' in French) (Splivallo *et al.*, 2011; Streiblová *et al.*, 2012). Napoli *et al.* (2010) showed that fungal communities within *brûlé* soils, which were dominated by *Tuber melanosporum*, had significantly lower fungal species richness compared with soil outside of *brûlés*. The production of antibiotics may also be coupled with other environmental changes favoring EM fungal growth. Mucha *et al.* (2009) demonstrated that *Suillus bovinus* was able to inhibit the growth of a saprotrophic and a pathogenic fungus *in vitro* via coupling of a reduction of pH and the production of antibiotics. These changes in growth media by *S. bovinus* induced abnormalities in hyphal cytoskeleton components and mitochondria of the two competing fungi. Collectively, these chemical-mediated influences on fungal communities are likely to have important consequences on litter and SOM decomposition processes.

Despite the rich literature on the biosynthesis of antibiotics and other secondary metabolites by EM fungi, it remains unknown to what extent these compounds affect saprotrophic fungal communities and whether or not this effectively reduces litter or SOM decomposition rates at the ecosystem level. While useful in determining the potential role in ecosystem processes, nearly all of the research on EM antifungal production has been conducted in pure culture systems, which does not provide the necessary link between secondary metabolite production and alteration of ecosystem-scale C cycling.

3. Mechanism 3: mycoparasitism

Parasitism is one of the more common resource-acquisition strategies that have evolved throughout the main lineages of fungi (James *et al.*, 2006). Along with parasitism of plants and animal hosts, mycoparasitism (parasitism on other fungal organisms) is also widespread (Lee & Koske, 1994; Werner & Zadworny, 2003; Mucha *et al.*, 2006; Kubicek *et al.*, 2011). With regard to the 'Gadgil effect', EM fungi may directly utilize nutrients found in the biomass of saprotrophic fungi, which may lead to the suppression of litter and SOM decomposition processes (Lindahl *et al.*, 1999; Cairney & Meharg, 2002). Because fungal biomass is generally more labile relative to most plant tissues present in forest soils (Koide *et al.*, 2011; Drigo *et al.*, 2012; Fernandez & Koide, 2012), parasitizing saprotrophic (or other EM fungi) fungi may be an efficient way to access nutrients and effectively short-circuit nutrient cycles. Support for the plausibility of this mechanism comes from Lindahl *et al.* (1999), who used ^{32}P to show the direct acquisition of resources by EM fungi from the mycelia of wood saprotrophic fungi in a microcosm experiment. In addition, Werner & Zadworny (2003) observed strong suppression and degradation of saprotrophic biomass of *Mucor hiemalis* by the EM fungus *Laccaria laccata* in a pure culture study.

The generality of these mycoparasitic interactions and whether or not this mechanism would have a large enough effect to scale up to the ecosystem level are currently unknown. These types of interactions are almost certainly dependent on the presence of particular EM taxa that utilize parasitic strategies, which may be related to exploration type. Specifically, one might expect that EM fungi that invest in long-distance exploration to seek nutrient-rich patches in the soil (e.g. patches of saprotrophic mycelium) would be more likely to engage in these interactions. By contrast, EM fungi that have shorter distance exploration types would seem less likely to engage in these interactions, as they are limited to exploring the volume of soil immediate to the ectomycorrhizal root tip.

4. Mechanism 4: altering water availability

Water availability is a major rate-limiting factor in decomposition processes, with increases in soil moisture generally increasing decomposition rates of litter and SOM (Orchard & Cook, 1983; Holden *et al.*, 2015). As such, the removal of water by EM fungi and their associated roots may be responsible for the decreases in decomposition observed in trenched plots (Staaf, 1988). Support for the effect of EM-mediated water removal comes from Fisher & Gosz (1986), who compared soil respiration and inorganic nitrogen concentrations in control, irrigated, and trenched plots. They found that trenched soil had higher respiration rates and increases in inorganic N, which could be explained by the higher soil moisture in those plots. Interestingly, when soil moisture content across treatments was later equilibrated in the laboratory, the authors found no differences in respiration between soils collected from the control and trenched plots. A similar field-based result was later found by Koide & Wu (2003), who showed that much of the variation in litter and SOM decomposition was explained by the percentage moisture of the substrate, which itself was largely explained by the EM root density occupying a volume of soil. In the earlier work of Gadgil & Gadgil (1975), however, the effect of trenching on litter water content was inconsistent during the course of their experiment, suggesting that EM fungi did not strongly influence soil moisture content.

Given the high abundances of EM-colonized roots in most forests where they occur, the possibility of this mechanism driving the 'Gadgil effect' at large spatial scales is high. However, it seems logical that the strength of this mechanism would be strongly contingent on water limitation during the growing season, which may be a reason for the lack of evidence for the 'Gadgil effect' in wet tropical EM forests (Bending, 2003; Koide & Wu, 2003). In some ecosystems, there is also evidence that tree roots are involved in redistributing water from deeper to shallower horizons, which allows EM fungi to stay active during periods of lower water potential (Querejeta *et al.*, 2003). In this case, the mechanism of the 'Gadgil effect' would not be directly related to soil moisture content, but rather one of the other mechanisms described earlier. Synergy among the four mechanisms (or others not mentioned) is also possible. For instance, in a water- and N-limited pine system, mechanisms 1 and 4 may both suppress saprotrophic activity but be completely absent in a wet and phosphorus-limited dipterocarp rainforest. For this reason, after discussing the potential role of EM fungi in priming SOM decomposition, we focus on why recognizing the environmental context in which these interactions occur seems particularly important in understanding how the 'Gadgil effect' works in different study systems.

V. Priming and the 'Gadgil effect'

'Priming effects' are relevant to consider in discussions of the 'Gadgil effect' because they represent a different interaction outcome between EM fungi and soil saprotrophic organisms. In contrast to negative impacts on decomposition associated with the 'Gadgil effect', the presence of EM fungi may benefit saprotrophic fungi if they facilitate nutrient mineralization. Recent studies have shown that in certain ecosystems and under certain environmental conditions (e.g. elevated atmospheric CO_2 concentration), EM fungi do appear to stimulate the decomposition of SOM via priming (Phillips *et al.*, 2012; Brzostek *et al.*, 2015). 'Priming effects' could be the result of multiple mechanisms, but have been most commonly linked with the exudation of labile C compounds by fine roots and mycorrhizal fungi (Kaiser *et al.*, 2015). These exudates relieve free-living saprotrophs (both fungal and prokaryotic) of C limitation and stimulate nutrient mineralization rates, which can increase EM fungal access to resources held in SOM (Kuzyakov, 2002). Alternatively, 'priming effects' may be a result of the turnover of EM fungal necromass that can stimulate free-living saprotrophs in a similar fashion (Phillips *et al.*, 2012). In this case, priming effects would be largely dependent on the recalcitrance of the EM fungal necromass (Drigo *et al.*, 2012; Fernandez & Koide, 2012, 2014; Fernandez *et al.*, 2013). Finally, some EM fungi are known to produce oxalic acid (Cromack *et al.*, 1977), which may be responsible for stimulating microbial mineralization by liberating

organic compounds from protective associations with soil minerals (Keiluweit *et al.*, 2015).

It is possible that, within a given site, the activity of certain EM fungi may suppress soil saprotrophs when acquiring resources (see Mechanisms 1–4), while other EM species may actively 'prime' soil saprotrophs in order to access those same resources. Thus, the net effect of EM fungi on decomposition processes may be governed by magnitude of these contrasting phenomena. That said, it should be noted that 'priming effects' and the 'Gadgil effect' mechanisms discussed earlier may not be mutually exclusive. For instance, if the extraction of water from soil horizons (mechanism 3) is a driving mechanism of the 'Gadgil effect', that would not preclude the occurrence of a 'priming effect' by EM fungi and roots. Additionally, it is possible that the release of labile C forms from EM fungi may not be directed at greater nutrient mineralization but rather represent a form of 'baiting' by EM fungi, which could facilitate their parasitism of saprotrophic fungi (see mechanism 3, discussed earlier).

VI. Is the 'Gadgil effect' context-dependent?

Ectomycorrhizal fungi are distributed globally across many hosts and biomes, which represent a wide range of resource levels and environmental conditions (Tedersoo *et al.*, 2010). We believe that both biotic and abiotic context-dependency probably explains the inconsistencies found among studies examining the 'Gadgil effect'. Rather than be confused by this variation, however, we suggest that explicitly testing the 'Gadgil effect' along environmental gradients represents a promising approach to understanding both the mechanisms and the generality of the phenomenon. In the following, we discuss a suite of ecological factors that seem likely to play a key role in modulating the magnitude and direction of the 'Gadgil effect' (Fig. 2). We realize that much of this section is speculative, but given the lack of a mechanistic understanding of the 'Gadgil effect', we believe that clearly discussing how biotic and abiotic factors might drive the variability in this phenomenon is useful in focusing current and future research.

1. Soil effects

Soil fertility limits the growth of both plants and microorganisms in most forest systems (Kaye & Hart, 1997). These limitations are result of litter stoichiometry and chemistry and probably regulate competitive interactions for nutrients between saprotrophic fungi and EM fungi. In systems where litter and SOM have relatively high C : N ratios, heterotrophs are strongly limited by N (Kaye & Hart, 1997) and are therefore likely to be involved in strong competitive interactions for N with EM fungi (and associated host plants). This

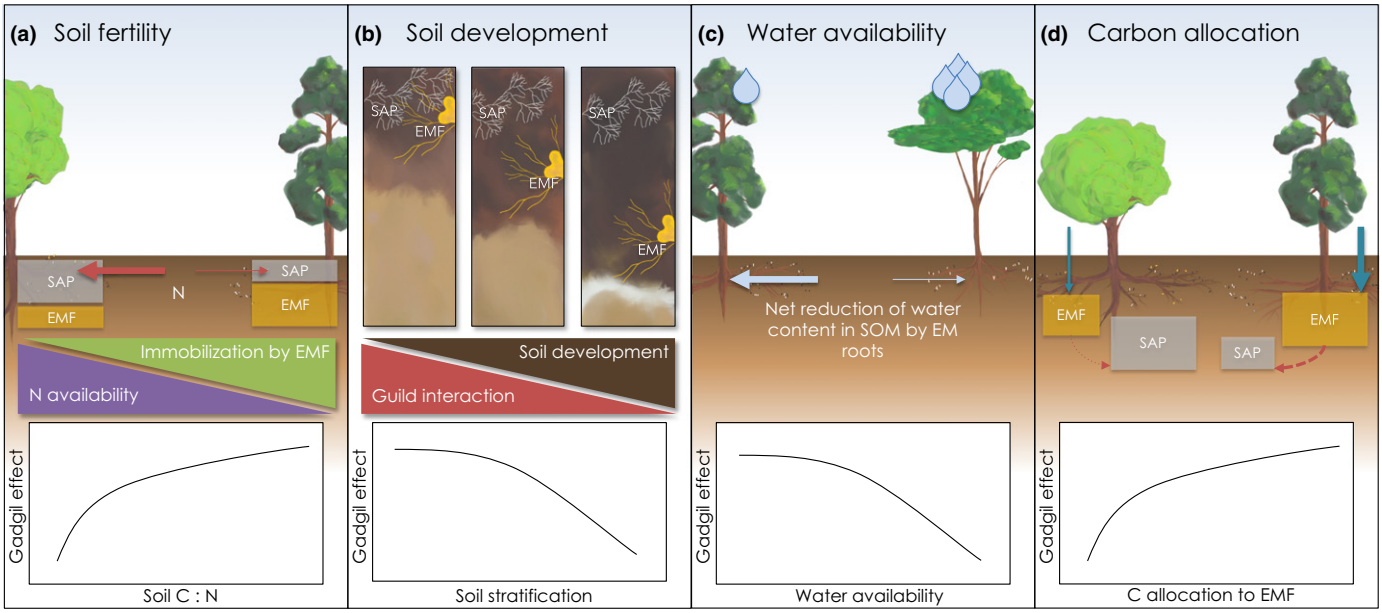

Fig. 2 Hypothesized examples of biotic and abiotic environmental factors that may be important modulators of the influence of ectomycorrhizal (EM) fungi on saprotrophic fungi (SAP) and associated decomposition processes. Box and arrow sizes designate the magnitude and size of fluxes and pools, respectively. Dashed arrows indicate negative biotic interactions. The 'Gadgil effect' is defined as the suppression of organic matter decomposition rates by EM fungi. (a) As nitrogen (N) becomes more limiting, a higher proportion of N is immobilized in EM fungal biomass. By exacerbating saprotrophic fungal N limitation, this suppresses saprotrophic fungal growth and organic matter decomposition rates. (b) Competition for soil resources in litter and soil organic matter (SOM) between saprotrophic and EM fungi may be strongest when soils are poorly developed as a result of the two fungal guilds occupying similar vertical depths and targeting the same litter and SOM substrates for growth. As soils develop and there is more heterogeneity in substrates, these competitive interactions probably become relaxed, resulting in a weaker 'Gadgil effect'. (c) Water availability directly limits the decomposition of organic matter. In ecosystems where water limitations are common, EM fungi and associated roots extract water from the soil, reducing the activity of saprotrophic fungi. As water becomes less limiting, the 'Gadgil effect' weakens. (d) Carbon (C) allocation to EM fungi by plant hosts varies considerably across taxa and ecosystem. The amount of C that is allocated to EM fungi probably has a significant influence on the amount of EM fungal biomass, which may have a subsequent effect on the ability of EM fungi to engage in competitive interactions with saprotrophic fungi. This weakening of competitive interactions (i.e. a smaller 'Gadgil effect') may, in turn, increase organic matter decomposition rates.

will lead to greater N immobilization, which will further hasten competition, leading to a stronger 'Gadgil effect'. By contrast, in more fertile systems, where low soil C : N ratios are common, saprotrophic fungi may become relatively less limited by N. If N competition is the mechanism driving the 'Gadgil effect', lower N limitation would reduce competitive interactions with EM fungi and weaken this effect (Fig. 2a). Consistent with these scenarios, Sterkenburg *et al.* (2015) found that litter-associated saprotrophic fungi were found to inhabit lower hummus layers on the fertile end of a C : N gradient, which suggests that there may be a relaxation of competition for N between fungal guilds.

Soil organic layer development, which results in steep stratification of chemical and physical properties in the soil profile, corresponds with forest succession (Huggett, 1998). It is well known that the structure of both saprotrophic and EM fungal communities coincide with this development, resulting in strong vertical gradients in guild and species composition (Dickie *et al.*, 2002; Rosling *et al.*, 2003; Genney *et al.*, 2006; Lindahl *et al.*, 2007; Anderson *et al.*, 2014 ; Bahram *et al.*, 2015; Clemmensen *et al.*, 2015). As previously noted, this spatial structure is thought to be the result of competitive exclusion and/or niche partitioning through the substrate use specialization. Competition for resources in litter and SOM between saprotrophic and EM fungal guilds may be strongest when soils are poorly developed, as a result of fungal guilds occupying a similar vertical position in the profile and targeting the same litter and SOM substrates for growth-limiting resources (Fig. 2b). Correspondingly, it seems reasonable to expect (and experimentally possible to test) that as the soil profile develops, which will create greater vertical heterogeneity in the substrate, negative interguild fungal interactions will relax and the magnitude of the 'Gadgil effect' will lessen.

Soil texture, which governs nutrient retention in soil, may also play a critical role in determining the strength of competitive interactions between fungal guilds. Sandy soils, which retain nutrients poorly, owing to the coarse texture and low cation exchange capacity, have been found to have substantially higher densities of EM roots in O-layer, which have corresponded with nutrient immobilization and soil organic carbon (SOC) accumulation relative to loamy soils (Raulund-Rasmussen & Vejre, 1995). This was postulated to be the result of the increased competition between EM roots and saprotrophs for nutrients in those layers. Additionally, texture is a major driver of the water-holding capacity of soils, which in turn may exacerbate the effects of water limitations resulting from water extraction by EM roots (see discussion later).

2. Climatic effects

Ectomycorrhizal symbioses are prevalent across ecosystems with tremendous variation in climatic conditions. For instance, mean annual precipitation can range > 10-fold in EM-dominated forests, from as low as 280 mm in semiarid *Pinus edulis* stands (Gehring *et al.*, 1998) to as high as 4000 mm in tropical *Dicymbe corymbosa* rainforests (McGuire *et al.*, 2010). As decomposition processes are directly dependent on water availability, we suggest that this variation is likely to be a primary factor modulating the 'Gadgil effect' across study systems (Koide & Wu, 2003). Specifically, in ecosystems where water limitations are not as severe and seasonally dependent, such as wet tropical systems, this mechanism (see mechanism 4) would be weak relative to systems that are strongly water-limited (Fig. 2c).

Variation in mean annual temperature across ecosystems may also influence the outcomes of fungal interguild interactions via effects on enzyme kinetics. As mentioned earlier, saprotrophic and EM fungi typically employ different enzyme suites to break down and acquire resources from different substrates (Baldrian, 2009; Talbot *et al.*, 2015). Oxidative enzymes (used frequently by EM fungi) require relatively more energy than hydrolytic enzymes (used frequently by saprotrophic fungi) and are thus more responsive to elevated temperatures (Fierer *et al.*, 2005). Talbot *et al.* (2013) demonstrated significant positive correlations between EM fungal richness and peroxidase activity in organic and mineral horizons of a *Pinus muricata*-dominated site, with no such correlation found for saprotrophic fungal richness. Those results suggest that EM fungi may be disproportionately utilizing oxidative enzymes to acquire resources tied up in recalcitrant SOM. If this is the case, increasing temperatures may exacerbate the competitive dominance of EM fungi (i.e. strengthening the 'Gadgil effect'), although any gain in C storage from the suppression of saprotrophic fungi may be counteracted by increased decomposition of recalcitrant SOM by EM fungi.

3. Plant effects

Like climatic conditions, the amount of C allocated to EM fungi by plants can vary widely across hosts and ecosystems (Hobbie, 2006). We speculate this variation may have important consequences for extracellular enzyme production and nutrient acquisition by EM fungi. In particular, it seems likely that the more C that plants allocate to EM fungi, the more these fungi would be able to invest in extracellular enzyme production, which will facilitate their capture of organic N from the environment. This would intensify their competitive abilities for litter- and SOM-derived N and consequently increase the magnitude of the 'Gadgil effect' (Fig. 2d). Support for this scenario comes from Rineau *et al.* (2013), who found that in microcosms containing the EM fungus *Paxillus involutus*, the addition of glucose was a key trigger of litter decomposition and resulted in the up-regulation of genes coding for extracellular enzymes that were integral to litter decomposition and N acquisition. Overall, however, our understanding of EM fungal C allocation patterns across hosts and systems remains limited and represents an important area of future research related to this topic.

In addition to absolute levels of C allocation, plant effects can also manifest via litter quality, which has dramatic effects on decomposition processes (Melillo *et al.*, 1982). Ecosystems where plant litter is relatively recalcitrant (i.e. high lignin and low N concentration) may tie up nutrients in recalcitrant litter and favor access to EM fungi, which would strengthen the 'Gadgil effect' in these systems. Conversely, we expect that the effect of EM fungi on litter and SOM decomposition may be weaker in systems dominated by plants producing relatively labile litters that decompose rapidly.

4. Fungal effects

Given the range in functional traits of both EM and saprotrophic fungi, variation in the taxonomic composition of fungal communities has been hypothesized to have a profound influence on ecosystem processes (Read & Perez-Moreno, 2003; Crowther *et al.*, 2014; Koide *et al.*, 2014). Even within a single study system, it is well known that dominance of a given volume of soil by particular EM fungi can have a dramatic influence on soil biogeochemical cycles. For instance, mat-forming EM fungi can dominate large patches of soils in Douglas-fir forests of the Pacific Northwest, USA, and biogeochemical cycling within mat-dominated soils is dramatically different from that in adjacent nonmat EM fungal communities (Aguilera *et al.*, 1993). With specific relevance to the 'Gadgil effect', both cellulose and lignin decomposition were dramatically accelerated in mat communities dominated by *Hysterangium* spp. compared with nonmat EM community soil (Entry *et al.*, 1991). These results suggest that the presence or absence of specific species may have dramatic impacts on the magnitude of the 'Gadgil effect'. In addition to individual species effects, there may also be effects at the community level. Fungal decomposer communities usually have a negative diversity–decomposition rate relationship, which is thought to be a result of decomposers being aggressively antagonistic towards each other (Toljander *et al.*, 2006; Fukami *et al.*, 2010). The extent to which EM fungal community diversity has a negative or positive effect on ecosystem decomposition rates remains unknown.

Fungal and host effects may also be linked via the host specificity exhibited by some EM fungi (Ishida *et al.*, 2007; Tedersoo *et al.*, 2008). For instance, *Suillus* spp. are known to be specific colonists of hosts in the Pinaceae (Dahlberg & Finlay, 1999) and isolates of the genus have been demonstrated to have high competitive ability when grown with saprotrophic fungi in microcosm experiments (Lindahl *et al.*, 1999). Thus, the inclusion of *Suillus* spp. in an EM fungal community could have a positive effect on the 'Gadgil effect'. The specificity of saprotrophic fungi is less clear, although in many mushroom identification guides, certain saprotrophic species are noted to be present only in forests dominated by angiosperms or gymnosperms.

5. Human effects

It has been well documented that anthropogenic N deposition has drastic, usually negative, consequences on the activity and function of EM fungal communities (Avis *et al.*, 2003; Högberg *et al.*, 2003, 2010; Nilsson & Wallander, 2003). As plant N limitation is alleviated with inorganic N deposition, hosts shift C allocation away from maintaining EM symbioses (Högberg *et al.*, 2010), which may potentially lead to competitive advantage for saprotrophic fungi. Community shifts towards 'inorganic N-tolerant' EM fungi members have also been well documented in systems where inorganic N has been experimentally manipulated (Avis *et al.*, 2003) and across inorganic N deposition gradients (Lilleskov *et al.*, 2002). In both cases, if N competition between EM and saprotrophic fungal guilds is a mechanism for the 'Gadgil effect', then it is likely that increases in anthropogenic N deposition will lessen its magnitude by favoring saprotrophic fungi (Högberg *et al.*, 2003).

VII. Future research on the 'Gadgil effect'

1. Identify species and their relative roles

A major limitation in attaining a mechanistic understanding the 'Gadgil effect' has been the inability to observe and identify the organisms directly involved in the decomposition processes. Because of the difficulties of studying soil microbes *in situ*, these organisms and their activities have largely been treated as a black box in studies examining ecosystem processes (Horton & Bruns, 2001; Peay *et al.*, 2008). With the recent progress in high-throughput sequencing and bioinformatics (Lindahl *et al.*, 2013, Nguyen *et al.*, 2015), however, we are now able to identify fungal community members and guilds with relative ease. Tracking changes in fungal community composition with high-throughput sequencing in plots with trenching or girdling treatments has been useful in identifying specific fungi associated with decomposition processes (Yarwood *et al.*, 2009; Lindahl *et al.*, 2010). Despite this progress, a sequence-based approach alone can only provide correlative evidence of functional roles and does not directly assess resource use by the fungal guild members. To fully elucidate the relative roles of different fungal guilds, coupling of DNA-stable isotope probing methodologies (Neufeld *et al.*, 2007) with high-throughput sequencing would provide a much-needed link between fungal community structure and function (i.e. allow investigators to trace and quantify C and N fluxes from labeled substrate into specific fungal guild pools).

2. Recognize strengths and weaknesses of different experimental approaches

As trenching represents a simple way to sever C allocation to fine roots and EM fungi with little long-term system impact, it has been a popular choice for researchers assessing the 'Gadgil effect' (Table 1). However, there are a handful of issues associated with trenching that need to be kept in mind. As mentioned earlier, trenching undoubtedly increases soil moisture relative control plots by cutting off root water uptake. In addition, there is a rapid flux of newly generated detritus and labile C exudates from severing roots as well as the generation of EM fungal necromass. This C and N flux into the detrital cycle may prime the decomposition of the SOM in these plots (see Section V). That said, Gadgil & Gadgil (1975) incorporated treatments to control for this effect by removing coarse and fine roots from a subset of their trenched plots. They found that the decomposition dynamics in the root removal plots did not differ significantly from those that were trenched and with intact roots. Fisher & Gosz (1986) also found no evidence that the generation of labile inputs following trenching had any effect on the decomposition rates of litter or SOM. While Lindahl *et al.* (2010) did demonstrate that trenching leads to an increased relative abundance of fungal opportunists capitalizing on new generated labile substrates, the extent to which these opportunists persist after

the initial few weeks following trenching and influence longer-term litter or SOM decomposition dynamics remains uncertain.

Similar to trenching-based experiments, tree girdling also halts C allocation below ground to EM fungi, which allows researchers to measure the response of the soil microbial community to the absence of EM fungi. With girdling, however, there is a gradual turnover of root and fungal biomass instead of a rapid flux as a result of the disturbance associated with trenching. In addition, soil water content is not as dramatically affected by these methods. Both of these characteristics may be more favorable for assessment of the 'Gadgil effect', but killing trees by girdling presents a major issue when environmental impact is a concern. Because of its destructive nature, girdling also limits the ability to replicate treatments when reducing impact is a goal. A final important issue with girdling is that encroachment of roots and EM fungi from untreated trees just outside treated plots may obscure any signal by partly suppressing saprotrophs and decomposition.

3. Use gradients to clarify the influence of environmental variation

The use of climatic, edaphic, topographical, successional and anthropogenic gradients has been a fruitful endeavor in teasing out ecological signals from complex systems (McGill *et al.*, 2006). The application of trenching and/or girdling treatments across natural gradients would allow for a much better understanding of how various ecological factors modulate the direction and magnitude of the effect of EM fungi on SOM decomposition. To date, all of the studies examining the 'Gadgil effect' have focused on single sites or contrasted EM host-dominated stands with AM host-dominated stands. By implementing treatments across gradients, this would allow researchers to regress environmental factors on an index of the 'Gadgil effect'. For instance, applying trenching treatment plots along a successional chronosequence and utilizing high-throughput sequencing techniques may reveal important patterns in relation to the development of soil (Clemmensen *et al.*, 2013, 2015). While the factors outlined in Fig. 2 can be considered a starting point to identify relevant gradients, other factors, such as anthropogenic N deposition, EM host diversity, and soil type, are also probably important. Additionally, coordinated research networks, where researchers implement standardized methodologies across a broad range of ecosystems and conditions, is an effective way to gain a broad-scale understanding to various ecosystem processes (Callaway *et al.*, 2002; Borer *et al.*, 2014). Such a network could be created to tackle questions regarding EM fungal influence on C and nutrient cycles and allow the fungal ecology research community to address key questions in a standardized manner across broader scales than are possible for any single research group.

4. Explicitly consider scaling effects

Most of the research to date on the effects of fungal–fungal interactions on ecosystem processes has been conducted without serious consideration as to how results might scale up to the ecosystem level, both spatially and temporally. Sequestration of C in soils is a process that occurs on extensive temporal scales and extrapolating initial decomposition stages to SOM formation could result in significant inaccuracies, as chemistry alone does not dictate the fate of SOC (Schmidt *et al.*, 2011). Currently, the majority of studies that have examined the 'Gadgil effect' have been conducted on the scale of months, but when the absence of an effect is found, this may not reflect the true impact of fungal–fungal interactions, as the accumulation of C in SOM may only occur at longer timescales (i.e. decades to millennia; e.g. Clemmensen *et al.*, 2015). Similarly, the high spatial heterogeneity of soil processes combined with the typical approaches used to study the 'Gadgil effect' (i.e. trenching), which are done at small spatial scales and are typically not designed in a spatially explicit manner, may lead to considerable noise in the data obtained from these kinds of studies. The spatial and temporal distributions of individual EM fungi often differ as well (Izzo *et al.*, 2005), which is probably the result of differences in dispersal and soil exploration strategies (Lilleskov *et al.*, 2004; Pickles *et al.*, 2010). For instance, some *Cortinarius* spp. have been shown to have clumped distributions, whereas *Cenococcum geophilum* has been found to have a notably even spatial distribution (Pickles *et al.*, 2010). If different EM fungi differentially suppress the decomposition of litter or SOM through antagonistic interactions with saprotrophic fungi (a largely untested but probably

Table 2 Outstanding questions for future research regarding the 'Gadgil effect' and relevant references

Questions	References
How common is ectomycorrhizal (EM) fungal priming of soil organic matter (SOM) decomposition and what is the mechanism(s)?	Brzostek *et al.* (2015)
Are EM fungi effective competitors with wood decay fungi? Is the 'Gadgil effect' present in coarse woody debris?	Bending & Read (1995)
Do arbuscular mycorrhizal fungi suppress saprotrophic fungal activity? If so, what is the mechanism(s)?	Leifheit *et al.* (2015)
How do changes in carbon (C) availability (e.g. thinning, shading) to EM fungi drive litter and SOM decomposition?	Moore *et al.* (2015)
How does the composition of EM hosts (monodominant vs mixed) influence the magnitude of the 'Gadgil effect'?	McGuire *et al.* (2010)
Does coinvasion of EM fungi and plant hosts lead to reductions or increases in decomposition of litter and SOM?	Nuñez & Dickie (2014); Parker *et al.* (2014)
Does plant host phenology and seasonality favor certain fungal guilds?	Högberg *et al.* (2010)
Does the presence of ericaceous plants, which host ericoid mycorrhizal (ERM) fungi, strengthen or weaken the 'Gadgil effect'?	Bending & Read (1997)
Do soil fauna mediate fungal competition and alter litter and SOM decomposition rates?	Crowther *et al.* (2011)
Does incorporating interguild interactions into ecosystem C models improve our understanding of C cycling?	Orwin *et al.* (2011)

reasonable assumption based on known variation in EM traits), then it is reasonable to expect that the overall ecosystem effect of this fungus would be determined by its spatial distribution. For example, an abundant and evenly distributed EM fungus that is a supreme competitor may suppress decomposition across larger areas of soil than a patchily distributed fungus possessing similar competitive ability. We recommend that keeping spatial and temporal context in mind when designing experiments will be helpful in reducing unexplained variation.

VIII. Conclusions

Although the 'Gadgil effect' represents a frequently referenced phenomenon, our survey of the literature suggests its generality is much less well established than previously recognized. This is probably a result of multiple factors, but particularly the lack of mechanistic understanding of the phenomenon. With this review, we hope to stimulate a new generation of 'Gadgil effect' experiments, which will not only benefit our basic understanding of forest C cycling but also foster efforts to mitigate global atmospheric CO_2 concentrations. The application of next-generation sequencing tools, coupled with experiments across natural environmental gradients, seems to be a particularly fruitful approach to more thoroughly understand the nature of 'Gadgil'-related interactions. As a guide for helping direct future research, we provide a selected list of questions that remain unanswered about the 'Gadgil effect' (Table 2), which we believe are well primed for further investigation.

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