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DIPLOMARBEIT

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Effects of resource stoichiometry and stress on the structural and functional microbial community composition of decomposing beech litter

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Wien, im

I dedicate this work to my grandmother Emma Sophie Emilie Frank.

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Contents

„Und wenn ich weissagen könnte und wüßte alle Geheimnisse und alle Erkenntnis und hätte allen Glauben, also daß ich Berge versetzte, und hätte der Liebe nicht, so wäre ich nichts.“

1. Korinther, 13

Summary in English

Decomposition of plant material is the major process of nutrient recycling in ecology being driven by fungi and bacteria, processing about 90% of of the global terrestrial plant biomass. The decomposing microbial community composition (MCC) may be affected in three different ways:

(1) Ecological stoichiometry theory predicts microbial community composition being subject to the relative elemental composition of the substratum assimilated.
(2) Within different taxa unequal abilities of converting complex and recalcitrant compounds like ligno-cellulose into smaller ones (mono- and oligomers) by producing depolymerising exoenzymes exist. Thus, recalcitrance of the substratum will most likely determine composition of the microbial community.
(3) Due to differences in metabolic adaption and optimum, community composition may be altered differently by environmental stress.

To address these three hypothesis, we conducted a laboratory mesocosm experiment with beech (*Fagus sylvatica*) litter from 4 different sites in Austria (Achenkirch, Klausenlopoldsdorf, Schottenwald, and Ossiach) all of which possessing different stoichoimetric ratios of carbon, nitrogen and phosphorous.

Litter was sterilized and subsequently inoculated with the same suspension of soil containing microbes from one of the sites. Microbial community composition and differential growth within this community was assessed via analysis of phospholipid fatty acids (PLFA) and stable isotope probing of PLFA with ^{13}C enriched amino acids.Microbial biomass by extraction-fumigation-extraction method and respiration was measured.

Protein depolymerisation, nitrification, nitrogen mineralization and phosphorous mineralization via pool dilution assays of (stable) isotopes, as well as enzyme activities, mass loss and stoichiometry of the litter, and pool sizes of several elements were measured in parallel by other parts of the MICDIF-project. Two harvest with three months in between were performed.

Under equilibrium conditions we found a community change between the two harvest by analysis of similarity (Global R: 0.924, $p < 0.001$), multidimensional scaling (MDS) and cluster analysis. This was change went along with a decrease of fungal-bacterial dominance (R^2: 0.552, $p < 0.001$). We found a strong effect of litter quality and

chemistry on structural microbial community composition with a positive correlation of fungi with relative lignin content and C:N of the litter. Nitrification and nitrate immobilization, and cellulase and chitinase production were enhanced by fungi, while bacteria had positive effects on protein depolymerization, and to a lower extent protease and phosphatase activity. Under “equilibrium” conditions we found a restricted accordance between abundance and growth of the microbial community. Resolution between the different microbial community compositions according to litter type and therefore to their elemental stoichiometry was better when using the abundance- then the growth-data.

When temperature-stressed, this different communities were differently strong altered. With decreasing litter C:N and increasing bacterial dominance, stress resistance increased. After three months the communities were still distinguishable with regard to litter type, and no selection for community members being generally more resilient or faster growing was found.

We conclude that litter stoichiometry had a strong influence on microbial community composition and fungal bacterial dominance, resulting in differential resistance to temperature stress and a relative high resilence after 3 months which was not subject to litter type.

Zusammenfassung auf Deutsch

Die Kompostierung von Pflanzenmaterial ist der wichtigste Prozess der Nährstoff-Mineralisierung in der Ökologie. Sie wird angetrieben durch Pilze und Bakterien, welche etwa 90% der globalen terrestrischen pflanzlichen Biomasse umsetzen. Die Zusammensetzung dieser mikrobiellen Gemeinschaft kann auf drei verschiedene Arten beeinflusst werden:

(1) Die Theorie der ökologischen Stöchiometrie sagt voraus, dass die Zusammensetzung der mikrobiellen Gemeinschaft der relativen elementaren Zusammensetzung des Substrats, welches assimiliert wird unterliegt.
(2) Es ist bekannt, das die Fähigkeit Enzyme herzustellen, die die Umwandlung von komplexen und schwer abbaubaren Verbindungen, wie Lignin-Cellulose in kleinere Einheiten wie Mono-und Oligomere katalysieren, bestimmten Taxa vorbehalten ist. So ist es anzunehmen, dass die Abbaubarkeit des Substrats die Zusammensetzung der mikrobiellen Gemeinschaft beeinflusst.
(3) Aufgrund von Unterschieden in der metabolischen Anpassungsfähigkeit und der Unterschiedlichkeit der optimalen Nische der in der Synusie beteiligten Organismen, lässt sich erwarten, dass die Zusammensetzung der Mikrobiozönose durch unterschiedliche äußere Einwirkungen, insbesondere Störungen, verändert werden kann.

Um diese drei Hypothesen zu überprüfen führten wir ein Mesokosmos-Experiment unter Laborbedingungen durch.

Es wurde Laubstreu (Blätter) der Rotbuche (*Fagus sylvatica*) mit jeweils unterschiedlichen stöchiometrischen Verhältnissen von Kohlenstoff, Stickstoff und Phosphor von vier verschiedenen Standorten in Österreich (Achenkirch, Klausenlopoldsdorf, Schottenwald und Ossiach) aufgesammelt und sterilisiert. Anschließend wurden die gesamte Laubstreu mit jeweils der gleichen Boden-Suspension (und den darin enthaltenen Mikroben) eines der Standorte inokuliert. Die Zusammensetzung der mikrobiellen Gemeinschaft und die Zuwächse innerhalb dieser Gemeinschaft wurden über die Analyse von Phospholipid-Fettsäuren (PLFA) und sog. „Stable Isotope Probing“ von PLFA mit ^{13}C angereicherten Aminosäuren gemessen. Es wurden die mikrobielle Biomasse durch ein Präextraktions-Chloroform-Extraktionsverfahren und die Atmung gemessen.
Die Proteindepolymerisation, Nitrifikation, Stickstoff- und Phosphor- Mineralisierung,

über sogenannte Pool-Verdünnungs-Ansätze mit (stabilen) Isotopen, sowie Enzymaktivitäten, Masseverlust, als auch die Stöchiometrie der Laubstreu, sowie die darin enthaltene Poolgröße einiger Elemente wurden parallel in anderen Teilen des MICDIF-Projekts gemessen.

Unter Gleichgewichtsbedingungen fand zwischen den beiden Ernten eine Sukzession statt, welche mit Hilfe der Ähnlichkeitsanalyse (Globales R: 0,924, $p < 0,001$), der multidimensionalen Skalierung (MDS) und Clusteranalyse nachgewiesen werden konnte. Diese Veränderung der Mikrobiozönose ging mit einem Rückgang der Dominanz der Pilze zugunsten der Bakterien einher (R^2: 0,552, $p < 0,001$). Wir konnten eine starke Wirkung der stöchiometrischen und qualitativen Eigenschaften der Laubstreu auf die strukturelle Zusammensetzung der mikrobiellen Gemeinschaft nachweisen. Dies äußerte sich durch positive Korrelationen von Pilzen mit dem relativen Ligningehalt einerseits, als auch dem C:N Verhältnis der Streu andererseits. Nitrifikation und Nitrat-Immobilisierung als auch Cellulase- und Chitinase-Produktion wurden durch Pilze verbessert, während Bakterien positive Auswirkungen auf die Protein-Depolymerisierung , und in geringerem Umfang auch auf die Protease- und Phosphatase-Aktivität hatten. Wir fanden nur eingeschränkte Übereinstimmung zwischen dem Auftreten und Wachstum bestimmter Organismengruppen innerhalb der mikrobiellen Gemeinschaft unter Gleichgewichtsbedingungen. Zusätzlich war und Gleichgewichtsbedingungen eine bessere Auflösung der unterschiedlichen Mikrobiozönosen nach Laubstreutypen und damit nach ihrer elementaren Stöchiometrie unter Verwendung der Abundanz-Daten gegenüber den Wachstums-Daten möglich.

Nach dem Temperaturstress, waren diese verschiedenen Gemeinschaften unterschiedlich stark verändert. Mit abnehmender C: N Verhältnis der Laubstreu ergab sich eine zunehmende bakterielle Dominanz und Stressresistenz. Drei Monate nach der Stress-Behandlung waren die Gemeinschaften immer noch im Hinblick auf das Substrat unterscheidbar. Jedoch waren keine Unterschiede zwischen Behandlungen und Kontrollen nachweisbar.

Wir folgern, dass die Laubstreu-Stöchiometrie auf die Mikrobiozönose, im Speziellen auch auf die Pilz-Bakterien-Dominanz eine starke Kontrolle ausübt. Diese hatte unmittelbaren Einfluss auf die Temperatur-Resistenz eben jener. Desweiteren wurde eine von der Laubstreu unabhängige, relativ hohe Resilienz (Rückstellvermögen, Widerstandsfähigkeit) drei Monate nach der Temperatur-Auslenkung gefunden.

General introduction

Decomposition of organic matter

Decomposition of organic matter is a major process of nutrient cycling in ecosystems. This process is driven by microorganisms, mainly fungi and bacteria in temperate ecosystems. On the global scale, plants are by far the most abundant eukaryotes in terms of terrestrial biomass. It is therefore crucial to elucidate the processes of decomposition of plant litter in order to understand their fundamental ecological function.

Litter decomposition is a continuous process. A concept to describe this process has been formulated based on a model of sequential serial stages of decomposition. Berg and McClaugherty (2008) distinguished an early from a late, and a humus-near stage (Berg and McClaugherty 2008). During the different stages specific factors, which control the decomposition process, change. Namely, different classes of organic compounds dominate the decomposition process throughout these phases (Berg, Hannus et al. 1982). Depending on the plant species, and therefore on structural and chemical composition of the litter different initial stages may occur, with net mineralization or immobilization of organic nitrogen and/or phosphorus. For some plant species a two-phase model where the early stage is omitted due to the absence of large quantities of labile substances in the litter is more accurate.

Soil animals are involved in the process of litter decomposition, especially in enlarging the surface of the debris material by feeding activities. This makes the substrate more accessible to decomposer organisms and degrading enzymes (Swift, Heal et al. 1979; Ziegler and Zech 1991; Chapin III, Matson et al. 2002; Berg and McClaugherty 2008). The dwelling of soil animals in the soil can enhance oxygen-levels which may accelerate decomposition of polymeric substrates such as lignin (Reid and Seifert 1982). Soil animals also feed on decomposer microorganisms as well as on other soil animals performing this task (Swift, Heal et al. 1979). Despite these multiple activities of soil animals that can affect litter decomposition (Huhta, Persson et al. 1998; Setala, Laakso et al. 1998; O'Hanlon and Bolger 1999; Couteaux, Aloui et al. 2002; González, Seastedt et al. 2003), microorganisms play the predominant role in litter decomposition in temperate and boreal ecosystems. They transform more than 95% of plant litter carbon in boreal forests (Berg and

McClaugherty 2008) and globally decompose 90% of the terrestrial plant biomass (Swift, Heal et al. 1979).

On an ecosystem scale the most important factors governing litter decomposition:

- Litter quantity
- Carbon quality (e.g. lignocellulose content)
- Stoichiometry (e.g. litter C:N and C:P ratio)
- Oxygen availability, temperature, and moisture.

Climatic factors play a direct and indirect role. Soil and litter moisture and temperature depend directly on climate, while litter amount, carbon quality and litter C:N ratio are mediated over so-called interactive controls such as prevailing plant functional types and soil resources. These controls in turn are influenced by climate as state factor (Chapin III, Matson et al. 2002) and feed back on litter decomposition via litter quality (Kooijman and Cammeraat 2010). Furthermore, climate has effects on soil faunal activity thereby potentially altering litter decomposition rates (Gonzalez and Seastedt 2001).

Shortly before death and abscission of leaves certain (i.e. prior to initialization of litter decomposition), formerly strictly controlled cellular structures, biochemical components and nutrients (e.g. membranes, nucleic acids, and proteins) are broken up, mobilized and re-translocated to internal stores or growing sink tissues of plants. The intrinsic controls of nutrient resorption are the type of nutrient, the initial concentration of this nutrient, and the plant species (Hagen-Thorn, Varnagiryte et al. 2006). The nutrient resorption efficiencies are particularly high for nitrogen, phosphorus and potassium. Climate, as indicated by actual evapotranspiration (AET) (Meentemeyer 1978), was shown to have a major effect on the concentrations of nitrogen in shed leaves.

The subsequent initial stage of decomposition is dominated by decomposition of non-lignified carbohydrates and soluble compounds such as sugars, polyphenols, hydrocarbons, and glycerides (Chapin III, Matson et al. 2002; Berg and McClaugherty 2008). Leaching of highly soluble compounds from senescent and dead leaves before abscission may occur, the compounds being consumed by external microorganisms (McClaugherty 1983). Besides soluble substrates, hemicellulose

and cellulose are degraded by cellulolytic enzymes which are produced by fungi and bacteria (Fujii, Sugimura et al. 2010; Schneider, Gerrits et al. 2010). Nutrient availability and local climate appear to dominate the early stage of decomposition (Berg and McClaugherty 2008). Fractionation by freeze-thaw cycles and soil animals can accelerate this initial step. Breakage of spatial confinements, like the cuticle of the leaf or the lignin-stabilized cell wall, provides access to depolymerizing enzymes produced by the decomposer community (Blanchette, Krueger et al. 1997; Chapin III, Matson et al. 2002) which also enhances the decomposition process.

Uptake of nutrients through the cell membranes of microorganisms is limited with respect to the size of solutes: Molecules with masses up to 600 g mol^{-1} (Weiss, Abele et al. 1991) can pass freely or through carrier proteins into microbes, depending on water solubility (Benz and Bauer 1988). Larger molecules must be broken down to smaller components before they can be taken up, a process called depolymerisation (Ratledge 1994). Besides temperature, water potential, and pH, the depolymerisation of larger molecules, i.e. proteins, waxes, cellulose, and lignin, is dependent on the degree of branching, complexity, and presence of functional groups determining the chemical potential and the availability of starting points for extracellular enzymes (Swift, Heal et al. 1979). For the breakdown of some high-molecular weight substrates specific extracellular enzymes are required. For instance, for lignin decomposition specific oxidative enzymes (ligninases) are needed, enzymes which belong to the oxidoreductases (EC 1.14.99-).

Especially in the second or so called “late” phase of decomposition in which remaining substances tend to be more recalcitrant, i.e. more lignified, the activities of such lignolytic enzymes increase. Ligninases are produced by fungi (Worrall, Anagnost et al. 1997) and some bacteria (Uma, Kalaiselvi et al. 1994), especially under nitrogen deficiency (Leatham and Kirk 1983).

The process of decomposition of lignified plant debris is traditionally split into three categories, originally differentiated by visual aspects of lignin decomposition. Lignolytic consortia of fungi and bacteria can be divided into three different classes causing white-rot, brown-rot, and soft-rot. It has been shown that this simple classification is based on different taxonomic classes of decomposer organism and is also related to differences in the functional taxonomy of lignin decomposition.

Surprisingly, this classification system can also be used for categorizing the decomposers of cellulose and hemicelluloses (Worrall, Anagnost et al. 1997; Goyal, Samsher et al. 2010). Although sets of lignolytic enzymes vary between different species within the different classes, due to historic reasons, the knowledge of lignin-degrading fungi is, compared to that of bacteria, much more developed. This has often led to the mis-interpretation that fungi are the sole lignin decomposers in terrestrial ecosystems (Chapin III, Matson et al. 2002).

The white-rot type is the only one in which complete decomposition of lignin is reached. Aerobic conditions are required (Reid and Seifert 1982; Eriksson K-E, Blanchette et al. 1990) and basidomycetes dominate this group. Some organisms within this group preferentially degrade lignin over cellulose (Hakala, Maijala et al. 2004). Manganese peroxidases (MnP) are most common among white-rot types (Hofrichter 2002). MnP is dependent on Mn for its activity (Perez and Jeffries 1992) via oxidation of Mn^{2+} to Mn^{3+}. The latter, being more reactive than the former, can be chelated and stabilized by organic acids like oxalic and malic acid. Mn^{3+} reacts with the phenol residues of lignin.

Similar to the white-rot type, the activity of brown-rot organisms is linked to low nitrogen levels (Keyser, Kirk et al. 1978; Bono, Gas et al. 1983; Leatham and Kirk 1983; Kirk and Shimada 1985), although some studies presented data with fungi showing no repression of lignin-decomposition by enhanced nitrogen (Freer and Detroy 1982; Leatham and Kirk 1983). In contrast to the white-rot type, brown-rot can also be caused by anaerobic bacteria (Berg and McClaugherty 2008). Brown-rot organisms degrade mainly cellulose and hemicelluloses, but can chemically alter lignin. In particular, methoxyl groups are removed from aromatic rings (Crawford, Crawford et al. 1981), producing methanol (Eriksson K-E, Blanchette et al. 1990). MnP is found rather seldom in the set of enzymes from brown-rot organisms. Reactive oxygen species are considered to be mainly involved in lignin decomposition (Illman 1991).

Soft-rot consortia can degrade lignin to a substantial degree but do not mineralize it completely. There is indication that the degree of depolymerisation by soft-rot organisms is negatively related to the fraction of guaiacyl units in the lignin. This

would explain the greater decomposability of wood of deciduous trees (syringyl-type lignin) than of conifers (guaiacyl-type lignin) (Nilsson, Daniel et al. 1989).

When recalcitrance has reached a certain point, the decomposition ceases. This represents the third, “humus-near” stage of litter decomposition.

Ecological Stoichiometry

Since Liebig it is known that limitations in plant growth will occur if one essential elements is in the minimum (Von Liebig 1840). The understanding of the necessity of stoichiometric balance of nutrients since then increased with time. Nowadays it is clear that the stoichiometry of resources does not only affect plant growth but is central to every living organism including consumers. Actually, the importance of stoichiometric balance of nutrients is so profound that R. W. Sterner and J. J. Elsner in their book “Ecological Stoichiometry” summarized their objective with the following sentences ”Organisms can be thought of as complex evolved chemical substances that interact with each other and the abiotic world in a way that resembles a complex, composite chemical reaction. Like any other "normal" chemical rearrangement at the surface of the Earth, when organisms interact, mass must be conserved and elements are neither created nor destroyed (…). There is stoichiometry in ecology, just as there is in organic synthesis in a test tube”(Sterner and Elsner 2002).

Homeostasis accounts for this preservation of stoichiometry in organisms throughout different environmental conditions (Kooijman 1995). The term homeostatis is used to indicate that in all organisms the elmental composition is bounded, i.e. to indicate that organisms have the ability to maintain their chemical composition constant, despite large variation in the chemical composition of the environment and resources. As individual organisms take up substrates for growth, respiration, reproduction, formation of enzymes, steroids, and so forth, they have to handle ratios of carbon to nitrogen and phosphorus quite different from their needs. Although different metabolic states of microorganisms can vary in their stoichiometric balance, there are constraints to the cellular stoichiometric variability. General ranges can be given (Killham 1994): bacteria for instance are considered to have C:N ratios of about five while fungi tolerate a wider variability of this ratios (Sterner and Elsner 2002).

Plants, and therefore litter, can cover wide ranges of elemental composition due to fluctuations of storage products within their cells and differences in structural

components of their tissues. The more variable stoichiometric response of plants to their chemical environment is sometimes called partial homeostasis. Generally speaking, microbes in contrast to plants exhibit more restricted ranges of elemental composition. This requires metabolic processes which balance the fluctuations of substrates present in the environment and/or taken up, in comparison to the actual elemental need of the individual microorganism. For example, if under nitrogen deficiency substances with high C:N ratio are processed by the microorganisms, so-called overflow respiration can be observed. Overflow respiration represents an enhanced respiratory activity, presumably to remove the excess carbon from the resource substrate, and therefore increase the relative abundance of nitrogen in microbial cells (Manzoni, Jackson et al. 2008). It is therefore practical to apply the concept of carbon-use efficiency in ecological stoichiometry, defined as the ratio of fixed carbon relative to carbon taken up. To measure microbial carbon-use efficiency in environmental samples, all organic compounds taken up, those left or exuded into the external medium, and respiratory use of organic compounds must be considered and quantified accurately which represents a daunting task in mesocosms and in situ (Keiblinger, Hall et al. 2010). On the other hand, if C:N ratio of the resource is considerably below the needs of the microbial consortia, net nitrogen mineralization occurs.

Differences in C:N ratios of resources and C:N requirements of different microbial groups lead to differentiation of microbial communities in soils and litter (Swift, Heal et al. 1979; Hogberg, Hogberg et al. 2007). This is not limited to the ratio of fungal to bacterial biomass but functional diversity within bacteria is controlled as well. (Allison 2005) has developed a model for computing the dependency of different functional participants in the decomposition process where microbial community composition is controlled by resource C:N ratios to meet the nitrogen demand for enzyme production. The ratio of carbon to nitrogen of a resource is an easily quantifiable parameter, and therefore often has been used for characterization of the complexity and ecomposability of resources (Killham 1994).

In conclusion, besides absolute nutrient concentrations the ratios of elements and the recalcitrance of substrates towards decomposition play major roles in nutrient fluxes, rates of decomposition, and microbial community composition. On the other hand, the efficiency of nutrient uptake and biomass production by different decomposer

organisms varies throughout different C:N environments (Killham 1994; Hodge, Robinson et al. 2000). Microcosm experiments suggest that this may also be true for the process of decomposition and for N:P ratios as well (Guesewell and Gessner 2009).

Phospholipid fatty acids as measure of microbial biomass

The membranes of living cells, except for many *Archaea,* consist mainly of phospholipid fatty acids (PLFA), the major lipids in bacteria, fungi and other eukaryotes (White 1979). PLFA are believed to be present in similar amounts throughout the life of microbial cells, whereas they rapidly decompose by hydrolysis of the phosphate group when cells die (White, Davis et al. 1979; Tollefson and McKercher 1983; Zelles 1999). This makes PLFA analysis a good proxy for determination of living microbial biomass in environmental samples (Zelles, Bai et al. 1994; Frostegard and Baath 1996; Zelles 1999). As shown earlier by Balkwill et al. conversion factors can be established for relating PLFA concentrations to other measures of microbial biomass such as ATP content, lipid and glycerol phosphate concentration, and direct cell counting (Balkwill, Leach et al. 1988). Microbial biomass is often expressed as total lipid phosphate which is relatively easy to determine in a reproducible manner. Fifty micromoles of lipid phosphate per gram dry weight is “a reasonable estimate of the mass of the detrital microflora”(White 1979).

Phospholipid fatty acid nomenclature

There are two types of chemical nomenclatures for PLFA in use. Their difference lies in the starting point of counting double bonds, also called unsaturated bonds. If a PLFA is named 18:2(9,12), it consists of 18 carbon atoms and possesses two double bonds. However, the correct structure still remains undefined when the location of the double bonds is not given. This is determined by addition of the Greek letters □□□α□ or □. These letters annotate that counting starts at the first carbon atom (□) or the last carbon atom of the fatty acid (□), based on the rule of chemical counting from the carbon with the highest oxidation state, in this case the carboxyl-group, which is numbered as one. The index □ is not used any longer, as “□“□and□“□“ serve as indices for carbon atoms bearing a functional residue such as a hydroxyl group (Zelles 1999). There are good reasons for the use of either the □ or the □

index. Traditionally, □ is used when biochemical pathways of desaturation or chain elongation are concerned. The use of □ is founded in the process, likewise the enzyme class introducing double bonds into saturated fatty acids, namely desaturases or dehydrases. These reactions occur on existing saturated free fatty acids and even those bound to membrane phospholipids (Rock and Jackowski 2002; Aguilar and de Mendoza 2006). Another minor way of forming double bonds in fatty acids is during elongation, i.e. in the anaerobic formation of unsaturated fatty acids (Bloch 1969). In the medical literature, especially when inflammatory processes are concerned, the □-index is more commonly used (Calder and Grimble 2002), where □ is sometimes replaced by the letter n. For the sake of simplicity, in this text the □-nomenclature is used.

In addition to determining the position of double bonds as described above, the letters *c* or *t* are used (despite IUPAC nomenclature would suggest Z and E) to indicate the geometry of the four carbon atoms involved in this part of the molecule. The prefix “c” refers to the cis (Z) configuration, where the carbon atoms attached to either side of the planar and rigid double bond point in the same direction, ”t” refers to the trans configuration (E) where they are oriented in opposite directions. Methyl-branching at the next to the last carbon (iso) is indicated by the prefix i, or an a if branching occurs at the next lower carbon atom (anteiso). When branching positions are unknown, br is used. Indication of a cyclopropyl fatty acid is expressed by cy prefix.

Phospholipid fatty acids as biomarkers for changes in microbial community structure

Since PLFA can undergo a wide range of biochemical modifications, in parts characteristic for specific groups of organisms, they may be used a biomarkers for assessment of particular microbial community patterns and their changes (Zelles 1999; Moore-Kucera and Dick 2008).

In several studies, the outstanding value of PLFA for distinguishing between fungal and bacterial groups has been emphasized (Bardgett, Hobbs et al. 1996; Frostegard and Baath 1996). In the majority of articles, the fatty acid 18:2(9,12)c – linoleic acid - is used as biomarker for fungal biomass (Baath and Anderson 2003; Joergensen and Wichern 2008), since its amount is strongly correlated to ergosterol, another

biomarker for fungal biomass (Baath and Anderson 2003; Klamer and Baath 2004). Ergosterol is a membrane-bound steroid considered to be predominantly present in fungi (Seitz 1979) and is often used as a marker for living fungal biomass (Suberkropp, Gessner et al. 1993) or rather fungal membrane (Ruzicka, Edgerton et al. 2000), since the late 1970s when Seitz et al. developed a method for detection of fungal contaminants (Seitz 1977) and fungal growth (Seitz 1979). However, the relationship between fungal biomass and ergosterol is not always that simple; recent studies have shown that egosterol should be used cautiously as a biomarker for living fungi (Mille-Lindblom, von Wachenfeldt et al. 2004) since ergosterol decomposition after fungal death can be quite slow. Thus, Klamer and Baath came up with conversion factors for both egosterol and 18:2(9,12)c to fungal biomass (Klamer and Baath 2004). For a summary of conversion factors of fungal PFLA to fungal biomass the reader is refered to (Joergensen and Wichern 2008).

Other PLFAs can also be applied for the estimation of fungal biomass if the presence of living plant material or other eucaryotic cells can be excluded. This is the case in particular for oleic acid 18:1(9)c (Joergensen and Wichern 2008), which is well correlated to 18:2(9,12) (Hogberg 2006), 18:3(9,12,15)c (Potthoff, Steenwerth et al. 2006; Joergensen and Wichern 2008) and other even-numbered polyunsaturated (polyenoic) phospholipid fatty acids since they are exclusively produced by eucaryotes (Erwin 1973; Federle, Dobbins et al. 1986; Klamer and Baath 2004). Actinomycetes, gram-positive filamentous bacteria, can be monitored by the sum of i17:1, 10Me16:0, 10Me17:0 and 10Me18:0 (Potthoff, Steenwerth et al. 2006). An overview of assignments used in numerous articles is given in Table A. An attempt to summarize the literature used for PLFA assignments in Table A is made in Table B. This complicated form of presentation is because assignments in the recent literature has often been used without thorough presentation of background literature leading to these assumptions.

Table A) Assignment of specific groups of PLFA to specific groups of organisms. Notes: a: E1: found in Seeds of *Citrus sp.*, b: E4: found in dried leaves of *Sinapis sp.*", c: E5: "11.8 µmol / g C(fungi)", d: R1: "almost exclusively in bacteria and absent in fungi", R1: "bacteria with branched FA normally distributed to proportion of branched FA" (others random concentration; later assigned as g+) , f: R1: "limited to photosynthetic organisms", g: R1: occurs in "some Zygomycota" h: R1: "the data suggests…normally distributed…estimate relative abundance", i: R1: "unique to actinomycetes", R4: "<0,5 = unstressed", k: R4: "occur in g+ and eukaryota in lower amounts", l: R4: "occur in some g- (sulfate reducers)", m: R4: "occur in other eukaryotes & bacteria", n: R4: "rare in bacteria"

Type PLFA	Specific Marker	used as biomarker for	but occures in less amounts in	References	Comments
Saturated straight chain <20C		Bacteria in general	Fungi	E4, E5, R1, R3-4	
Saturated straight chain >20C		Eucaryonts	-	R1, R2, R4, E4	d, l
Saturated branched		Bacteria in general and gram-positve bacteria	Gram-negative bacteria and fungi	E4, R1-4	e, d, h, l
Saturated branched with C_{10}-methyl		Actinomycetes (g+) and sulfate reducers	gram-positve bacteria in general	E4, R1-4	i, l
Cyclopropyl (cy)		Bacteria in general and gram-negative bacteria	gram-positve bacteria	E4, R1-4	e, d, k
enoic, w3, >20		Plants		R1	f
enoic, w8		Methan oxidizing bacteria		R2	
Monoenoic, branched		Sulfate reducers	-	R3	
Monoenoic			gram-negative bacteria and plants	R1	
	16:1d7	Bacteria in general and gram-negative bacteria	gram-negative bacteria and plants	R1, R3	d, o
	16:1d7c	gram-negative bacteria	bacteria in general	R4	k
	16:1d8c/t	Methan oxidizing bacteria	gram-negative bacteria and plants	R3	
	16:1d9	Aerobes	gram-negative bacteria and plants	R3	
	16:1d9c	Fungi	gram-negative bacteria and plants	E5, R4	k
	16:1d9t	General bacteria	gram-negative bacteria and plants	R1	d, k
	16:1d11	General bacteria	gram-negative bacteria and plants	R1, R3	d
	16: 1d11c	Methan oxidizing bacteria and Fungi	gram-negative bacteria and plants	E1, R3	k
	16:1d13	Plants	-	R1	f
	18:1	g- bacteria	gram-negative bacteria and plants	R4	k
	18:1d9	Fungi	bacteria in general and plants	E4, R3	
	18:1d9c	Fungi	gram-negative bacteria and plants	R4	m, k
	18:1d10c/t	Methan oxidizing bacteria	gram-negative bacteria and plants	R3	
	18:1d11c	Fungi and gram-negative bacteria	gram-negative bacteria and plants	E4, R1, R4	a, k
	18:1d11t	General bacteria, aerobes	gram-negative bacteria and plants	R1, R3	o
	18:1d12c	Methan oxidizing bacteria	gram-negative bacteria and plants	R3	
	18:1d13	General bacteria	gram-negative bacteria and plants	R1, R3	d
	18:1d13c	g- bacteria	gram-negative bacteria and plants	R4	k
polyenoic			Plants	E4	
	16:3d7,10,13	Microalgae	Plants	R3	
	18:2d9,12	Fungi / fungal BM / fungal SA and dead plants and cyanobacteria	Plants	E4, E5, R1, R3, R4	b, c, m
	18:3d6,9,12	Fungi	Plants	R1, R3	g
	18:3d9,12,15	Fungi	Plants	E4, R3, R4	m
	20:2	Fungi and plants	Plants	E4	
	20:3d8,11,14	Protozoa	Plants	R3	n
	20:3d9,12,15	Protozoa and plants	Plants	E4, R3	
	20:4d5,8,11,14	Protozoa	Plants	R4	n
	20:5	Barophilic psychrophulic bacteria	Plants	R3	
	22:6	Barophilic psychrophulic bacteria	Plants	R3	
Ratio cis vs. Trans monenoic	16:1d11t/16:1d11c	Stress indicator		R4	j
	16:1d8t/16:1d8c	Stress indicator		R4	j
Ratio monenoic precursers vs cyclopropane	16:1d8c/cy19:0	Stress indicator		R4	j
	161d11c/cy17:0	Stress indicator		R4	j
Ratio polyenoic vs branched	18:2d9,12c/branched	Fungal/Bacterial ratio		R4	k
	18:2d9,12/ general bacterial	Fungal/Bacterial ratio			

Table B) List of References for Table A, E = Experimental study, R = Review.

References	first author	journal	year (s)	contribution	used References (in Review)
E1	Nordby	Agric Food Chem 396	1981	Experimental 1	
E2	Kroppenstedt	Chem Meth Bact 173	1985	Experimental 2	
E3	Frostegard	Appl Envir Microb 3605	1993	Experimental 3	
E4	Zelles	Chemosphere 275	1997	Experimental 4	
E5	Klamer	Soil Bio Biochem	2004	Experimental 5	
R1	Federle	Persp. Micro Eco 493	1986	Review 1	Erwin,1973; Lechevalier,1977; Weete,1980; O'Leary,1982
R2	Zelles	Biol Fertil Soils 111	1999	Review 2	Yano,1972; Yano,1978; Harwood,1984; Balkwill,1988; Brennan,1988; Lechevalier,1988; Lösel,1988; O'Leary,1988; Ratledge,1988; Lechvalier,1989; Galbraith,1991; Kroppenstedt,1992; Bowman,1993; Haak,1994; Zelles,1994; Alugupalli,1995; Zelles,1995a
R3	Hill	Appl Soil Eco 25	2000	Review 3	"Our knowledge of such siguature molecules comes from the use of fatty acid analysis for bacterial taxonomy"
R4	Leckie	Forest Eco Man 88	2005	Review 4	Wilkinson,1988; Lechevalier,1988; Lechevalier,1977; Federle,1986; Frostgard,1996; Klamer,2004; Zelles,1999; Guckert,1986; Ratledge,1988;
O1	O'Leary	Microbial lipids 117	1988, 1982	NA, Book	NA
O2	Wilkinson	Microbial lipids 299	1988	NA, Book	NA
O3	Weete	Lipid Biochem. Fungi & Other Org.	1980	NA	NA
O4	Erwin	LIPIDS BIOMEMBRANES	1973	NA	NA
O5	Lechevalier	Crit Rev Microbio	1977	NA	NA

Isotope fractionation and stable isotope probing (SIP) in PLFA

The use of stable isotopes as tracers has become a widely used technique for determining, for example, the rates of microbial processes such as the uptake of nutrients, respiration, or mineralization (Boschker and Middelburg 2002). The applicability of naturally-occurring stable isotopes of low abundance as tracers for their more abundant analogues results from the fact that the former have nearly identical chemical properties as the naturally more abundant, usually lighter analogues. Nevertheless, discrimination of light and heavy isotopes can occur in biochemical and physical processes and at biosynthetic branching points (Hayes 2001). This is due to their slightly differing chemical potentials based on their differences in mass. The term 'isotope fractionation' or discrimination embraces this process. The degree of isotope fractionation is defined as the difference in isotopic composition between the reactant and the product, conventionally given as □□□‰:

$$= \left(\frac{\frac{H_b}{L_b}}{\frac{H_S}{L_S}} - 1 \right) \times 1000\ [‰] - \left(\frac{\frac{H_a}{L_a}}{\frac{H_S}{L_S}} - 1 \right) \times 1000\ [‰]$$

where R^h is the ratio of the heavy to the light isotope. The subscripts refer to the product , the reactant a and the international standard S (e.g. Vienna PeeDee Belemnite for ^{13}C, with $R^{13}C$ = 0,0112372). The nucleide number h of the heavy isotope is given as a superscript following the Greek letter □, followed by the letter of the corresponding element E. The letters H and L stand for the number or percent of the heavy and the light isotope of the element.

Fractionation results in depletion or enrichment in the heavy isotope in a product relative to the reactant. In specific biochemical reactions fractionation can be rather high, e.g. 27‰ for autotrophic fixation of CO_2 via ribulose 1,5-bisphosphate carboxylase/oxygenase (RUBISCO) (Farquhar, Oleary et al. 1982), with discrimination of the heavy ^{13}C-CO_2 against the light ^{12}C-CO_2. Several studies have investigated the isotope fractionation during biosynthesis of PLFA in cultured heterotrophic aerobic and anaerobic microorganism in laboratory isolates, as well as in enriched cultures (Blair, Leu et al. 1985; Van Der Meer, Schouten et al. 1998;

Teece, Fogel et al. 1999; Hayes 2001; Londry, Jahnke et al. 2004; Cowie, Slater et al. 2009). Considering aerobic heterotrophic microorganisms, these studies reported rather low values ranging from 4‰ enrichment to 3‰ depletion relative to the given carbon source. High values of depletion have also been reported, especially for facultative and obligate autotrophic organisms (Van Der Meer, Schouten et al. 1998; Londry, Jahnke et al. 2004; Cowie, Slater et al. 2009).

Nevertheless, tracing the uptake of ^{13}C-labeled substrates into specific components such as PFLA can be employed to monitor the relative metabolic activity of different participants of a community. This approach is commonly referred to as stable-isotope probing (SIP). The term SIP was first introduced by Boschker et al. (Boschker, Nold et al. 1998) to monitor the turnover of PLFA.

Application of the PLFA-SIP method has allowed detailed studies, such as to the importance of specific members of a community to carbon cycling processes. When the method is applied with substrates which can be used only by a specific group of microorganisms, e.g. methane by methanotrophs, PLFA-SIP can provide further insight into their specific ecological relevance (Crossman, Abraham et al. 2004; Mohanty, Bodelier et al. 2006). Another possibility is to determine whether different microbial taxonomic groups use different or the same sources of carbon (Elfstrand, Lagerlof et al. 2008), e.g. plant residues or exudates from living plant roots. Pulse-labeling experiments with ^{13}C-CO_2 have been employed to quantitatively trace ^{13}C-photosynthates via rhizodeposition into soil biota (Griffiths, Manefield et al. 2004). Thus, critical components of the global terrestrial carbon-cycle can be elucidated based on this technique. In other words: “It is possible to directly link microbial functional groups or even individual species with specific processes in the soil carbon cycle” (Leake, Ostle et al. 2006).

As a note of caution it must be mentioned that the concentration and the duration of labeling must be carefully considered to avoid ambiguous data. For instance, upon extended duration of experiments labeling can occur in organisms that not directly use the ^{13}C-labeled substrate, through a phenomenon referred to as cross-feeding; or, if substrate concentrations are too high, the original community composition can be altered (Neufeld, Dumont et al. 2007).

The applications of PLFA-SIP to ecosystem studies with respect to different environments or substrates, and the possibilities of combining it with other methods are limitless. Judicious selection of the specific substrates for experiments involving gas measurements and subsequent PLFA analysis (Qiu, Noll et al. 2008) is necessary, and so-called push-pull tests in aquifers combined with fluorescence in situ hybridization (FISH) (Pombo, Pelz et al. 2002) are state of the art (Neufeld, Wagner et al. 2007). Given the importance of SIP, recently several reviews on SIP have been published (Evershed, Crossman et al. 2006; Neufeld, Wagner et al. 2007).

Stability of communities and network theory

The stability of ecosystems and the relationship to their complexity have been discussed in ecological science for several decades. Charles Elton is believed to be one of the first ecologists who stated that the stability of an ecosystem is positively correlated to its complexity (cited in(McCann 2000)). This intuitive point of view was questioned by a mathematical model of Robert May (May 1973). In his model, complexity was manipulated by adding or removing participants in the system. Stability was measured as the ability to re-establish a balanced system after having been disturbed by e.g. the addition of novel participants or altered 'environmental' conditions. May's model suggests that simple systems are more stable than those with many participants. This picture was not corrected until Peter Yodzis, using a hierarchical network approach instead of a model based on random graphs, found that real ecosystems are networks with high complexity and stability (Yodzis 1981). The basic difference in the two types of networks is that all interactions in models based on random graphs are random, i.e. the number of links or relations fluctuate around a mean value. In hierarchical models some participants are distinguished by having significantly more or stronger interactions then others which is a consequence of the history of the network (Barabasi and Albert 1999; Albert and Barabasi 2002). In addition, in natural networks the strength and number of relationships stand in an anti-proportional context, i.e. exclusive consumption by one participant of one specific substance/prey is linked to a strong relationship between both participants of the network and vice versa. Conversely, if many connections exist they tend to be weaker. Nevertheless, weaker food web connections play an outstanding role in stabilizing ecosystems (McCann, Hastings et al. 1998).

Stability as term can be divided into two different categories: (1.) “stability definitions that are based on a system's dynamic stability,” and (2.) “stability definitions that are based on a system's ability to defy change” (McCann 2000). May for example defined stability as a situation where the resulting community is balanced at the same values as the system before a disturbance occurred (second category) (May 1973). This is a definition close to that of Holling’s “engineering resilience” (as cited in (Gunderson 2000)). McCann et al. used a stability-definition where changes in organism assemblage could occur if they result in persisting communities, often accompanied by small changes in gild biomass (first category) (McCann, Hastings et al. 1998). This definition is close to that which Holling sketches in an earlier attempt to disentangle the various meanings of stability by introducing the term “resilience” (Holling 1973), later called “ecological resilience” for distinction from “engineering resilience”. Engineering resilience represents the existence of one single equilibrium of the system with no oscillation when the system experiences no perturbation (Holling 1973; Gunderson 2000). For the remainder of this work, McCann’s suggestion is followed to use “general stability” and “general variability” in preference to resilience and resistance to examine stability (McCann 2000).

Aims of the Study

The aim of this study was to assess the effects of litter stoichiometry and abiotic stress (heat and freeze) on the stability and functionality of the litter decomposer community. This was performed in terms of:

a. monitoring the change of the structural microbial community composition by analyzing PLFA
b. assessing controls on ^{13}C-incorporation into PLFA (PLFA-SIP) and therefore on the functional microbial community composition
c. linking this findings to ecosystem processes, and uptake efficiencies of nitrogen and carbon by measuring respiration, microbial carbon, and nitrogen uptake from a labeled amino acid pool.

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Manuscript

Effects of resource stoichiometry and stress on the structural and functional microbial community composition of decomposing beech litter

Introduction

Decomposition of organic matter is a major process in the nutrient cycles of terrestrial ecosystems. In temperate ecosystems plant litter decomposition is driven by microorganisms, mainly fungi and bacteria, as they transform more than 95% of plant litter carbon in boreal forests (Berg and McClaugherty 2008) and globally decompose about 90% of the terrestrial plant biomass (Swift, Heal et al. 1979). The major factors controlling litter decomposition are litter quality and quantity, climate, and the microbial communities (Aerts 1997). While hundreds of studies have investigated in depth the climatic and litter quality controls, much less is known on the effect of microbial communities per se. Thus, to understand one of the fundamental ecological functions in terrestrial nutrient cycles, it is crucial to elucidate the control of microbial community composition (MCC) on litter decomposition. In many ecosystems, attempts have been made to link MCC with specific functions encompassing the decomposition process (Six, Frey et al. 2006). This task was most often tackled with indirect measurements, for example by measuring extracellular enzymes produced by microorganisms (Schimel and Weintraub 2003; Romani, Fischer et al. 2006), "while less attention has been given to community-level responses" (Hill, Mitkowski et al. 2000). At least some studies demonstrated changes in decomposer community with litter decomposition (see (Berg and McClaugherty 2008) and references herein).

In their seminal review (Sterner and Elsner 2002) called attention to the applicability of ecological stoichiometry theory (EST) on litter decomposition and microbial functions. According to EST differences in C:N ratios of resources and C:N requirements of microbes,is expected to lead to a differentiation of microbial communities between different litter types and possible also during litter decomposition, particularly in fungal: bacterial dominance (FBD) (Swift, Heal et al. 1979; Hogberg, Hogberg et al. 2007; Strickland and Rousk 2010). Recently, in a review on fungal: bacterial dominance (Strickland and Rousk 2010) the authors

supported earlier findings that bacteria seem to be more homeostatic and have narrower C:N ratios than fungi (6 versus 12-14, respectively). Fungi exhibited wider C:N ratios but also had a wider range of C:N ratios (McGill, Hunt et al. 1981; Killham 1994; Sterner and Elsner 2002), though C:N ratios overlapped between bacteria and fungi (Strickland and Rousk 2010). *In situ* manipulations of resource quality and consequently of soil microbial communities reported changes in FBD in line with EST (Hogberg, Baath et al. 2003; de Vries, Hoffland et al. 2006; Demoling, Nilsson et al. 2008), but some contradicting results have been found with the intensity of management (i.e. nitrogen availability) (Bardgett and McAlister 1999; de Vries, Bloem et al. 2007; Mulder and Elser 2009). A few theoretical models have also addressed the possible interactions between resource stoichiometry and changes of MCC at different taxonomical or functional depth (Schimel and Weintraub 2003; Allison 2005). Beside the ecological impact of resource stoichiometry on the structure and function of microbial communities (Cleveland and Liptzin 2007), C:N ratios have often been used as a proxy for the complexity and decomposability of resources (Killham 1994), with litter of low C:N decomposing more rapidly than litter with high C:N.

In addition to C:N ratios and the strong influence of climatic factors (Aerts 1997), lignin content is believed to have major influence on microbial colonization and litter decomposition, especially in the late phase of litter decomposition (Wright and Covich 2005; Berg and McClaugherty 2008). Though there is evidence for some bacteria producing oxidative enzymes to decompose lignin (Perestelo, Rodriguez et al. 1996; Vargas-Garcia, Suarez-Estrella et al. 2007), it is widely accepted that fungi are dominating the lignin decomposition (de Boer, Folman et al. 2005).

Analysis of phospholipid fatty acids (PLFA) as microbial biomarkers has proven highly useful to investigate shifts in structural microbial community composition (SMCC) in the environment (Frostegard, Baath et al. 1993; Frostegard, Tunlid et al. 1996; Zelles 1999; Haubert, Birkhofer et al. 2009). When using PLFA-Stable Isotope Probing (PLFA-SIP), i.e. measuring the ^{13}C incorporation from some labile or recalcitrant ^{13}C-labelled resource into specific PLFAs, questions concerning the functional MCC (FMCC) can be addressed (Moore-Kucera and Dick 2008; Bapiri, Baath et al. 2010).

In this mesocosm study, which comprises two different experiments, we investigated:

1. If there is a control of litter stoichiometry on MCC and ecological function?
2. If MCC more strongly controls ecosystem processes under non-equilibrium conditions, i.e. after stress treatments?
3. Are fast-growing microbes (r-strategists) less resistant to stress than slow-growing ones (K-strategists)?

We hypothesized that microorganisms exhibit different elemental requirements (i.e., C:N:P demands) and that the stoichiometric composition of plant litter thereby exerts a major control on MCC and ecosystem functioning during litter decomposition (Experiment 1 (E1)). Furthermore, we hypothesized that MCC has only a minor effect on ecosystem processes under equilibrium conditions. Under non-equilibrium conditions, however, the structure of the microbial community would strongly determine the functional response of the system (Experiment 2 (E2)). Moreover we hypothesized that along the r-K selection continuum and based on trade-offs in life history theory (Winogradsky 1924; MacArthur and Wilson 1967; Shipley and Keddy 1988; Notley-McRobb, King et al. 2002; Fierer, Bradford et al. 2007). fast-growing microbes (r-strategists), showing high PLFA turnover and ^{13}C incorporation into related biomarkers, would be less resistant to stress than slow-growing microbes (K-strategists).

Experimentally we tested these hypotheses using stoichiometrically different beech litters that were gamma irradiated, inoculated with a common O horizon homogenate and kept at 15 °C for up to six months (E1).,Stress treatment was performed through exposure of beech litter to realistic temperature excursions, either by heat (+30°C) and freeze (-15°C) treatment, respectively. To examine the stoichiometric controls (E1) and the resistance and resilience of the microbial community structure and function in response to stress (E2), we measured a large set of microbial processes, microbial biomass, PLFA composition and ^{13}C incorporation into PLFA. In E2 these measurements were performed one week (H2) and three months (H3) after the stress treatment. In this study structural microbial community composition (SMCC) was investigated by PLFA analysis (mol%), while the functional microbial community composition (FMCC) was assessed by PLFA-SIP, i.e. ^{13}C incorporation from labeled amino acids into PLFA.

Materials and Methods

Mesocosms

Four beech litter types with distinct stoichiometries (Achenkirch, Klausenleopoldsdorf, Ossiach, and Schottenwald; Supplementary Table 11) were collected, dried, cleaned, cut and sieved (0.2 - 1 cm mesh). Subsequently, the litter was sterilized with gamma radiation and inoculated with a mixture of soil (O-horizon) and litter, both from Klausenleopoldsdorf in a 1:1 proportion (Wanek, Mooshammer et al. 2010). Inoculation took place in March 2009. For each litter type and each harvest five replicates of 60 g litter fresh weight were placed into PVC tubes (10 cm high, 12.5 cm in diameter, perforated plastic grid as bottom, micromesh cloth and parafilm as top lid). These “mesocosms” were kept at 15 °C and the water content of the litter was weekly adjusted to 60% fresh weight by addition of autoclaved tap water (experiment 1, E1).

To obtain the elemental composition of the litter, samples were dried and ground in a ball mill (MM2000, Retsch, Haan, Germany) to obtain a fine homogeneous powder. Total carbon and nitrogen contents were determined by an elemental analyzer (Leco CN2000, LECO Corp. St Joseph, MI, USA). The ground samples were wet-oxidized with 6 mL H_2SO_4 (95-97%, pa) and 2 mL HNO_3 (65%, pa) in a microwave oven (MARS Express, CEM Corp., Matthews, NC, USA). Element concentrations (P, K, Mg, Mn, Ca, Fe) were determined by inductively-coupled plasma atomic emission spectroscopy (Vista PRO, Varian Inc.(now Aglient Technologies).

Concurrently, a second set of mesocosms (experiment 2, E2) with three of the four litter types (K, O, S) were set up. After three months, E2 mesocosms were split into three sets for performing two different stress treatments, keeping one set as untreated controls. Mesocosms were subjected to a hot (+30 °C) or a cold treatment (-15 °C) which was done by gradual adjustment to the treatment temperatures within 72 hours. The mesocosms were maintained at the respective temperatures for five days. Gradual readjustment of the mesocosms back to 15° C took again 72 hours. Half of the mesocosms were harvested 72 hours after having reached the temperature of 15 °C (H2-E2), the other half was harvested three months later (H3-E2).

Determination of ^{13}C (^{15}N) in respiratory CO_2, dissolved organic matter, and microbial biomass

Out of each mesocosm one litter aliquot (1 g fresh weight) was weigehd into a sterile 50-mL polypropylene tube. An amino acid labeling solution (see below) containing 250 µg amino acids in 3 mL deionized water was added to each sample. The labeling solution was prepared from two amino acid mixtures i.e. one part ^{15}N-labeled amino acid mix (>98 atom percent ^{15}N, 20 amino acid mixture, Spectra Gases Inc., Columbia, USA) and three parts ^{13}C-labeled amino acid mixture (algal amino acid mixture, U-13C, 97-99%, Cambridge Isotope Laboratories, Andover, USA). Carbon and nitrogen concentrations as well as isotopic composition of the amino acid mixture were determined after dilution with an unlabeled standard (1:10 v:v), drying of the solution and isotopic measurement by means of an elemental-analyzer coupled to an isotope-ratio mass spectrometer (EA-IRMS) (elemental analyzer: NA 1108, CE Instruments, Milan, Italy; Interface: ConFlo III, Finnigan MAT, Bremen, Germany; IRMS Delta Plus, Finnigan MAT, Bremen, Germany). For PLFA, microbial biomass, DOM, and respiration analysis, pooled unlabelled samples for determination of natural abundance of ^{13}C and ^{15}N were run in parallel.

To measure respiratory CO_2 during the incubation a 15-mL narrow polypropylene tube was introduced and fixed with a wire to the rim of the outer tube. This inner tube was filled with 6 mL 0.25 M NaOH and 2 mL 1 M $BaCl_2$. The outer tube was closed with a rubber stopper. Ten replicates without litter were prepared in the same way for blank measurements. After 48 h incubation at 15 °C the rubber plug was removed and the concentration of NaOH in the inner tube was determined by titration with 0.1 M HCl and phenolphthalein as pH indicator. The precipitated $BaCO_3$ was immediately transferred into a 2-mL micro test tube, and centrifuged for 1 minute at 14,000 g (Beckmann Microfuge E, Palo Alto, CA). The pellet was repeatedly (>three times) washed with deionized water until pH 7 was reached. Then the $BaCO_3$ was dried in a Speedvac system (Eppendorf Concentrator 5301 connected to KNF laboport pump), and aliquots of about 0.5 mg analyzed with respect to their $\delta^{13}C$ values by EA-IRMS. Directly after removing the inner tube 30 mL K_2SO_4 (50 mM) was added to the litter and the mixture was shaken for 30 minutes on a horizontal shaker (SM25, Edmund Bühler Lab Tec, Hechingen, Germany). The solution was filtered (folded

cellulose filter type 595 ½, d = 150 mm, Whatman Schleicher & Schüll) and aliquots of 1.5 mL were transferred into 2-mL micro test tubes and dried in a Speedvac. The dried salt was then weighed, and aliquots (8-9 mg) weighed into tin capsules on a microbalance (M2P, Sartorius, Goettingen, Germany). The relative abundances of ^{13}C and ^{15}N were determined by means of the EA-IRMS. Non-purgeable organic carbon (NPOC) and total dissolved nitrogen (TDN) content of the solution was determined using a TOC-$V_{CPH/CPN}$ / TNM-1 analyzer (Shimadzu, Japan). To assess microbial biomass N, C, ^{15}N and ^{13}C by means of extraction-fumigation-extraction technique (Dijkstra, Ishizu et al. 2006) the wet litter was washed three times with 10 mL K_2SO_4 (50 mM) in the filter, then the wet filter with the pre-extracted litter transferred in a new 50-mL polypropylene tube and weighed. Addition of 30 mL K_2SO_4 (50 mM) and 1 mL chloroform was followed by shaking for 60 minutes at room temperature. After passing through a second ash-free filter the solutions were analyzed for NPOC and TDN, and aliquots dried and analyzed in the same way as mentioned above,.

Phospholipid fatty acids

From each mesocosm a litter sample of approximately 0.5 g fresh weight was transferred into a muffled 40-mL clear glass vial (screw top, cap with PTFE silicon septa, O.D. × height 29 mm × 81 mm, Supelco) and 1.5 mL of the above described amino acid solution was added. To prevent the samples from drying while allowing gas exchange, the vials were closed with a plug of aquarium wool. After 48 hours at 15°C, the vials were frozen on dry ice and stored at -24 °C. Lipids were extracted from the litter according to the method of Frostegard (Frostegard, Tunlid et al. 1991), based on White (White, Davis et al. 1979) and Bligh and Dyer (Bligh and Dyer 1959). Phospholipids were converted to fatty acid methyl esters (FAME) by alkaline methanolysis. FAME were analyzed by gas chromatography (Trace GC Ultra, Thermo Fisher Scientific) on a DB23 column (J&W 60 m, 0.25 mm, film thickness 0.25 µm, 50%-Cyanopropyl-methylpolysiloxane) coupled via a self-made capillary oxidation reactor to an Isotope-ratio mass spectrometer (Delta V Advantage, Thermo Scientific). The capillary reactor was based on the design of Sacks et al. (Sacks, Zhang et al. 2007) with four 25 cm long copper wires (50 µm diameter) placed in a methyl-silicone deactivated capillary (ID 0.32mm, 4m) heated to 960 °C in a GC/C III-

Interface (Thermo Scientific) and oxidized prior to use in a stream of oxygen. A mixture of bacterial FAME (bacterial fatty acid methyl ester mix, Supelco; and 37Comp. FAME Mix, Supelco) was used as qualitative standard. The concentrations of the single FAME were calculated using nonadecanoic acid (19:0) as internal standard to eliminate variations of recovery introduced after the alkaline methanolysis. An example of a sample analyzed by capillary GC/C-IRMS is presented in Supplementary Data Fig. 8.

Identification of peaks was performed by comparing retention times using Origin (8.1 student version) by overlaying of the chromatograms of sample and standards, and by identification via GC-MS (Finnigan TRACE GC-DSQ, database: NIST 2.0). Isotope values were calculated using ISODAT 2.5 (Thermo Scientific). Various integration parameters and baseline settings were tested to minimize the variance of area and $\delta^{13}C$-values over different concentrations of PLFA standards and injection volumes. Background calculations were then based on “low-pass filtered” or “base fit background” of ISODAT2.5. Of the 74 FAME peaks obtained, 53 peaks were identified as PLFA by GC-MS. Of these, 29 PLFA were selected because of their unambiguous identification, their major contribution and good separation for further analysis. The sum of these 29 PLFA was hereafter referred to as total PLFA and made up 96 $\pm$ 0.05% (mean $\pm$ SD, n=116) in terms of carbon mass of all the peaks, which could be identified as PLFA in the chromatogram. The taxonomic assignment of these PLFA is given in Table 1. One sample had to be excluded because of poor chromatographic resolution (OH3-H3).

Calculations

Measured isotopic signatures of methylated PLFA were corrected for addition of one methyl group by methanolysis using the mass balance equation:

$$\delta^{13}\boldsymbol{C_x} * \boldsymbol{n_x} = \delta^{13}\boldsymbol{C_z} * \boldsymbol{n_z} - \delta^{13}\boldsymbol{C_y} * \boldsymbol{n_y} \quad \text{eq. 1}$$

where n is the number of carbon atoms, z is the derivatized compound, x represents the underivatized compound, and y the derivatizing agent. The $\delta^{13}C$ of the methanol used was determined by EA-IRMS ($\delta^{13}C$ = -34,2 or -48,7 ± 0,1‰ for H2 and H3, respectively). For PLFA, microbial biomass, and respiration analysis pooled unlabelled samples where used to correct labeled samples for natural abundance of ^{13}C. Atom percent excess (APE) was calculated by the following approximation:

$$\boldsymbol{APE} = \boldsymbol{ats} - \boldsymbol{atn} \quad \text{eq. 2}$$

where *ats* is the atom percent value of the compound of interest and *atn* is the atom percent value of the same substance at natural abundance. To estimate the incorporation of ^{13}C (and ^{15}N) into microbial biomass and PLFA, APE was used:

$$\boldsymbol{m_l} = \boldsymbol{m_s} * \frac{\boldsymbol{APE}}{\boldsymbol{100}} \quad \text{eq. 3}$$

where m_s is the mass of the measured compound and m_l is the mass of the labelled fraction in the measured compound.

To calculate the carbon use efficiency (CUE) of the microbial communities we applied the following approach. Assuming that microorganisms suffered nitrogen starvation due to wide C/N_{litter} ratios ranging from 37 to 62 (Keiblinger Manuscript in progress), we hypothesized that all nitrogen taken up from the amino acid mixture was immobilized. Therefore one can state the following equation:

$$^{15}\boldsymbol{N_o}/\boldsymbol{R}^{15}\boldsymbol{N_a} = \boldsymbol{N_u} \quad \text{eq. 4}$$

where $^{15}N_o$ is the APE-corrected amount of ^{15}N measured in the microbial biomass, $R^{15}N_a$ is the ratio of ^{15}N to the sum of $^{15}N+^{14}N$ in the labeling solution, and N_u is the amount of nitrogen taken up of from the labeling solution. When using the measured ratio of carbon to nitrogen in the amino acids (C/N_a=3.05), the amount of labelled carbon taken up from the labeling solution ($^{13}C_u$) can be calculated as:

$$^{13}C_u = R^{13}C_a * C_u = R^{13}C_a * N_u * C/N_a$$ eq. 5

where $R^{13}C$ is the ratio of labeled carbon in the amino acid mixture and C_u is the amount of carbon taken up. The carbon use efficiency (CUE) is then calculated as the ratio of immobilized carbon (C_i) over carbon taken up (C_u):

$$CUE = {}^{13}C_i/{}^{13}C_u = (C_o * APE)/{}^{13}C_u$$ eq. 6

where ^{13}C is the amount of heavy carbon derived from the label.

Statistics

Analysis of variance (ANOVA) and (multiple) regressions were calculated using STATGRAPHICS plus 5.0. Analysis of similarity (ANOSIM), cluster analysis (CA), principal component analysis (PCA), and multidimensional scaling (MDS) were performed with PRIMER 6.1.8. For analyzing SMCC, mol% data of total PLFA were used. The data set was square root transformed and Bray Curtis similarity was used for calculating the resemblance matrix out of which two-dimensional representations of multidimensional scaling (MDS) and cluster analysis (CA) were performed. For analyzing differences between groups of interest, SIMPER analysis and ANOSIM were performed after data treatment as mentioned above. The same procedure was used for the analysis of ^{13}C-incorporation into PLFA (FMCC).

Results

EXPERIMENT 1

Control of litter stoichiometry on the structural microbial community composition

Performing two way ANOVA (Table 2) on sums of characteristic PLFA assigned to broad taxonomic groups revealed significant effects of harvest on general bacterial, and eucariotic markers, as well as on 18:2(9,12)c. The sum of gram positive markers and 20:4(5,8,11,14) showed no response to harvest. When using one way ANOVA, significant decreases between H2 and H3 were found in total PLFA content, 18:2(9,12)c, bacterial, and eukaryotic PLFA for all litter types. Differences between litter types on this parameters could only be revealed for H2, while eukaryotic PLFA showed no dependency on litter type (Fig. 1). All three approaches to calculate fungal-bacterial ratios produced values, which were affected by harvest and litter type (Table 2, Fig. 2).

Multivariate analyses of SMCC showed highly significant differences between H2 and H3 based on two-way analysis of similarity (ANOSIM) (across all litter types) (Global R: 0.924, $p < 0.001$). SIMPER analysis of the same data showed a 8% difference between both harvests. Furthermore, highly significant differences were found between the different litter types (across both harvests) (Global R: 0.794, $p < 0.001$) (for details on pair wise tests see Appendix Table 19). One-way-ANOSIM (Supplementary Table 12) revealed statistical significant differences between all litter types at each harvest and between both harvests for each litter type.

No clustering in MDS plots was observed for litter type or harvest based on absolute values. In contrast MDS of mol% data showed similarities of up to 96% within single litter types, and all samples were similar at the 90% level. Clustering of litter types was more pronounced in H2 than in H3. Especially the community composition of Schottenwald differed from the other litter types in H2 to a greater extent. MDS and cluster analysis revealed clear differences in SMCC between both harvests (Fig. 3). Furthermore a higher degree of dissimilarity and clustering between litter types was apparent in H2 than in H3 (Supplementary Fig. 9).

MDS 1 axis was primarily separating H2 and H3, while litter types separated on MDS 2 axis (Fig. 3). As seen for absolute values for FBD i.e. the FB3 ratio, fungal:bacterial ratios dropped from H2 to H3, which is reflected in a highly significant negative correlation between FBD ratios and MDS 1 (Table 4). Saturated, methyl-branched fatty acids were positively correlated with MDS 1, which is a strong indication for a relative increase in gram positive bacteria with time. Markers indicating bacteria in general increased with MDS 1. With exception of 18:0 all of them were significantly correlated with MDS 1. With the exception of 16:1(9)c and 18:2(9,12)t all eukaryotic PLFA decreased along MDS 1. Of these negatively correlated markers only correlations of 18:1(9)c and 20:0 with MDS 1 were not significant. On MDS 2 highly significant positive correlations with bacterial (14:0, 16:0, 17:0, i17:1(9)c) and fungal (16:1(9)c) markers, and 18:1(11)c were found. Highly significant negative correlations with MDS 2 were found for 18:3(9,12,15)c, and FB3, indicating a relative decrease of fungi.

In terms of elemental stoichiometry, pools, enzyme activities and microbial processes (Table 4) strong positive correlations of MDS 2 with nitrogen and phosphorous content of the litter were found, while C:P and N:P showed no significant correlation, and C:N of the litter was strongly negatively correlated. Concerning other proxies for litter chemistry, significant negative correlations of MDS 2 were found for lignin, cellulose and the ratio of lignin to nitrogen. Amino acids, ammonium, and nitrate concentrations were also positively correlated with MDS 2. Concerning processes, only one highly significant correlation was found with MDS 1, i.e. protein depolymerization (R^2=0.4772, p<0,001) while nitrification showed a rather weak negative correlation (R^2= 0.2258, p<0,01) with MDS 1. In contrast, all processes, with exception of phosphate immobilization, showed significant positive correlations with MDS 2, although nitrate immobilization only to a minor extent. With respect to potential enzyme activities, highly significant correlations were only found with MDS 2, though protease did not correlate. Only a very weak negative correlation between CUE and MDS 1 was found. Microbial biomass carbon and nitrogen showed significant positive correlations with both MDS axes, while microbial biomass phosphorous showed only a weak correlation with MDS 2. A highly significant negative correlation of microbial C:N with MDS 1 was also evident.

Controls of litter stoichiometry on the functional microbial community structure (^{13}C-PLFA)

Two-way ANOVA resolved significant effects of harvest on FMCC i.e. ^{13}C incorporation into eukaryotic PLFA, 18:2(9,12)c, and 20:4(5,8,11,14)c (Table 3). Harvest also affected FBD as reflected in all ^{13}C-FB ratios. With exception of ^{13}C-FB 1, all above mentioned parameters were also significantly affected by litter type. Significant interaction terms of litter type and harvest were found for 18:2(9,12)c and all FB-ratios, showing that FMCC did not change monotonously for all litter types with time. Nevertheless, when using one-way ANOVA, significant differences between litter type could only be revealed for 18:2(9,12)c regarding H2, where KLausenleopoldsdorf and Ossiach showed higher values than Achenkirch, and Schottenwald was intermediate. While a total increase of ^{13}C uptake into C_{mic} between H2 and H3 was seen in Achenkirch, Klausenleopoldsdorf and Ossiach, no similar effect could be observed for ^{13}C uptake into total PLFA. Furthermore, a decrease of ^{13}C-uptake was evident for 18:2(9,12)c and eukariotic PLFA for several litter types (Fig. 1).

A recognizable effect of the time of harvest, and, to a minor extent, of litter type on FMCC could be extracted from the MDS plot (Fig. 3, Supplementary Data Fig. 8). Based on two-way analysis of similarity (ANOSIM), highly significant differences were found between H2 and H3 (across all litter types) (Global R: 0.866, $p< 0.001$). SIMPER analysis of the same data showed a 10% difference between the two harvests. Furthermore, highly significant differences, with less degree of explanation, were found between the different litter types (across both harvests) (Global R: 0.52, $p< 0.001$). One-way ANOSIM of FMCC (Supplementary Data Table 13) resulted in a lower significance level for harvest and litter type in comparison with the one-way ANOSIM of SMCC (Supplementary Data Table 12). With the exception of Ossiach H2 vs.H3, all differences decreased in comparison with the analysis of SMCC. No significant difference in FMCC of Achenkirch and Ossiach at H3 was found any more, the difference being also rather small in SMCC analysis. In comparison with SMCC-several PLFA in the MDS of FMCC (compare Tables 4 and 5) were correlated in the same direction (i14:0, a15:0, i16:0, i17:1(9)c, 18:1(11)c, and 23:0) while others were still significant but correlated in the opposite direction (cy17:9(9/10), 18:2(9,12)t, cy19:9(9/10), 18:3(9,12,15)c, and 24:0). Again others showed lower significance in

the FMCC in comparison to the SMCC data, while a few were found with higher significant correlations (i15:1(4)c, 16:0, 18:0, 18:1(9)c, 20:0, and 20:4(5,8,11,14)c.

Coupling between structural and functional microbial community composition in experiment 1

For 18:2(9,12)c and the sum of eukaryotic PLFA the correlation between concentration and the respective ^{13}C incorporation were highly significant (R^2 = 0.71 and 0.80, $p < 0.01$ each) while this was not the case for PLFA content, gram positive and general bacterial markers (Fig. 6, Supplementary Data Table 18).

EXPERIMENT 2

Response of structural microbial community composition to stress treatment in terms of resistance and resilience

Three-way ANOVA (Table 6) of relevant single and sums of taxonomical most important PLFA resolved significant effects of harvest on total, bacterial, eukaryotic, and gram positive PLFA as well as on 18:2(9,12)c, 20:4(5,8,11,14)c and all FB ratios. Litter type had no effect on FB1 and treatment effects were not found for 20:4(5,8,11,14)c, FB1 and FB3. Interactions between harvest and litter type, litter type and treatment, harvest, litter type and treatment were limited to 18:2(9,12)c and FB2. In contrast, significances of interactions between harvest and treatment were not found for FB1 and FB3.

One-way ANOVA (Fig. 4, Fig. 2) resulted in significant differences between heat and freeze treatments only for C_{mic} from Schottenwald at H3 and for FB1 from Ossiach at H3. No further significant differences were found for H3. In contrast, for H2 a significant ($p<0.05$) decrease of total PLFA for all litter types in response to stress treatment was revealed by one-way-ANOVA. Regarding bacterial PLFA, effects of treatment were found for all litter types. Eukaryotic PLFA in Ossiach and Klausenleopoldsdorf significantly ($p<0.01$) decreased after stress treatment, while for Schottenwald only the freeze treatment had a significantly negative effect ($p<0.01$). In response to heat treatment gram positive markers decreased significantly for Klausenleopoldsdorf and Ossiach, while for Klausenleopoldsdorf only freeze treatment had a significant effect. The PLFA 18:2(9,12)c decreased significantly ($p<0.001$) in response to stress treatment in Klausenleopoldsdorf and Ossiach, while

not in Schottenwald samples . Considering FB1 no effect of treatment was revealed by one-way ANOVA. Concerning FB2, Klausenleopoldsdorf and Ossiach responded to stress treatment with significant decreases ($p<0.05$). No significant effect of stress treatment on FB3 was found.

By using one way ANOSIM highly significant differences were found between H2 and H3, neglecting any influence of litter type or treatment (Global R: 0.845, $p< 0.0001$). Simper analysis of the same data resolved 10% difference between both harvests. A strong separation of H2 and H3 was also evident by MDS analysi (Fig. 5A) and the supplementary CA (Supplementary Fig. 9C). Therefore, further statistical analysis of samples was split with respect to harvest.

Harvest 2 (Resistance of SMCC)

For H2, two-way ANOSIM showed highly significant differences between litter type (Global R: 0.712, $p < 0.0001$) and between treatments (0.44, $p < 0.0001$), although no difference could be found between heat and freeze treatment. By using one-way ANOSIM (Supplementary Data Table 14) on groups defined as combinations of litter type, harvest and treatment (12 groups), no significant differences between freeze and heat treatments were apparent, while all differences between controls and stress treatments were significant.

For Klausenleopoldsdorf and Ossiach separation regarding control and both stress treatments was achieved by the MDS (Fig. 5C) and the CA (Supplementary Data Fig. 9E). For Schottenwald no separation between control and stress treatments was evident. By rotating the MDS it was possible to differentiate the more sensitive communities (Klausenleopoldsdorf and Ossiach) from the more stable communities (Schottenwald) on MDS 1. Correlating the relative content of individual PLFA with MDS 1 (Table 8) resulted in highly significant positive correlations ($p<0.001$) for 16:0, 16:1(9)c, i17:1(9)c, cy17:0(9/10), 18:1(11)c, 18:2(9,12)t, and 20:4(5,8,11,14)c. Negative correlations ($p<0.001$) were found for 18:3(9,12,15)c and FB3 with MDS 1. MDS 2 was highly significantly positively correlated though with less degree of explanation ($R^2 < 0.45$) for 18:1(9)c, 18:1(11)c, cy19:0(9/10), 22:0, and 23:0 and FB2, while correlation with 24:0 had a R^2 of 0.6152. Highly significant negative correlations, with high relevance ($R^2 > 0.45$) on MDS 2, were found for i15:0, a15:0, 15:0, i16:0, i15:1(4), 18:2(9,12)c, 18:3(6,9,12)c and total PLFA, while for 14:0, MDS2

showed slightly less dependence (R^2 = 0.4102). Significant correlations of beech litter chemistry were found on MDS 1 (Table 10). Here, especially C:N ratio showed a highly significant negative correlation, being reflected in a highly significant positive correlation with nitrogen content of the litter. Lignin content and N:P ratio did not produce significant correlations with MDS 1. With decreasing significance, cellulose, starch, the ratio of lignin to nitrogen, and the ratio of carbon to phosphorous, were negatively correlated with MDS1.

Harvest 3 (Resilience of SMCC)

For H3, the two-dimensional representation of MDS (Fig. 5E) and CA (Supplementary Data Fig. 9F) showed no distinct separation between controls and stress treatments while litter types separated on MDS1. Two-way ANOSIM resolved highly significant differences between litter type (Global R: 0.789, $p < 0.0001$) but treatment effects were very low (0.082, $p < 0.0001$). By using one-way ANOSIM (Supplementary Data Table 14) on groups defined as combinations of litter type, harvest and treatment (12 groups), significant difference between treatments and between treatments and control were not found. Correlating the relative content of individual PLFA with MDS axes (Table 8) resulted in highly significant correlations only on MDS1, i.e. negative correlations with i15:0, a15:0, and 18:3(9,12,15), and positive correlations with 16:0 and 16:1(9)c, all of these showing only a weak linear dependence ($R^2 < 0.26$) with MDS 1.

Response of the functional microbial community composition to stress treatment, ^{13}C-PLFA

Three-way ANOVA (Table 7) of FMCC i.e. ^{13}C incorporation into relevant single and sums of important PLFA showed significant effects of harvest on total, bacterial, and gram positive PLFA as well as on 18:2(9,12)c, 20:4(5,8,11,14)c and all FB ratios. Litter type had no effect on FB1 and FB2. Treatment effects were highly significant for all parameters measuring ^{13}C uptake into PLFA. Significant interactions between litter type and treatment, as well as between harvest, litter type and treatment were limited to uptake of ^{13}C into 18:2(9,12)c. In contrast, significant interactions between harvest and treatment were found for uptake of ^{13}C into bacterial and gram positive PLFA, and significant interactions between harvest and litter type for uptake into gram positive PLFA, 18:2(9,12)c, 20:4(5,8,11,14)c, FB2 and FB3. Significant

differences by one way ANOVA (Fig. 4) between ^{13}C-PLFA were only found for H2. Here significant decreases in response to treatment were again only found for Klausenleopoldsdorf and Ossiach, while not for Schottenwald samples. Incorporation of ^{13}C into total, bacterial, eukaryotic, and gram positive PLFA as well as into 18:2(9,12)c decreased significantly when exposing Klausenleopoldsdorf and Ossiach litter to the heat treatment. The freeze treatment had no significant negative effect on incorporation of ^{13}C into total, and bacterial PLFA for Klausenleopoldsdorf and Ossiach, while for eukaryotic PLFA and 18:2(9,12)c it had (Fig. 4). While having no effect on Ossiach, freeze treated microbial communities showed significantly lower uptake of ^{13}C into gram positive bacterial PLFA. Multidimensional scaling showed that H2 and H3 were well separated along MDS 1 (Fig. 5B) with 10% dissimilarity (Supplementary Data Fig. 9D).

Harvest 2 (Resistance of FMCC)

Two way ANOSIM testing for effects of litter type and treatment in H2 revealed a significant effect of litter type (Global R=0.66; p=0.0001) and treatment (Global R=0.550; p=0.0001). When using one-way ANOSIM (Table 15), significant differences between heat and freeze treatment were obtained only for samples from Klausenleopoldsdorf. Significant differences between controls and both stress treatments occurred for all litter types. Concerning H2, the MDS (Fig. 5D) based on the ^{13}C incorporation into PLFA revealed good separation between stress-treated and control samples at H2. This shift of the functional community in a uniform direction was projected along MDS 1. Positive, highly significant correlations ($p<0.001$) between MDS 1 and underlying ^{13}C-PLFA (

Table 9) were found for no fungal, but several bacterial markers. This was also reflected in highly significant negative correlations of MDS 1 with all three FBD ratios (R^2 between 0.60 and 0.82),

Harvest 3 (Resilience of FMCC)

Performing two-way-ANOSIM of the effects of litter type and treatment in H3 showed a significant effect of litter type (Global R=0.62; p=0.0001) while treatment had only a subordinate though still highly significant effect (Global R=0.168; p=0.0006) compared to H2. When using one-way ANOSIM (Table 15), significant differences between heat- and freeze-treatment were only obtained for Schottenwald samples. Significant differences between control and stress treatment were limited to Schottenwald with regard to freeze treatment, and Klausenleopoldsdorf with respect to heat treatment. For H3 separation due to litter type corresponded to MDS 1 (Fig. 5F), but no clear treatment effect was evident on either MDS axis. For H3, FB1 and FB3 correlations were highly significant with MDS 2 (R^2 = 0.719 and 0.888, respectively). Differences in FMCC due to litter type were thoroughly described and analyzed in E1.

Coupling of functional and structural microbial community composition when exposed to stress treatment.

The absolute amounts of PLFA classes and absolute ^{13}C incorporation rates into the same PLFA classes were strongly correlated ($R^2 > 0.81$, $p < 0.001$) in E2 H2 for PLFA content, 18:2(9,12)c, eukaryotic and gram positive associated PLFA. Bacterial PLFA were also correlated well ($R^2 = 0.72$, $p < 0.01$) though less significant and explaining less variation. For E2 H3 less strong but still significant coupling was restricted to total, and gram positive PLFA and 18:2(9,12)c, but was not found for general bacterial, and eukaryotic PLFA (Fig. 6, Supplementary Table 18).

Trade-off between stress resistance and growth of microbial populations.

We further tried to link stress resistance with growth of microbial populations based on biomarker analysis. The analysis was based on the correlation between ^{13}C incorporation into individual PLFA biomarkers in controls of E2 (as measure for PLFA turnover and proxy for growth rate) and stress resistance of the same PLFA biomarker. The latter “resistance” proxy was based on the correlation coefficient determined for each individual PLFA with MDS 1 and MDS 2 of SMCC of H2.

Positive correlation coefficients on both MDS axes were related to higher stress resistance of the biomarker to stress treatment, negative correlation coefficients with stress sensitivity of the biomarker. Interestingly, no significant correlation was found overall or for fungal or bacterial groups though we would have expected a negative relationship between stress resistance and growth rate (Fig. 7).

Discussion.

Comparison of biomass measuring methods

The significant increase in microbial carbon in all litter types from H2 to H3 by 50% suggests growth of the microbial community, while a decrease in total PLFA content by 50% suggests otherwise. Similar anti-correlations have been reported earlier (Balkwill, Leach et al. 1988; Frostegard, Tunlid et al. 1991). Several different explanations may account for this pattern, e.g. (1) It could be a major decrease in surface to volume ratio (SVR), since PLFA as membrane components do not correlate to "biomass *per se*, but to the (…) surface area" (Klamer and Baath 2004). There are indications that fungal hyphae vary in thickness with nutritional status, i.e. being thinner when starving (Robinson and Smith 1979). Furthermore, differences in hyphal thickness between fungal taxa are to be expected. The amount, and therefore the surface, of linoleic-acid PLFA, which is considered to be well correlated with fungal biomass .(e.g. (Klamer and Baath 2004)), decreased by approximately 50% between H2 and H3 (Fig. 1). Following the above argument, and supposing a 1:1 correlation of biomass to volume, an increase in microbial biomass to 150% would then result in a surface to volume ratio decreasing by three fold. To allow that the diameter would have to increase to somewhere between twelve-fold (when approaching hyphal geometry with a cylinder of negligible diameter in comparison to its length) and eighteen-fold (when assuming spherical geometry) of its former state, which is highly unlikely. (2) A shift of bacterial to fungal dominance would have affected the SVR in the direction we encountered, due to large differences between fungal and bacterial size, but FBD changed in the opposite direction (Fig. 2). (3) A different explanation is that PLFA content can vary in different stages of the life cycle of e.g. ascomycetes (Tsukahara 1980; Sancholle, Weete et al. 1988), which were the dominant group of fungi according to parallel metagenomic and metaproteomic measurements (Urich Manuscript in progress). (4) It cannot be ruled out completely, that differences in environmental conditions during sample preparation and PLFA extraction, like ambient temperature, could result in significant differences in extraction efficiencies. We were not able to discriminate between these potential mechanism but want to stress that PLFA-based and C_{mic}-based microbial biomass results cannot be directly compared.

Litter stoichiometry, recalcitrance and succession of the microbial community on decomposing leaf litter

Regarding the successional pattern of microbial communities during decomposition of the different litter types, clear changes and actually directional changes of SMCC in all litter types were reflected by all the different approaches taken to evaluate the PLFA data. Using (1) correlations of biomarker PLFA (rooting in mol% data) with MDS 1 (separating SMCC of the two harvests), and (2) by comparing FB3 for both harvests (rooting in absolute PLFA data), we found a strong decrease of fungi over bacteria within the period of three months in the mesocosm system, which was only to a minor extent depending on litter type (Fig. 1, but Table 2). This relative increase of bacteria was seen for gram positive bacteria as well (Table 4). We expected an increase in fungi over time, due to the increasing complexity and recalcitrance of the substrate when easily decomposable pools of C, N and P are exhausted after the initial phase of litter decomposition (Ziegler and Zech 1991; Berg 2000; Aneja, Sharma et al. 2006; van der Heijden, Bardgett et al. 2008). This increase in complexity would be in great parts linked to a relative increase of ligno-cellulose in plant debris (Aneja, Sharma et al. 2006; Berg and McClaugherty 2008). This, we assumed, would be met by an adjusted set of microorganisms and their complement enzymes (cellulases, oxidative enzymes), which are known to be produced especially by fungi and only some bacteria (Uma, Kalaiselvi et al. 1994; Perestelo, Rodriguez et al. 1996; Worrall, Anagnost et al. 1997; de Boer, Folman et al. 2005; Wright and Covich 2005; Vargas-Garcia, Suarez-Estrella et al. 2007). Moreover, the ability of fungi to relocate nutrients from other sources (Ames, Reid et al. 1983) has been suggested for this increasing dominance of fungi with time. However, no such shift of decomposing litter to a more complex, recalcitrant substrate within the here presented time frame was found, as neither the content of lignin and cellulose, nor the ratio of lignin to nitrogen changed (Table 4). Similar increases of bacterial dominance with litter decomposition have been reported by others as well (e.g. Strickland et al. 2009), which depended on the litter being decomposed. Fungal dominance during early phase litter decomposition may also be explained by the recalcitrance of the outer layers of litter (epidermis, cuticle) which can be easily bypassed by fungi due to their hyphal growth form, but not by bacteria (Hendrix et al. 1986).

Support for the shift towards a more bacterial dominated community can be seen in the decrease of the C:N ratio of the microbial community along MDS 1. This is founded on the argument, that bacteria tend to have C:N ratios which are more constraint to smaller values, while fungi often have wider C:N ratios (Killham 1994; Sterner and Elsner 2002). In a recent review (Strickland and Rousk 2010), based on ~1100 observations of C:N ratios of saprotrophic and ectomycorrhizal fungi, and bacteria,,fungi had a markedly higher C:N ratios (mean C:N 13-15) than bacteria (mean C:N ~6), though the authors noted a large overlap of fungi and bacteria with respect to biomass C:N. However, conflicting results have been reported on the influence of nitrogen availability on FBD (see Strickland and Rousk 2010 for review).

It is this difference in C:N requirements of different microbial populations (e.g. fungi versus bacteria) that have often been invoked to explain the higher bacterial dominance and faster decomposition on low C:N litter compared to fungal dominance on high C:N litter with lower decomposition rate. In this study SMCC of different litter types separated on the MDS 2 axis which was strongly related to litter quality and litter stoichiometry. Total nitrogen content of litter was strongly positively, and litter C:N strongly negatively correlated with this MDS axis (MDS 2). In contrast, relationships with litter phosphorus content or litter C:P were much weaker. The differences in SMCC on MDS 2 were therefore clearly dominated by litter C:N stoichiometry, and were for example related to FBD as represented by FB3 showing a decrease of fungal: bacterial domimance at lower litter C:N (i.e. Schottenwald litter). Several in situ studies on soil microbial communities reported that increased nitrogen availability altering FBD towards a more bacteria dominated SMCC ((Bardgett and McAlister 1999; Hogberg, Baath et al. 2003; de Vries, Hoffland et al. 2006; Demoling, Nilsson et al. 2008), while others did report otherwise (de Vries, Bloem et al. 2007; Rousk and Baath 2007; Mulder and Elser 2009). Recently a microcosm study of litter decomposition reported that FBD patterns and decomposition were controlled by the litter N:P ratio rather than litter C:N (Guesewell and Gessner 2009). In contrast to “common” belief they reported higher FBD at lower C:N ratios, when P was limiting, and increased dominance of bacteria on higher C:N ratios under sufficient P availability. Microbial community N:P showed a weak but significant correlation with MDS 2, which would be in concordance with the above mentioned study. Nevertheless, it could also be possible, that this pattern was the

reflection of increased P content of the litter in tandem with a less homeostatic behaviour of the microbial community towards litter C:P or N:P (Sterner and Elsner 2002). However, complicating the stoichiometric controls MDS 2 was also strongly negatively correlated with litter lignin and cellulose content, as well as to the ratio of lignin:N. As stated above, all these litter quality parameters would favor higher bacterial dominance on high quality litter with low lignin, low lignin:N ratios and low litter C:N which was reflected in this mesocosms study. Schottenwald litter with the lowest fungal: bacterial dominance had lowest lignin content, lignin:N and C:N ratios which was indicated also by FB3 ratio, 18:2(9,12)c and 18:3(9,12,15)c.

We found significant changes, and strong correlations of FBD with both MDS axes (Fig. 2, Fig. 3,Table 4), allowing statistical analyses of the relation between microbial processes and shifts/differences in FBD. We therefore argue that significant correlations of enzyme activity and related microbial processes could be assigned to those changes. Given that our knowledge of PFLA as biomarkers is restricted to broad groups only, we focussed on FBD as represented by FB3, though it must be noted, that divergent PLFA markers were responsible for the directional shifts in FBD. Regarding the successional changes in FBD as represented by MDS 1, positive correlations would point to an enhancement of this process by bacteria. Following this rational bacteria primarily promoted protein depolymerization, and to a lower extent protease and phosphatase activity. The huge differences in coefficients of determination between MDS 1 and in situ rates of protein depolymerization compared to MDS 1 and potential protease activity underline the importance of in situ measurements of processes i.e. based on stable isotope pool dilution measurements of such processes (Wanek, Mooshammer et al. 2010). Fungi would, following our rational, intensify nitrification and nitrate immobilization, and cellulase and chitinase production. In fact metaproteomic analyses of the same material suggested that the extracellular hydrolytic enzymes investigated (cellulases, pectinases) were solely produced by fungi (Schneider Manuscript in progress). Moreover, similar results based on MDS 2 correlations with FBD and enzymes/processes pointed towards bacterial dominance of the gross processes of protein depolymerization, amino acid immobilization, N mineralization, ammonium immobilization, nitrification, P mineralization and respiration, as well as of the enzymes cellulase, chitinase, phosphatase, peroxidase and phenoloxidase. The study obviously produced

contradictory results for fungal (MDS 1) and bacterial (MDS 2) dominance of the processes of nitrification, and the enzymes cellulose and chitinase. Part of this difference may be reconciled as completely different biomarkers were responsible for these correlations (see Table 4). These results actually point to the cooperation between bacteria and fungi in mediating specific decomposition processes, and to different fungal and bacterial populations being mostly responsible for these processes as indicated by distinct PLFA biomarker that correlated with MDS 1 and MDS 2. Second correlations between MDS based on mol% PLFA and “absolute” processes ignore the importance of microbial biomass per se. Partial correlations should be used to account for the unseen variability in microbial biomass or the correlations performed against specific activities, normalized to microbial biomass. This has been demonstrated as absolute enzyme activities reported by Romani et al (2006) were higher when fungi were present, while specific enzyme activities, normalized to the respective microbial biomass, were at least two-fold higher for bacteria.

In a former study on FBD and related enzyme activity (Romani, Fischer et al. 2006), *Phragmites* leaves where incubated with three different inocula composed of (1) only bacteria, (2) only fungi and (3) a mixed inoculum of fungi and bacteria. Activities of phosphatase, cellobiohydrolase, phenoloxidase, ß-xylosidase, ß-glucosidase and ß-glucosaminidase were at least eight times higher in fungal inoculated then in bacterial inoculated samples at the end of the experiment. With exception of phosphatase, enzyme activities of the mixed samples were always significantly lower than for fungi alone, pointing to suppression of fungi by bacteria in mixed culture. The attempt of using selective inhibition with antibiotics was criticized for having untargeted effects by (Landi, Badalucco et al. 1993), who used the approach directly on forest soil, instead of a cultivation prior to incubation. Nevertheless, when comparing their results with an earlier study (Moller, Miller et al. 1999), which did use a different method (Faegri, Torsvik et al. 1977) to gain a fungi-free inoculum, similar results were reported. Enzyme activities (ß-N-acetylglucosamidase and endo-exo-cellulase) were always higher when fungi were present, than bacteria alone (Moller, Miller et al. 1999), and similar results were presented by (Schneider, Gerrits et al. 2010). All these results point towards fungi being the most important microbial decomposers of litter. However, our data showed otherwise i.e. that most processes

increased with bacterial dominance. Moreover, the strong (positive) relationship between bacterial dominance and oxidative enzymes is counterintuitive and stands in stark contrast to other studies reporting that most oxidative enzymes are produced by fungi (see above). However, bacteria may also produce and exude oxidative enzymes (e.g. Vargas-Garcia et al. 2007). One possible explanation may therefore be, as suggested above, that though absolute enzyme activities were higher when fungi were present, but specific enzyme activities were higher for bacteria (Romani et al. 2006). Leucine-aminopeptidase for instance showed specific activities in bacteria nearly 1000-fold that of fungi. Although the exact relations between enzyme activity and the specific microbial community remain complex, the results support our hypothesis, that the stoichiometric composition of organic matter input exerts a major control on microbial community composition and ecosystem functioning.

Divergence of functional and structural microbial community composition

Direct linking of microbial populations to specific biogeochemical processes by ^{13}C-labelling of biomarkers (Boschker, Nold et al. 1998) has been an advantageous attempt to overcome certain possible ambiguities. As pointed out by (Evershed, Crossman et al. 2006), the presence of ^{13}C-labelled PLFA unequivocally elucidates the presence of an active community producing this specific PLFA. Quite recently, a report of differences in the response of growth and biomass of bacteria and fungi to a stress treatment (Bapiri, Baath et al. 2010) has been published. The reported discrepancies between growth- and biomass-based assessments of stress responses, especially considering FBD, led to the suggestion to revise aspects of microbial community with respect to what is actually measured. (Strickland and Rousk 2010) determined four different aspects of FBD published so far, those which are measuring (1) residues, (2) biomass, (3) contribution to substrate induced respiration, and (4) growth rates. Following this argumentation, our experiment was measuring surface contribution (SMCC) and growth rates would be presented by the FMCC. Although significant differences between the harvests in both SMCC and FMCC plots (MDS plots, Fig. 3) and one way ANOSIM were obvious, the picture was more complex for litter types. Litter types did not separate as well as in FMCC data they did in the SMCC data. However, concerning the successional patterns,

correlations of PLFA, processes and enzyme activities were performed in same manner for FMCC as for SMCC data. All fungal bacterial ratios showed a decrease with time, indicating less fungi in H3, as supported by a decrease in microbial C:N. Albeit this similarity between SMCC and FMCC, less PLFA showed a highly significant correlation with ^{13}C-MDS 1 and several flipped the direction to which they were correlated with SMCC. In contrast, based on broader microbial groups and absolute data of PLFA content and ^{13}C incorporation, we found a strong relationship between structural and functional attributes of microbial community structure for the main fungal biomarker (18:2(9,12)c and the sum of eukaryotic (here fungal) biomarkers and no correlation for bacterial biomarkers. Under “equilibrium” conditions we therefore found only a restricted accordance between SMCC and FMCC, and a better resolution between litter types according to their elemental stoichiometry in SMCC. It is therefore of utmost importance to decide which microbial community measure to use, being functional or structural in nature, for later interpretation of data and comparability to other studies.

Conclusion Experiment One

(1) We found a decrease in FBD with time, which is not in contradiction with the literature, because the conditions, which would suggest otherwise (increasing recalcitrance), were not met.

(2) We found a strong effect of litter quality and chemistry on structural microbial community composition.

   a. Relative abundance of fungi increased with lignin contribution.
   b. Relative abundance of fungi increased with increasing C:N of the litter.

(3) We could relate relevant processes and enzyme activities to the structural microbial community composition.

   a. Bacteria enhanced most processes including protein depolymerization and other N and P transformation processes, protease, oxidative enzymes and to a lower extent phosphatase activity.
   b. Fungi promoted nitrification, nitrate immobilization, cellulase, and chitinase activity. Some processes were conducted both by fungal and bacterial populations.

(4) We could identify a weak relationship between biomass-dependent and growth-dependent measurements of microbial community structure, though not for the bacterial part of the community.

Resistance and resilience of structural and functional microbial community composition to temperature stress

As an immediate response of SMCC to stress we saw dramatic decreases in the total PLFA values while this was accompanied by an increase of microbial biomass carbon. This result may be explained by similar considerations as made concerning the first experiment. Nevertheless, it should be noted that differences in extraction efficiency seem unlikely in E2, since changes in environmental conditions (ambient temperature) were not apparent during preparation of these samples of H2 or H3.

Although litter decomposition has been thoroughly studied with regards to stoichiometric controls on microbial community composition (e.g. (Smit and Wieringa 1953; Manzoni, Jackson et al. 2008; Moore-Kucera and Dick 2008; Guesewell and Gessner 2009; Hossain, Okubo et al. 2010; Schneider, Gerrits et al. 2010), the literature concerning stress responses of microbial decomposer communities is scarce. As stated in (Allison and Martiny 2008), until 2008 no study(ies) have addressed the relationship between phylogeny and microbial responses to disturbance. Given the absence of data on litter communities we can compare our data only to studies on the response of soil microbial communities to temperature or drying-rewetting stress. It has to be further noted, that in soils the microbial ecology, activity, and dynamics of microbial populations is known to be strongly dependent on the physical structure and porosity of soils (Edgerton, Harris et al. 1995; Ranjard and Richaume 2001; Nannipieri, Ascher et al. 2003). The comparability of our study to the recent literature is therefore limited.

Soil microbial diversity has been suggested to have a positive influence on the efficiency of nutrient-cycling in decomposition processes, based on theoretical models (Ekschmitt, Klein et al. 2001; Loreau, Naeem et al. 2001). To test this hypothesis, some studies initially reduced microbial biomass by thermal disruption. One of these studies (Chaer, Fernandes et al. 2009) found no negative effect of a 15 min heat shock at 40 °C and 50 °C on microbial biomass. At higher temperatures, changes in SMCC (monitored with PLFA) of a native tropical forest soil were linked to a decrease of arbuscular mycorrrhizal fungi (which were not present in our study), saprotrophic fungi, and gram negative bacteria (which we did not assign, due to ambiguous assignments in literature) 30 days after the treatment. In contrast 3 days

after the treatment, no difference in MCC between treated and untreated samples were reported for this soil and a soil exposed to agricultural cropping for 14 years. This is in contrast to our study, where differences in SMCC and FMCC due to stress treatment were much more pronounced in H2 than in H3. As described, highly significant differences were found between both harvests. We interpreted the immediate response of SMCC to stress (H2) in terms of resistance of specific microbial populations and communities to stress, i.e. some biomarkers were highly sensitive others highly resistant to stress treatment. The nearly complete disappearance of differences in SMCC between untreated and stressed litter three months after treatment (H3) points to a high resilience (recovery) of these communities.

In detail, both stress treatments (heat and freeze) did significantly alter SMCC of Klausenleopoldsdorf and Ossiach, while this was not the case for Schottenwald (Fig. 5C, Supplementary Table 14 and 15). In a study on the adaption of soil microbial communities to temperature (Barcenas-Moreno, Gomez-Brandon et al. 2009), optimal growth rates of fungi and bacteria of an arable soil from Sweden were determined to be at 30 °C. It therefore would have been conceivable to find differential effects of heat (30 °C) and freeze (-15 °C) treatment on FMCC, and possibly also on SMCC. Surprisingly, the response to heat and freeze as stress factors did not alter SMCC differently. It was possible to differentiate the more resistant SMCC of Schottenwald from the less resistant communities, represented in Ossiach and especially Klausenleopoldsdorf by rotating the MDS data. For the more sensitive communities, changes along MDS 2 were associated with the stress-response itself i.e. resistant biomarkers plotted towards high scores, sensitive biomarkers towards low scores on MDS 2 (Table 8). No clear pattern considering stress resistance of eco-functional or taxonomic groups could be seen. On both axes of the MDS of SMCC, general and gram positive bacterial as well as fungal markers behaved differently, some showing stress resistance, some being sensitive to stress treatment. Significant correlations between FBD itself and each MDS axis were in both cases restricted to only one of the three approaches to calculate FBD, rejecting a clear effect on FBD. All absolute biomarker values, be it fungal or bacterial, showed strong decreases after stress treatment, which explains the lack of overall changes in FBD. This is similar to what has been reported on the temperature adaption of soil

microbial communities (Barcenas-Moreno, Gomez-Brandon et al. 2009), but differs from that of effects of drying-rewetting cycles on MCC (Bapiri, Baath et al. 2010). By correlating all individual PLFA against the MDS axes (SMCC), the complexity of the community shift was revealed. This analysis indicates that resistance or sensitivity to temperature stress may be well distributed within different taxa and broad groups such as bacteria and fungi. In contrast to this finding, based on the FMCC data, a clear shift towards a more bacterial dominated community, as consistently indicated by all three ratios measuring FBD, was apparent. In a study on the response of MCC of an arable soil to repeated drying rewetting cycles (Bapiri, Baath et al. 2010) total PLFA, bacterial PLFA, 18:2(9,12)c, as well as SIR were used to detect changes in the microbial communities. Fungal growth was measured by uptake of acetate into egosterol (Newell and Fallon 1991). In this study, stress had stronger effects on growth-related than on biomass-related microbial community measures. This was especially true for the fungal response. In our study, concerning FMCC, we also found patterns being quite different from SMCC responses, with FBD being altered towards a more bacterial dominance. Nevertheless, similar to SMCC, differential effects on biomarkers within each taxonomic group were seen. This finding is in line with a review on the stability of microbial communities (Allison and Martiny 2008), where 110 publications were taken into account, 10% of which assessed responses to temperature mediated stress. The authors reported that they were not able to discern whether particular taxonomic or functional groups are more or less sensitive to particular disturbance types. Similar, it has been reported that fungi and bacteria, when exposed to a wide range of temperature treatments, (Barcenas-Moreno, Gomez-Brandon et al. 2009) similar response of growth was found. This homogenous stress-response of fungal and bacterial communities was also reported by a study on boreal forest soils, where temperature was increased by 0.5 °C (Allison and Treseder 2008).

Albeit this controversial finding for FBD, in contrast to the SMCC data growth-related measurements of H2 showed significant differences between stress treatments and related controls for all litter types, though with less significance for Schottenwald (Fig. 5D). Furthermore, the impact of the freeze treatment on the Klausenleopoldsdorf community was significantly stronger than the heat treatment. Similar to this, we had expected to find differential effects of both treatments more often, given that the hot

treatment was only a rise in temperature by 15 °C to 30 °C, close to the optimum temperature range of many but not all microbes, while the freeze treatment was expected to negatively affect all microbes. A study on the heat and freeze resistance of *Vibrio* bacteria (Johnston and Brown 2002), also found them not to differ between resistance to heat and freeze treatment.

Uptake of ^{13}C within broad groups of PLFA (gram positive, bacterial, eukaryotic, total, and 18:2(9,12)c) was well correlated ($R^2 > 0.70$) to the overall abundance of each group in the sample. Therefore, SMCC and FMCC were strongly coupled directly after stress treatment, the significance declining slightly thereafter during the recovery period. Microbial community structure was therefore more strongly coupled to ecosystem function or FMCC under non-equilibrium conditions than in unstressed controls. This points to a rather limited level of functional redundancy in litter decomposing communities. Overall, the results indicate a relatively high resilience of the decomposer community, where stoichiometry plays a dominant role in the resistance of SMCC and FMCC to stress.

Initially all litter types were inoculated with the same community. Based on differences in the stoichiometry and recalcitrance of the litter, this initial community was altered significantly and these microbial communities responded differently in terms of stress resistance. With decreasing litter C:N and increasing bacterial dominance, stress resistance increased. In contrast to stress resistance, stress resilience was high overall for all litter types and no effect of litter stoichiometry on stress resilience was found. Hence, communities were still distinguishable with regard to litter type, three months after the stress treatment, and no selection for community members being generally more resilient or fast growing was found. We found similar stress responses in terms of community shifts to very different stress types, indicating universal adaption mechanisms, or generally more stable members of the community for both type of stresses. Using growth- and biomass-dependent measurements showed that differences between treatments were greater using growth dependent measurements. Growth-dependent measurements would suggest fungi being less resistant than gram positive and general bacteria. This pattern is not as clear, when focusing on biomass-dependent measurements or even when considering the divergent behaviour of single PLFA markers within each taxonomic

group. To overcome these ambiguities it would be helpful to increase the understanding of deeper phylogenetic affiliation of single PLFA biomarkers in environmental samples, by comparing PLFA to other community profiling techniques, such as metagenomics or metaproteomics. Last but not least, we hope this study will enhance the knowledge of "the relationship of between phylogeny and microbial responses to disturbance" (Allison and Martiny 2008).

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Tables and Figures

Table 1 Taxonomic assignment of PLFA identified, with more than one taxonomic group being mentioned if found also for other groups. Bold formatted text shows the assignment used here. References: a, Federle et al (1986) (Federle 1986); b, Zelles (1997) (Zelles 1997); c, Zelles (1999) (Zelles 1999); d, Hill (2000) (Hill, Mitkowski et al. 2000); e, Klamer (2004) (Klamer and Baath 2004); f, Leckie, 2005 (Leckie 2005).

Type PLFA	Specific Markers	used as biomarker for	less amounts in	References
Saturated straight chain <20C	14:0, 15:0, 16:0, 17:0, 18:0	Bacteria in general	fungi	a, b, d, e, f
Saturated straight chain >20C	20:0, 22:0, 23:0, 24:0	Eucaryonts	-	a, b, c, f
Saturated branched	i14:0, a15:0, i15:0, i16:0, i17:0	**Gram-positve bacteria and bacteria in general**	Gram-negative bacteria and fungi	a, b, c, d, f
Cyclopropyl (cy)	cy17:0(9/10), cy19:0(9/10)	**Bacteria in general** and gram-negative bacteria	gram-positve bacteria	a, b, c, d, f
Monoenoic, branched	i17:1(9)c, i15:1(4)c	Sulfate reducers -> **bacteria in general**	-	d
Monoenoic			gram-negative bacteria and plants	a
	16:1(9)c	Fungi	gram-negative bacteria and plants	e, f
	16:1(11)t	General bacteria	gram-negative bacteria and plants	a, d
	18:1(9)c	Fungi	gram-negative bacteria and plants	f
	18:1(9)t	Fungi	bacteria in general and plants	b, d
	18:1(11)c	Fungi and gram-negative bacteria => none in this study	gram-negative bacteria and plants	a, b, f
Polyenoic			Plants	b
	18:2(9,12)c/t	Fungi / fungal biomass	Plants	a, b, d, e, f
	18:3(6,9,12)c	Fungi	Plants	a, d
	18:3(9,12,15)c	Fungi	Plants	b, d, f
	20:4(5,8,11,14)c	Protozoa	Plants	f
Ratios	18:2(9,12)c/branched	Fungal :Bacterial ratio 1		f
	18:2(9,12)c/ general bacterial	Fungal : Bacterial ratio 2		
	eucariotic/ general bacterial	Fungal : Bacterial ratio 3		

Table 2 Two-way ANOVA of important groups of PLFA for the effect of harvest and litter type, i.e. total PLFA, bacterial PLFA, gram positive PLFA, eukaryotic PLFA according to assignment stated in Table 2.

Parameter	Harvest			litter type			interaction		
	df	F	p	df	F	p	df	F	p
total PLFA (nmol g^{-1} d.w.)	1	97.31	**<0.0001**	3	5.46	**0.0031**	3	0.49	0.6943
bacterial PLFA (nmol g^{-1} d.w.)	1	44.00	**<0.0001**	3	10.29	**<0.0001**	3	0.69	0.5638
eukarytotic PLFA (nmol g^{-1} d.w.)	1	192.03	**<0.0001**	3	0.73	0.5324	3	0.64	0.593
gram positive PLFA (nmol g^{-1} d.w.)	1	0.69	0.4112	3	4.48	**0.0085**	3	1.18	0.3314
18:2(9,12)c (nmol g^{-1} d.w.)	1	148.67	**<0.0001**	3	0.71	0.5513	3	1.49	0.2336
20:4(5,8,11,14)c (nmol g-1 d.w.)	1	0.57	0.4534	3	8.87	**0.0003**	3	2.35	0.0875
F|B1	1	46.86	**<0.0001**	3	4.50	**0.0083**	3	2.43	0.0802
F|B2	1	119.00	**<0.0001**	3	11.04	**<0.0001**	3	10.67	**<0.0001**
F|B3	1	207.93	**<0.0001**	3	54.36	**<0.0001**	3	4.45	**0.0088**

Table 3 Two-way ANOVA of ^{13}C incorporation into important groups of PLFA for the effects of harvest and litter type.

Parameter	Harvest			Litter type			Interaction H X L		
	df	F	p	df	F	p	df	F	p
C mic (µg g^{-1}d.w.)	1	27.87	**<0.0001**	3	1.27	0.3008	3	2.82	0.0548
total PLFA (ng^{13}C g^{-1}d.w.)	1	1.2	0.2816	3	0.81	0.4992	3	0.11	0.9535
bacterial PLFA (ng^{13}C g^{-1}d.w.)	1	<0.01	0.9656	3	0.1	0.9602	3	0.15	0.9269
eucariotic PLFA (ng^{13}C g^{-1}d.w.)	1	21.18	**0.0001**	3	3.15	**0.039**	3	0.73	0.5393
gram positive PLFA (ng^{13}C g^{-1}d.w.)	1	0.08	0.7844	3	0.99	0.4094	3	0.56	0.6433
18:2(9,12)c (ng^{13}C g^{-1}d.w.)	1	95.57	**<0.0001**	3	6.28	**0.0019**	3	4.42	**0.0107**
20:4(5,8,11,14)c (ng^{13}C g^{-1}d.w.)	1	60.87	**<0.0001**	3	6.06	**0.0023**	3	1.17	0.3355
F|B 1	1	80.76	**<0.0001**	3	2.17	0.1115	3	4.03	**0.0157**
F|B 2	1	97.4	**<0.0001**	3	7.39	**0.0007**	3	6.73	**0.0013**
F|B 3	1	105.95	**<0.0001**	3	14.64	**<0.0001**	3	6.88	**0.0011**

Table 4 Linear correlation analysis between MDS axes shown in Fig. 3 (SMCC) and the 29 different identified PLFA underlying the MDS and three different fungal to bacterial ratios (refer Table 1) on the left side, and element contents, stoichiometric ratios, pools, enzymes and processes on the right side. The abbreviations g+, b, and e in column pa, the primarily assigned biomarker, stand for gram positive, bacteria in general, and eukaryotic (fungal) markers. Clit, Nlit, Plit, C:Nlit, C:Plit and N:Plit represent the respective elemental contents and elemental ratios of beech leaf litter; C:Nmic and Pmic the C:N ratio and P content of microbial biomass measured by chloroform fumigation extraction. C(mic) and N(mic) represent microbial biomass carbon and nitrogen,measured by the extraction-fumigation-extraction method. Lig:N represents the ratio of lignin to nitrogen content. AA conc., NH4 conc. and NO3 conc. represent the concentrations of total free amino acids, ammonium and nitrate in litter. Abbreviations for processes are: ProtDepol, protein depolymerization; AA imm., amino acid immobilization; N min, nitrogen mineralization; NH4 imm., ammonium immobilization; Nitr, nitrification; NO3 imm, nitrate immobilization; P min, phosphate mineralisation; P imm, phosphor immobilization; Cellulase, Chitinase, Phosphatase, Protease, Peroxidase, Phenoloxidase are to be understood as potential activities. Numbers represent correlation coefficients of linear regressions (R^2>0.45 in bold),

with direction of correlation, and significance level indicated: *, p<0.05; **, p<0.01; ***, p<0.001.

Parameter	pa	MDS1	MDS2	Parameter	MDS1	MDS2
i14:0	g+	**0.7416 *** **	0.0039	C_{lit}	0,0035	-0,0141
14:0	b	**0.5569 *** **	0.3046 ***	N_{lit}	0,0065	**0.6704 *** **
i15:0	g+	**0.8333 *** **	0.0398	P_{lit}	0,0014	0.2094 **
a15:0	g+	**0.7079 *** **	0.044	$C:N_{lit}$	-0,0049	**-0.703 *** **
15:0	b	**0.6775 *** **	0.0849 *	$C:P_{lit}$	0,0008	-0,0781
i16:0	g+	**0.8206 *** **	0.0107	$N:P_{lit}$	0,0036	0,0015
i15:1(4)	b	0.1751 **	0.0739	Lignin	-0.0402	-0.2561 **
16:0	b	0.1112 *	**0.6749 *** **	Starch	-0.0569	-0.0089
16:1(9)c	e	0.1221 *	**0.7951 *** **	Cellulose	-0.0817	-0.3572 ***
16:1(11)t	b	**0.6579 *** **	-0.001	Lig:N	-0.0441	**-0.4735 *** **
i17:0	g+	**0.6793 *** **	0.0398	AA conc.	0,013	**0.6523 *** **
a17:0	g+	**0.538 *** **	0.0368	NH_4 conc.	0.1194 *	**0.6725 *** **
i17:1(9)c	b	**0.6002 *** **	0.3159 ***	NO_3 conc.	0.3087 ***	0.3856 ***
17:0	b	0.1652 **	**0.5325 *** **	Mass Loss	0,069	0,0079
cy17:0(9.10)	b	0.4231 ***	0.057	ProtDepol	**0.4772 *** **	0.2419 **
18:0	b	0.0156	0.077	AA imm	0,0334	0.3213 ***
18:1(9)t	e	**-0.4835 *** **	-0.0351	N min	-0,0451	**0.5266 *** **
18:1(9)c	e	-0.0623	0.0183	NH_4 imm	-0,0145	**0.5453 *** **
18:1(11)c		0.3284 ***	**0.6338 *** **	Nitr.	-0.1289 *	0.2745 ***
18:2(9,12)t	e	**0.4583 *** **	0.1061 *	NO_3 imm	-0.2258 **	0.1793 *
18:2(9,12)c	e	-0.1751 **	**-0.4714 *** **	P min	0,0039	**0.4877 *** **
18:3(6,9,12)c	e	-0.4371 ***	0.0124	P imm	-0,0929	0,0332
cy19:0(9.10)	b	**0.4535 *** **	-0.0034	Cellulase	-0.1553 *	0.3382 ***
18:3(9,12,15)c	e	-0.2745 ***	**-0.8925 *** **	Chitinase	-0.1684 **	**0.4297 *** **
20:0	e	-0.0242	0.0526	Phosphatase	0.1486 *	**0.5227 *** **
20:4(5,8,11,14)c	p	0.0911 *	0.0799	Protease	0.1674 **	0,059
22:0	e	**-0.4887 *** **	0	Peroxidase	0,057	**0.6139 *** **
23:0	e	**-0.5058 *** **	-0.0461	Phenoloxidase	0,0111	**0.6096 *** **
24:0	e	**-0.5435 *** **	-0.0034	calc CUE	-0.1308 *	-0,0058
F|B1		**-0.6526 *** **	**-0.191 ** **	C-CO2	0,0847	0.4336 ***
F|B2		**-0.4589 *** **	0.0016	C(mic)	0.3052 ***	**0.6132 *** **
F|B3		**-0.552 *** **	**-0.6612 *** **	N(mic)	**0.4928 *** **	0.1821 **
totPLFA		**-0,5695 *** **	0,0107	P_{mic}	0,0004	0.1989 **
				$C:N_{mic}$	-0.4771 ***	0,0102
				$C:P_{mic}$	-0,0002	-0
				$N:P_{mic}$	0.1285 *	-0,001

Table 5 Linear Correlation analysis between MDS axes shown in Fig. 4 (FMCC) and the 29 different identified PLFA underlying the MDS and three different ways of calculating fungal to bacterial ratios given in Table 1 on the left side; Clit, Nlit, Plit, C:Nlit, C:Plit and N:Plit represent the respective elemental content and ratios of beech leaf litter; Cmic, Nmic and C:Nmic the carbon and nitrogen content and C:N ratio accounting for microbial biomass measured by chloroform fumigation extraction. C(mic) and N(mic), represent carbon and nitrogen content accounting for microbial biomass, measured by the pre-extraction-chloroform-extraction method. AA conc., NH4 conc. and NO3 conc. represent the concentrations of total free amino acids, ammonium and nitrate in litter. Abbreviations for processes are: ProtDepol, protein depolymerization; AA imm., amino acid immobilization; N min, nitrogen mineralization; NH4 imm., ammonium immobilization; Nitr, nitrification; NO3 imm, nitrate immobilization; P min, phosphate mineralisation; P imm, phosphor immobilization; Cellulase, Chitinase, Phosphatase, Protease, Peroxidase, Phenoloxidase are to be understood as potential activities. Numbers represent correlation coefficients of linear regressions, with direction of correlation, and significance level indicated: *, p<0.05; **, p<0.01; p<0.001.

Parameter	pa	MDS1	MDS2	Parameter	MDS1	MDS2
i14:0	g+	0.2847 ***	-0.1382 *	C_{lit}	0.0571	0.0023
14:0	b	0.0838	-0.7299 ***	N_{lit}	0.0408	0.2923 ***
i15:0	g+	0.0001	-0.7469 ***	P_{lit}	0.0003	0.0903
a15:0	g+	0.2761 ***	-0.2433 **	$C:N_{lit}$	-0.0358	-0.2878 ***
15:0	b	0.0238	-0.7042 ***	$C:P_{lit}$	0.0069	-0.0414
i16:0	g+	0.384 ***	-0.2688 ***	$N:P_{lit}$	0.022	-0.0003
i15:1(4)	b	0.3941 ***	0.0443	AA conc.	0.0706	0.3465 ***
16:0	b	0.2637 ***	0.3402 ***	NH_4 conc.	0.1885 **	0.3073 ***
16:1(9)c	e	-0.005	-0.1168 *	NO_3 conc.	0.3894 ***	0.0921
16:1(11)t	b	0.0482	-0.0087	Mass Loss	0.1715 **	0.019
i17:0	g+	-0.0868	-0.3432 ***	ProtDepol	0.4063 ***	0.0053
a17:0	g+	0.0786	-0.0522	AA imm	0.0674	0.1014 *
i17:1(9)c	b	0.3655 ***	-0.0554	N min	-0.02	0.3 ***
17:0	b	0.0354	0.0488	NH_4 imm	<0.0001	0.43 ***
cy17:0(9.10)	b	-0.2564 **	-0.0153	Nitr.	-0.04	0.51 ***
18:0	b	-0.6699 ***	0.0146	NO_3 imm	-0.1	0.42 ***
18:1(9)t	e	-0.711 ***	-0.0745	P min	0.01	0.14 *
18:1(9)c	e	0.6592 ***	0.0514	P imm	-0.01	0.1
18:1(11)c		0.0284	-0.0936	Cellulase	-0.1263 *	0.209 **
18:2(9,12)t	e	-0.9253 ***	-0.0066	Chitinase	-0.141 *	0.2351 **
18:2(9,12)c	e	-0.0281	0.1912 **	Phosphatase	0.1234 *	0.0594
18:3(6,9,12)c	e	0.0032	-0.0427	Protease	0.1666 **	0.0134
cy19:0(9.10)	b	-0.6026 ***	0.062	Peroxidase	0.0577	0.1733 **
18:3(9,12,15)c	e	0.4455 ***	-0.0545	Phenoloxidase	0.0209	0.3019 ***
20:0	e	-0.5226 ***	0.0633	direct CUE	0.54 ***	-0.02
20:4(5,8,11,14)c	p	-0.6096 ***	0.0886	calc CUE	-0.2166 **	0.0014
22:0	e	-0.0039	-0.0062	C-CO2	0.1092	0.2254 **
23:0	e	-0.4864 ***	0.149 *	C(mic)	0.2663 ***	0.0387
24:0	e	0.2761 ***	-0.4699 ***	C_{mic}	0.0262	0.1277 *
F|B1		-0.833 ***	0.0592	N(mic)	0.4204 ***	-0.0042
F|B2		-0.8823 ***	-0.0002	N_{mic}	0.3549 ***	0.0008
F|B3		-0.5748 ***	0.162 *	P_{mic}	-0.0145	0.0161
				$C:N_{mic}$	-0.4688 ***	0.0601
				$C:P_{mic}$	0.0077	-0
				$N:P_{mic}$	0.2024 **	-0.042
				13C/15N	-0.2166 **	0.0014
				15N(mic)	0.3594 ***	-0.1292 *
				13C(mic)	0.235 **	-0.1326 *

Table 6 Three-way ANOVA of important groups of PLFA. Total PLFA, sum of the 29 identified and for community analysis used PLFA listed in text; bacterial PLFA, gram positive PLFA, eukaryotic PLFA according to assignment stated in Table 1**.**

Parameter		total PLFA (nmol g^{-1}d.w.)	bacterial PLFA (nmol g^{-1}d.w.)	eukaryotic PLFA (nmol g^{-1}d.w.)	gram positive PLFA (nmol g-1	18:2(9,12)c (nmol g^{-1}d.w.)	20:4(5,8,11,14)c (nmol g^{-1}d.w.)	F|B 1	F|B 2	F|B 3
	df	1	1	1	1	1	1	1	1	1
Harvest	F	47.78	10.42	156.11	16,66	76.1	16.47	75,66	9,65	293,15
	p	**<0.0001**	**0.0018**	**<0.0001**	**0,0001**	**<0.0001**	**0.0001**	**<0.0001**	**0,0026**	**<0.0001**
	df	2	2	2	2	2	2	2	2	2
Litter type	F	25.11	29.91	12.84	7	21.45	22.62	1,75	6,77	64,52
	p	**<0.0001**	**<0.0001**	**<0.0001**	**0,0016**	**<0.0001**	**<0.0001**	0,1796	**0,0019**	**<0.0001**
	df	2	2	2	2	2	2	2	2	2
Treatment	F	15.46	9.62	28.13	5,68	50.31	3.06	1,38	11,64	1,24
	p	**<0.0001**	**0.0002**	**<0.0001**	**0,0049**	**<0.0001**	0.0524	0,2575	**<0.0001**	0,2937
	df	2	2	2	2	2	2	2	2	2
Interaction **H** X **L**	F	1.61	1.06	1.95	2,32	10.25	5.96	2,66	6,16	1,55
	p	0.206	0.3514	0.1486	0,1046	**0.0001**	0.0039	0,076	**0,0032**	0,2182
	df	2	2	2	2	2	2	2	2	2
Interaction **H** X **T**	F	15.28	11.06	24.66	9,41	41.08	3.81	0,02	4,96	0,59
	p	**<0.0001**	**0.0001**	**<0.0001**	**0,0002**	**<0.0001**	**0.0264**	0,9841	**0,0093**	0,5592
	df	4	4	4	4	4	4	4	4	4
Interaction **L** X **T**	F	0.89	0.63	1.77	0,4	3.07	0.46	0,44	3,12	0,56
	p	0.4742	0.6415	0.1437	0,8071	**0.0208**	0.7635	0,7802	**0,0194**	0,6916
	df	4	4	4	4	4	4	4	4	4
Interaction **H** X **L** X **T**	F	0.53	0.19	1.78	0,18	3.73	0.52	0,74	3,54	1,46
	p	0.7128	0.9409	0.1408	0,9465	**0.0078**	0.7211	0,5698	**0,0103**	0,2229

Table 7 Three-way ANOVA of several PLFA markers, ratios and sums (see Table 1 for detailed information) of ^{13}C labeled PLFA..

Parameter		C mic (µg g^{-1}d.w.)	total PLFA (nmol g^{-1}d.w.)	bacterial PLFA (nmol g^{-1}d.w.)	eukaryotic PLFA (nmol g^{-1}d.w.)	gram positive PLFA (nmol g-1 d.w.)	18:2(9,12)c (nmol g^{-1}d.w.)	20:4(5,8,11,14)c (nmol g^{-1}d.w.)	F|B 1	F|B 2	F|B 3
	df	1	1	1	1	1	1	1	1	1	1
Harvest	F	<0.01	8.46	10.44	0	13.05	17.67	63.75	4.24	11.88	17.02
	p	0.9736	**0.0049**	**0.0019**	0.9782	**0.0006**	**0.0001**	**<0.0001**	**0.0433**	**0.001**	**0.0001**
	df	2	2	2	2	2	2	2	2	2	2
Litter type	F	3.6	12.85	7.31	23.97	4.13	5.44	30.21	0.4	1.32	7.29
	p	0.0328	**<0.0001**	**0.0013**	**<0.0001**	**0.0203**	**0.0065**	**<0.0001**	0.6692	0.273	**0.0014**
	df	2	2	2	2	2	2	2	2	2	2
Treatment	F	2.04	11.11	8.2	32.37	7.93	66.96	10.6	5.16	15.04	21.99
	p	0.1386	**0.0001**	**0.0007**	**<0.0001**	**0.0008**	**<0.0001**	**0.0001**	**0.0082**	**<0.0001**	**<0.0001**
	df	2	2	2	2	2	2	2	2	2	2
Interaction **H** X **L**	F	0.92	1.66	3.51	0.35	5.53	4.13	15.41	2.38	4.06	4.83
	p	0.4026	0.1971	0.0354	0.7069	**0.006**	**0.0203**	**<0.0001**	0.1007	**0.0217**	**0.011**
	df	2	2	2	2	2	2	2	2	2	2
Interaction **H** X **T**	F	9.23	4.49	2.3	17.81	3.81	69.59	6.91	5.76	18.94	13.77
	p	0.0003	**0.0148**	0.1081	**<0.0001**	**0.0271**	**<0.0001**	**0.0019**	**0.0049**	**<0.0001**	**<0.0001**
	df	4	4	4	4	4	4	4	4	4	4
Interaction **L** X **T**	F	1.79	1.77	1.69	2.84	2.05	8.85	1.41	0.33	1.95	0.62
	p	0.1402	0.1455	0.1619	0.0308	0.0972	**<0.0001**	0.2414	0.8553	0.1119	0.6505
	df	4	4	4	4	4	4	4	4	4	4
Interaction **H** X **L** X **T**	F	2.24	0.57	0.54	1.97	0.47	5.84	1.14	1.09	2.21	1.95
	p	0.074	0.6864	0.7088	0.1098	0.7586	**0.0004**	0.3441	0.3666	0.0776	0.1117

Table 8 Linear Correlation analysis between both axis of two-dimensional scaling shown in Fig. 5C and Fig. 5E and the respective 29 different identified PLFA underlying each MDS, the three different ways of calculating fungal to bacterial ratios given in Table 1, and the total PLFA of each sample. Numbers represent correlation coefficients of linear regressions, with direction of correlation, and significance level indicated: *, p<0.05; **, p<0.01; ***, p<0.001.

	Harvest 2			Harvest 3		
pa	PLFA	MDS1	MDS2	PLFA	MDS1	MDS2
g+	i14:0	-0.1708 **	-0.033	i14:0	-0.145 **	-0.0005
b	14:0	0.0645	-0.4102 ***	14:0	0.0015	0.0762 *
g+	i15:0	-0.0038	**-0.6023 *** **	i15:0	-0.2207 ***	-0.008
g+	a15:0	-0.0102	**-0.4144 *** **	a15:0	-0.2298 ***	-0.0023
b	15:0	-0.0071	**-0.7846 *** **	15:0	-0.1406 **	-0.0064
g+	i16:0	-0.0241	**-0.4851 *** **	i16:0	-0.2591 ***	-0.1272 **
b	i15:1(4)	-0.0004	**-0.5037 *** **	i15:1(4)	-0.0299	0.0552
b	16:0	**0.4923 *** **	-0.0463	16:0	0.213 ***	0.1255 **
e	16:1(9)c	**0.7516 *** **	-0.0455	16:1(9)c	0.2445 ***	0.0236
b	16:1(11)t	-0.0775	0.0031	16:1(11)t	-0.0518	-0.0782 *
g+	i17:0	0.1446 **	-0.0585	i17:0	-0.1371 **	-0.1313 **
g+	a17:0	0.1993 **	-0.0151	a17:0	-0.1964 **	-0.1579 **
b	i17:1(9)c	**0.4794 *** **	-0.1065 *	i17:1(9)c	-0.0565	-0.1045 *
b	17:0	0.3777 ***	0.001	17:0	0.1008 *	0.002
b	cy17:0(9.10)	**0.5035 *** **	-0.0001	cy17:0(9.10)	-0.0043	-0.1227 *
b	18:0	0.0037	0.1822 **	18:0	0.0017	-0.0169
e	18:1(9)t	-0.048	0.2214 **	18:1(9)t	-0	-0.1161 *
e	18:1(9)c	-0.0029	0.2253 ***	18:1(9)c	-0.0374	-0.0903 *
	18:1(11)c	0.4382 ***	0.2964 ***	18:1(11)c	0.1838 **	-0.0079
e	18:2(9,12)t	0.3664 ***	-0.0002	18:2(9,12)t	-0.0019	-0.0369
e	18:2(9,12)c	0.0079	**-0.4776 *** **	18:2(9,12)c	-0.0836 *	-0.0505
e	18:3(6,9,12)c	-0.044	**-0.4776 *** **	18:3(6,9,12)c	0.0578	0.0352
b	cy19:0(9.10)	-0.0127	0.2869 ***	cy19:0(9.10)	-0.0302	-0.0724
e	18:3(9,12,15)c	**-0.8852 *** **	0.0012	18:3(9,12,15)c	-0.2017 ***	-0.0034
e	20:0	-0.0039	0.0627	20:0	-0.005	-0.0251
p	20:4(5,8,11,14)(	0.3324 ***	-0.0128	20:4(5,8,11,14)(	-0.152 **	-0.0526
e	22:0	0.0179	0.4049 ***	22:0	0.033	-0.0071
e	23:0	-0.0007	0.2968 ***	23:0	0.0628	-0
e	24:0	-0.0378	**0.6152 *** **	24:0	0.0306	-0.008
	F|B1	0.0084	0.0708	F|B1	0.0791 *	0.0001
	F|B2	-0.0666	0.4429 ***	F|B2	0.0396	0.0228
	F|B3	**-0.6603 *** **	0.0533	F|B3	-0.1446 **	-0.0539
	total PLFA	0.1524 **	-0.58 ***	total PLFA	0.098 *	0.1046 *

Table 9 Linear Correlation analysis between both axis of two-dimensional scaling of H2 and H3, shown in Fig. 5D and Fig. 5F and the respective the ^{13}C-mol% values of the 29 different identified PLFA underlying the MDS, three different ways of calculating fungal to bacterial ratios given in Table 1, and total ^{13}C-PLFA amount of each sample. Numbers represent correlation coefficients of linear regressions, with direction of correlation, and significance level indicated: *, p<0.05; **, p<0.01; ***, p<0.001.

	Harvest 2			Harvest 3		
pa	PLFA	MDS1	MDS2	PLFA	MDS1	MDS2
g+	i14:0	-0.0137	-0.4068 ***	i14:0	-0.3266 ***	-0.0201
b	14:0	-0.0887	-0.3763 ***	14:0	-0.0155	-0.0151
g+	i15:0	-0.4059 ***	-0.2852 ***	i15:0	**-0.6741 *** **	0.0236
g+	a15:0	-0.2112 **	-0.2494 ***	a15:0	**-0.6344 *** **	0.0067
b	15:0	**-0.5734 *** **	-0.0035	15:0	-0.0397	0.1219 *
g+	i16:0	-0.3966 ***	0.0028	i16:0	**-0.832 *** **	0.0822
b	i15:1(4)	**-0.664 *** **	-0.0079	i15:1(4)	-0.1993 **	0.0062
b	16:0	**0.499 *** **	-0.173 **	16:0	0.0601	0.0001
e	16:1(9)c	0.1844 **	-0.4082 ***	16:1(9)c	**0.7004 *** **	-0.3811 ***
b	16:1(11)t	0.11 *	-0.0003	16:1(11)t	-0.1676 **	0.0633
g+	i17:0	0.3173 ***	0.035	i17:0	-0.4301 ***	-0.0006
g+	a17:0	0.1305 *	0.0558	a17:0	**-0.7433 *** **	0.1075 *
b	i17:1(9)c	-0.3368 ***	0.0001	i17:1(9)c	-0.1872 **	0.0055
b	17:0	-0.0978 *	-0.0661	17:0	-0.2282 **	0.2477 ***
b	cy17:0(9.10)	**0.6465 *** **	-0.0033	cy17:0(9.10)	-0.0455	-0.3104 ***
b	18:0	-0.0931 *	0.4285 ***	18:0	-0.0254	0.1294 *
e	18:1(9)t	0.2165 **	0.0029	18:1(9)t	-0.1908 **	0.0636
e	18:1(9)c	**-0.641 *** **	0.188 **	18:1(9)c	-0.109 *	**0.8504 *** **
	18:1(11)c	**0.8134 *** **	0.1066 *	18:1(11)c	0.0267	**-0.5325 *** **
e	18:2(9,12)t	0.0983 *	-0.0004	18:2(9,12)t	-0.2119 **	0.172 **
e	18:2(9,12)c	**-0.8463 *** **	0.0696	18:2(9,12)c	-0.0441	**0.9152 *** **
e	18:3(6,9,12)c	**-0.4635 *** **	-0.0261	18:3(6,9,12)c	**0.5158 *** **	0.0625
b	cy19:0(9.10)	0.4245 ***	0.1118 *	cy19:0(9.10)	**-0.578 *** **	0.0005
e	18:3(9,12,15)c	**-0.8795 *** **	0.0064	18:3(9,12,15)c	0.0896	0.0926
e	20:0	0.0099	-0.0016	20:0	-0.0694	0.0026
p	20:4(5,8,11,14)c	-0.1961 **	-0	20:4(5,8,11,14)c	-0.0029	0.1828 **
e	22:0	-0.1991 **	-0.0005	22:0	-0.0137	0.0096
e	23:0	0.2256 **	-0.0013	23:0	0.0088	-0.0064
e	24:0	-0.1964 **	0.0073	24:0	0.4399 ***	0.1467 *
	F|B1	**-0.6018 *** **	0.2599 ***	F|B1	0.0703	**0.7192 *** **
	F|B2	**-0.8167 *** **	0.0922	F|B2	-0.0003	**0.8875 *** **
	F|B3	**-0.7765 *** **	0.0492	F|B3	**0.6268 *** **	0.1121 *
	total PLFA	-0.2734 ***	-0.2195 **	total PLFA	0.0478	-0.1554 **

Table 10 Linear correlations of beach litter chemistry with both MDS axis of the SMCC data of H2.

stoichiometric	Harvest 2	
Parameter	MDS1	MDS2
Lignin	-0,1054	0,0057
Starch	-0,4135 *	-0,0904
Cellulose	-0,5439 **	-0,0041
N_lit	**0,8734 *** **	0,0604
Lig:N	-0,3525 *	-0,0002
C:NLit	**-0,8307 *** **	-0,0605
C:PLit	-0,3048 *	-0,0268
N:PLit	-0,0331	-0,0044

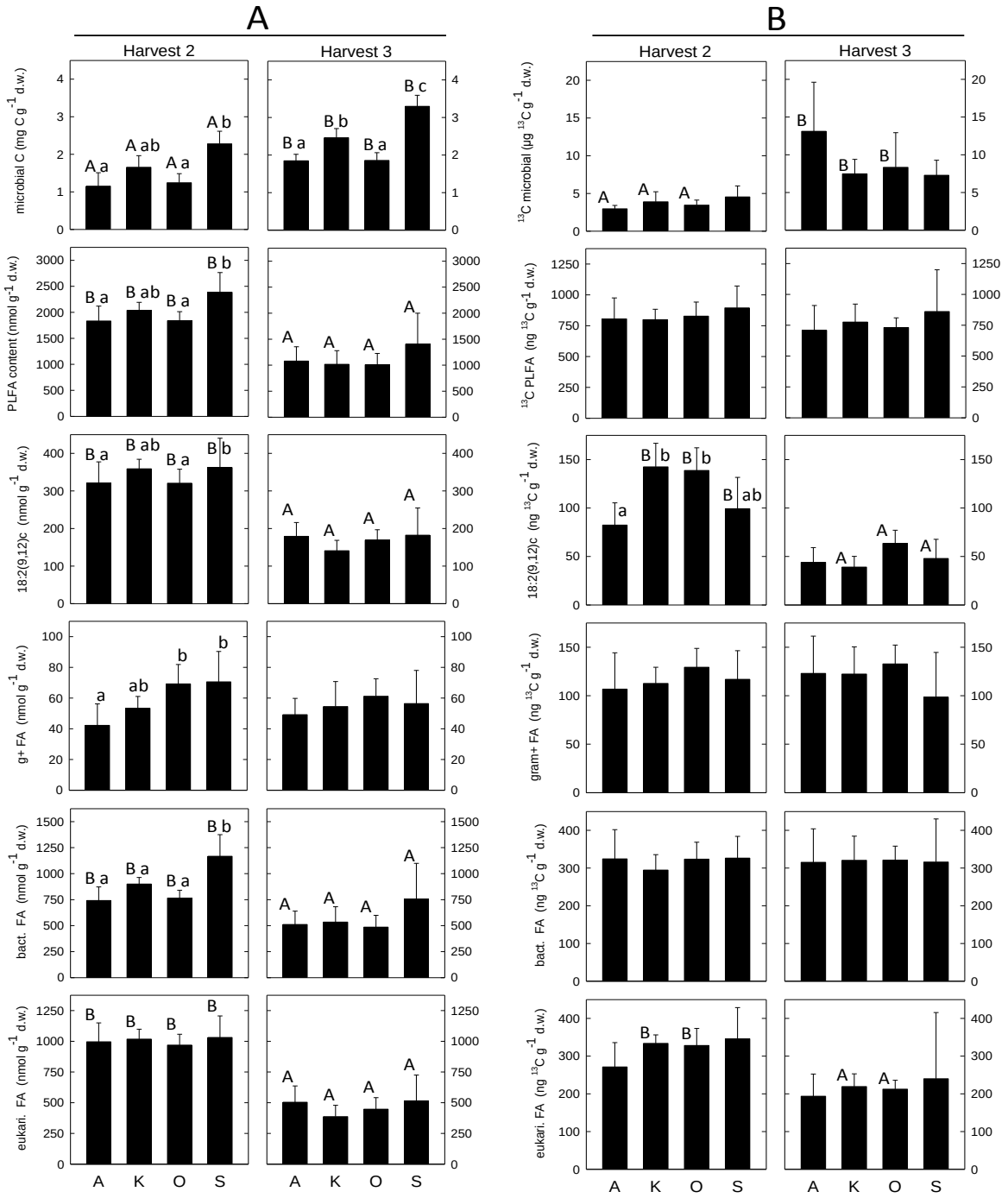

Fig. 1 (A) Absolute amount of; and (B) uptake and distribution of ^{13}C label into: microbial carbon, PLFA content, different PLFA markers and subgroups assigned to different taxonomic groups as stated in Table 1. Error bars indicate standard deviation; letters represent homogeneous groups from one-way-ANOVA. Capital letters for comparing differences regarding harvest within same litter type; small letters for comparing litter types within each harvest.

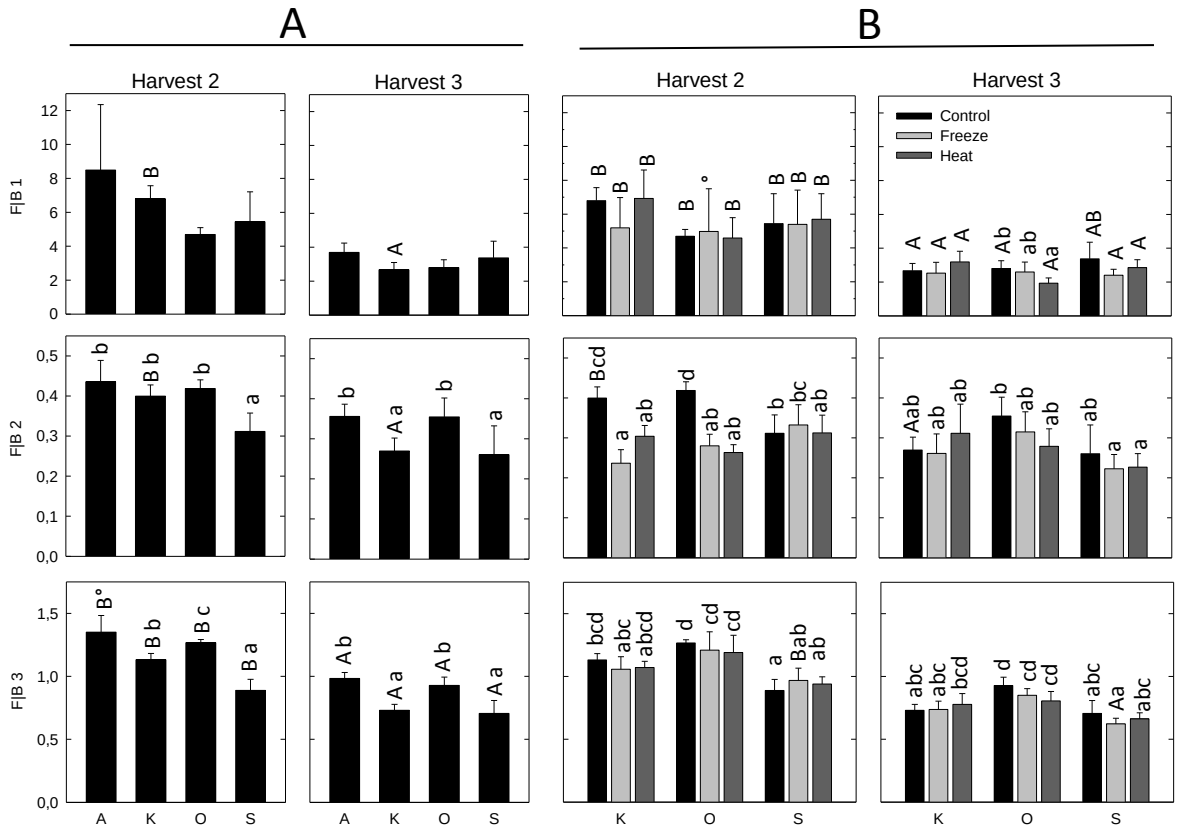

Fig. 2 Fungal-Bacterial ratios of E1 (A), and E2 (B) according to Table 1. Small (capital) letters indicate homogeneous groups considering significant differences within (between) harvests. °, litter type had to been taken out for ANOVA

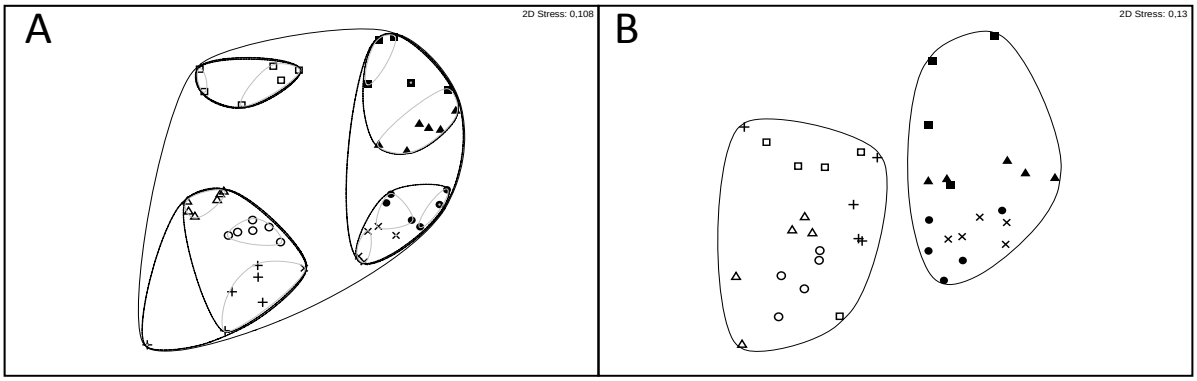

Fig. 3 Multidimensional scaling based on Bray Curtis similarity of square root transformed mol% data of (A) total PLFA and (B) ^{13}C enriched, APE corrected total PLFA. Similarity derived from CA is overlaid in MDS. Open symbols, H2; filled symbols, H3; triangles, Klausenleopoldsdorf; circles, Ossiach; squares, Schottenwald; + Achenkirch H2; x, Achenkirch H3. (A) Solid black line, 91% similarity; broken black line, 92% similarity; dotted black line, 94% similarity; solid gray line, 96% similarity. (B) Solid black line, 90% similarity. CA given in supplementary data : (A) , .

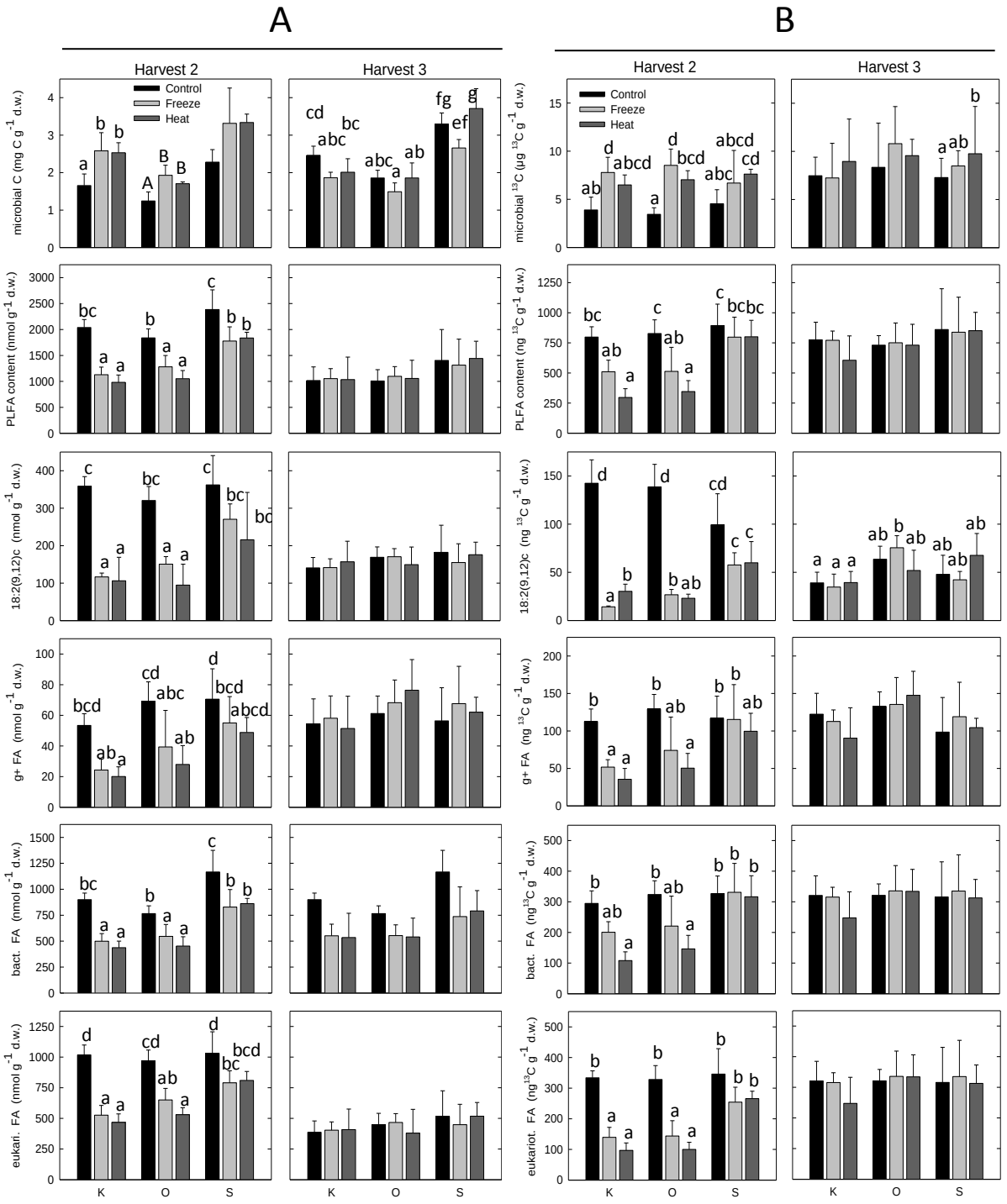

Fig. 4 Amount of (A), and 13C label uptake and distribution into (B) microbial carbon, PLFA content, different PLFA markers and subgroups assigned to different taxonomic groups as stated in Table 1. Error bars indicate standard deviation; letters represent homogeneous groups from one-way-ANOVA; when capital letters appear separate analysis between treatments for each litter type was performed.

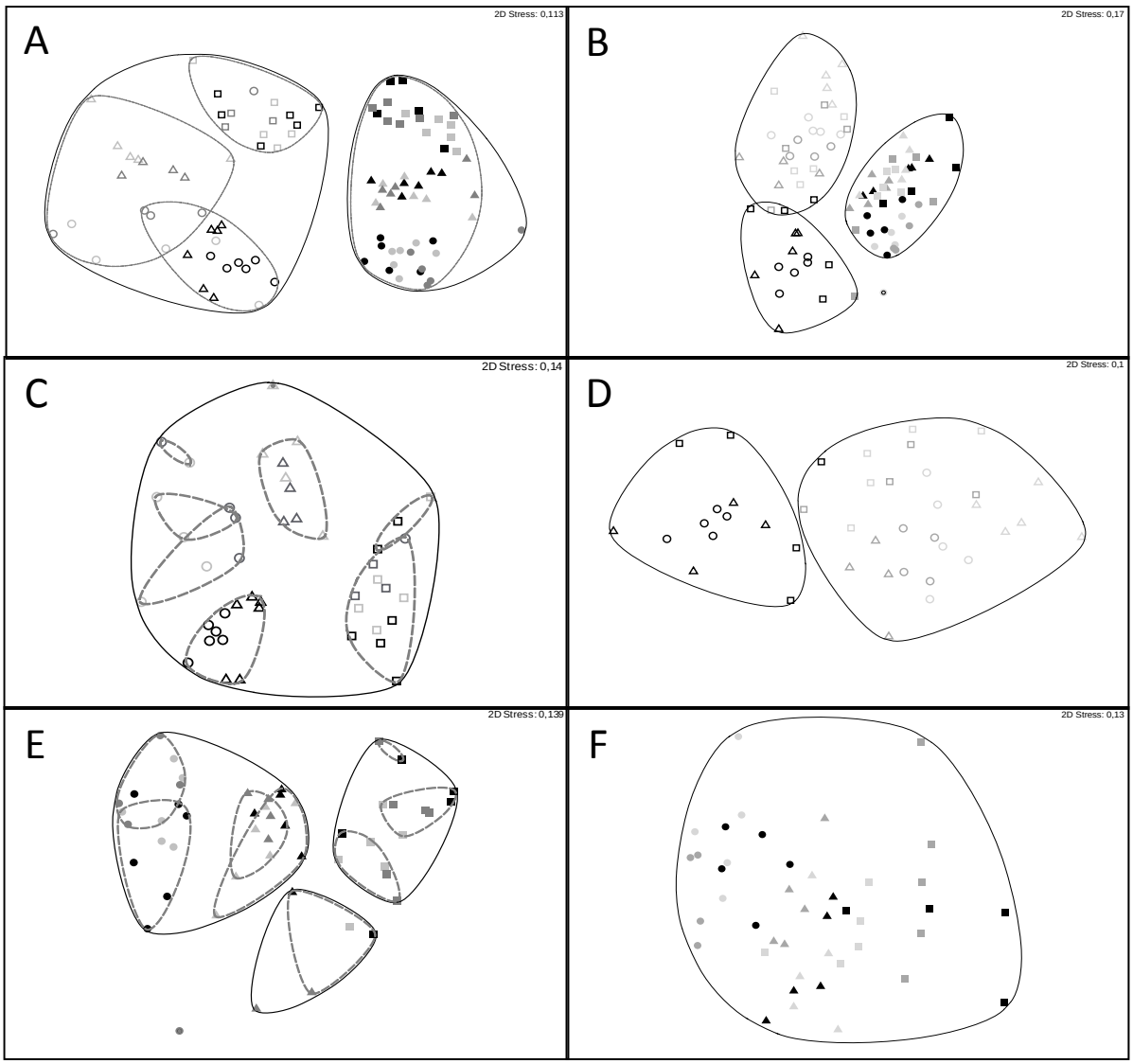

Fig. 5 MDS of amount (A; C; E) of, and incorporation of label into (B; D; F) total PLFA, based on mol% and ^{13}C-mol% data, respectively. Bray Curtis similarity, after square root transformation. A; B, both harvests together. C;D, H2. E; F H3. Open symbols, H2; filled symbols, H3; triangles, Klausen-leopoldsdorf; circles, Ossiach; squares, Schottenwald. Similarity derived from CA is overlaid: (A) solid black line, 90%; broken gray line 93%; (B) solid black line, 90%; (C) solid black line, 92%; broken gray line, 95%; (D) solid black line, 90%; (E) solid black line, 92%; broken gray line, 94%; (F) solid black line, 90%. For detailed CA see Supplementary Data Fig. 9.

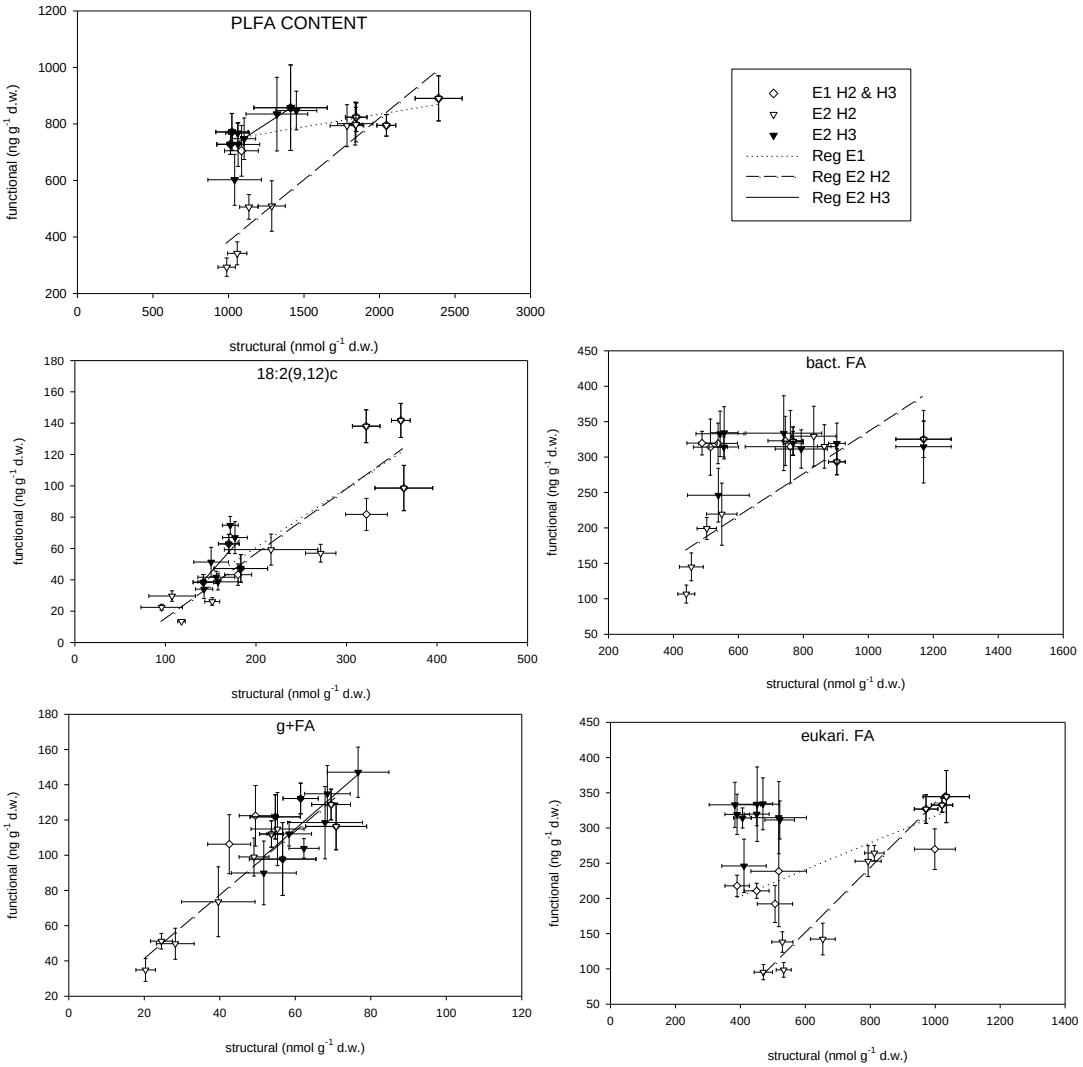

Fig. 6 Correlations of structure/abundance and function/^{13}C-uptake. Error bars represent standard error. N=5. Statistical parameters of regressions are given in Table 18.

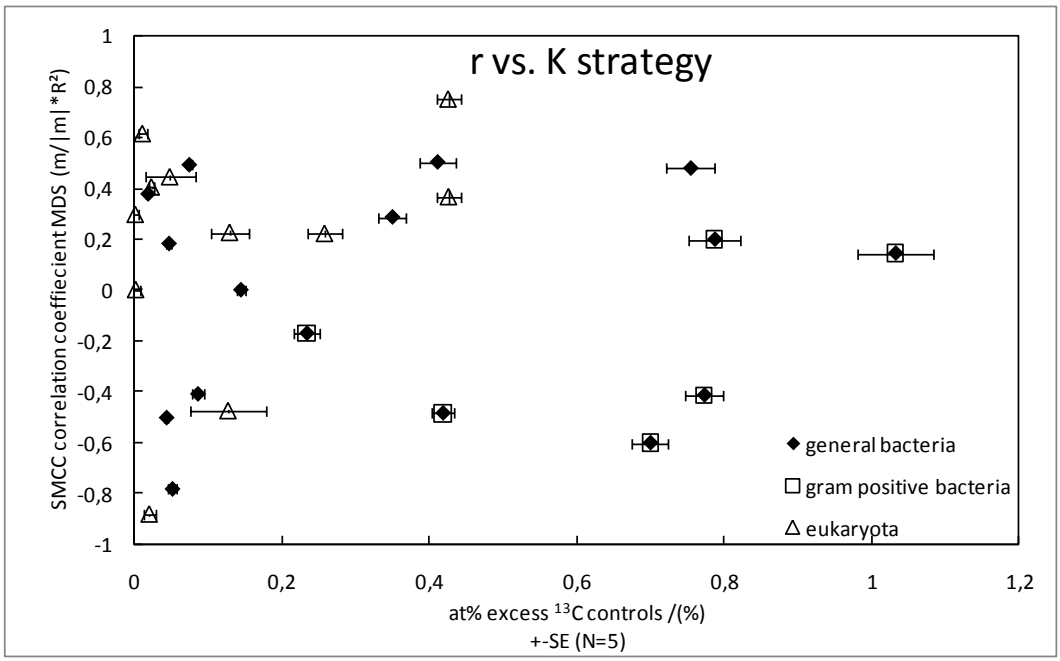

Fig. 7 The uptake of ^{13}C into PLFA (at% excess) is not correlated with resistance (as correlation index) of the SMCC data of H2 (Table 8). R^2, correlation coefficient; m/|m|, direction of correlation. Highest values on y are most resistant PLFA

Supplementary Data

Table 11 Stoichiometric data of the used litter. A, Achenkirch; K, Klausenleopoldsdorf; O, Ossiach; S, Schottenwald. For further information on the locations see (Kesik, Ambus et al. 2005; Ambus, Zechmeister-Boltenstern et al. 2006; Wanek, Mooshammer et al. 2010).

Litter	%C ± SD		%N ± SD		% P ± SD		C:N ± SD		C:P ± SD		N:P ± SD	
A	49.1	1.0	0.84	0.02	0.04	<0.01	58.6	1.6	1230	25	20.9	0.4
K	48.0	<0.1	0.89	0.01	0.03	0.01	53.9	0.6	1470	250	27.2	4.7
O	47.0	0.8	0.71	0.02	0.05	<0.01	66.0	1.8	940	16	14.2	0.3
S	47.6	0.1	1.06	0.02	0.07	0.01	44.8	0.8	650	50	14.6	1.2

N=5

Table 12 Statistical parameters of performed one way ANOSIM for each separate litter type based Bray Curtis similarity of square root transformed mol% data of 29 PLFA.

Litter Type	Harvest	Difference to	R	p
Achenkirch	2	Klausenleopoldsdorf	**0.867**	**0.002**
		Ossiach	**0.776**	**0.002**
		Schottenwald	**0.998**	**0.002**
		Harvest 3	**0.807**	**0.002**
	3	Klausenleopoldsdorf	**0.883**	**0.002**
		Ossiach	0.422	**0.013**
		Schottenwald	**0.992**	**0.002**
Klausenleo-poldsdorf	2	Ossiach	**0.874**	**0.002**
		Schottenwald	**0.869**	**0.002**
		Harvest 3	**0.999**	**0.002**
	3	Ossiach	**0.796**	**0.002**
		Schottenwald	**0.712**	**0.002**
Ossiach	2	Schottenwald	**0.952**	**0.002**
		Harvest 3	**0.999**	**0.002**
	3	Schottenwald	**0.992**	**0.002**
Schottenwald	2	Harvest 3	**0.880**	**0.002**

Table 13 Statistical parameters of performed one way ANOSIM for each separate litter type based on 13C enriched, APE-corrected PLFA.

Litter Type	Harvest	Difference to	R	p
Achenkirch	2	Klausenleopoldsdc	**0.524**	**0.008**
		Ossiach	**0.648**	**0.008**
		Schottenwald	0.312	**0.040**
		Harvest 3	**0.78**	**0.008**
	3	Klausenleopoldsdc	**0.692**	**0.008**
		Ossiach	0.136	0.135
		Schottenwald	**0.806**	**0.008**
Klausenleo-poldsdorf	2	Ossiach	0.312	**0.024**
		Schottenwald	0.356	**0.008**
		Harvest 3	**0.944**	**0.008**
	3	Ossiach	**0.708**	**0.008**
		Schottenwald	**0.594**	**0.008**
Ossiach	2	Schottenwald	**0.632**	**0.008**
		Harvest 3	**0.999**	**0.008**
	3	Schottenwald	**0.948**	**0.008**
Schottenwald	2	Harvest 3	**0.706**	**0.008**

Table 14 Statistical parameters of performed one way ANOSIM for each separate litter type based Bray Curtis similarity of square root transformed mol% data of 29 PLFA .

Litter Type	Harvest	Treatment	R	p
Klausenleo-poldsdorf	2	Control, Freeze	**0.931**	**0.002**
		Control, Heat	**0.999**	**0.005**
		Freeze, Heat	0.206	0.079
	3	Control, Freeze	-0.002	0.446
		Control, Heat	0.106	0.139
		Freeze, Heat	0.085	0.158
Ossiach	2	Control, Freeze	**0.632**	**0.002**
		Control, Heat	**0.849**	**0.005**
		Freeze, Heat	-0.10	0.659
	3	Control, Freeze	-0.063	0.662
		Control, Heat	0.168	0.095
		Freeze, Heat	0.107	0.171
Schottenwald	2	Control, Freeze	0.099	0.206
		Control, Heat	0.289	0.286
		Freeze, Heat	0.08	0.500
	3	Control, Freeze	0.253	0.061
		Control, Heat	-0.04	0.580
		Freeze, Heat	0.165	0.067

Table 15 Statistical parameters of performed one way ANOSIM for each separate litter type based on 13C enriched, APE-corrected PLFA.

Litter Type	Harvest	Treatment	R	p
Klausenleo-poldsdorf	2	Control, Freeze	**0.999**	**0.008**
		Control, Heat	**0.831**	**0.008**
		Freeze, Heat	**0.975**	**0.008**
	3	Control, Freeze	0.008	0.397
		Control, Heat	0.444	**0.032**
		Freeze, Heat	0.228	0.103
Ossiach	2	Control, Freeze	**0.999**	**0.008**
		Control, Heat	**0.999**	**0.008**
		Freeze, Heat	-0.075	0.643
	3	Control, Freeze	<0.001	47.6
		Control, Heat	0.281	0.079
		Freeze, Heat	0.100	0.198
Schottenwald	2	Control, Freeze	**0.600**	**0.008**
		Control, Heat	**0.544**	**0.024**
		Freeze, Heat	-0.088	0.714
	3	Control, Freeze	**0.500**	**0.024**
		Control, Heat	-0.100	0.738
		Freeze, Heat	0.272	**0.024**

Table 16 Concentration of PLFA in controls, given in nmol per gram dry weight litter. A, Achenkirch; K, Klausenleopoldsdorf; O, Ossiach; S, Schottenwald; C, Control; 1-5, Replicate; P, Pooled sample out of replicates 1-5, unlabeled (cursive); H2/3, harvest 2/3;

Identifier	i14:0	14:0	i15:0	a15:0	15:0	i16:0	i15:1(4)	16:0	16:1(9)c	16:1(11)t	i17:0	a17:0	i17:1(9)c	17:0	cy17:0(9.10)	18:0	18:1(9)t	18:1(9)c	18:1(11)c	18:2(9,12)t	18:2(9,12)c	18:3(6,9,12)c	cy19:0(9.10)	18:3(9,12,15)c	20:0	20:4(5,8,11,14)c	22:0	23:0	24:0
AC1-H2	1,13	3,73	11,36	15,33	5,99	6,12	6,59	477,10	82,98	9,58	2,45	4,14	2,46	22,70	28,60	67,73	5,55	95,39	76,30	1,31	259,62	7,78	12,07	306,18	6,99	3,98	27,30	9,51	11,09
AC2-H2	2,00	7,36	13,76	18,65	8,07	6,30	9,15	652,50	101,41	8,14	2,25	4,84	2,09	30,59	28,95	58,49	5,89	118,47	80,88	0,91	339,12	4,66	10,88	446,75	9,06	4,27	33,36	12,15	13,55
AC3-H2	2,52	5,22	10,82	14,71	6,50	6,00	4,44	531,44	78,26	10,39	2,28	3,82	2,20	27,74	27,27	50,64	4,49	110,67	85,80	1,33	370,87	6,97	11,87	422,91	7,77	4,35	35,46	11,72	14,93
AC4-H2	1,28	2,23	4,63	5,27	2,80	3,19	8,39	471,02	63,20	8,03	2,01	2,77	1,53	26,59	27,73	65,88	3,02	107,16	87,30	0,43	306,04	15,84	12,03	398,31	15,47	4,04	35,08	16,50	13,90
AC5-H2	3,52	9,41	16,97	24,00	10,64	9,10	13,30	705,29	117,82	12,20	3,01	5,63	2,89	32,87	37,45	67,09	6,22	139,28	96,41	1,18	392,53	10,17	13,98	458,53	12,77	4,02	39,21	13,58	15,29
ACP-H2	3,14	6,71	12,45	17,37	6,86	5,66	9,88	463,30	63,13	10,97	1,84	3,29	1,55	21,19	21,62	48,01	2,23	86,32	58,72	0,70	258,29	5,45	8,92	358,12	11,76	2,82	23,73	8,54	10,95
KC1-H2	2,44	11,39	16,82	24,65	10,80	7,27	16,37	742,48	112,32	10,61	2,73	5,96	3,58	34,81	27,41	67,13	6,47	136,51	120,20	0,53	352,36	70,84	7,82	330,76	12,18	4,39	39,86	14,49	19,32
KC2-H2	2,13	10,95	12,80	21,30	9,09	6,14	15,22	643,28	110,08	7,02	2,36	4,58	2,99	28,90	24,44	60,97	5,76	114,43	96,85	0,70	326,04	53,33	9,66	262,08	12,05	2,30	31,78	11,19	15,52
KC3-H2	1,60	10,11	12,92	23,41	10,20	6,52	12,39	674,46	109,45	7,40	2,97	5,58	3,26	29,41	25,17	75,36	7,21	142,59	112,32	0,49	374,30	45,41	9,05	275,63	12,57	4,15	30,66	11,96	15,15
KC4-H2	1,31	8,65	12,04	20,85	9,33	6,00	11,42	645,74	95,88	6,54	2,32	4,75	3,00	31,20	21,16	64,46	6,43	130,97	101,40	0,54	372,96	45,44	7,63	291,91	10,93	1,79	34,07	12,67	16,80
KC5-H2	2,77	1,08	19,00	26,95	13,22	7,41	23,74	775,37	115,07	7,34	2,77	6,25	4,97	34,63	21,65	58,78	7,18	140,28	94,14	1,13	392,64	47,31	6,84	340,96	11,98	3,04	29,93	12,15	15,76
KCP-H2	2,02	11,18	11,07	20,36	9,69	5,89	10,03	670,21	75,50	5,73	1,84	4,79	3,18	30,85	18,02	68,37	3,47	121,79	73,64	0,53	335,52	27,21	5,04	279,38	12,00	1,83	29,75	10,36	15,34
OC1-H2	1,49	5,93	12,80	22,86	8,01	6,84	7,03	485,59	80,89	7,74	2,12	4,88	2,72	23,05	22,49	53,32	6,28	110,25	74,08	0,60	258,55	33,06	7,63	285,30	8,24	3,57	29,28	9,30	12,18
OC2-H2	4,40	11,04	22,30	32,18	10,83	8,84	12,64	585,40	102,70	12,33	3,25	6,11	3,66	27,51	26,34	69,72	8,08	131,11	97,97	0,83	327,43	62,18	12,26	356,15	10,54	4,44	37,72	11,12	13,51
OC3-H2	3,39	8,38	15,30	24,60	9,62	7,25	7,94	495,78	84,98	9,41	2,45	4,15	3,16	24,80	21,88	57,65	5,41	112,76	76,77	0,54	301,55	45,88	7,76	287,86	8,92	3,90	28,88	8,21	10,34
OC4-H2	3,53	10,85	20,36	32,43	11,55	8,24	12,76	537,14	102,00	11,69	2,21	4,59	3,53	24,23	26,64	57,72	6,83	116,74	85,20	0,70	324,31	72,61	8,81	284,45	8,31	4,60	30,21	8,80	12,51
OC5-H2	3,78	8,98	21,39	30,88	11,55	9,13	11,03	563,25	107,67	11,16	2,99	6,69	3,60	27,21	31,22	54,04	7,97	138,87	97,45	0,84	348,19	32,72	11,84	308,13	10,07	5,23	37,44	10,77	15,83
OCP-H2	4,30	12,95	22,41	38,93	12,13	10,06	14,40	597,58	95,97	11,99	2,82	5,41	3,67	26,92	27,76	65,23	7,54	144,18	86,79	0,82	364,09	22,15	11,73	333,94	10,75	3,39	33,54	10,19	13,09
SC1-H2	1,57	14,55	20,17	31,28	10,70	7,94	11,11	772,47	158,31	8,85	3,51	6,17	4,89	32,91	36,13	72,18	7,05	124,38	133,51	1,47	252,77	53,50	6,30	128,42	13,56	6,23	40,72	12,32	15,85
SC2-H2	0,45	2,65	10,24	17,29	6,07	6,81	7,84	665,64	141,17	9,91	4,03	6,67	5,57	33,89	36,99	75,60	7,22	147,47	175,02	0,56	319,07	42,35	10,94	150,04	15,01	10,46	47,56	12,98	16,47
SC3-H2	3,45	21,60	20,87	27,93	13,96	9,55	16,28	876,82	203,00	12,14	4,43	8,98	6,47	40,49	35,27	92,66	4,59	151,30	147,12	0,94	334,46	64,53	7,60	151,65	15,07	5,40	40,30	13,61	17,21
SC4-H2	5,48	26,09	25,97	41,81	16,39	10,55	34,50	1033,87	232,09	11,64	2,54	7,14	5,40	43,64	39,13	82,07	4,62	169,55	156,45	2,10	386,98	43,19	6,67	167,99	19,20	11,04	46,31	14,93	17,42
SC5-H2	1,22	7,40	13,14	19,46	10,38	7,09	10,31	839,37	157,17	7,43	2,88	5,80	4,45	42,73	40,56	98,12	7,90	181,19	167,11	2,52	400,62	51,17	15,49	158,88	18,84	5,18	53,23	16,26	20,59
SCP-H2	3,36	25,69	23,55	39,41	15,50	11,00	16,75	1106,18	205,32	10,97	3,09	8,63	6,75	51,78	40,21	103,44	8,02	203,16	162,27	2,28	479,68	71,47	8,43	210,66	30,98	9,89	58,62	17,27	22,33
AC1-H3	5,77	7,11	14,60	20,18	7,28	7,48	8,28	366,18	57,89	10,15	1,94	4,03	2,36	16,10	18,45	25,96	1,68	63,90	56,08	0,71	177,47	3,39	7,41	166,88	3,61	2,71	12,10	4,67	5,11
AC2-H3	5,96	6,89	13,45	18,46	7,44	6,90	6,89	355,12	57,75	11,27	1,81	3,64	2,03	16,01	15,52	28,49	1,16	62,73	50,16	0,67	181,23	1,93	6,03	175,18	3,58	2,59	10,72	3,70	3,95
AC3-H3	5,48	11,07	15,73	21,02	8,27	7,76	7,55	450,05	65,55	12,14	2,12	4,00	2,17	19,02	18,63	55,16	1,08	70,83	62,86	0,82	205,31	2,48	7,95	213,63	4,64	2,82	13,23	4,76	5,22
AC4-H3	4,64	5,62	16,51	20,74	6,60	8,04	6,54	342,65	59,95	10,22	2,54	4,17	2,66	16,90	21,86	26,45	1,88	59,81	60,66	0,62	168,91	3,59	10,12	161,72	3,89	2,94	13,28	5,50	5,98
AC5-H3	2,03	3,86	8,14	9,54	4,11	4,79	2,53	186,50	25,08	5,11	1,49	2,44	1,20	10,06	12,54	28,32	0,59	40,93	32,80	0,55	117,01	3,43	6,46	68,01	3,65	1,91	8,92	3,21	3,60
ACP-H3	3,95	6,06	13,85	18,45	6,56	7,48	6,30	470,92	56,70	9,03	2,25	3,91	2,14	22,42	19,98	42,48	0,85	78,00	63,93	0,59	224,94	5,32	8,68	264,69	5,05	3,22	21,87	7,45	8,57
KC1-H3	3,37	7,04	11,64	17,38	5,75	5,95	6,12	366,63	58,58	8,64	2,25	3,86	2,93	16,62	15,86	30,71	2,02	58,68	81,21	1,04	145,65	4,52	6,73	91,00	5,36	2,30	13,91	4,87	6,47
KC2-H3	3,55	8,22	11,74	18,30	6,26	5,95	7,27	320,26	56,95	6,79	2,12	3,64	2,86	15,53	15,20	26,77	1,30	53,04	63,79	0,59	140,16	2,30	5,30	80,68	4,24	1,93	9,95	3,46	4,05
KC3-H3	5,12	13,77	16,41	27,60	8,50	8,80	15,78	448,63	79,34	7,38	2,71	4,41	4,18	21,39	20,66	41,54	2,05	71,64	86,95	0,82	160,81	2,76	8,47	102,30	5,94	2,14	14,60	4,64	6,07
KC4-H3	6,32	11,44	14,21	22,97	7,19	7,57	12,73	402,50	62,26	6,72	2,72	3,87	3,12	19,23	17,21	37,73	1,40	67,10	78,56	0,87	135,62	1,83	7,93	88,46	7,26	2,07	16,29	7,05	8,22
KC5-H3	6,19	15,26	20,59	32,93	9,73	11,61	17,16	499,52	96,46	8,80	3,25	4,96	4,37	23,79	25,16	62,05	2,24	76,01	111,38	1,17	171,21	2,15	12,01	104,65	11,26	2,73	17,35	6,32	8,25
KCP-H3	2,86	6,40	10,20	13,32	4,72	4,65	5,66	208,02	37,42	5,45	1,65	1,96	1,72	9,69	11,61	28,19	0,80	37,74	53,49	0,71	91,65	3,32	6,44	38,46	3,15	1,80	8,83	2,94	3,91
OC1-H3	2,54	4,46	12,30	17,29	5,40	7,64	4,46	242,78	45,30	10,33	2,77	4,21	2,99	12,03	15,16	28,74	1,97	58,73	54,75	0,99	154,17	5,15	6,77	86,85	8,46	3,50	12,93	4,17	5,77
OC2-H3	5,50	9,72	15,92	23,71	7,65	7,50	11,98	279,29	47,64	8,62	2,01	3,71	4,33	13,08	13,58	29,65	1,00	56,53	43,99	0,54	137,01	4,07	5,14	95,84	4,02	2,04	10,68	3,00	3,99
OC3-H3	2,80	5,74	14,91	21,47	7,56	8,63	4,82	324,92	57,36	8,99	2,80	5,13	3,58	16,21	20,63	30,12	1,61	71,04	60,77	0,85	192,97	1,82	8,59	120,41	4,04	2,99	12,26	3,62	4,44
OC4-H3	5,57	8,52	21,11	32,15	8,83	10,37	7,72	457,37	74,46	12,08	3,42	5,78	4,01	22,21	22,53	39,72	2,14	79,39	76,13	0,96	205,48	2,07	9,92	184,48	7,66	3,32	17,39	6,94	7,28
OC5-H3	5,25	8,97	18,37	28,65	8,37	10,24	10,31	395,41	60,85	9,58	2,93	5,41	3,56	20,15	20,73	39,40	1,36	75,42	71,39	0,70	179,83	4,53	9,61	155,01	7,35	5,09	18,58	6,06	7,89
OCP-H3	4,27	6,38	16,64	21,39	7,36	8,69	7,62	246,06	46,97	8,33	2,33	3,65	2,72	13,39	17,00	28,25	1,14	55,23	54,01	0,85	144,30	4,46	8,38	78,01	6,44	3,29	11,99	3,89	4,35
SC1-H3	3,86	12,05	18,24	20,05	9,42	7,27	13,11	615,16	157,09	11,73	2,46	4,02	5,35	26,08	24,81	48,48	1,61	95,10	131,55	0,90	271,78	6,19	9,51	89,06	8,47	4,21	20,74	7,90	8,75
SC2-H3	5,34	12,88	19,54	29,77	8,70	9,16	10,21	481,16	99,04	14,35	2,88	6,23	4,13	22,49	22,92	40,01	1,24	75,33	109,44	1,07	165,93	4,77	9,52	66,63	6,80	3,79	16,53	4,60	5,60
SC3-H3	1,37	3,29	6,01	7,33	2,95	2,68	1,57	147,97	36,65	3,00	0,94	1,32	1,44	7,69	10,07	18,26	0,60	29,81	40,96	0,39	73,55	1,58	4,79	19,52	2,10	1,18	6,76	1,93	2,73
SC4-H3	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!
SC5-H3	3,81	13,42	18,68	23,59	10,35	9,19	7,89	728,38	178,90	14,17	3,26	4,41	5,03	31,17	31,06	54,12	0,74	110,00	144,63	1,40	190,04	7,69	11,60	93,67	8,19	4,53	23,84	7,00	8,87
SCP-H3	5,11	19,20	21,79	26,68	11,43	8,91	9,63	844,72	164,58	14,13	2,81	5,28	5,68	34,71	27,58	79,65	1,75	110,38	152,88	1,15	209,87	10,65	11,55	100,03	10,63	4,49	25,41	9,70	11,05

Table 17 Concentration of PLFA in stress treatments, given in nmol per gram dry weight litter. A, Achenkirch; K, Klausenleopoldsdorf; O, Ossiach; S, Schottenwald; F, Freeze; H, Heat; 1-5, Replicate; P, Pooled sample replicates 1-5, unlabeled (cursive); H2, harvest 2; H3, harvest 3.

Identifier	i14:0	14:0	i15:0	a15:0	15:0	i16:0	i15:1(4)	16:0	16:1(9)c	16:1(11)t	i17:0	a17:0	i17:1(9)c	17:0	cy17:0(9.10)	18:0	18:1(9)t	18:1(9)c	18:1(11)c	18:2(9,12)t	18:2(9,12)c	18:3(6,9,12)c	cy19:0(9.10)	18:3(9,12,15)c	20:0	20:4(5,8,11,14)c	22:0	23:0	24:0
KF1-H2	2,36	4,66	6,27	12,75	3,67	3,58	5,47	448,35	79,40	8,27	1,23	3,23	1,94	19,95	19,45	66,65	5,82	84,82	97,89	0,86	119,84	186,59	7,07	126,95	14,27	1,16	24,15	7,57	12,28
KF2-H2	2,11	5,36	8,56	14,51	4,07	3,40	7,94	407,54	75,99	6,64	1,48	3,74	1,90	18,53	16,88	33,76	5,25	78,12	87,45	0,71	109,60	40,65	8,21	116,40	6,99	1,22	20,52	6,44	10,60
KF3-H2	1,84	3,86	5,48	7,85	2,70	2,54	3,72	314,00	55,66	5,33	1,13	2,67	1,43	14,52	13,17	35,21	3,86	65,58	86,04	0,40	103,14	75,73	7,41	118,04	8,18	1,14	21,42	6,76	11,20
KF4-H2	0,99	2,14	3,77	5,56	1,88	1,95	3,41	364,25	61,12	6,63	1,28	2,86	1,65	18,51	16,09	35,97	4,97	78,17	106,41	0,62	128,21	50,63	9,60	131,23	8,51	2,16	30,27	8,62	13,43
KF5-H2	0,94	2,90	4,91	7,40	2,70	2,65	4,47	361,15	67,15	5,34	1,11	3,36	1,76	16,86	15,06	37,10	6,10	81,90	93,96	0,24	122,72	45,62	5,81	135,96	8,00	1,26	24,01	8,18	12,38
KH1-H2	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!
KH2-H2	0,98	1,86	2,72	5,40	1,75	1,79	2,40	313,81	43,05	3,48	1,38	2,41	1,39	16,21	11,97	32,75	2,09	70,00	72,24	0,31	136,77	45,29	6,10	113,89	6,32	1,69	21,46	6,83	10,38
KH3-H2	0,86	3,02	3,98	12,22	3,40	2,70	3,61	387,71	60,72	4,17	1,47	3,29	2,00	18,41	12,70	36,57	5,72	83,01	77,90	0,48	150,72	41,30	5,07	122,06	6,63	2,35	23,16	7,29	11,42
KH4-H2	1,85	4,96	5,94	10,66	3,31	2,97	5,38	374,17	64,97	5,26	1,45	3,62	1,95	18,14	12,89	34,28	2,30	82,53	76,05	0,32	144,40	59,32	5,16	127,35	7,48	1,27	20,95	6,78	10,73
KH5-H2	0,66	3,03	3,83	6,01	1,62	1,42	2,93	291,35	44,88	3,52	0,87	1,91	0,88	12,36	7,27	25,73	3,70	61,66	58,46	0,32	99,82	35,03	4,18	91,25	5,96	1,11	17,30	5,56	8,75
OF1-H2	4,65	7,52	13,48	31,26	6,79	4,90	10,59	526,15	94,71	15,70	2,05	3,88	2,38	20,69	19,50	44,43	7,54	113,19	94,20	0,75	184,83	58,68	9,97	251,10	20,98	2,84	29,10	8,05	12,39
OF2-H2	0,71	1,75	3,60	6,27	2,10	1,97	3,06	335,39	45,52	4,34	1,14	2,08	1,61	15,49	10,50	32,74	4,68	79,46	55,66	0,49	133,16	16,38	6,08	217,09	7,60	1,18	25,13	6,94	11,40
OF3-H2	6,21	6,61	14,16	36,85	5,78	5,74	14,09	436,07	79,33	19,01	2,42	4,02	2,63	16,74	18,32	33,31	4,92	93,56	77,78	0,94	148,95	35,78	8,51	215,32	22,87	2,15	26,87	7,46	12,15
OF4-H2	1,80	4,30	7,03	12,13	3,44	2,61	5,39	377,01	57,30	5,45	1,17	3,13	1,77	16,21	12,73	33,15	5,47	84,87	64,45	0,53	138,34	10,13	7,08	228,99	7,72	1,45	25,91	7,50	11,53
OF5-H2	1,73	2,84	5,60	8,11	3,45	2,71	3,83	367,55	61,84	7,13	1,51	3,85	1,75	18,43	16,55	47,96	5,07	100,61	70,30	0,43	147,90	108,48	6,25	217,41	8,58	1,91	28,12	7,67	12,25
OH1-H2	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!
OH2-H2	2,05	4,13	6,07	10,25	3,15	2,96	4,24	320,52	54,50	6,32	0,68	3,27	1,36	12,48	12,92	38,63	3,79	78,20	59,09	0,47	106,47	49,81	4,91	149,52	9,47	1,73	22,35	6,08	9,75
OH3-H2	1,16	3,19	5,11	9,32	2,41	2,75	3,26	347,10	53,81	6,29	1,43	3,01	1,29	15,44	14,06	37,29	4,86	87,54	67,68	0,60	131,04	23,54	6,13	176,04	8,96	1,44	25,64	6,42	9,95
OH4-H2	2,10	5,32	10,11	22,83	5,45	5,32	7,98	431,91	76,87	7,96	1,81	3,64	2,28	16,91	16,21	35,38	6,13	93,73	72,23	0,62	140,77	54,27	6,32	187,97	8,10	1,73	24,82	7,58	10,31
OH5-H2	1,35	2,46	3,90	7,62	2,47	2,01	3,02	263,66	40,98	4,45	0,92	2,19	1,24	12,04	10,34	36,96	3,84	59,81	45,69	0,48	95,70	123,73	4,45	133,04	5,61	1,33	15,83	4,79	8,22
SF1-H2	0,86	3,32	5,48	10,29	2,49	2,55	3,37	462,42	114,08	7,89	2,31	5,40	5,40	22,87	32,33	46,29	6,29	119,03	134,81	1,85	235,61	32,93	7,31	117,21	11,24	13,19	31,64	7,75	11,69
SF2-H2	2,68	10,36	18,60	32,64	7,66	6,81	12,69	673,27	170,84	10,57	3,62	5,75	5,17	28,12	34,56	67,57	7,44	121,35	135,80	0,89	234,84	101,57	9,34	113,87	13,24	5,08	35,05	9,25	12,59
SF3-H2	1,93	6,60	11,63	25,45	5,21	5,58	6,53	509,55	109,30	9,47	2,61	4,84	4,66	22,36	26,01	47,93	4,43	104,70	126,52	1,33	252,94	36,91	9,07	103,37	13,49	6,73	35,07	8,99	13,23
SF4-H2	1,97	10,70	14,14	28,76	7,87	5,76	12,61	720,66	153,32	13,67	2,59	6,38	4,73	30,79	30,06	54,85	6,65	137,31	144,39	2,02	320,84	38,71	9,51	143,65	13,53	4,81	36,33	9,94	14,13
SF5-H2	3,65	12,67	17,15	31,19	7,92	5,41	15,81	774,34	178,25	9,86	2,69	6,49	4,75	29,53	32,07	53,44	9,20	135,23	145,28	2,16	308,11	35,84	9,33	144,08	11,27	4,87	33,81	10,25	13,97
SH1-H2	2,99	6,87	9,93	18,40	4,73	4,63	6,73	607,07	136,27	10,10	3,15	5,97	4,24	27,95	34,83	52,66	6,90	120,73	166,62	2,95	213,73	35,31	13,44	112,14	13,14	2,66	38,66	10,06	15,22
SH2-H2	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!	#NA!
SH3-H2	2,32	9,05	15,84	29,85	7,99	5,30	10,42	652,76	166,60	7,90	3,19	6,42	4,88	28,86	37,14	57,24	6,07	131,76	162,74	1,76	257,46	50,63	10,52	125,76	14,59	4,08	34,76	9,40	14,46
SH4-H2	1,61	8,31	9,87	19,45	6,44	3,06	6,95	728,52	160,12	11,01	2,40	4,33	3,40	29,46	26,98	61,55	6,98	130,27	148,26	2,08	293,66	47,02	9,99	139,19	12,92	6,36	41,91	11,22	15,57
SH5-H2	1,82	8,83	10,38	23,33	6,51	3,95	10,32	663,01	150,32	6,85	2,17	4,93	3,67	27,29	25,25	54,43	7,35	133,37	118,57	1,80	313,68	65,32	6,58	120,49	10,49	4,76	32,94	9,64	13,88
KF1-H3	3,91	10,61	13,21	19,36	6,06	5,99	10,42	361,41	60,10	8,16	2,28	3,30	2,84	16,20	15,21	31,43	1,53	52,38	74,53	0,59	119,94	2,63	6,51	83,51	5,10	1,98	13,25	4,39	6,04
KF2-H3	5,11	10,04	14,17	20,73	5,96	10,48	9,15	305,28	50,55	8,54	2,62	4,29	3,02	14,33	18,31	39,30	1,32	52,42	70,78	0,90	122,44	1,16	8,84	77,85	16,95	1,77	10,15	3,25	4,59
KF3-H3	1,92	5,77	11,64	16,22	5,58	6,37	4,46	312,80	49,42	8,77	2,61	4,16	3,22	16,53	16,13	33,22	1,69	59,75	75,26	0,90	160,92	2,12	7,21	85,59	6,85	1,91	12,47	4,06	5,44
KF4-H3	2,98	6,14	12,49	18,64	5,54	8,89	5,68	389,02	59,23	9,03	2,66	4,74	2,89	19,19	20,80	31,45	1,98	66,89	88,41	1,15	130,78	1,93	10,24	101,33	5,11	1,97	15,21	6,36	7,84
KF5-H3	6,63	10,78	18,49	24,76	7,41	10,28	9,95	410,48	68,22	15,07	2,80	5,21	3,47	19,58	19,67	37,91	1,65	64,36	90,90	1,21	137,22	2,63	9,45	104,52	6,81	1,72	15,42	5,40	7,59
KFP-H3	6,97	13,25	21,55	31,73	9,79	12,43	14,37	530,58	79,68	13,66	3,76	5,41	4,63	25,57	24,35	42,72	0,83	82,84	106,57	1,94	178,47	7,33	9,66	133,31	6,20	2,24	21,84	6,84	9,28
KH1-H3	2,23	5,52	6,97	9,83	3,66	4,98	3,57	172,41	28,38	4,24	1,38	2,30	1,64	7,60	12,08	37,15	1,27	34,11	45,45	0,63	83,41	2,94	7,01	27,50	5,08	1,66	9,07	3,68	4,49
KH2-H3	3,53	7,39	11,50	18,47	6,78	7,68	5,52	338,66	53,56	7,62	2,03	4,35	3,02	16,03	16,39	37,36	1,89	57,88	70,63	0,79	138,36	3,05	6,86	77,67	4,64	1,64	11,87	4,27	5,43
KH3-H3	1,27	3,07	6,31	9,23	3,97	4,83	2,28	161,88	29,01	4,40	1,53	2,51	1,70	8,45	12,18	20,96	1,57	39,79	48,52	0,85	113,80	1,11	8,30	35,09	3,25	1,39	6,70	2,20	2,73
KH4-H3	5,36	9,41	17,35	27,64	8,20	10,49	10,81	523,23	67,56	9,58	3,61	6,01	4,00	26,11	24,74	42,43	1,64	82,98	95,95	1,00	194,70	4,43	12,09	154,71	7,91	2,15	19,73	7,14	9,92
KH5-H3	4,80	10,83	17,41	29,86	10,23	11,03	10,79	562,49	82,32	9,14	3,07	5,48	4,30	28,39	27,77	41,24	2,06	94,15	117,03	0,97	229,58	3,82	13,32	137,17	7,88	2,64	21,16	7,53	9,79
KHP-H3	5,17	11,87	17,22	25,91	9,05	9,85	9,17	502,24	62,68	10,22	3,09	4,28	3,71	23,26	22,47	43,71	0,99	82,93	95,95	1,46	182,91	3,78	11,27	126,74	6,08	2,24	18,96	8,34	10,05
OF1-H3	5,41	8,65	17,90	25,38	9,28	10,47	7,29	361,85	59,59	13,74	2,96	5,15	3,39	17,39	18,15	39,26	1,52	73,38	70,24	1,21	174,64	2,06	9,82	120,79	5,58	4,20	12,86	4,34	5,42
OF2-H3	4,50	7,53	15,47	22,27	7,99	9,69	6,12	372,25	57,33	11,38	2,72	5,36	3,39	18,76	18,20	41,49	1,50	78,34	60,94	0,90	188,06	1,83	7,94	128,20	4,87	3,33	13,85	3,91	4,84
OF3-H3	3,46	6,60	12,11	16,53	6,69	6,73	5,13	252,60	39,88	8,43	1,30	3,22	1,93	11,70	11,27	23,60	0,76	49,51	39,81	0,63	144,74	1,60	4,32	89,34	3,23	2,39	8,46	2,62	3,13
OF4-H3	7,32	8,59	21,68	33,42	8,36	11,02	10,94	368,20	63,52	14,50	3,20	5,94	3,55	17,91	21,07	32,92	1,48	68,94	70,73	0,88	162,29	1,85	10,57	126,87	4,70	2,45	13,71	4,98	6,01
OF5-H3	5,87	10,80	21,90	31,23	9,92	9,88	14,41	476,21	60,85	12,64	2,79	5,14	3,32	22,07	20,31	38,32	2,15	76,71	65,45	0,85	201,38	4,58	9,29	186,93	5,62	2,73	16,53	5,31	7,11
OFP-H3	6,38	10,24	22,08	31,30	9,03	11,18	10,66	424,60	57,28	12,62	3,31	5,26	3,59	19,53	19,26	36,36	1,63	71,73	65,84	0,93	152,66	3,72	7,85	160,33	7,16	3,32	17,84	6,12	7,40
OH1-H3	5,66	7,64	19,80	26,83	8,17	9,14	9,77	305,17	53,55	11,21	2,62	4,74	3,11	15,99	16,69	22,63	1,42	61,40	58,49	0,90	150,64	1,75	7,59	109,89	4,04	2,18	11,70	4,13	4,69
OH2-H3	7,55	9,70	22,20	33,03	9,66	10,73	10,39	366,77	63,94	11,67	2,50	5,27	3,63	18,02	19,82	26,35	1,94	75,27	65,09	0,76	181,04	1,65	8,47	138,25	4,22	1,98	12,34	3,74	4,61
OH3-H3	0,23	0,51	0,88	1,20	0,97	0,79	1,48	51,66	4,33	0,49	0,30	0,53	0,18	3,92	2,68	8,04	0,05	16,47	11,19	0,16	43,64	5,48	2,36	16,49	0,93	0,99	3,29	1,04	1,11
OH4-H3	8,42	11,81	24,45	34,66	9,47	12,57	13,47	484,37	77,57	13,93	3,69	6,06	6,98	23,66	23,15	40,19	3,16	80,41	83,31	1,08	179,57	2,12	10,60	188,60	6,65	3,18	19,51	6,44	8,41
OH5-H3	4,07	6,32	12,99	17,85	4,67	5,98	7,82	159,38	30,13	6,36	2,12	2,79	1,81	7,84	12,17	24,80	1,75	32,46	35,45	0,55	68,22	3,43	6,78	35,39	9,13	1,39	7,80	2,64	3,45
OHP-H3	8,95	14,17	26,49	40,05	11,02	12,44	18,02	479,67	61,09	14,55	3,12	5,26	3,35	20,97	22,42	38,40	1,65	74,10	65,54	1,04	168,06	3,31	8,00	179,83	6,26	2,84	17,40	6,54	8,25
SF1-H3	9,73	12,37	21,85	31,07	8,32	9,38	12,95	474,22	90,33	14,15	2,89	5,69	3,58	21,84	24,05	38,07	1,09	82,94	103,09	1,47	166,48	4,43	13,20	59,03	6,64	3,74	19,28	5,72	7,30
SF2-H3	1,88	3,61	6,75	8,48	3,07	4,09	3,33	165,81	32,04	4,81	1,26	1,57	1,56	8,64	10,94	20,24	0,56	29,97	42,70	0,87	68,47	2,57	7,38	19,31	2,70	1,17	7,70	1,98	2,95
SF3-H3	3,08	9,24	14,70	18,38	6,21	6,54	7,40	389,19	80,05	8,22	2,21	3,90	3,05	17,54	22,66	36,27	0,96	63,44	96,04	1,29	130,29	4,84	11,79	47,14	5,80	2,97	12,58	3,62	4,35
SF4-H3	5,92	13,51	23,07	30,38	8,97	10,86	11,45	720,64	134,58	14,16	3,71	5,50	5,90	34,55	32,82	56,21	2,27	108,83	159,72	1,48	190,13	9,67	17,44	97,43	9,37	2,73	27,38	8,65	10,99
SF5-H3	5,98	15,30	19,72	25,90	9,41	11,16	10,52	623,40	105,13	17,71	3,52	6,18	4,44	29,52	28,48	60,72	1,35	94,65	120,33	1,23	182,59	5,91	15,94	79,55	9,39	4,81	24,03	7,60	9,71
SFP-H3	9,41	24,23	30,56	38,06	11,95	12,74	18,77	786,86	139,78	15,90	4,04	5,60	6,28	32,45	32,82	64,86	1,69	107,72	143,86	1,43	192,93	9,53	15,02	96,24	9,82	3,67	23,26	8,63	10,60
SH1-H3	4,46	8,75	17,39	20,59	6,79	9,44	8,92	402,40	95,94	24,83	3,03	5,53	3,60	18,53	25,03	33,24	3,05	68,25	95,26	0,91	131,40	4,32	7,20	51,81	9,79	1,37	15,49	5,07	6,30
SH2-H3	2,31	6,29	13,25	15,37	5,69	7,23	7,34	398,85	81,81	9,52	3,06	4,58	3,90	18,39	22,15	33,97	2,12	72,53	91,37	1,46	137,32	7,47	9,66	54,21	5,68	3,08	14,05	4,05	5,14
SH3-H3	3,15	14,98	16,74	24,27	9,26	6,96	13,92	545,11	109,90	9,11	1,92	4,00	3,61	23,81	17,26	44,80	0,77	82,66	94,02	0,69	206,20	7,49	5,56	83,60	6,86	1,85	17,79	4,76	5,61
SH4-H3	4,53	14,90	21,80	27,59	11,07	9,84	12,61	765,03	158,85	13,38	3,34	4,97	4,78	35,98	32,03	58,26	2,62	116,63	147,15	2,41	208,17	15,54	12,55	101,90	9,67	4,53	30,94	10,19	11,12
SH5-H3	5,61	16,08	20,04	25,39	10,56	8,58	9,56	698,73	144,91	12,26	3,19	4,91	4,91	31,42	26,42	59,71	2,03	100,28	142,40	1,89	184,27	13,56	10,83	93,23	8,34	2,70	25,06	7,87	9,87
SHP-H3	5,53	19,45	22,76	25,30	9,94	8,90	16,04	688,11	117,77	16,40	2,60	4,10	4,41	28,98	29,32	56,20	1,54	91,15	123,39	1,33	187,27	6,53	12,62	87,89	9,54	3,72	25,80	7,83	9,11

Table 18 Statistical parameters of linear correlation between amount/structure and ^{13}C-uptake/function. m, slope; b, axis intercept.

PLFA content	E1	E2-H2	E2-H3
R^2	*0,4974*	**0,891**	*0,6038*
p	*0,0305*	**<0,0001**	*0,0137*
m	0,0896	0,4366	0,3477
b	658,9945	-52,1472	365,5127
18:2(9,12)c	E1	E2 H2	E2 H3
R^2	0,7133	**0,8117**	*0,3755*
p	0,0051	**0,0006**	*0,0467*
m	0,3799	0,4132	0,6503
b	-14,4418	-25,8483	-52,8611
g+ FA	E1	E2 H2	E2 H3
R^2	0,0452	**0,9291**	*0,561*
p	0,2925	**<0,0001**	*0,0123*
m	0,5096	1,8047	1,8598
b	88,6728	5,3054	3,2825
bact. FA	E1	E2 H2	E2 H3
R^2	0	0,7174	0
p	0,9173	0,0024	0,6818
m	-0,0019	0,2973	0,0202
b	319,2259	38,7075	300,7175
eukari. FA	E1	E2 H2	E2 H3
R^2	0,8006	**0,9698**	0
p	0,0017	**<0,0001**	0,761
m	0,1895	0,4602	0,062
b	129,1278	-124,2065	288,044

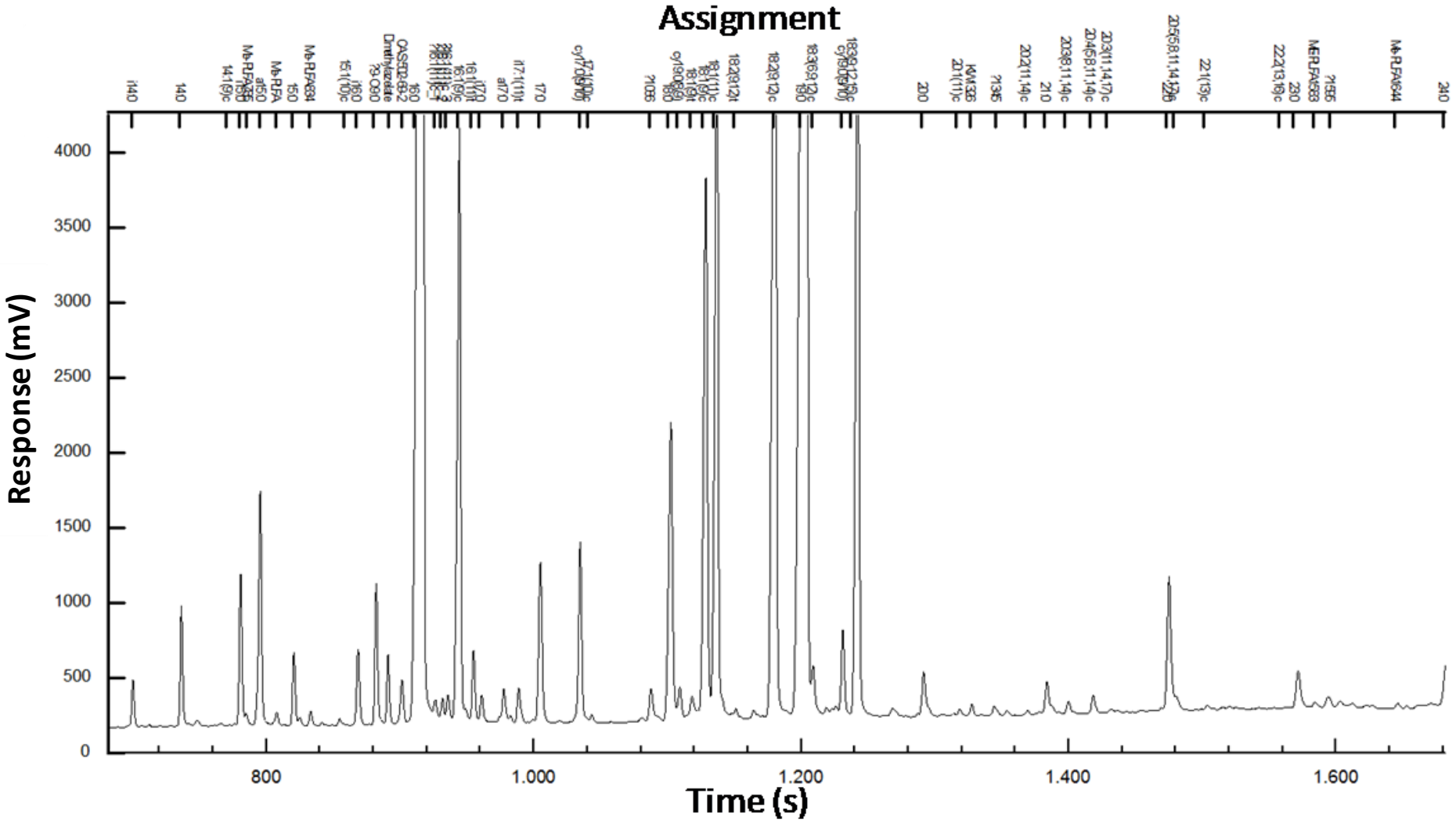

Fig. 8 Typical chromatogram of one mass (44) with indication of identified PLFA in upper x-axis.

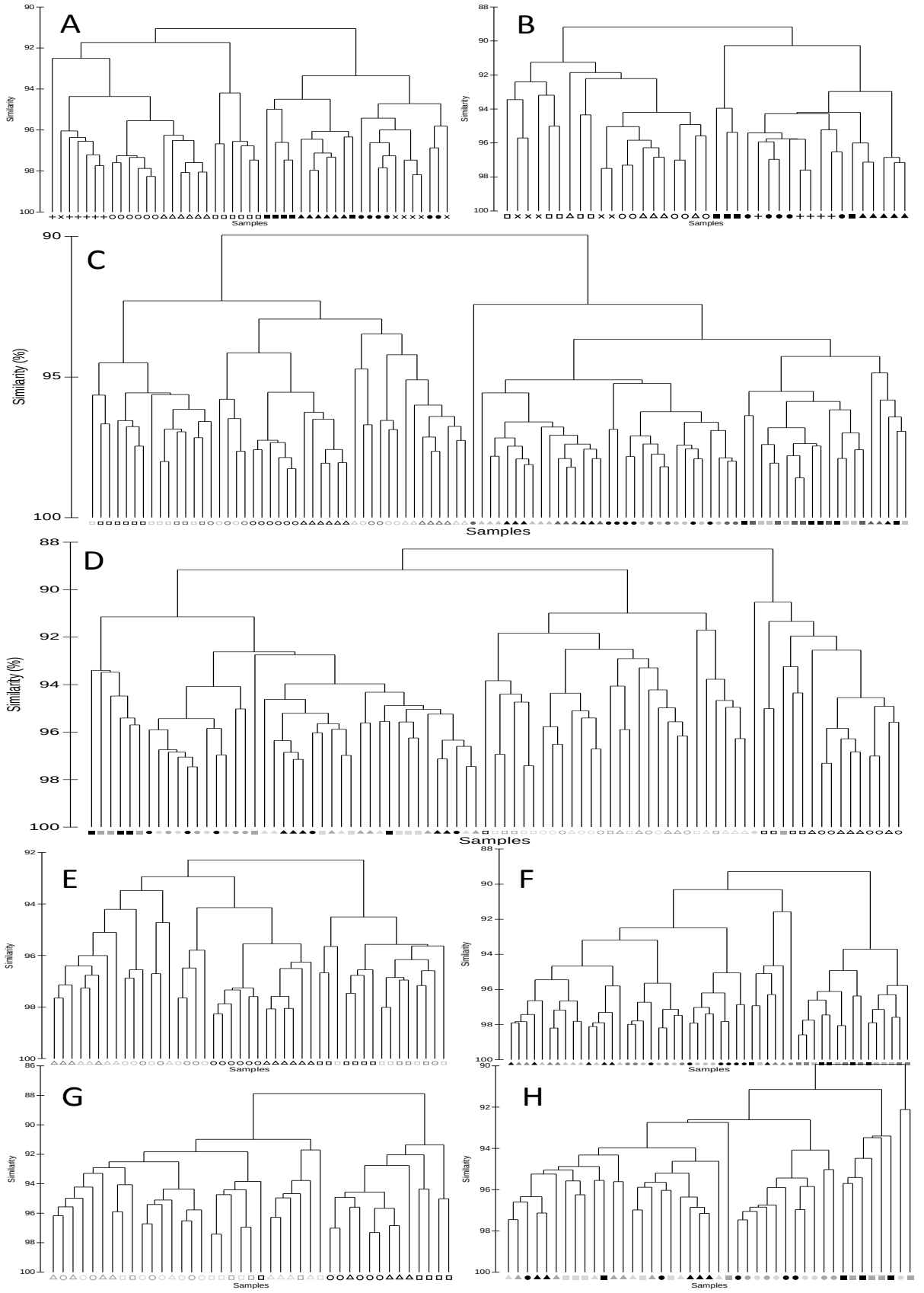

Fig. 9 CA of several NMDS given in Fig. 3 and Fig. 5: (A), Fig. 3A; (B), Fig. 3B; (C), Fig. 5A; (D), Fig. 5B; (E), Fig. 5C; (F), Fig. 5E; (G), Fig. 5D; (H), Fig. 5F

Appendix

Since for both harvests concerning the response of the SMCC on stress treatment, significant differences between beach litter types were found, it is legit to separate analysis in regard to this. Results founded on this attempt are given below.

Klausenleopoldsdorf

Two way ANOSIM on the data from Kausenleopoldsdorf, shows an highly significant difference between H2 and H3 with a global R of 0.999 and a significance level of smaller than 0.001. The explanation of difference due to treatment is less, but still highly significant (R=0.344; p<0.001). Pair wise tests on treatment groups give highly significant differences between control and freeze, and control and heat treatments (R=0.421 and 0.475, respectively). No significant difference between freeze and heat treatment could be found (R = 0.126; p = 0.055). Using one way ANOSIM significant differences between controls and both treatments occur only for the second harvest; see Table 14.

Ossiach

Two way ANOSIM on the data from Ossiach, shows an highly significant difference between H2 and H3 with a global R of 0.99 and a significance level of smaller than 0.001. The explanation of difference due to treatment is less, but still highly significant (R: 0.275; p: < 0.001). Pair wise tests on treatment groups give highly significant differences between control and freeze, and control and heat treatments, with R = 0.252 and 0.481 respectively. No significant difference between freeze and heat treatment could be found (R = 0.027, p = 0.366). Using one way ANOSIM significant differences between controls and both treatments occur only for the second harvest; see Table 14.

Schottenwald

Two way ANOSIM on the data from Schottenwald, shows an highly significant difference between H2 and H3 with a global R of 0.936 and a significance level of smaller than 0.001. Treatment has no significant influence on similarities from a Bray Curtis resemblance matrix, derived from mol% PLFA data treated by square root transformation (R: 0.11, p: 0.075). Pair wise tests on treatment groups give no significant difference. Using one way ANOSIM no significant differences between controls and both treatments occur; see Table 14.

Table 19 Two-way-ANOSIM and SIMPER pair wise tests on mol% PLFA between groups of E1. On the principal diagonal SIMPER similarities within group are given, SIMPER dissimilarities between groups are given below R (first line) and p values (second line) of upper triangular matrix.

	A	K	O	S
		0.875	0.599	0.995
A	95.85	<0.001	<0.001	<0.001
		6.45	5.48	9.20
			0.835	0.798
K		96.77	<0.001	<0.001
			4.83	6.16
				0.97
O			97.76	<0.001
				7.67
S				95.55

Table 20 Two way ANOSIM and SIMPER pair wise tests on ^{13}C-PLFA between groups of E1. On the principal diagonal SIMPER similarities within group are given, SIMPER dissimilarities between groups are given below R (first line) and p values (second line) of upper triangular matrix

	A	K	O	S
		0.608	0.392	0.531
A	94.62	<0.001	<0.001	<0.001
		7.51	6.37	8.71
			0.510	0.461
K		94.76	<0.001	<0.001
			6.29	8.05
				0.720
O			95.66	<0.001
				8.87
S				92.93

Table 21 Two way ANOSIM and SIMPER pair wise tests on mol% PLFA between groups of E2H2. Litter type: K, Klausenleopoldsdorf; O, Ossiach; S, Schottenwald; Treatment: C, 'Control'; F, 'Freeze'; H, 'Heat'.

Groups	R (ANOSIM)	p	Average dissimilarity (SIMPER) /%
K, O	0.606	0.001	5.5
K, S	0.864	0.001	7.0
O, S	0.811	0.002	7,9
C, F	0.554	0.001	6.4
C, H	0.634	0.001	6.0
F, H	-0.007	50	5.0

Table 22 Two way ANOSIM and SIMPER pair wise tests on mol% PLFA between groups of E2H3. Litter type: K, Klausenleopoldsdorf; O, Ossiach; S, Schottenwald; Treatment: C, 'Control'; F, 'Freeze'; H, 'Heat'.

Groups	R (ANOSIM)	p	Average dissimilarity (SIMPER) /%
K, O	0.684	0.001	5.4
K, S	0.696	0.001	5.4
O, S	0.986	0.001	7.5
C, F	0.051	0.223	3.8
C, H	0.08	0.107	4.3
F, H	0.12	0.036	4.2

Table 23 Pair wise results of two-way-ANOSIM and SIMPER analysis of ^{13}C labeled PLFA in E2H2.

Groups	R (ANOSIM)	p	Average dissimilarity (SIMPER) /%
K, O	0.544	0.001	6.8
K, S	0.579	0.001	8.7
O, S	0.586	0.001	8.2
C, F	0.857	0.001	12.6
C, H	0.805	0.001	10.5
F, H	0.271	0.012	7.2

Table 24 Pair wise results of two-way-ANOSIM and SIMPER analysis of ^{13}C labeled PLFA in E2H3.

Groups	R (ANOSIM)	p	Average dissimilarity (SIMPER) /%
K, O	0.680	0.001	8.2
K, S	0.484	0.001	7.2
O, S	0.752	0.001	9.9
C, F	0.145	0.06	5.53
C, H	0.189	0.022	6.8
F, H	-0.177	0.021	6.8

Table 25 SIMPER analysis of each harvest of E1 separately, in the crossing of two same indices similarity within this group is given, otherwise dissimilarities between the goups of E1.

H2	A	K	O	S
A	95,84	8,53	7,38	10,01
K		94,35	6,49	7,19
O			94,14	7,98
S				95,5

H3	A	K	O	S
A	95,81	6,46	5,39	8,35
K		96,05	5,28	5,38
O			95,9	7,53
S				96

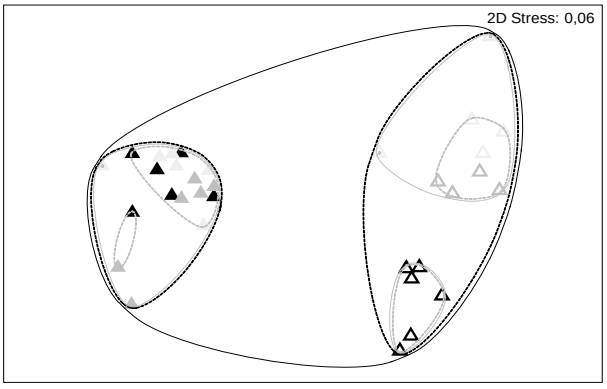

Fig. 10 two-dimensional scaling of litter from Klausenleopoldsdorf based on Bray Curtis similarity of square root transformed mol% data of 29 PLFA. Similarity derived from cluster analysis (Fig. 11) is overlaid; black symbols, controls; dark gray symbols, 'heat'-treatment; light gray symbols, 'freeze'-treatment. Solid black line, 85% similarity; broken black line, 90% similarity; solid gray line, 93% similarity; broken gray line, 96% similarity.

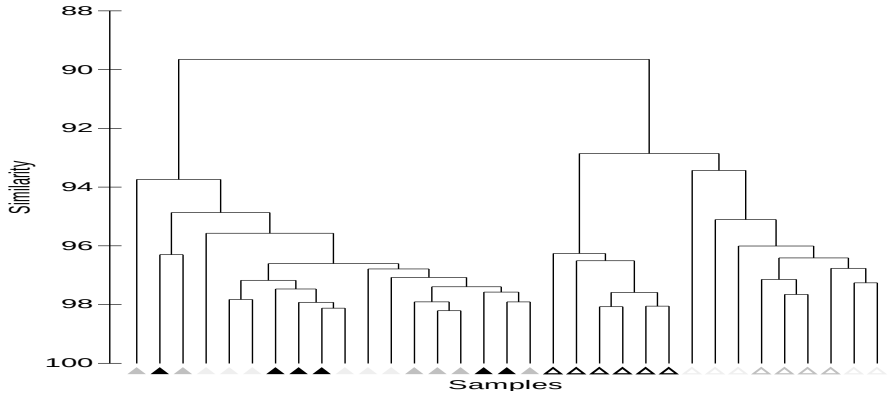

Fig. 11 Cluster analysis based on Bray Curtis similarity of square root transformed mol% data of 29 PLFA for Klausenleopoldsdorf. Black symbols, controls; dark gray symbols, 'heat'-treatment; light gray symbols, 'freeze'-treatment. Open symbols, H2; filled symbols H3.

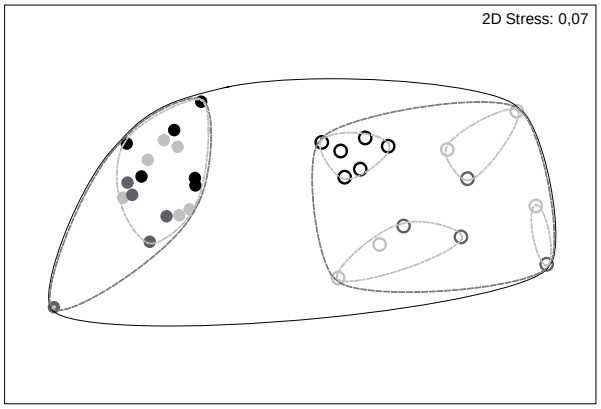

Fig. 12 two-dimensional scaling of litter from Ossiach based on Bray Curtis similarity of square root transformed mol% data of 29 PLFA. Similarity derived from cluster analysis (Fig. 13) is overlaid; black symbols, controls; dark gray symbols, 'heat'-treatment; light gray symbols, 'freeze'-treatment. Solid black line, 85% similarity; broken black line, 90% similarity; solid gray line, 93% similarity; broken gray line, 96% similarity.

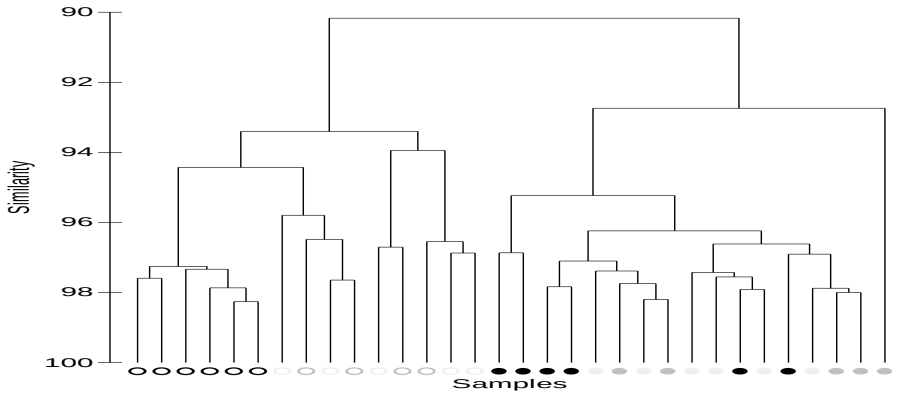

Fig. 13 Cluster analysis based on Bray Curtis similarity of square root transformed mol% data of 29 PLFA for Ossiach. Black symbols, controls; dark gray symbols, 'heat'-treatment; light gray symbols, 'freeze'-treatment. Open symbols, H2; filled symbols H3.

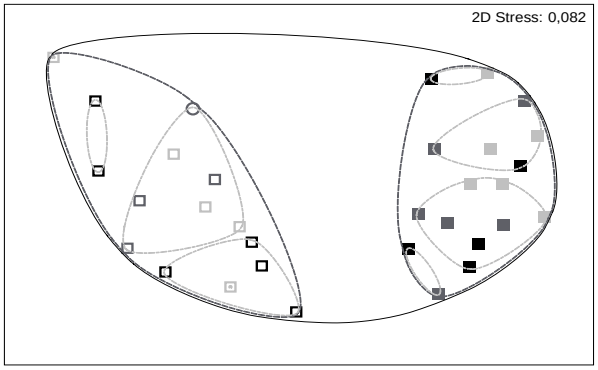

Fig. 14 two-dimensional scaling of litter from Schottenwald based on Bray Curtis similarity of square root transformed mol% data of 29 PLFA. Similarity derived from cluster analysis (Fig. 15) is overlaid; black symbols, controls; dark gray symbols, 'heat'-treatment; light gray symbols, 'freeze'-treatment. Solid black line, 85% similarity; broken black line, 90% similarity; solid gray line, 93% similarity; broken gray line, 96% similarity.

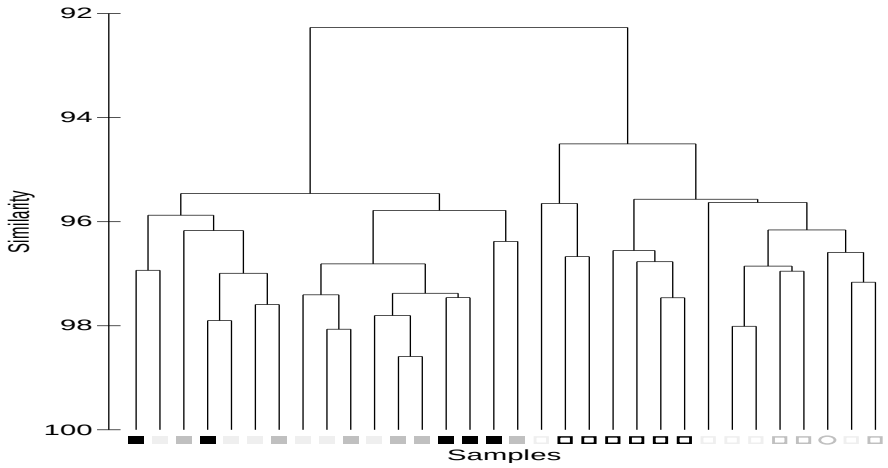

Fig. 15 Cluster analysis based on Bray Curtis similarity of square root transformed mol% data of 29 PLFA for Schottenwald. Black symbols, controls; dark gray symbols, 'heat'-treatment; light gray symbols, 'freeze'-treatment. Open symbols, H2; filled symbols H3.

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Publikationen

Kaiser, C., A. Frank, et al. (2010). "Negligible contribution from roots to soil-borne phospholipid fatty acid fungal biomarkers 18:2[omega]6,9 and 18:1[omega]9." Soil Biology and Biochemistry **42**(9): 1650-1652.

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