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Full Length Research Paper

The theoretical approach of ecoplexivity focusing on mass outbreaks of phytophagous insects and altering forest functions

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Epidemics of forest insects can have deep impacts on ecosystem functioning and dynamics, with consequences for forest economics and forest carbon feedback to climate change. Despite the many roles that insects fulfil in terrestrial ecosystems, their importance in nutrient cycling is not well known (Kosola et al., 2001) . The only instances where herbivores are recognized to have a large effect on ecosystem function are mass outbreaks of particular species like herbivores. However, the climate change induced alterations in precipitation and temperature patterns will undoubtedly affect occurrence, intensity, frequency, magnitude and timing of these phenomena and thus, provoke an increasing susceptibility of hosts and a significantly larger habitat presence of pests. Records show that, in an increasing number of cases severe outbreaks can even cause the complete devastation of vast areas and thus, imply considerable economic losses at a large scale. Down to the present day, it remains uncertain how forest ecosystems will respond to the changing environmental conditions in the long run. This work reports on the possible alterations of forest functions due to mass outbreaks of phytophagous insects with respect to the changing ecosystem service of carbon sequestration ability of forests on the northern hemisphere.

Key words: Forest disturbances, insect mass outbreaks, forest functioning, carbon sequestration.

INTRODUCTION

The growing interest in the impacts of global climate change on forest ecosystems is not surprising as forests cover about 43% of the world's surface and account for some 70% of terrestrial net primary production (NPP) (Melillo et al., 1993), which transforms into 359 Gt of carbon in biomass and 787 Gt of carbon deposited in soils (WBGU, 1998). Forests are being bartered on world markets for carbon mitigation purposes since they represent 46% of the globally sequestered terrestrial carbon (WBGU, 1998; Nilsson, 1995).

According to the latest IPCC (2007) assessment report, disturbances in the form of insect infestations which will most certainly increase in areas featuring sub-continental to continental climatic conditions as a result of a decline in precipitation and rising temperatures, however, depending on the modelled warming scenario (IPCC, 2007; Dale et al., 2000). Yet till the present day, it remains uncertain how European forest ecosystems will respond to the changing environmental conditions in the long run. It can be assumed that, in specific regions, forests will not feature sufficient resilience capabilities to

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adapt to these fast changing climatic conditions characterized by the increased occurrence of forest disturbances like wild fires and mass outbreaks of insects. Until this very day, the conception and opinion has prevailed that forests on the northern hemisphere serve as gigantic carbon sinks. However, feedback effects indicate that, the assumption that forests represent one of the key mitigation factors for reducing the emission of greenhouse gases (IPCC, 2007) has become debatable (Stern et al., 2006), meaning that, forests are likely to become carbon sources.

Forest disturbances are inherent to natural forest dynamics (Ayres and Lombardero, 2000) . On the other hand, disturbances such as wild fires and wind throw as well as mass outbreaks of insects often cause devastating ecological effects and substantial economic losses. In the United States of America, more than 20 million hectares of forested land are annually affected by insect mass outbreaks, resulting in drastic economic losses in the magnitude of about 20 billion US $ (Ayres and Lombardero, 2000). However, studies suggest that insect herbivore can also act as a regulator of forest primary production, leading to increasing above ground biodiversity after defoliation (Hartley and Jones, 2004).

Apparently, canopy herbivore plays an important role with respect to carbon (C) and N inputs by altering timing and quality of organic material reaching forest floor and affecting below ground processes (herbivore mediated production of organic matter (OM)), thus, directly as well as indirectly affecting ecosystem functioning. However, despite the many purposes insects serve in terrestrial ecosystems, their importance in nutrient cycling and advanced forest functions are not well understood (Rouault et al., 2006).

The assessment report of the IPPC predicts that, forest perturbations such as mass outbreaks of insects will increase dramatically in the future due to changes in precipitation and temperature patterns, thus, leading to the depletion of water resources and subsequently, increase the susceptibility of trees for diseases and insects attacks (IPCC, 2007).

Other than an expected drop in net primary production (NPP) (Ciais et al., 2005) the resultant diminishing C storage in wood biomass as well as alterations in carbon cycling characteristics (Baldocchi, 2005) are likely to have fatal consequences for the overall stability of forest stands resulting in a curtailed adaptability and resilience of forest ecosystems (Bale et al., 2002). Climate change induced alterations in precipitation and temperature patterns will undoubtedly affect the occurrence patterns of these phenomena (Dale et al., 2001) by changing the natural cycles of mass outbreaks through modifying magnitude, frequency, intensity and duration of the reproduction characteristics of pest insects (Begon et al., 1991; Cambell and Madden, 1990; Dale et al., 2001). This is based on indirect (accelerated reproduction turnover, lower mortality, decreased defense potential of trees) and direct processes (change in population density of antagonists, parasitoids, predators) (Dale et al., 2001; Hunter, 2001). All in all, it can be postulated with confidence that global warming provokes an increasing susceptibility of hosts and a significantly larger habitat presence of pests (Hunter, 2001) . Records show that, in some cases severe outbreaks can even cause the complete devastation of large areas and thus, imply considerable economic losses at a large scale.

Enhanced nutrient input to the soil-transformation from recalcitrant to easily degradable matter

During mass outbreaks of phytophagous insects, high amounts of organic matter (OM) enter the forest floor dry as insect modified fragments (pellets, damaged needles and leaves) or in solution by throughfall. Under these conditions, the matter transfer from the canopy source to the soil is enlarged. Studies have shown that, input of organic carbon into the forest floor can reach about 180 kg C ha^{-1} 6 $months^{-1}$ (by throughfall) and up to 520 kg C ha^{-1} 6 $months^{-1}$ (by frass pellets) during the vegetation season (le Mellec and Michalzik, 2008). Peak fluxes occurred within a short period of 5 weeks during June/July, where about 80% of the overall inputs enter the ground under herbivore activity, thus, stressing the relevance of altered timing of organic matter cycling (le Mellec and Michalzik, 2008). Guggenberger and Zech (1994) could demonstrate that, 40 to 50% of the organic carbon in throughfall consists of easily degradable carbohydrates and therefore, can be considered as a promoting co-substrate for decomposition processes. In this context, various studies have demonstrated that herbivorous insects are able to transform needle biomass or leaf constituents into more easily degradable secondary products (insect pellets, honeydew) (Chapman et al., 2003; Hunter, 2001; Schowalter et al., 1991; Stadler et al., 2001). Through the transformation into more easily decomposable organic matter, herbivorous insects are likely to promote decomposition activity and lead to an accelerated and quantitatively increased decomposition rate and release of nutrients (Ritchie et al., 1998; Hollinger, 1986; Chapman et al., 2003; Lovett and Ruesink, 1995; Stalder et al., 2001). In this context, studies suggest that mass outbreaks of insects affect above and below ground carbon sequestration by their defoliating activity: (1) due to a limited above ground C fixation as a result of frass induced tree mortality (limited net primer production (NPP)) (Langstrom et al., 2001; Amour et al., 2003; Cedervind and Långström, 2003); (2) due to the quantitatively increased and qualitatively changed matter input that causes altered soil processes (Lovett et al., 1995). This in consequence might lead to a limitation of below ground C sequestration and the reduction of soil organic carbon (SOC) storage caused by an enhanced release of DOC (dissolved organic carbon per soil percolates), CO_2 as well as nitrous oxide (N_2O) (Madritch and Hunter, 2003).

However, it remains still unclear to what extent those nutrient entries have the potential to change biogeochemical processes and therefore, the above and below ground functioning in forest ecosystems. From this point of view, forest stands with an enhanced vulnerability to mass outbreaks (due to limited above and below ground C sequestration ability and an enhanced production and release of CO_2 and N_2O) might expose themselves as forest stands with an increasing global warming potential. However, this scenario appears to be in stark contrast with the general perception that, forests of the northern hemisphere are supposed to act as C sinks. If climate change does in fact affect frequency, magnitude and interannual activity of forest disturbances like wild fires and insect outbreaks, forest ecosystems will certainly lose their ability to sequestrate C very significantly.

Here, we present a theoretical approach that deals with this phenomenon in application of new terms. This approach provides information of possible altered forest functions due to mass outbreaks on small (compartment), meso (ecosystem) and large scale (ecosystems).

METHODS

The model of ecoplexivity

Ecosystems can be considered as self-organized open systems Ellenberg (1972), in which various biological, chemical and physical processes determine processes through energy and matter fluxes. Within and between ecosystems, ecopartments (compartments in ecosystems) are linked by an exchange of energy and matter transfer under participation of different trophic levels (connectivity). The more diverse ecopartments are linked to each other, the more complex ecosystems are featuring a broad range of diversity (structural and biological). The degree of complexity within an ecosystem, is governed by the quantity and quality of trophic levels (feeding hierarchy in a food web such as primary producers, herbivores and primary carnivores), the quality and amount of information in cross linking (level of connectivity) as well as ecopartment involvement (multi-various ecopartments with overlapping schemes, particularly key ecopartments like the soil). Based on the fact that forest functioning is critically determined by connective and complex structures, we created the new term of “ecoplexivity” (connectivity + complexity).

The structure of this theoretical ecosystem approach is based on three scales: Small scale (process scale of ecopartments); meso scale (energy and matter transfer between ecopartments within an ecosystem); large scale (energy and matter exchange between (eco) systems).

The small scale (solid line ellipse) is the key level of ecosystem functioning comprising all chemical, physical and biological processes within ecopartments (canopy and soil). All functions within and between ecosystems are governed by these processes. The resulting compartment function (CF, canopy function and SF, soil function)) represents the sink or source capability for energy, water and matter characterised by processes (triangle) of either release (mobilisation) and/or sorption (immobilisation) processes (Figure 1).

The meso scale (dashed/dotted ellipse) is based on the energy, water and matter transfer between ecopartments like the canopy-to-soil transfer (Figure 1). Functions resulting from this level are intra-ecosystem functions, such as above and below ground production (C sequestration) and biodiversity. The interaction between (eco) systems (forests-atmosphere interactions) is based on the largest scale through the exchange of energy, water and matter fluxes. Large scale functions can be reflected in source and sinks abilities of these systems like forests on the north hemisphere (dashed/dotted ellipse) acting as enormous sinks for C. The exchange of energy, water and matter between (eco) systems is called ecosystem-cross-linking (ECL) (double arrows).

Mass outbreaks of phytophagous insects and altering forest functions

Insect outbreaks are temporal and spatial dynamic disturbances which take place in ecosystems as a result of process cascades affecting different ecosystem compartments, time scales and trophic levels. According to Hollinger (1986), these disturbances (associated with the “Figure 8 model”), although being destructive, can become a driving force for constructive rebuilding processes for ecosystems in cases when ecosystem development (succession) is inhibited. The ecoplexivity approach has been devised to reflect possible alterations in ecosystem functioning due to mass outbreaks of phytophagous insects and the related elevated input of mediated organic matter.

Alteration of function on a small scale

Defoliating processes in the canopy compartment can provoke an alteration in the functionality by decreasing photosynthetic rates and by transferring large amounts of organic matter from one compartment (canopy) to another (soil). Studies suggest that, these elevated and chemically transformed matter inputs can trigger processes in the soil compartment due to increased soil microbial activity (mineralization and decomposition). Subsequently, the source functionality of both compartments (canopy and soil) is increased (Figure 2).

Alteration of function on a meso scale

The big black arrow in the graph indicates the alteration within the canopy-to-soil transfer due to increasing matter inputs by phytophagous insect frass from the canopy compartment during mass outbreak situations. The alterations of small scale processes (Canopy: reduced photosynthetic activity, soil: accelerated decomposition) also have effect on the meso scale by reducing carbon assimilation due to frass attack. In consequence, the above ground carbon fixation is limited by reduced photosynthesis resulting in reduced biomass production (enhanced tree mortality, limited timber growth and reduced fine root production) . Therefore, NPP (net primary production) is reduced. NEP (net ecosystem production) is additionally reduced, particularly due to below ground carbon release. According to the acceleration hypothesis (Ritchie et al., 1998), SOM is mineralized at higher rates resulting in enhanced production of CO_2. Secondly, there is more vertical water percolation which includes DOC transport (loss) to the groundwater. This is due to reduced transpiration activity of infested or dead trees. As a possible consequence, it can be presumed that forest stands experience a shift from carbon sinks to carbon sources.

Alteration of function on a large scale

The largest scale which is represented by the ECL reflects the relation between the forest ecosystem and external systems such

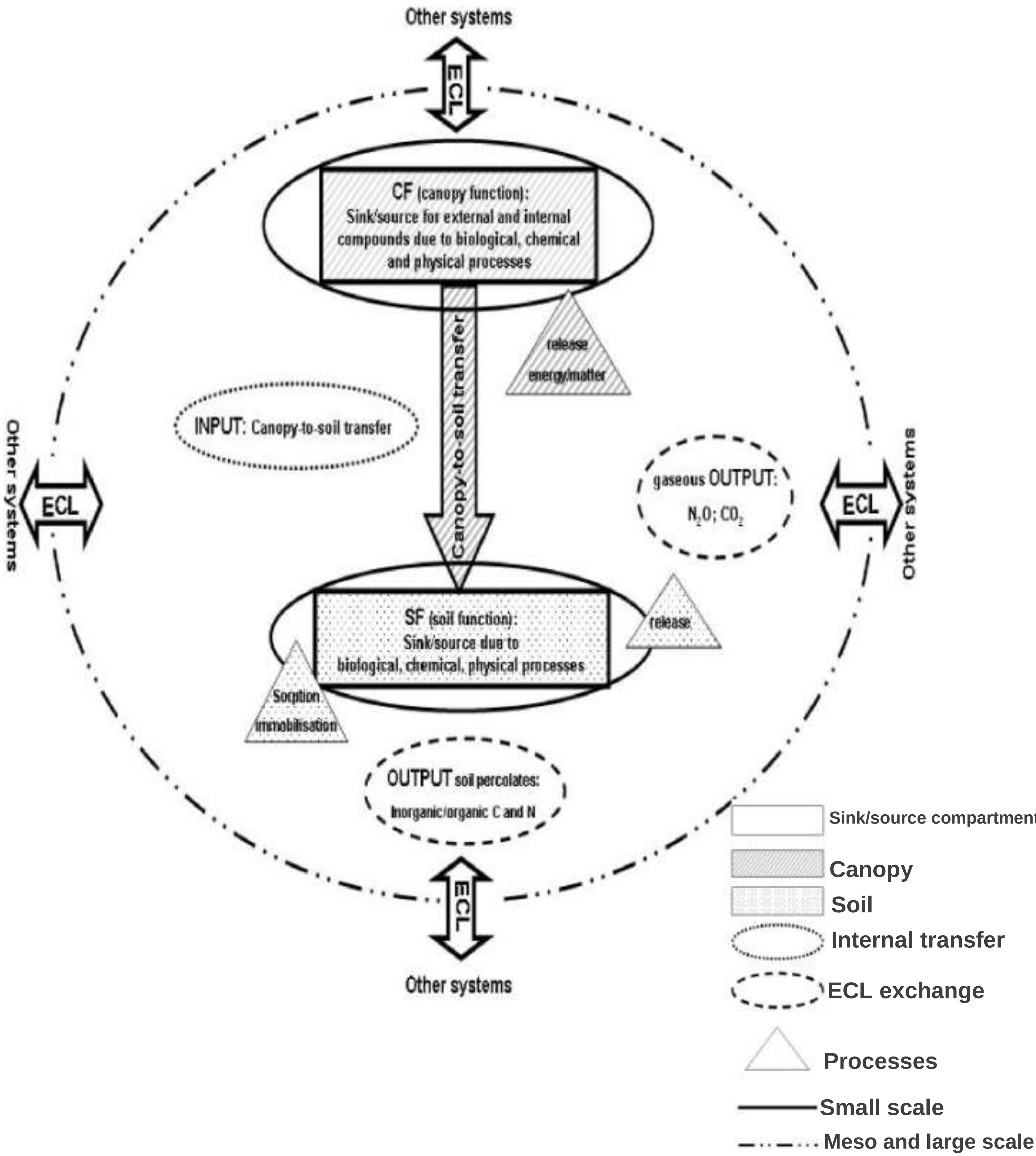

Figure 1. The model of ecoplexivity without mass outbreaks of phytophagous insects. The theoretical approach of ecoplexivity: Sink/source functionality of the canopy and the soil compartment due to abiotic and biotic processes (small scale: solid line ellipse). The meso scale (dashed dotted line) shows the boundary between ecopartments through the canopy- to-soil transfer (under participation of various trophical levels and processes). There exist exchanges to other ecosystems (four double arrows) on meso and large scale (dashed dotted line) due to ecosystem-cross-linking (ECL).

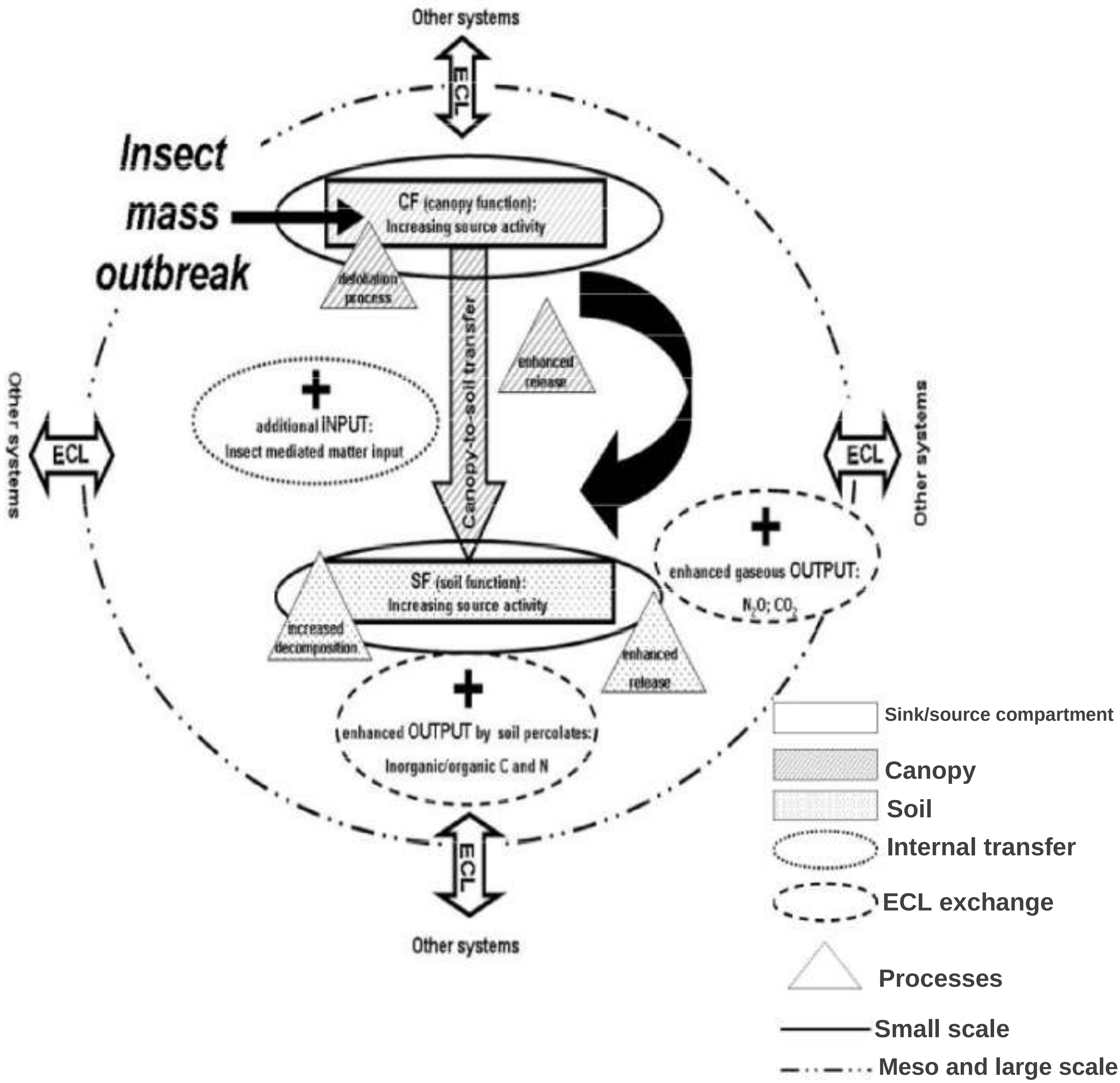

Figure 2. The model of ecoplexivity with mass outbreaks of phytophagous insects. Due to mass outbreaks of phyotophagous, insects the canopy compartment becomes more the character of a source for energy and organic matter compounds. This leads to an increase of the canopy-to-soil transfer (big black arrow). Consequently, the soil processes alter due to these enhanced and qualitatively changed inputs. The soil compartment also becomes the character of a source due to the enhanced release of CO_2 and DOC. On meso as well as large scale, mass outbreaks lead to altered forest functions by reducing the forest abilities of carbon sequestration.

as the atmosphere; no matter which scenario will prove to be the 'true' one (increase of mean temperature by 1.4 to 4°C (WBGU, 1998), it can be foreseen that, heat waves like the ones in 2003 will increase in frequency and intensity in Europe and thus, affect forest ecosystems. Furthermore, it is expected that not only summer temperatures will increase, but additionally, the amount of precipitation during the summer period will drop substantially for vast areas in Europe. This baleful scenario featuring a decline in precipitation and the reduction of soil water reservoirs will certainly induce severe limitations of water being available to plants (drought stress), which subsequently, become more susceptible to insect attacks. In the near future, climate change will undoubtedly impinge on the occurrence, intensity, frequency, magnitude and timing of mass outbreaks of pests (Dale et al*.,* 2001). In the wake of this trend, tree hosts are likely to become extremely predisposed and will have to face an ever increasing habitat presence of pests. The earlier mentioned alterations on the small and meso-scale also bear the potential to make an impact on the large scale functionality through an increase in the soil-atmosphere transfer (increased release of CO_2 due to enhanced microbial decomposition).

DISCUSSION

To what magnitude those temporally limited available matter inputs will affect forest ecosystems remains worth discussing. However, studies have shown that those matter inputs can lead to an improvement in the nutrition scheme due to matter transformation from recalcitrant to more degradable compounds (quality aspect), as well as resulting in an increase in matter quantity provided that defoliation rate is below 70% (light frass) . Defoliations under light frass conditions might appear as “first aid scenario” in monoculture coniferous stands of continental/sub-continental regions, where a large percentage of biomass (essential elements and nutrients) is accumulated in the canopy compartment, and where nutrient and water availability is limited. Here, outbreaks of canopy phytophagous insects might refill the internal matter cycling due to an enhanced matter release (frass activity) and canopy-to-soil transfer during insect outbreaks.

On the other hand, severe defoliation can cause a serious dieback of the host trees. This situation can be denominated as a “worst case scenario”. Due to the absence of nutrient uptake by the trees, essential elements will simply disappear through runoff and with seepage output and thus, resulting in a nutrient loss for the ecosystem. Furthermore, forest stands which are marked by a negative NEP due to limited above and below ground C sequestration ability (and enhanced production and release of CO_2 and N_2O), might easily contribute to the increasing global warming potential. This aspect seems to contrast the general perception of forests of the northern hemisphere serving as vast C sinks. If climate change has the potential to modify frequency, magnitude and inter-annual activity of forest disturbances such as insect outbreaks (as the IPCC report predicts), then, forest ecosystems will certainly loose their ability to sequestrate C to a great extend and subsequently, might even take a shift from carbon sinks to carbon sources, as one of the most dramatic examples of an ECL.

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