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Grazing by collembola controls fungal induced soil aggregation

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ABSTRACT

Fungi affect soil aggregation and hence soil structure. Soil aggregation by saprotrophic fungi has been linked to various fungal traits but not tested during interactions with other organisms such as grazing soil fauna. Here we investigated how fungal identity and traits such as mycelial extension rate and biomass production affect aggregation across 49 fungal species isolated from sandy soils with different land uses. We tested each fungus and its effect on aggregation in the presence and absence of a grazer (*Folsomia candida*). We show that fungal species vary widely in their ability to aggregate soil, that the ability to aggregate soil was not phylogenetically conserved and the best trait predictor for aggregation was mycelial extension rate. Moreover, we show that the interactions between fungi and collembola affect the ability of fungi to aggregate soils. We conclude that identity of fungal species and their interaction with grazers affects soil aggregation and thus soil structure.

1. Introduction

Soil structure is one of the most important factors influencing soil quality as it largely determines water storage, the amount of gas that is exchanged, nutrient cycling and carbon storage (Lal, 2015). It is defined as the three-dimensional arrangement of carbon and mineral particles and pore spaces, and it is often described by the size and/or stability of soil aggregates. These soil aggregates are particles of soil that bind together more strongly than surrounding particles. They can have a range of sizes ranging from microaggregates (<0.25 mm) to macroaggregates (>0.25 mm) (Tisdall and Oades, 1982). The latter are formed directly or indirectly by plants roots and a range of soil organisms. Fungi in particular have a positive effect on soil aggregation (Rillig and Mummey, 2006; Busse et al., 2009; Hannula and Morriën, 2022). Many studies have focused on the interaction between fungi and soil aggregation (Miller and Jastrow, 1990; Rillig et al., 2015) showing that there is a positive relationship between biomass of the fungus measured as mycelial density and its ability to aggregate soils (Lehmann et al., 2020).

During fungal growth and foraging within the soil, fungi entangle the soil aggregates and particles because of their filamentous growth style (Rillig et al., 2010). Furthermore, the biopolymers produced by fungi can function as surface sealants for soil aggregates (Lehmann et al., 2020). Additionally, hydrophobins, released by fungi, can modify the moisture level of aggregates and have soil aggregate stabilizing functions (Lehmann et al., 2020; Wright and Upadhyaya, 1998). Therefore, fungi are considered to play a key role in soil aggregate formation and stabilization. The ability and efficiency to stabilize aggregates is fungal species specific (Lehmann et al., 2020) and fungi have multiple morphological, physical, chemical and biotic traits that lead to differences in their ability to aggregate soils (Six et al., 2004). As a chemical trait, fungi exude extracellular compounds that stick aggregates together (Tisdall et al., 2012) while physical and morphological traits include enmeshing particles while growing filamentous through the soils foraging for nutrients (Daynes et al., 2012; Tisdall and Oades, 1982). Fungi also produce extracellular enzymes decomposing organic matter which can have opposing effects, namely they can break the formed aggregates (Baldrian et al., 2011). Earlier studies focus on the interaction between fungi and soil aggregation (Miller and Jastrow, 1990; Rillig et al., 2015) and previous research has shown that there is a positive relationship between biomass of the fungus measured as mycelial density and its ability to aggregate soils (Lehmann et al., 2020). No association between foraging or mycelial growth rate of the fungus were found in earlier studies while fungal decisions to exploit or explore the environment do depend on its growth rate (Veresoglou et al., 2018).

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Furthermore, it is assumed that higher growth rates imply higher metabolic costs and shorter lifespan (Andrews and Rouse, 1982) and therefore a higher turnover and a potential larger buildup of necromass which may act as a C stabilizing factor (Buckeridge et al., 2020).

Yet, fungi are rarely alone in the soil and soil fungi have a range of biotic interactions (Lussenhop, 1992; Maraun et al., 2003) that are likely to affect their ability to aggregate the soil. Especially organisms grazing on fungi such as collembola can have a large effect on fungal biomass (Crowther et al., 2012a) and in this way on soil aggregation. Collembola are soil-inhabiting microarthropods, widely known as springtails. Several species such as *Folsomia candida* are reported to be mycophagous from feeding habit observations and the presence of spores or mycelia in their gut content (Hedĕnec et al., 2013; Hiol et al., 1994). It is further confirmed that they prefer saprotrophic fungi over mycorrhizal fungi (Klironomos et al., 1999). Collembola like other micro-arthropods have been shown to have a direct effect on soil aggregation through formation of aggregates around their fecal pellets that also serve as source organic matter (Lussenhop, 1992). However, the indirect effects through grazing on fungi are likely to be at least of a similar magnitude as direct effects. The presence of sufficient numbers of collembola in the soil can have an effect on soil fungi. A decline in the fungal biomass caused by collembola grazing may negatively influence the soil aggregation as well as C sequestration. Although Bengtsson and Rundgren (1983) concluded that fungal growth increased greatly as a response to grazing by collembola, Hanlon (1981) concluded that the stimulation of collembola grazing on fungal activity has an optimum value, after which the response of fungal activity would reduce with further increases in grazing intensity. Indeed, at low to moderate densities collembola can stimulate fungal growth through removal of old hyphae and creation of labile nutrient pools. (Visser, 1985). This means that fungal growth is negatively influenced when collembola feeding surpasses this optimal threshold value. An earlier study investigated the relationship between arbuscular mycorrhizal fungi (AMF) and native collembola on soil stable aggregates and found that both collembola alone and AMF alone affected soil aggregation yet the combination had non-additive effect (Siddiky et al., 2012). The effects of this grazing on soil aggregation through reduction on soil saprotrophic fungal biomass are, however, still unknown.

Here, we investigated how collembolan grazing on fungi affects the soil aggregation across fungal species using a model soil microcosm system. We tested the effect of 49 fungal species on soil aggregation with and without added *Folsomia candida*. This species of collembola was selected due to its general feeding preference across fungal species and high grazing intensity (Tordoff et al., 2008). We expected that fungal species would vary in their ability to aggregate the soil but also in their sensitivity to grazing. This could be related to their palatability (i.e. dark mycelia; Maraun et al., 2003), defence (Addison and Parkinson, 1978; Mills and Sinha, 1971), or growth rate. More fungal biomass is likely to support a larger population of grazers (Morriën et al., 2017). Hence, we expect that aggregation will not only be affected by fungal species and identity but also by the interaction of fungal species and collembolan grazing. We further expected that the fungi producing most biomass would maintain the largest number of collembola and hence that the grazing would disrupt the biomass – aggregation relationship detected earlier (Lehmann et al., 2020).

2. Material and methods

2.1. Soils

Soils used in this study were collected from four sites within The Netherlands with varying land use. All soils were characterized as sandy soils. Soil 1 was collected from a pasture used for conventional farming in Helvoirt, North-Brabant (N51.6423, E5.1998). This was characterized as a sandy soil with relatively low organic matter content of 2%. Soil 2 was collected from neighboring farm to soil 1, also in Helvoirt, North-Brabant (N51.6460, E5.2172). This soil was managed as an organic pasture and had the same soil type as soil 1. Soil 3 soil was collected at the experimental farm of Wageningen University and Research located at Vredepeel, Limburg (N51.3219, E5.5105). This soil is characterized as sandy soil with relatively high organic matter content (6%; Clocchiatti et al., 2020). Lastly, soil 4 was collected from a grassland abandoned from intensive agricultural management 2 years prior to the sampling in Empe, Gelderland (N52.0830, E6.0639). This soil was also sandy soil with low organic matter content (around 2%). All soils were collected in April 2020. We further sequenced the soil fungal communities using methods described in detail elsewhere (Hannula et al., 2021)and compared the list of species obtained with MiSeq amplicon sequencing of the same soils to the representatives obtained by culturing (Supplementary Table 1).

2.2. Collembola

The colony of *F. candida* was acquired from a company (Baitshop, Balk, The Netherlands) in April 2020. They were transferred in a box with charcoal and kept in constant temperature 20 °C in the dark and fed with sterile yeast culture.

2.3. Fungi

Fungal strains were isolated using a serial dilution method with NaCl buffer from the collected soils using different media all supplemented with antibiotics (15 mg l^{-1} Ampicillin, 15 mg l^{-1} Streptomycin and 30 mg l^{-1} Chlortetracycline) to prevent bacterial growth. Multiple media were used to cover different growth conditions and groups of fungi. The media used were: Rose-Bengal agar (RBA), Malt Extract Agar (MEA), Czapek's agar (CZA) and Yeast Extract Peptone Dextrose Agar (YEPD), Water Agar (WA), PDA (Potato Dextrose Agar), PDA with supplemented benomyl (0.5 ml l^{-1} agar) and 1:10 PDA. All fungi were grown initially in 20 °C for 2 weeks and thereafter in 10 °C until new colonies appeared. This approach of growing fungi for longer and in lower temperature was adapted due to COVID-19 related entry restrictions to the labs in April 2020. Unique colonies were constantly isolated from the plates upon appearance.

To measure colony radial extension rate (in μm h^{-1}), the fungi were cultivated both on full strength PDA to imitate nutrient rich conditions (Lehmann et al., 2020) and on 1:10 PDA to imitate nutrient poor conditions often found in soils. For all fungal strains, five replicates were used. The fungi were aseptically transferred as plugs to the middle of the Petri dish and grown in 20 °C in darkness for 4 weeks. At day 0, 2, 4, 7, 9, 11, 21 and 28, all plates were observed for growth and new growth was marked in the bottom of the Petri dish. The growth was measured by measuring the radius in four directions (0°, 90°, 180°, and 270°) with the agar plug as center point to the colony and the four values were averaged. For each replicate, the mean colony radius was plotted over time to identify the linear growth phase. The slope of the linear growth phase represents the colony radial extension rate and was estimated by linear regression standardized by the length of the linear growth phase (Lehmann et al., 2020).

The data for colony biomass density (in g mm^{-2}) were obtained in an experiment in which fungal colonies were grown on PDA. For each fungus, 5 replicate agar plugs were transferred to new petri dished and grown as described above. When fungi reached half of their linear growth phase determined previously, colony area was measured, then biomass was harvested by dissolving the agar in a water bath in a Falcon tube and filtering the resulting liquid including fungal biomass onto a sterile filter paper (Whatmann). The filter paper including fungus were dried at 45 °C and weighed (Reeslev and Kjoller, 1995). Extraction from Petri dishes without fungus served as control. Finally, the biomass was standardized by the colony area.

For molecular identification, approximately 0.2 g of tissue was collected from each fungal culture under sterile conditions and immediately frozen. DNA was extracted using Zymo Fungal DNA extraction

kit, amplified using ITS1 and ITS4 primers (White et al., 1990), purified and sequenced at Macrogen (Amsterdam, the Netherlands). The fungal sequences were trimmed to remove the primer sequences in MEGA-X-software and identified by comparing them against curated UNITE SH database (Nilsson et al., 2019). Due to problems in sequencing quality few of the fungi could not be definitely assigned to types and species and are here categorized as 'unknown'. These unknown species are included in analyses of phyla or classes. The obtained sequences are deposited in Genbank under accession numbers OR134023-OR13409.

2.4. Soil aggregation

The procedure for measuring soil aggregate formation (SAF) was modified slightly from Lehmann et al. (2020). Firstly, the 6 cm Petri dishes were filled with around 12 ml PDA. Then 10 g of soil (here soils 1–4) from which the fungus was isolated was gently added on top of the agar. All fungi were incubated on the soil from which they were isolated. Before that, the soils were sieved with a 1 mm sieve and autoclaved twice (at 121 °C for 2 × 20 min). After that, the soil was equilibrated on agar for 2 d before inoculation. In this way, the soil was rewetted via capillary action to provide a moist environment for fungal growth. Each fungal species was transferred to soil in a Petri dish (6 cm diameter) with 10 replicates per species. The 10 controls only consisted of PDA without a fungus and 10 g soil. Finally, all the plates were sealed and incubated in complete darkness at 20 °C. After 7 days of incubation, 10 same sized *F. candida* adults from same colony were added to each of the Petri dishes. There were a total of 49 fungal species and the control without added fungus on each soil with 5 replicates each. This resulted in 530 experimental units (49 fungi + 4 controls x 2 (no collembola/-collembola) x 5 replicates). *F. candida* was added after the fungi had grown to a sufficient size to ensure they had enough to feed on. All petri dishes stayed in complete darkness at 20 °C for 5 weeks until further measurements. The number of living (moving away from light) collembola were observed using a stereomicroscope at the end of the experiment prior to drying.

For SAF analysis, the plates were reopened and dried at 50 °C for 2 d. To obtain the soil aggregates >1 mm that formed during experiments, the soil was carefully sieved with a 1 mm sieve. After that, the soil fraction >1 mm was weighed. The following equation was used to calculate the final SAF:

$$\mathrm{SAF}\% = (\text{aggregates} > 1\ \text{mm} / 10) * 100$$

The SAF of control groups without *F. candida* for the groups without collembola was applied for background value while for units with collembola, control soils with *F.candida* were used as reference value. There was no visible fungal growth in any of the control (sterilized) soils.

2.5. Statistical analysis

The relationship between aggregation with and without grazing, extension rates and biomass were evaluated using linear models and polynomial fitting (R packages 'psych', 'rcompanion', and 'PerformanceAnalytics'). The best fit for models was evaluated using BIC and residuals of the (polynomial) models were fitted against normality. Best fitting models (lowest BIC, normal residuals) are reported in the text. The effect of the phylum, the class and the order of fungal species on growth rates and biomass was evaluated using the same models. The effect of soil, fungal species and grazing on aggregation were evaluated using linear models (lme) in R (R Core Team (2020)).

3. Results

3.1. Representation of culturing approach

We evaluated if the fungal species captured by culturing were representative of the soil fungal diversity. Of the 25 major taxa of Ascomycota (representing >60% of the relative abundance in terms of sequencing reads) detected by amplicon sequencing across soils, we obtained a culture of 13 of them (Supplementary Table 1). We did not capture in our culturing efforts representative of orders *Chaetothyriales*, *Pezizales*, *Saccharomycetales*, or *Xylariales* while other orders detected had a representative culture. Further, one species cultured from two different soils was not captured by sequencing (namely *Oidiodendron truncatum*). As expected, we did not reach as good coverage of cultures for Basidiomycota eventhough they made up around 20% of the community in terms of average reads in all soils. Out of 7 major orders of Basidiomycota, we only got cultures of Tremellales (Tremellomycetes; *Apiotrichum lignicola*, Tremellomycete sp., and *Apiotrichum* sp.). No representative of Agaricomycete was achieved using our methods. We further did not achive any cultures of Chytridiomycota (<1% of total reads), Glomeromycota (<1% of total reads) or Rozellomycota (<1% of total reads; Supplementary Table 1). For Mortiriellomycetes (~2% of community) we had a representative culture (*Mortierella elongate*) and representative cultures for both Mycoromycotina (~2% of total reads) families detected (e.g. *Umbelopsidomycetes* and *Mucoromycetes*).

3.2. Extension rate or biomass production of the different fungal species

We first evaluated if the species identity of the fungi isolated was related to its extension rate or biomass production. We detected that extension rates measured on both nutrient rich and nutrient poor media were higher for Mucoromycota as compared to Ascomycota, Basidiomycota and Mortiriellomycota (Fig. 1A&B) while biomass density was not significantly affected by the phylum of the fungal species (Fig. 1C). As the design was unbalanced in terms of number of cultures per phyla, complimentary analyses were run only to compare Ascomycota and Mucoromycota which showed that Mucoromycota had higher extension rates on PDA ($F = 10.28$, $p = 0.003$) and on 1:10 PDA ($F = 8.21$, $p = 0.007$) than Ascomycota. The lower taxonomic levels (i.e. classes or orders) did not differ in their extension rates although we note that especially Eurotiomycetes exhibited large variation in their extension rates within the class, especially compared with variation within other classes (Fig. 1D and E). Species with highest extension rates in nutrient rich conditions on PDA were *Penicillium chrysogenum, Penicillium echinulatum* (Eurotiomycetes), *Mucor circinelloides, Mucor moelleri,* and *Mucor hiemalis* (Mucoromycetes) while species growing slowest on PDA were *Penicillium canescens* (Eurotiomycetes), *Emericellopsis minima* (Hypocreales), *Cladosporium cladosporioides* (Capnodiales), and *Tetracladium furcatum* (Helotiales). On nutrient poor media (1:10 PDA) highest extension rates were detected for *Penicillium polonicum*, *Penicillium rubens* (Eurotiomycetes), *Mucor moelleri*, and *Mucor heterogamus* (Mucoromycetes; Table 1).

3.3. Soil aggregation, soil origin and fungal species identity

The 49 isolated fungi had different effects on aggregation of the soils (species: $n = 50$, $F = 3.11$, $p < 0.001$), and this variation in species effects was consistent across fungi isolated from different soils (soils 1–4: $F = 3.82–10.46$, $p < 0.005$). The soil where fungi were isolated from did affect the aggregation ($F = 5.23$, $p = 0.002$) and there was a further significant interaction between soil origin and fungal species identity ($F = 4.47$, $p < 0.001$). Remarkably, from soil 3 (arable soil) we detected species of fungi that negatively affected soil aggregation compared to the control of having no fungi (Fig. 2). This soil also contained the fungi that on average aggregated soils least which was followed by soil 4 (recently abandoned field). The pasture soils (1 and 2) harbored fungi with the highest aggregation potential (Fig. 2).

3.4. Soil aggregation and collembola grazing

Grazing by collembola did not affect aggregation across fungi but

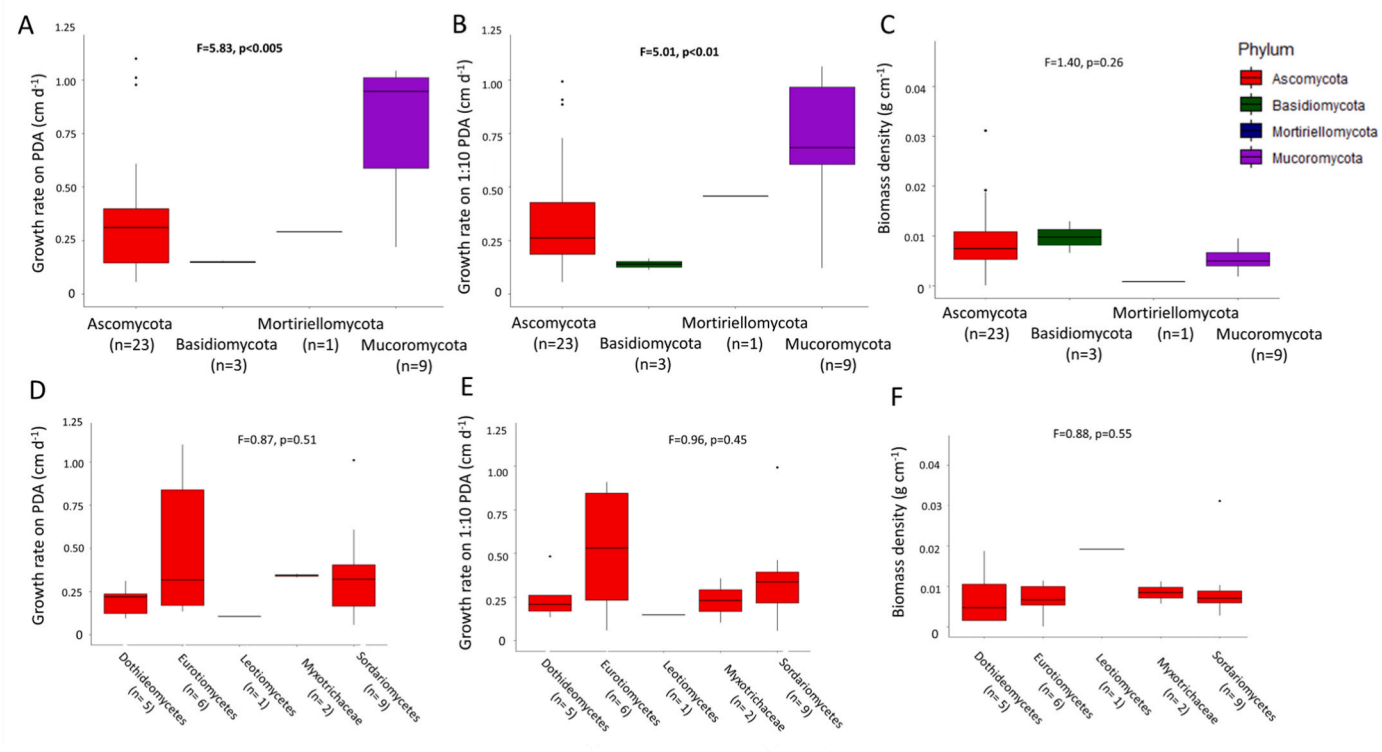

Fig. 1. Extension rates and biomass production of fungi per phylum (A–C) and per class for Ascomycota (D–F). The growth speed is measured as extension of hyphal growth per day (in cm) in nutrient rich media (A & D), and on nutrient poor media (B and E). Biomass density (C and F) is calculated as gram of hyphae produced per cm of outgrowing hyphae. The statistical significance and F-value of the linear model for phylum fungi belong to (A–C) and class it belongs to (D–F) explaining its growth rate of biomass are given in the figure. The fungal cultures without a definite identification were excluded from this analysis (n = 10).

there was an interaction between grazing by collembola and fungal species identity ($F = 2.04$, $p < 0.005$; Fig. 3). We further calculated the effect of collembola grazing on the fungal induced aggregation (the aggregation in the absence of collembola – aggregation in the presence of collembola). Grazing by collembola generally had a negative effect on soil aggregation: a significant negative effect on grazing on aggregation was detected for 16 fungal species while no significant positive effects of grazing on soil aggregation were found (Fig. 3). There was no effect of collembola themselves in a sterilized soil (without a fungus) on aggregation. The average decrease in aggregation caused by grazing by collembola on fungi was 5.5% while the values ranged from decrease of 76% to an increase of 26%.

3.5. Fungal identity, soil aggregation and collembola grazing

We did not detect a significant effect of fungal taxonomic identity at phylum or order-level on aggregation (for phyla $F = 0.59$, $p = 0.62$, for orders $F = 0.88$, $p = 0.56$) although species belonging to Basidiomycota tended to have lower soil aggregation ability than fungi belonging to other phyla (Fig. 4A). The fungal species that aggregated most soil compared to control were *Mortierella elongata*, *Cladosporium cladosporioides* and *Gibberella zeae*. We further tried to relate the effect of collembola grazing on fungal species to the taxonomic identity of the fungi but found that fungal phyla or order species belonged to did not explain the ratio of aggregation in presence and absence of collembola (for phyla $F = 0.38$, $p = 0.77$; for orders $F = 0.69$, $p = 0.73$; Fig. 4B). The species whose ability to aggregate soils was most (negatively) affected by grazing were *Penicillium polonicum* (Eurotiomycetes), *Talaromyces muroii* (Eurotiomycetes), *Apiotrichum lignicola* (Tremellomycetes), and *Pseudogymnoascus pannorum* (Dothideomycetes) (also seen in Fig. 3).

All collembola were dead at the end of the experiment when grown on cultures of *Mucor griseocyanus*, *Penicillium freii*, and *Penicillium fellutanum*. These species were among the fungi that were either slightly positively or not at all affected by grazing. In a small scale choise experiment we confirmed that these fungi were also the fungi least selected by collembola when offered three choises (*Penicillium freii* was selected in only 15% of the cases). In most other cultures, the number of collembola increased rather than decreased during the 5 weeks of the experiment due to reproduction in optimal conditions (Supplementary Table 2).

3.6. Fungal growth rate, soil aggregation and collembola grazing

There was a relationship between extension rate on nutrient poor agar (1:10 PDA) and aggregation in the absence of collembola, and that the optimal extension rates for aggregation were in the mid-range growth rates (polynomial relationship best fit evaluated by BIC, $R^2 = 0.17$, $p = 0.018$; Fig. 5A). In the presence of collembola no significant relationship between extension rate and aggregation was detected (polynomial model; $R^2 = 0.06$, $p = 0.264$; Fig. 5A). Similar to the extension rate in nutrient poor conditions (1:10 PDA), fungal growth in nutrient rich conditions (PDA) was correlated with aggregation in the absence of grazer (non-transformed lm: $R^2 = 0.10$, $p = 0.029$) but not in the presence of grazer ($R^2 = 0.01$, $p = 0.663$). Biomass density of fungi was negatively related to extension rate ($R^2 = 0.14$, $p = 0.014$ for 1:10 PDA and $R^2 = 0.18$, $p = 0.004$ for PDA) but was not related to aggregation by fungi in the absence (non-transformed lm: $R^2 = 0.00$, $p = 0.719$; Fig. 5C) or presence (non-transformed lm: $R^2 = 0.00$, $p = 0.768$) of collembola (Fig. 5D). Lastly, the effect of collembola on aggregation was positively correlated with the extension rate of the fungi (non-transformed lm: PDA $R^2 = 0.12$, $p = 0.018$ 4D; 1:10 PDA $R^2 = 0.09$, $p = 0.039$; Fig. 5B).

4. Discussion

We found that the mycelial extension rate in both nutrient rich and

Table 1
Extension rate and biomass production of the fungal cultures. The representative sequences are deposited in Genbank under accession numbers OR134023-OR13409.

Name	Growth rate on PDA (cm d^{-1})	Growth rate on 1:10 PDA (cm d^{-1})	Biomass density (g / cm^3)	Closest species	Phylum	Class	Order
1C	0.09	0.26	0.0016	*Cladosporium cladosporioides*	Ascomycota	Dothideomycetes	Capnodiales
3C	0.31	0.48	0.0016	*Aureobasidium pullulans*	Ascomycota	Dothideomycetes	Dothideales
3D	0.22	0.13	0.0079	*Aureobasidium pullulans*	Ascomycota	Dothideomycetes	Dothideales
3V	0.12	0.17	0.0188	*Pseudogymnoascus pannorum*	Ascomycota	Dothideomycetes	Dothideomycetes_ic.
3X	0.24	0.21	ND	*Paraphaeosphaeria sporulosa*	Ascomycota	Dothideomycetes	Pleosporales
3S	0.21	0.31	0.0004	Dothideales sp.	Ascomycota	Dothideomycetes	
2X	0.15	0.89	0.0114	*Penicillium canescens*	Ascomycota	Eurotiomycetes	Eurotiales
2Y	0.13	0.06	0.0078	*Penicillium fellutanum*	Ascomycota	Eurotiomycetes	Eurotiales
1E	1.10	0.33	0.0001	*Penicillium chrysogenum*	Ascomycota	Eurotiomycetes	Eurotiales
1L	0.42	0.73	0.0056	*Penicillium sp.*	Ascomycota	Eurotiomycetes	Eurotiales
3O	0.98	0.91	0.0053	*Penicillium freii*	Ascomycota	Eurotiomycetes	Eurotiales
3Y	0.21	0.20	0.0108	*Talaromyces muroii*	Ascomycota	Eurotiomycetes	Eurotiales
3N	0.10	0.15	0.0192	*Tetracladium furcatum*	Ascomycota	Leotiomycetes	Helotiales
2M	0.35	0.10	0.0112	*Oidiodendron truncatum*	Ascomycota	Myxotrichaceae	Myxotrichaceae
3AB	0.33	0.36	0.0057	*Oidiodendron truncatum*	Ascomycota	Myxotrichaceae	Myxotrichaceae
1X	0.06	0.06	0.0312	*Emericellopsis minima*	Ascomycota	Sordariomycetes	Hypocreales
2A	0.61	0.22	0.0047	*Gibberella zeae*	Ascomycota	Sordariomycetes	Hypocreales
3B	0.39	0.39	0.0063	*Fusarium oxysporum*	Ascomycota	Sordariomycetes	Hypocreales
3P	0.31	0.34	0.0084	*Fusarium solani*	Ascomycota	Sordariomycetes	Hypocreales
3Q	0.11	0.22	ND	*Plectosphaerella cucumerina*	Ascomycota	Sordariomycetes	Hypocreales
3T	0.41	0.46	0.0028	*Gibberella intricans*	Ascomycota	Sordariomycetes	Hypocreales
4C	1.01	0.99	0.0066	*Trichoderma harzianum*	Ascomycota	Sordariomycetes	Hypocreales
4Q	0.32	0.38	0.0074	*Gibberella fujikuroi*	Ascomycota	Sordariomycetes	Hypocreales
3R	0.16	0.22	0.0103	*Humicola grisea*	Ascomycota	Sordariomycetes	Sordariales
1B	1.09	1.05	0.0050	*Ascomycota sp.*	Ascomycota		
3E	0.14	0.11	0.0129	*Apiotrichum sp.*	Basidiomycota	Tremellomycetes	Tremellomycetes
3L	0.15	0.16	0.0066	*Apiotrichum lignicola*	Basidiomycota	Tremellomycetes	Tremellomycetes
3K	0.13	0.11	0.0046	*Tremellomycete sp.*	Basidiomycota	Tremellomycetes	Tremellomycetes
1D	0.29	0.46	0.0009	*Mortierella elongata*	Mortiriellomycota	Mortiriellomycota	Mortierella
1A	1.01	1.02	0.0026	*Mucor heterogamus*	Mucoromycota	Mucoromycota	Mucorales
2D	1.04	0.68	0.0063	*Mucor circinelloides*	Mucoromycota	Mucoromycota	Mucorales
2F	0.63	0.61	0.0069	*Mucor hiemalis*	Mucoromycota	Mucoromycota	Mucorales
3AC	0.24	0.20	0.0095	*Mucor hiemalis*	Mucoromycota	Mucoromycota	Mucorales
3I	0.59	0.61	0.0046	*Mucor circinelloides*	Mucoromycota	Mucoromycota	Mucorales
3M	0.22	0.12	0.0018	*Mucor griseocyanus*	Mucoromycota	Mucoromycota	Mucorales
4B	1.01	0.97	0.0040	*Umbelopsis isabellina*	Mucoromycota	Mucoromycota	Mucorales
4E	0.95	0.95	0.0067	*Mucor moelleri*	Mucoromycota	Mucoromycota	Mucorales
4V	1.02	1.06	0.0049	*Mucor moelleri*	Mucoromycota	Mucoromycota	Mucorales
4X	0.09	0.10	0.0069	Unknown	Unknown	Unknown	Unknown
1F	0.19	0.22	0.0135	Unknown	Unknown	Unknown	Unknown
2V	0.49	0.38	0.0069	Unknown	Unknown	Unknown	Unknown
3F	0.41	0.41	0.0096	Unknown	Unknown	Unknown	Unknown
3H	0.60	0.60	0.0022	Unknown	Unknown	Unknown	Unknown
3J	0.39	0.37	0.0025	Unknown	Unknown	Unknown	Unknown
3S	0.21	0.31	0.0004	Unknown	Unknown	Unknown	Unknown
3U	0.08	0.03	ND	Unknown	Unknown	Unknown	Unknown
3W	0.39	0.35	ND	Unknown	Unknown	Unknown	Unknown
3Z	0.99	0.93	0.0005	Unknown	Unknown	Unknown	Unknown

nutrient poor conditions – and not the hyphal biomass - was the best predictor of soil aggregation. This is contradictory to our expectation and previous findings on fungi isolated from and tested in loamy sand textured grassland soil (Lehmann et al., 2020). Here we used soils with different land uses and slightly different textures, and added fungi isolated from those soils directly to the same soil. The species we detected belonged to the same major groups (Ascomycota, Basidiomycota and Mucoromycota) as in the study by Lehmann et al., (2020). However, on species level only a few species of fungi that were the same between the studies. Lehmann et al. (2020) showed that Ascomycota were the most efficient aggregators followed by Basidiomycota and Mucoromycota. Here we show that Ascomycota and Mucoromycota had a similar ability to aggregate soils but that the variance within Ascomycota species is larger. We even detected negative effects of adding a fungus to the system on aggregation which could be due to degradation of naturally forming aggregates (Baldrian et al., 2011). This contrasts with the findings of Lehmann et al. (2020) who only found positive effects. Differences between studies could be explained by the differences in fungal species isolated from different soils under different land uses. We further detected an effect of soil origin on soil aggregation (Fig. 2), and an

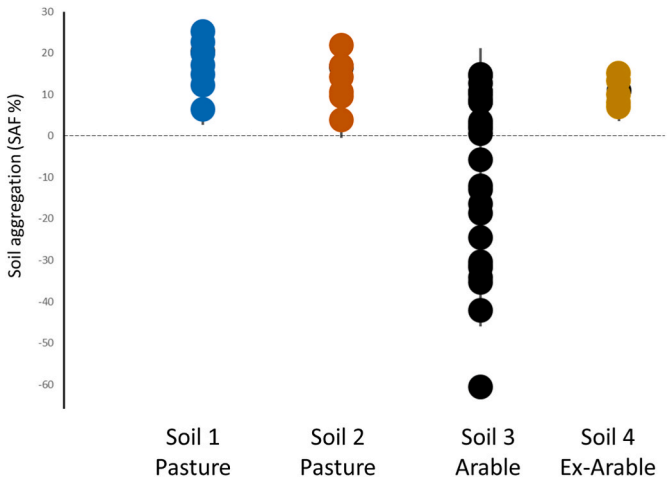

Fig. 2. The individual aggregation rates (SAF%) of fungi per soils. Each dot represents one fungus and error bars for the 5 replicates per fungi are shown. Soil 1 (pasture) is marked with blue, soil 2 (pasture) in orange, soil 3 (arable soil) in black and soil 4 (ex-arable soil) in yellow.

interaction between soil origin and fungal species on aggregation, which would hint towards differences in the fungal species that are major aggregators in those soils.

The study by Lehmann et al. (2020) did not use any Eurotiomycetes or Tremellomycetes which were major groups in our study showing the most adverse effects on aggregation. We further had more species of *Mucorales*, which also showed negative effects on aggregation. Their presence in our study and not in that of Lehman et al. (2020) could be due to our selection of more disturbed soils (arable soil, former arable soil and pastures) as starting material. These soils are known to harbor more fast growing yeast-like fungal species and *Mucorales*, and these fungi are likely the most important fungi in these systems related to carbon cycling (Hannula et al., 2012, 2020). It is also likely that in the more disturbed systems it is the extension rate and not biomass that most affects the ability to aggregate soils while in stable environments biomass production is favored.

We acknowledge that using culture based approach we do not capture the total diversity of soil mycobiome even that our dataset of 49 species across 4 different soils is one of the more complete datasets (Lehmann et al., 2020). For Ascomycota and Mucoromycota we covered here large part of the excisting diversity while for the other major group of saprotrophic fungi, Basidiomycota, we could only scratch the surface by having two cultures of Tremellomycetes and no Agaricomycetes. This potentially affects our conclusions related to the comparison between the phyla while we are confident that the analyses of families is valid. This is a common issue in studies of saprotrophs and we suggest future studies to pay more attention to capture yeasts and slower growing fungi such as Basidiomycota.

The major finding of our study is that the relationship between fungal traits and aggregation is sensitive to grazing by collembola. Species that were the fastest growing and also best at aggregating soils in absence of a grazer were consumed more by collembola. We found an optimal aggregation by fungal species in presence of collembola in intermediate hyphal extension rates. In accordance with the optimal foraging model, collembola should feed on the most energetically rewarding food source, one that will yield the greatest reproductive success (Stephens and Krebs, 1987). We did not absolutely quantify the numbers of collembola at the end of the experiment but did note that in many cases they had reached very high population numbers (Supplementary Table 2) and were visibly damaging the mycelia. Earlier studies have shown that collembola grazing affects fungal morphology and extension rates (Bretherton et al., 2006; Kampichler et al., 2004; Tordoff et al., 2008) but in most cases no effect on process rates (such as wood decomposition rates) have been observed in response (Tordoff et al., 2008). Here we show that this grazing on fast growing fungal species decreases their mycelial extension rate and at the same time has an effect on soil aggregation. Within the time scale of this study (5 weeks) we further did not detect an effect of *F. candida* alone on the aggregation of sterilized soils without the presence of a fungus which slightly contradicts the findings by Siddiky et al. (2012) which showed that the native collembolan community affects soil aggregation possibly through fecal matter and available SOM (Lussenhop, 1992). Our system is, however, quite artificial and aims to test the effects of interactions, and hence we cannot conclude on the effects of collembola alone on aggregation under natural conditions and microbiomes. This needs to be further tested using also broader range of species of collembola, in more realistic conditions in presence of native soil microbiome. Further, it would be interesting to test how biotic interactions between fungal species mediate their effects on aggregation in presence and absence of collembola (Crowther et al., 2012b).

We detected an effect of fungal species identity on aggregation albeit

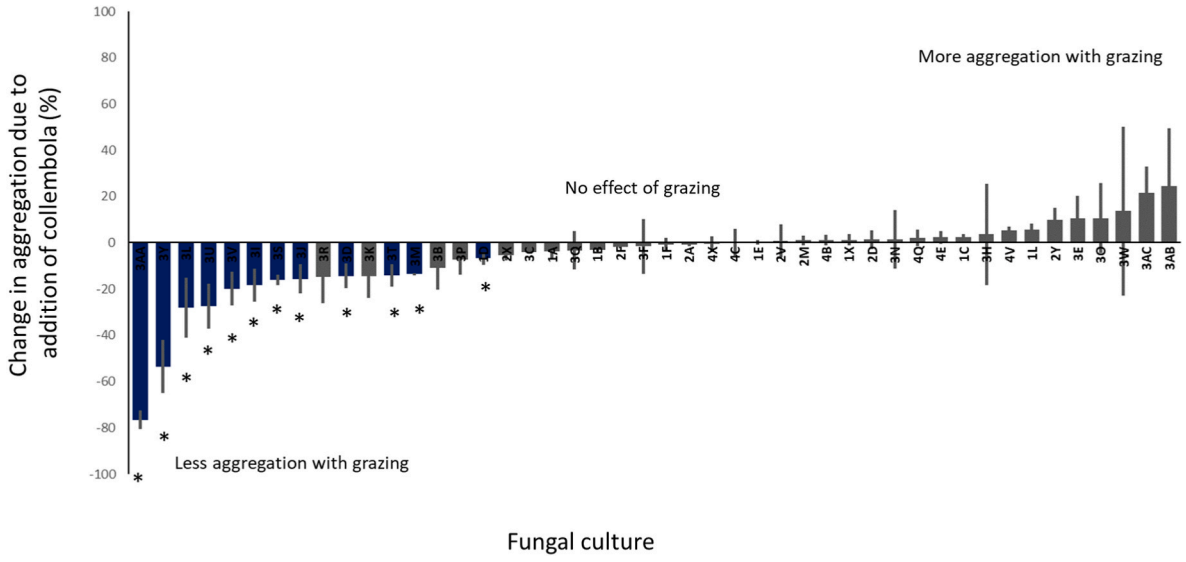

Fig. 3. The effect of collembola on aggregation of soil across fungal species. Statistically significant effects calculated between aggregation with grazing and without grazing are marked with blue colour and asterisk (*).

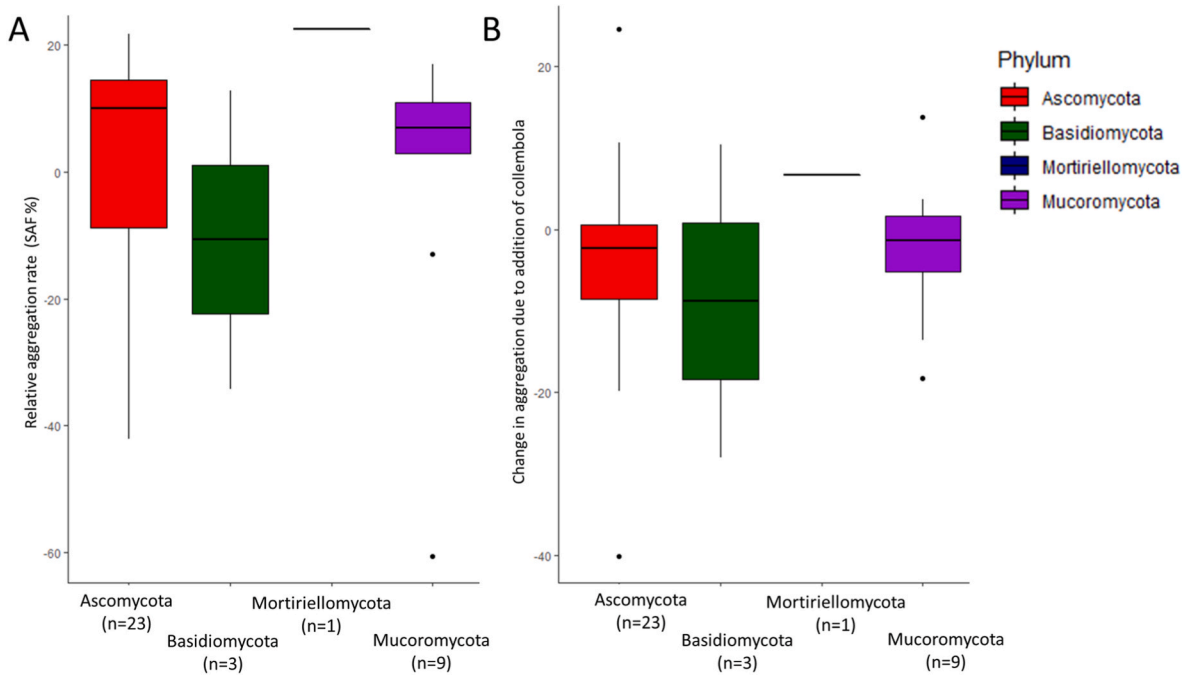

Fig. 4. The effect of fungal phylum on the aggregation rate (SAF %) (A) and the effect of fungal phylum on grazing induced effects on soil aggregation (B).

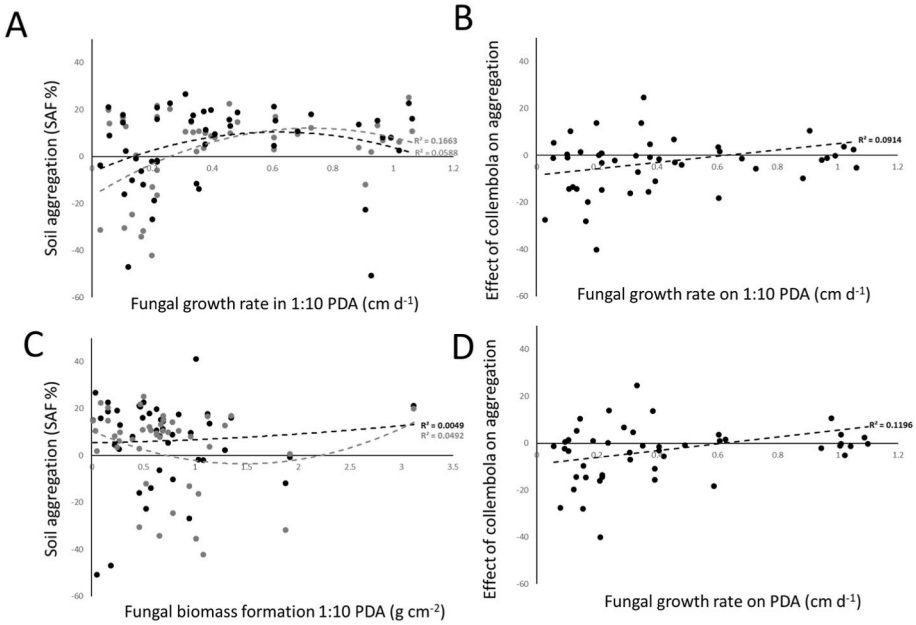

Fig. 5. Effect of fungal growth rate (A) and biomass formation (C) on soil aggregation compared to control (SAF%) in the absence of collembola (grey dots, grey trend lines) and in the presence of collembolan grazing (black dots, black trendline) and the effect of collembolan grazing on the relationship between growth rate measured on 1:10 PDA (B) and on PDA (D) on aggregation.

this seems not to be conserved in the phylum or class level, and variation is large sometimes even at the level of genera. Different fungal groups have different ways of stabilizing the aggregates while some stabilize aggregates through chemical binding of (clay) particles to the hyphae (common for ascomycetes) and some do it by holding particles together by restricting movement (*Mucor* sp.) which could affect the aggregation (Tisdall et al., 2012). Further, as we did not measure the aggregation under abiotic stresses but under stable conditions, the differential binding mechanisms might affect the stability even more.

The fungal species differed also in other traits which would affect preference by collembola and hence the relative effects of collembola on aggregation. The species most affected by grazing belonged to *Penicillium*, *Trichosporonales* and *Pseudogymnoascus*. Remarkably, we only detected significant negative effects of collembola on aggregation while no significant positive effects were observed (Fig. 2). We could not link the order or phylum of fungi to the grazing induced effects on aggregation, and importantly, there was variation in the response of fungi to grazing by collembola even within genera (e.g. *Penicillium*). Earlier research has postulated that dark pigmented fungi (for example *Cladosporium* and *Alternaria*) would be the preferred food source of collembola while other fungi might not even be eaten (such as *Trichoderma*; Maraun et al., 2003) or even be toxic to collembola (Visser and Whittaker, 1977).

However, it was noted that collembola species vary in their behavior and that despite occasionally observed strong preferences for certain fungi when given a choice (Moore et al., 1987), based on gut-content analysis, *F. candida* is a generalist species (Anderson and Healey, 1972) which might explain our results. For more specialist collembola or other microarthropod species the identity, and for example, coloring and palatability of mycelium might play a more important role in feeding preference which might have further consequences (Barnes et al., 2018) on ecosystem level processes such as soil aggregation. Hence, we urge future experiments to test more possible interactions between species and groups of fungi and microarthropods in order to gain a better understanding of the effects of grazing on fungal mediated soil processes. Furthermore, in soils, direct interactions between fungal species and indirect effects through preferential feeding (Moore et al., 1987) on one or few fungi by specialist and generalist species of microarthropods (Crowther et al., 2012a) will have effects on soil aggregation and consequently, the soil carbon cycling.

We also detected few fungal species that were able to directly kill or starve the collembola to death. It has been postulated that some *Penicillium* and *Trichoderma* species with high chitinolytic activities would entangle collembola in their hyphae and digest them while especially *Penicillium* is also known to have direct toxic effects on collembola (Mills and Sinha, 1971; Addison and Parkinson, 1978; Maraun et al., 2003). Further species like *Hypholoma fasciculare* are not preferred by collembola and can also kill them (Rotheray et al., 2009). Here the species having adverse effects on collembola were *Penicillium* species and a species of *Mucor*. We did not detect this to be specific to those groups as there were other species of *Penicillium* and *Mucor* that were not having adverse effects on collembola. We conclude that this is a species specific response which is in line with the large variation in extension rates and aggregation with and without collembola detected especially for Eurotiomycetes and Mucoromycota.

Soil aggregation is an important factor for stabilizing C in soils (Cotrufo et al., 2019). Next to carbon that binds to minerals as the mineral associated organic matter (MAOM) fraction, larger biopolymers of mainly litter inputs can be occluded by soil aggregates as particulate organic matter (POM) (De Gryze et al., 2006). This pool of occluded carbon material is traditionally not regarded to be stable (Lavallee et al., 2020), but if this pool is captured by aggregates that become relatively stable due to filamentous entanglement ((Rillig, 2004; Six et al., 2004; Tisdall et al., 1997), fine roots, and extracellular polymeric substances (EPS) (Bettermann et al., 2021) secreted by both bacteria and fungi. Fungi also produce hydrophobins (Lehmann et al., 2020; Wright and Upadhyaya, 1998) which might stabilize aggregates by making them water-repellant (Rillig et al., 2010). Fungi do not only play a physical role in stabilizing aggregates, but they can also serve as sources of organic matter themselves (Liang et al., 2016; Wang et al., 2021). Some fungi may have a high biomass turnover if they are dependent on extending their mycelial network to reach labile sugars such as root exudates (De Vries et al., 2009) although this turnover rate is highly context dependent (Anthony et al., 2020). Combined with a high carbon use efficiency (CUE), fungi are likely to sequester more carbon in biomass in the production of new tissue than they respire compared to bacteria (Kallenbach et al., 2016). Therefore, their old hyphae can serve as large bodies of new organic inputs in the form of necromass (Buckeridge et al., 2020) that, if melanized, can contribute to a relatively stable form of organic carbon. Once this necromass is fragmented it can also end-up as POM occluded in aggregates. Understanding trophic cascade controls such as by collembola grazing will ultimately contribute to carbon retention if we know how we can optimally stimulate top-down control on fungi to maximize aggregate stabilization.

In summary, we show that fungal species vary widely in their ability to aggregate soil and this could not be explained by their phylogeny. Moreover, the interactions they had with grazing collembola varied and this significantly affected how much they aggregated soil. We detected a positive correlation between fungal extension rate and aggregation but this relationship changed in response to grazing. Hence, we urge scientists to also take interactions with other organisms into account when studying the relationship between (fungal) traits and ecosystem functions. This research also links to soil carbon sequestration: it is not so straight forward to increase soil fungal biomass and growth to increase soil aggregation and carbon retention and here we show that intermediate extension rates are optimal in the presence of grazers.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: S. E. Hannula reports financial support was provided by Maj & Tor Nessling Foundation.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.funeco.2023.101284.

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