

# Chapter 12

## A Conceptual Framework for Up-Scaling Ecological Processes and Application to Ectomycorrhizal Fungi

Virgil Iordache, Erika Kothe, Aurora Neagoe, and Felicia Gherghel

### 12.1 Introduction

Molecular biologists do not attempt to simply up-scale knowledge concerning macromolecules to the scale of organisms, but use intermediary theories, while ecologists make intensive efforts to up-scale knowledge concerning the functioning of tiny organisms to the large scale of ecosystems and landscapes. There is an implicit recognition of the fact that the first case (up-scaling from macromolecules to organisms) represents a nested hierarchy of systems, with each hierarchical level characterized by new, emergent, and in principle irreducible properties (although reduction attempts are heuristically valuable). In the second case (up-scaling from tiny organisms to ecosystems), the underlying assumption is that ecological processes are basically of the same type over a large range of scales. The problem is to find a meaningful way to aggregate the processes over different hierarchical levels. Hence the question: Is the concept “hierarchy of systems” consistent in biological sciences?

Mycorrhizal fungi, particularly the ectomycorrhizal fungi – (EMF), are well suited to study up-scaling because of their important role in controlling the functioning of forest ecosystems in view of climate change (see O’Neill et al. 1991). Recent reviews deal with methodological aspects of the problem (Pickles et al. 2009) and with mechanisms controlling structural changes of the communities over

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V. Iordache (✉)

Department of Systems Ecology, University of Bucharest, Bucharest, Romania  
e-mail: virgil.iordache@g.unibuc.ro

E. Kothe

Microbial Phytopathology, Institute of Microbiology, Friedrich Schiller University, Jena, Germany

A. Neagoe

Research Center for Ecological Services (CESEC), Faculty of Biology, University of Bucharest, Bucharest, Romania

F. Gherghel

UMR 1136 Interactions Arbres/Microorganismes, INRA 54280, Champenoux, France

a wide range of scales (Wolfe et al. 2009). Wolfe et al. (2009) briefly discuss the functioning of mycorrhizal communities only to underline the need of research in this area.

In the present chapter, we focus on the functioning of EMF over scales, which, however, needs a clear concept about the structural aspects. The goal of the text is to provide an analytical framework for up-scaling processes involving EMF. Such a framework has not been proposed in literature but can be developed and then checked for consistency with the existing literature. As the processes involving EMF are ecological, one cannot look for the existence of an analytical framework specific only to EMFs. Consequently, we present a general up-scaling framework and then apply it to EMF.

We start with an overview of approaches to ecological up-scaling (Sect. 12.2), introduce a framework (Sect. 12.3), and within this framework identify the relevant scales for EMF functioning (Sect. 12.4.1) from a structural (Sect. 12.4.1.1) and functional (Sect. 12.4.1.2) point of view. The problems in interpretation of EMF responses to disturbances and their succession over scales (Sect. 12.4.2), of their management for ecosystem services (Sect. 12.4.3), and modeling (Sect. 12.4.4) provide a complementary perspective. Research directions are presented (Sect. 12.5) and conclusions end the text.

## 12.2 Addressing the Up-Scaling Problem

The idea to understand the relationship between patterns and processes at various scales within a hierarchy of nested systems is currently common to all ecological disciplines, including EMF ecology (Dahlberg 2001). The study of this relationship can start with the pattern (detection, description, and analyses of the underlying process) or with the process (description, simulation, and pattern generation) (Schroder and Seppelt 2006). The second approach is more interesting scientifically because it allows for mechanistic, theory-based research questions, a recognized need in the field of EMF ecology (Bruns and Kennedy 2009).

An objective hierarchy of systems has widely been assumed, but some researchers have arrived at the conclusion that “ecological hierarchy and associated scales do not exist per se; rather they represent an instrument constructed by the observer or modeler” (Lischke et al. 2006), and “hierarchy theory is but one way of viewing nature” (O’Neill 1996). Indeed, if one looks at the hierarchical approaches available in the literature, there is no general approach to the scale problem. The classic hierarchy of increasing scale systems accepted by most researchers is organism–population–community–ecosystem–landscape. The diversity of views comes when putting into practice this formal pattern. This can be illustrated by the study of Bailey (1987), looking for objective criteria for delineating large scale landscapes (ecoregions). The spatial scales of the landscape units are the plant ( $10^{-4}$ – $10^{-1}$  m<sup>2</sup>), the patch ( $10^0$ – $10^4$  m<sup>2</sup>), the flowpath

( $10^2$ – $10^5$  m<sup>2</sup>), the landscape (integrative flow system  $10^6$ – $4 \times 10^6$  m<sup>2</sup>), and the region ( $10^7$ – $10^{10}$  m<sup>2</sup>) (Reynolds and Wu 1999). According to these authors, the ecosystem concept fits in the patch level (patch ecosystems form a flowpath). At the ecosystem scale, the search for objective criteria is related to the delineation of boundaries between ecosystems (e.g., Fortin et al. 2000). Within ecosystems, food webs “are portrayed as static networks with highly aggregated trophic groups over broad scales of time and space” (Berg and Bengtsson 2007). Rillig (2004) uses three hierarchical levels when conceiving the effect of mycorrhizal fungi on ecosystem processes: the mycorrhizal fungi, the plants (community and composition), and the ecosystem. Within the soil compartment of terrestrial ecosystems, Miller and Lodge (1997) use a complex hierarchy of soil ecology systems, starting with detritosphere, aggregatusphere, and rhizosphere, continuing with drillosphere and porosphere, and ending with the soil as a whole. When studying the role of arbuscular mycorrhizal fungi (AMF) in controlling the effects of CO<sub>2</sub> on plants and ecosystems, Rillig and Allen (1999) use a hierarchy with two branches: host plant–plant population–plant community and host plant–functional group–ecosystem. Ettema and Wardle (2002) identify as relevant for soil ecology four scales: the fine scale (at root, organic particle and soil structure level), the plot scale, the field scale, and the large scale (gradients of texture and soil carbon, topography, and vegetation). No explicit dimensions in space and time are given for these scales, but they also associate specific ecological processes to each of these scales and discuss mechanisms of process’ disturbance at each scale and point out qualitatively the connection between scales (“spatial distribution of soil organisms influence both plant growth and plant community structure”). Scaling is also related to the research on species–area relationships (Dengler 2009a), including those of microbes (Zhou et al. 2008); these relationships depend both on grain size and on the type of organism (Rahbek 2005). A review on the sampling and mathematical issues of this research area (Dengler 2009b) suggests a stratified approach at large scale (by environmental gradients, vegetation types, and landscape sectors) coupled with a nested one at small scale with five subscales (0.01, 0.1, 1, 10, and 100 m<sup>2</sup>), thus at least six scales in all (five small and one large).

The limits of such approaches are:

- If the hierarchy does not exist per se, then there is no objective character of the entities at the hierarchical levels used, and there is no objective knowledge. This is a conclusion that is difficult to accept within a science.
- If the ecosystems and landscapes include both abiotic and biotic parts, it is not clear why the classical nested hierarchy includes only biological systems (organisms) as its elementary subsystems. Not including the abiotic factors at all levels leads to bizarre conclusions that the elementary units of the landscapes, such as the “area” proposed by Lepczyk et al. (2008) in a landscape ontology, refer only to biological systems such as populations and communities, and the abiotic factors appear only at larger scales (ecosystem and landscape).

- The aggregated trophic groups in ecosystems, including those of soil (Klironomos et al. 1999), are characterized by very different biomass turnover rates and species' dynamics in time; so it is not appropriate to treat the food web as characterized by an aggregated space-time scale.
- Stating that there is an "influence" of processes occurring at different scales is far from being enough because this influence depends also on the plastic phenotypic answer of organisms to soil heterogeneity (Maestre et al. 2003).
- An explicit statement of the time scale of the pattern is needed as well because the patterns can change in time in function of cyclic (e.g., seasonal) or long term driving forces (Wong and Asseng 2006). The evolutionary time scale should not be forgotten because evaluating the significance of biodiversity only at the time scale of ecosystems may lead to the unproductive (from conservation point of view) idea of functional redundancy not only in general but also in the case of soil (Beare et al. 1995).

Pickles et al. (2009) formulate in the end of their review a number of research questions, the first one of which is crucial for linking space-time scale with function: what constitutes a belowground community of EMF, and is it possible to determine the limits of a given "community"? In the next part, we will try to answer this question and to produce a theoretical framework surpassing the limits of existing approaches. Our method follows and generalizes Pahl-Vostl (1995), who came up with a singular approach for identifying ecosystems and clearly delineating communities. Besides the functional niche in differentiating the modules, she proposes the use of biomass turnover rate (inversely related to the length of the life cycle) and of the location in space-time. The application of these criteria would lead to a "trophic-dynamic module" (TDM). She defines a TDM as the group of biological populations having (1) similar rates of biomass cycling (inversely correlated with lifetime of the individuals), (2) the same location in space and time, and (3) similar roles of the species in the food web. Application of criterion one leads to dynamic classes of populations, and further, application of criterion two leads to dynamic modules, which by criterion three are split into TDMs. Pahl-Vostl's method of systems identification in this formulation still has two problems (a) it does not explicitly address the abiotic part of the ecosystem, so productivity can be described only at large ecosystem scales (or the problem is to exactly up-scale from smaller scale to ecosystem scale), and (b) some populations can have structural parts with very different turnover rates, or with different functional niches, and it is not clear how a population can, in this case, be included into a single TDM.

It is clear that a conceptual framework for integrating biotic and abiotic processes at all scales is needed. This is obvious now at least for theoreticians and modelers who are in a position to integrate the available information for fundamental or applied purposes. For instance, Seppelt et al. (2009) argue that modeling with reliable simulations of the human–environmental interactions necessitates linking modeling and simulation research much more strongly to science fields such as landscape ecology, community ecology, ecohydrology, etc. Such linking cannot be done in the absence of a formal cross-scales conceptual framework.

## 12.3 An Analytic Conceptual Framework for Integration Across Scales

A thorough conceptual analysis of the terms used in up-scaling research cannot have a place here for reasons of space, but it is useful to note that even some classic concepts such as ecosystem are under strong criticism in the current literature. O'Neill (2001) discusses logical and scientific problems associated with this concept in an article entitled "Is it time to bury the ecosystem concept?" He proposes that an ecological system is composed of a range of spatial scales from the local system to the potential dispersal range of all of the species within the local system. With the same critical attitude, Reynolds and Wu (1999) ask: "Do landscape structural and functional units exist?"

Looking for the ontological status of ecosystems and landscapes, in the last decade, we have approached the up-scaling problem in various contexts and produced step by step, new theoretical elements. Based on the analyses of biodiversity structure in large rivers, we introduced the concept of emergent TDM, characterizing each hierarchical ecosystem level (Vadineanu et al. 2001). Then, in the context of the natural capital management, we discriminated between the concepts of natural capital and of ecological systems (Iordache and Bodescu 2005). More recently, we advanced ideas about the integration across scales in the context of integrated modeling in the biogeochemistry of metals (Iordache et al. 2009a) and for assessing the effects of disturbance on ectomycorrhiza diversity (Iordache et al. 2009b). Here, we synthesize and further develop these ideas.

### 12.3.1 *Developmental System as the Basic Unit of Ecological Functioning*

In the most general sense, when we declare of an organism that "it functions," we mean that it produces biomass, that it reproduces, and that it has biological productivity. This process conceptually supports both the standard view of ecosystem functions (flow of energy, cycling of matter, self-regulation) and evolution (recall Darwin's 1859 "law of growth with reproduction" characterizing the organisms), but at different space and time (ST) scales. However, an organism as an isolated system cannot "function," because when the organism grows and reproduces, it uses natural resources and services. Darwin did not state this explicitly, but it is an implicit assumption of the fight for existence introduced in his explanatory argument for natural selection (the fight for existence cannot be directly deduced from an empirical "law of growth with reproduction" without scarcity of resources). Darwin avoided putting growth and reproduction in functional terms (i.e., to say "the organism uses natural resources and services *in order to* grow and reproduce") because he avoided making use of any teleological principle, being a convinced Newtonian. But in the current biological thinking, we are used to speaking about

teleonomic behavior of the organisms, the behavior *as if* they would pursue the goals to grow and to reproduce. From such a line of argument (developed in more detail in Iordache 2009b), we first provide a definition for the basic unit of ecological functioning: a developmental system (DS) is a teleonomic entity within its environment producing natural resources and services. Two remarks are needed now (1) if we include the abiotic resources in the developmental system, it is not clear why we would not include the biotic resources too because the DS productivity depends also on biotic resources, and (2) if we include entities with positive value (resources or entities producing services – e.g., dispersal services) for the biomass production, we should also include entities with negative value because both of them influence productivity. In definition, a DS is then a teleonomic entity (TE) and all environmental entities with value (EV) for it (Iordache 2009a). To avoid confusion, we mention that EVs are not isomorphic with the multidimensional niche in the ecological sense because they refer not only to external entities but also to internal ones. Another argument for this lack of overlapping is provided in Sect. 12.4.1.1.4.

DS is a useful theoretical concept because it fits the formal structure of any biological organism with structural (internal, e.g., genes) EVs and external EVs (as “perceived” in its environment), fits the formal structure of human organizations (with organizational leader in the position of TE and organizational goal as goal function, the organization system as an extended body with internal EVs, and the organizational environment in place of external EVs), and fits the structure of management projects (as short-lived organizations).

The fact that it accommodates both natural and human systems provides a common theoretical basis for describing coupled natural-human systems (socio-ecological systems), the connection between biological productivity and organizational productivity, and for modeling such coupled systems.

### ***12.3.2 Epistemic Status of the Developmental Systems***

Here, we provide a way to “translate” the conceptual framework introduced in Sect. 12.3.1 into measurable phenomena and empirically based scientific knowledge. A DS can be modeled by a state space and the “law of growth” can be formulated in a such state-space. Usually, any system’s “goal” is formulated as an attractor point or region in the state space of the properties of the systems or as a maximization or minimization of an index derived from the space parameters (e.g., ascendancy in ecology). Here, we introduce the goal of “growth” through an underived variable (e.g., biomass) or set of variables (accounting for the life cycle of the organism) in the state space and the laws of growth through mathematical functions relating the numerical values of goal variable(s) and the numerical values of other parameters of the state space. We mention without demonstration that efficiency and effectiveness of the DS can be introduced from the form of these mathematical functions, and apparent and general fitness can be related to

efficiency and effectiveness, respectively; this is a way to a common formalization of ecological and evolutionary theory. As far as the “reproduction” part of the Darwinian law is concerned, it cannot be formulated in the same organismic state space but actually involves a multiplication of the organismic state space within the integrating populational system (formally as subspaces). The full “law of growth with reproduction” presupposes the existence (and, from an epistemic point of view, the modeling) of a system with at least three hierarchical levels: parts of DS (TE and EVs), the DS per se, and a population of DS. In order to model the relationships between the DSs of a population or of a community, one needs to integrate the state spaces of each DS in a higher dimensional mathematical space. Part of this mathematical space should describe the “objective” environment between the DSs and include the mathematical functions showing how the common use of this environment by different TEs leads to a change in the value of its entities for other TEs. The integrated model would include two types of models: teleonomic (subjectivistic) of the DS and objectivistic (without goal parameters) submodels (Fig. 4 in Iordache et al. (2009a) illustrates this point). Both types of models need the concept of physical time, but the concept of physical space is requested only by the objectivistic models. The objectivistic model may be needed in two types of situations (a) the environment of the organisms is very heterogenous, and the organisms may deal with different values of the environmental parameters, (b) the organisms perceive the environment in different ways, the value of the environment for each organism being different as a result of their perceptual differences. If one assumes that such situations do not occur, then we arrive to a simplified state space having only one set of parameters for the environment and several goal parameters (reflecting the number of organisms in the intra- or interspecific group). In the case of natural selection modeling, this simplification leads to the replacement of the DS with the organism as the selection unit. However, it is currently accepted that the manner in which organisms perceive the environment is in itself a trait supporting the sorting of organisms by natural selection, and the role of environmental heterogeneity in the selection process is documented as well. For theoretical reasons (including compatibility with cultural and economic selection theories), it is more appropriate to consider the developmental system as the unit of selection, which boils down, in biology, to organisms as units of selection in a simplified model of the environmental pressure, as we have seen. Describing the formal structure of these models and deriving from them the Price equation (Price 1995) is a matter of ongoing research. Other aspects of the epistemic status of DSs as related to their scale will be tackled in Sect. 12.3.4.

### ***12.3.3 Scale and Productivity***

We limit this discussion to biological productivity. The timescale of DS productivity is short and limited to the life of the systems. One scale effect on biological productivity is given by the ST scale of the TE (organism here). Another scale

effect is related to the fact that populations of DS of the same species have a larger ST scale and productivity (due to intraspecific relationships and processes, including reproduction). Still another scale effect is related to the communities of DS of different species, larger in ST scale and having larger productivity as a result of interspecific relations. One could think further about metapopulations and meta-communities of DS and so on. All these systems with larger ST scales are ecological systems but with various degrees of complexity. This view of ecological systems is partly convergent with O'Neill's (2001) view mentioned above, according to which an ecological system crosses a range of scales. We underline that we have not introduced here the concept of "population" and "community" in the classic sense (of biological individuals) but as populations and communities of developmental systems, including both organisms and their environment. Also, there is not a simple ST nesting hierarchy of these systems, and actually there is no hierarchy at all (see next point for the hierarchy as epistemically conditioned) because each DS is characterized by its own ST parameters and usually does not "stay" within the limits of an ecosystem in the standard sense. The more appropriate representation is that of a network of overlapped basic ecological systems (DSs) functioning and interacting through objective (nonteleonomic) systems at various ST scales.

### ***12.3.4 Epistemic Status of Complex Ecological Systems***

The fact that the ecological systems more complex than a DS have no definite boundaries in the Newtonian space is a problem for their description and management. Operationally, one can study or manage only structures well defined in a three-dimensional physical space, not in an  $n$  dimensional mathematical space. Even one DS may spread over many scales, if the EVs from their ET's developmental system spread over many scales, namely from scales smaller than ET's source scale (e.g., fungi for plants) to scales much larger than the source scale (large herbivorous mammals, or seed eating birds, for plants). The solution to this problem is a rough discretization, the modularization of the system (pointing out its "compartmentalized architecture" – Moore et al. 2007).

For a modularization in the interest of scientific description, we adapt Pahl-Vostl's (1995) trophic-dynamic concept (in line also with Godbold's 2005 and Satomura et al. 2006 views) in the following way: a functional dynamic modules (FDM) is a group of TEs or of parts of TEs having (1) similar rates of TE biomass cycling (inversely correlated with lifetime of the individuals), (2) the same location in space and time, and (3) similar functional niches, i.e., relations with TEs of the same or of different scales. We prefer the term "functional" to "trophic" because not just the trophic relations count for the differentiation of functional niches. Another reason is that we want this concept to be applicable to nonbiological TEs as well. With this concept, we tackle the TE part of the ecological systems. The abiotic parts (physical solids, liquids, and gasses) might be tackled by an apparent nested hierarchy



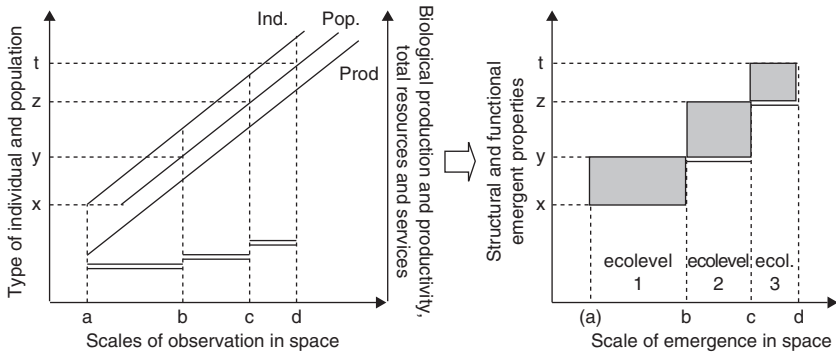
approach at the scales resulting from the TE systems modularization (Iordache et al. 2011). Down-scaling and up-scaling in their case is a problem of physical modeling in a large sense.

Specific to the scientific modularization is that the ST scale is not constrained by the manageability of the delineated system. Some populations of ETs can be included in more than one FDM at the same time because of their internal structural diversity (Iordache et al. 2009b) For instance, populations of deciduous tree DSs have parts with very different rates of biomass cycling, like leaves and wood (criterion 1), as well as parts with different locations in space like below- vs. aboveground (criterion 2). Thus, the trees will belong to at least three FDMs: two aboveground and one belowground. The notions of “same order of magnitude,” “same location in space and time,” and “same role in food web” are to be defined by the researcher and can be applied more stringently or relaxed. In the most stringent application, they will lead to a model identical with the “reality” (“isomorphic” model). If relaxed too much, they will lead to a model too aggregated, having lost the key characteristics of the real system (simplistic model). Only at an appropriate intermediate level will they lead to a model simple enough for explanatory value but keeping the basic characteristic of the system (“homomorphic” model). The scale of the FDMs varies hugely, which implies that there is not one “true” scale for ecological processes. Rather, emergence of new structural (e.g., new FDMs) and functional (e.g., increase in overall biological productivity or changes in the rates of biogeochemical processes) properties should be defined and used to derive the mathematical function that links scale and emergence of new properties in different areas and in different periods of time (“emergence function”).

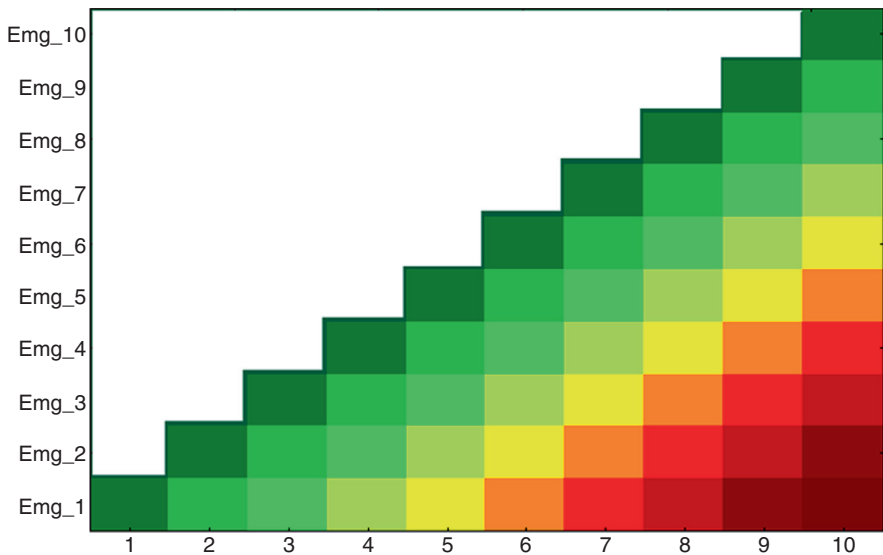
As for the functional niche, we have to clarify what it can mean in a context where there are interactions with systems of many scales. Luck et al. (2003) introduced the concept of a service production unit (SPU) as a subsystem of or a full biological population directly contributing to the production of a resource or service perceived as such by humans. The concept of SPU can be generalized from the perspective of all other species. For instance, roots can be interpreted as an SPU for fungi, and sporocarps as SPUs for fungivorous mammals. This generalization allows for a precise delineation of what part of an EV organism provides value for a TE organism. For EVs with a scale larger than that of the source scale, we answer this question as follows: one has to either produce a model linking the EV with the source scale SPU providing direct services (this works for instance for fine roots of plants as SPUs for EM fungi) or consider the use of source scale TEs by the large scale entity as a biotic internal control parameter connected to a fungal SPU (this could work for consumption of fungal sporocarps by mammals, for instance). By internal control parameters, we mean those describing the influence from inside the DS model, but from scales different than the source TE scale; by external control parameters, we mean those describing the factors influencing from outside the DS model – e.g., large scale physical ones or human action. For entities with a smaller scale than the fungal source scale (e.g., bacteria, tiny invertebrates), one needs to produce a model linking the source scale individual with small scale organisms through the smaller scale SPU providing direct resources and services (e.g., organic

exudates, hyphae) to these smaller scale organisms and then to up-scale the results of this model to the source scale to form another internal biotic control parameter. The particular interaction of the source scale individual with each small scale entity will not count, but the overall pattern resulting from the structural and functional characteristics of these small scale FDMs will. We can now interpret the functional niche of a TE as consisting of variables describing the source scale entities with value for the fungi, the source scale SPUs that are part of larger scale entities relevant for fungi, and the internal biotic control parameters. This concept of functional niche is an epistemic one, with no objective reality associated to it. It will not imply that the developmental system of fungi will not continue in reality to be spread across scales but that we have to modularize the scale continuum in order to obtain workable FDMs, which is a strategic part of the epistemic status of the DS. The DS of a TE (the DS's "world") will be modeled not only by the TE's FDMs but also by the entire homomorphic model reflecting also the EVs *direct* relevance for the TE, i.e., the epistemic status of a DS is related to the production of a structural homomorphic model and of the associated mathematical models (and of the hierarchically structured physical abiotic models). Of course, nobody produces such homomorphic models just for one DS, but for populations of DSs of different species. The homomorphic model for a single DS is a theoretical case with number of species one and number of individuals one. This theoretical case is important when one needs to move the discussion to natural selection, by providing a conceptual bridge between ecological and evolutionist theories. An important point is methodological: in an FDM of ecological use, the physical environment associated with it is considered homogenous and perceived identically not only for the individuals of the same species but also for all individuals of different species grouped in that FDM. This leads to the simplification of the state space used in modeling to make it workable for ecological purposes (where the evolution of the organisms is not taken into account) and especially for aggregation in view of up-scaling the ecological processes. Another point is that the space-time windows associated with the homomorphic models should be chosen, especially in the case of managerial modularization, such as to be compatible with the human practical possibilities of action.

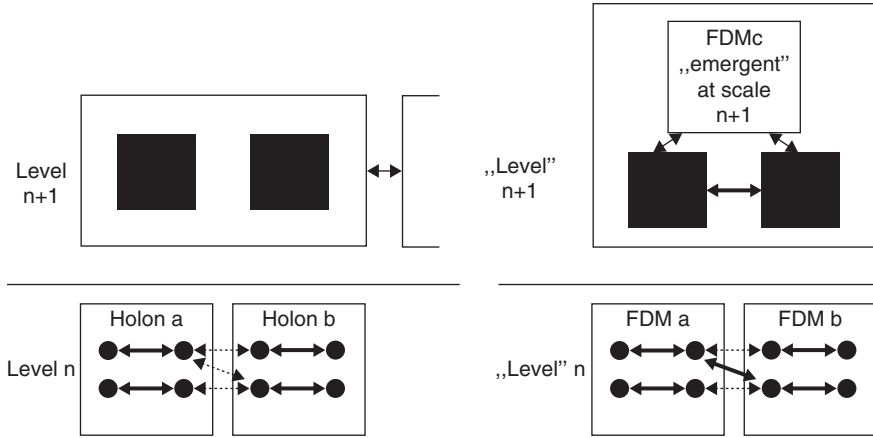
The scientific or managerial modularization leads to a nested hierarchy of ecosystems but not a true one (Fig. 12.1). In this framework, it is not the case that "holons at level  $n$  form the entities at level  $n + 1$ " (Lischke et al. 2006) because besides the  $n$  level entities, there are also new larger scale entities forming the  $n + 1$  level; each eco-level is characterized by structurally new types of FDMs that are not found at lower hierarchical levels (Fig. 12.2). Only the representational three dimensional physical spaces needed for scientific investigation or management are nested and not the productive systems analyzed within this three dimensional space. The standard homomorphic model of an ecological system (including compartments for primary producers, consumers, decomposers, etc.) will be then about interactions of different developmental ecosystems of different scales. What is not seen in the standard representation is the large number of smaller scale populations of TEs



**Fig. 12.1** The relationship between the scale of biological structural elements and processes (individuals, populations, *left graph* – left axes, production and productivity, *left graph* – right axes) and the hierarchical structure of ecosystems (*right graph*). At scales of observation from a to b (corresponding to ecological level 1), one can perceive all types of individuals (and their populations) from x to y but only some of the individual types from y to z (and not their populations). The FDMs including populations of type y to z are said to “emerge” at higher hierarchical ecological level 2. Grey areas on the *right graph* suggest the multidimensional spaces characterizing each ecological level in which the processes supporting the productivity of each level can be conceptualized. Note that the simplistic linear models (emergence functions) from the *left graph* can be cut in a different way, leading to alternative hierarchies. The real forms of the emergence functions are not linear and depend on the starting point of observation in space



**Fig. 12.2** Theoretical relationships between the number of eco-levels and the number of emergent FDMs (communities) of each type (Emg\_1 to 10) within an eco-level (1 to 10). The color change from *green* to *red* indicates an increase. Biodiversity of the overall biocenoses (system of communities) is related to the number of FDM types and instances and to the species diversity inside each FDM



**Fig. 12.3** Simplified representation of a true nested hierarchy (*left*, applicable, for instance, to molecules – level  $n$ , and cells level  $n + 1$ ) and the apparent hierarchy of systems (*right*, resulted from the epistemic modularization of ecological systems). In the apparent hierarchy (abiotic physical parts not represented), the holon at  $n + 1$  level includes subsystems that are not present at  $n$  level, which is not the case for true hierarchies. In the true hierarchy, the interactions within the subsystems of a holon are strong and between holons are weak, while in the apparent hierarchy, they may be very strong between holons (when, for instance, the FDMs include parts of the same population of DSs with different functional niches, or parts of the same DSs with different location in space and time, or different turnover rates)

compared to the large scale ones. Many small scale FDMs are coupled at the same time to a relatively larger FDM (Fig. 12.3).

Usually, the term ecosystem is used both for scientific and for management purposes. This leads to conceptual confusion and, as we have seen, even to proposals of rejecting the ecosystem concept with scientific arguments. Here, we separate the scientific use from the applied, managerial use, by the additional term natural capital. An ecosystem is natural capital when the modularization of the emergence function is done for management goals, i.e., of interest is the value of the ecosystem for humans. Promoting a separation between basic and applied studies is in line with other opinions from the literature. For instance, in a conceptual analysis Yarrow and Marin (2007) conclude that the concept of ecological boundary will find its primary utility within scientific circles, whereas the system-specific transition zone is quite useful in public discourse and socioeconomic decision-making. For a modularization in the interest of management, leading to a *theoretical* hierarchy of the natural capital, one has to use only scales appropriate for the coupling of natural DSs with human developmental systems (organizations, management projects) by natural resources and services relevant to humans. The theoretical natural capital hierarchy resulting from a managerial modularization of the emergence function is a hierarchy of the natural capital, with specific natural resources and services produced at each level (Iordache and Bodescu 2005) and

with specific managerial organizations created for (“emergent at”) each level. An emergence function for human developmental systems (organizations) can be constructed and modularized leading to a hierarchy of socioeconomic systems, with the importance difference being that this modularization is no longer at the latitude of the researcher but imposed by national and international institutional reality. Actually, the theoretical natural capital hierarchy may follow the socioeconomic current hierarchy for reasons of manageability of the natural modularized entities.

An analysis of the socioeconomic systems (the construction of the organizational emergence function just mentioned) reveals that the *real* structure of the natural capital is not the theoretical one, simply because the modularization of the natural emergence functions is not only a scientific process but also an institutional one associated with the functioning of a socioeconomic system that includes the scientists’ organizations. What is interesting in real management is how particular organizations and projects deal with the ecological system, what they perceive as valuable, and how they interact when they want to maximize their separately perceived values (when they are in a conflict of interests, leading eventually to an environmental crisis). Exactly at this point, the key role of the theoretical concept of natural capital is revealed as an attractor for the structure of the real natural capital if one envisages the maximization of the privately and publicly intercepted natural resources and services. There is an institutional evolution of the real natural capital (Iordache 2004) and a cultural history of the natural capital as part of the overall cultural and institutional evolution. The theoretical concept of natural capital is useful also as a reference for conceiving the deterioration process – as structural change leading to the decrease of overall (whatever the intercepting organization is) natural resources and services produced by the natural capital – and for conceiving the restoration process (the inverse of deterioration).

Another important distinction to make is that between production and management of the natural resources and services. The production takes place at all scales of the ecological emergence function, but the management can occur only at the human-relevant scales. One problem is how to take into account the contribution of small scale organisms (like EMF) to the overall natural resources and services production at the management scale. This can be done through the SPU concept. From a managerial perspective, the TEs’ populations of the same species (or fragments of such populations) found in an FDM constitute service productive units (SPUs). The SPU concept allows the identification of each species’ contribution to the overall theoretical or real natural capital value, and on this basis, the design of targeted management measures. All services provided by SPUs are dependent on the production of biomass, and the material fluxes associated with it, but they can range from providing a source of carbon to a simple physical support (e.g., for smaller scale organisms). One needs long term field studies in order to appropriately assess the biomass production (Staddon et al. 2002), and hence the importance of long term ecological research. Besides this ecological knowledge, one will need for its application socioeconomic knowledge concerning the optimal institutional framework. Optimally, this framework has to allow for the integrated action of the organizations perceiving different values of the natural

capital and the integrated implementation of management projects having different standpoints.

### 12.3.5 *Up-Scaling the Ecological Processes*

Up-scaling the biomass production function from original DSs of scale 1 to a larger target scale 2 is not a simple physical space-time (ST) procedure because it involves an increase in the complexity of the state space from the original to the target system. The scale issues are related to the position in space-time (ST) of the original TEs as grouped in FDMs of their internal and external EVs, of DSs of larger scale to which they are directly connected, and to the ST patterns of physical processes of larger scale controlling the value of abiotic parameters relevant for the original and large scale TEs.

Up-scaling the biomass production function from the FDMs of source scale to target scale may involve previous down-scaling of other processes. One of these situations occurs when the source scale DSs use as EV an organism of larger scale (for instance as a carbon source). In this case, one needs a model down-scaling the biomass production of that organism to the specific portion of biomass/carbon made available for source scale organisms, which is different from the model describing the overall biomass production of that large scale organism. Another situation is connected to the pattern (perceived at large scale) of distribution in space of the biomass of source scale FDMs, a pattern controlling the choice of mathematical tools for up-scaling (excellently reviewed by Lischke et al. 2006). This pattern may depend in time on external control parameters that can be modeled in space and time only at large, target scale. For instance, if one predicts with hydrogeomorphological models the dispersion of a toxic pollutant with a resolution of  $50 \times 50$  m, this information should be down-scaled if the DSs controlled by this pollutant, whose up-scaling we are looking for, have a much smaller scale. The particular distribution at small scale can be influenced by the external control parameters, by changing the species location in space, changing the species location in time, or changing the turnover rate of the biomass, with overall consequences on the FDMs structure and associated productivity.

Within the presented analytical framework, the steps for up-scaling the biomass production (and related biogeochemical processes) from the original (source) DS systems could be based on *structural aspects* like (1) ST location and turnover rate of the source TEs (characterizing biomass turnover and position in ST of the TEs by one or several modules reflecting their life cycle and morphological properties), (2) entities providing resources and services to the original TEs (identifying the EVs relevant for each TE type by module and characterizing their ST position), (3) entities using resources and services of the original TEs (identifying the use of source ET modules as EVs by developmental systems centered on types of TE of larger scales and identifying the position of these large scale DSs in the system of target scale), (4) external control factors (identifying the large scale abiotic factors,

described as external parameters, influencing the DS of the original scale identified above) and (5) the homomorphic model of the system of DSs and of its integrating system (identifying the overall ST scale of the system of FDMs characterizing the source DS, the relationships of these FDMs with larger scale ones and the external control parameters). In addition, *functional aspects* include (6) biomass production functions at source scale (characterization of the production functions at DS, populations of DSs, and FDMs of the source TEs at the original scale in the field, i.e., implicitly taking into account the influence of smaller scale DSs), (7) large scale DSs' influence on the production function (characterizing the mathematical functions describing the influence of large scale DSs on the productivity of the original DSs), (8) large scale abiotic factor's influence on the production function (characterizing the mathematical relationships underlying the influence of large scale abiotic parameters on DSs at the original scale, the space distribution of the abiotic parameters in the system of target scale with a resolution of original scale, and the mathematical functions predicting their space-time dynamic and the abiotic processes involved at the target scales) and (9) large scale abiotic factor's influence on large scale DSs connected to the source scale (the same as in point 6 done for the large scale FDMs mentioned at point 3 keeping into account only the abiotic processes influencing all DSs whatever the scale). The *integration* relies on (10) stratification (stratifying the system of target scale into strata having the scale of the system of FDMs characterizing the original DS as identified) , (11) production function by strata as controlled by large scale DSs and abiotic factors (assessment of the productivity or other associated processes of interest of original DSs by types of strata, as modeled by the system of FDMs developed within stratum under the control of larger scale DSs and abiotic parameters, providing the possibility to correct for results obtained in step 6 by results from steps 7, 8 and 9, and (12) model up-scaling (extrapolation of production function to the target area of interest by types of strata).

## 12.4 Application to Ectomycorrhizae

It follows from above that the up-scaling of the function of EMF cannot be done without modeling their function. We are still far from reaching this level of understanding EMF ecology. Below, we will concentrate on the structural and functional aspects, and less on the modeling side (touched on in Sect. 12.4.4) and in, particular, on the following questions:

- How many hierarchical levels do we need to construct and study from the natural emergence function in order to fully understand the role of EMF DSs in the ecological productivity of ecosystems and landscapes?
- What are the appropriate modularization scales for understanding the role of EMFs? (“which are the most relevant scales of analyses for these organisms?” Lilleskov et al. 2004)

- How many types of FDMs are needed for the structural and functional modeling of EMF communities?

These questions are directly relevant to the discussion of EMFs biodiversity. We have shown elsewhere that (Iordache et al. 2009b), for instance, it is not meaningful to interpret EMF patterns of alpha diversity at an ecosystem scale ( $10^4$ – $10^6$  m<sup>2</sup>), but that this should be done at a much smaller scale (subtree level differentiated by soil layer). Here, we will not develop, however, this line of interpretation but only take the steps of the analytical framework introduced in the previous part.

### ***12.4.1 Scales Relevant for EMF Developmental Systems***

#### **12.4.1.1 Structural Issues**

The criteria for delineating FDMs are, as we have seen, the biomass turnover rate, the location in space-time, and the functional niche. The functional niche is discussed in terms of resources used by EMF and organisms using parts of EMF as service providing units.

#### Dimension and Turnover Rate of EMFs

The simple parameters characterizing an organism are difficult to determine in the case of fungi and even more difficult for EMF. The reasons for this are the complex structure and life cycle of these organisms and the underground location of most of their parts. An analysis of the EMF individual should in principle differentiate between fungal tissue (fruiting body – sporocarp, sclerotium, spore), the plant fungal interface (ectomycorrhizae (EM), also referred to as “root tips” in the literature and further below), and the soil fungal interface (extraradical mycelium or extraradical hyphae, which can differentiate rhizomorphs for long distance transport of nutrients and water) (Satomura et al. 2006). Anatomical details like the dimensions of hyphae, cell walls, etc., are provided in an excellent series of studies on ectomycorrhizae (e.g., Agerer and Weiss 1989 and references therein). The hyphae have diameters of 3–5  $\mu$ m, smaller than many soil pores (Smith et al. 2010). The importance of each of these potential parts varies with the species. For instance, relatively few EMF are known to form sclerotia, but when present, they support resistance to disturbance and recolonization (Münzenberge et al. 2009). Rhizomorphs can be associated with root tips, with the extraradical hyphae network between trees, or with the sporocarps. Further complications (many plant fungal interfaces) occur in the case of fungi linking several plants. Ectomycorrhizae, rhizomorphs, hyphae, and sporocarps perform different functions, respond differently to environmental conditions, and their life span has consequences on soil biogeochemical processes (Treseder et al. 2005). Most microbial measurements to date, such as biomass or hyphal length, have been single time-point measurements (Allen et al. 2007).



The delineation of a fungal individual starting from its various parts can be done by direct physiological continuity or by genetic identity (Smith et al. 1992). Most of the reported sizes refer to the genets. This may be a false indicator when a physical fragmentation of an individual, especially at ERH level, occurs. In the case of plants, a distinction between genets and ramets (physiological individuals separated from the clone) is made. For fungi, the term “ramet” is not used since anastomoses of physically separated units may occur. Lamour et al. (2007) analyze, for instance, the network of an *Armillaria* species in two 25 m<sup>2</sup> plots of natural soil. They found a density of 4.3–6.1 rhizomorphs per mm<sup>2</sup>. At one site, the network consisted of 169 rhizomorphs as edges and 107 rhizomorphs as nodes. Only two critical rhizomorph bridges would lead to the separation of significant physiologically independent fragments, so there was “low probability that amputation of a randomly chosen edge would separate the network into two disconnected components” (Lamour et al. 2007). So the dimension of a genet is a fairly good approximation for the dimension of the biological individual in the case of fungi.

Smith et al. (1992) reported a 15 ha large, 1,500 year old genet of a parasitic fungi with an estimated biomass of 10,000 kg. Similar investigations are missing for EMF. While ectomycorrhiza life span depends to some extent on the life span of the host tree, interconnections between trees are generally found and may be seen as indication of similar sizes and life times for EMF. Griffiths et al. (1996) reported that EMF mats may persist 2 years after their host trees have been cut down. The patch size of individual EMF mats studied by Agerer and Göttlein (2003) were several dm<sup>2</sup>. Within the mats, some species were positively correlated to N–NH<sub>4</sub><sup>+</sup> concentration, to total K, Na, Mg, Fe, Mn concentrations and pH, but other species distribution revealed no such correlation. The sizes of the genets of three EMF species studied by Redecker et al. (2001) were 1.5, 9.3, and 1.1 m<sup>2</sup>. Bruns et al. (2002b) have mapped and genotyped the fruiting bodies of EMF in a forest in order to compare the pre- and postdisturbance distributions and identify the causes of community reestablishment (dispersal or regeneration from local forms of resistance), and the size of the genets ranged from 1 to 10<sup>2</sup> m<sup>2</sup> (estimates from their map). In reviews, the size of genets is estimated to vary from 10<sup>-1</sup> to 10<sup>2</sup> m<sup>2</sup> (Lilleskov et al. 2004), 1 m<sup>2</sup> to more than 10<sup>2</sup> m<sup>2</sup> (Godbold 2005), and between 1 and 300 m<sup>2</sup> (Wolfe et al. 2009). Inside a genet, the root tip abundance itself may be patchy (Pickles et al. 2009).

The size of the genets is related to the physiological and reproduction strategies of the fungi (Table 12.1). The extent of extraradical mycelium for the same species

**Table 12.1** Comparison of early- and late-stage ECM species characteristics (Iordache et al. 2009b). The relation to exploration types is hypothetical; the other relations are documented by the literature

Species/ characteristic	Reproduction	Genetic diversity	Requirement of C, N, P	Exploration type
Early	Primarily by spores	Higher	Small	Mainly medium and long distance
Late	Primarily by clonal expansion	Lower	Greater	Mainly contact and short distance

may depend on environmental variables (Scattolin et al. 2008), and consequently, the individuals of the same species may have different locations in space as a function of abiotic factors.

The information about the life time of a genet is very important for understanding the speciation process, but from a short and average timescale perspective, the turnover rate of the biomass of a genet's parts is of interest as well. The turnover rate may be estimated not only from the life span of the parts but also as a function of the decomposition of the associated organic matter.

Rygiewicz et al. (1997) found an average median lifetime for mycorrhizal tips of 139 days (lifespan + decomposition), ranging from 123 to 185 days for the eight treatments in the 18 month study period. These authors also review the older literature, some of which report a much longer life time of individual root tips (2–4 years). Treseder et al. (2004) screened the literature showing that ages extended from 1 to 6 years (including errors and sample variability), a range that overlaps with the 0.25–4 year life spans reported in other studies that have visually tracked ectomycorrhizae. The fine root turnover rate is dependent on external, large scale abiotic parameters such as CO<sub>2</sub> concentration (Tingey et al. 2000), with consequences on the root tip FDMs. But “ECM turnover need not precisely mirror root turnover. A number of ecological factors may influence fungal lifespan independently of roots, including life history of the fungal species, predation on the fungi, and shifts in the allocation of host plant C to the fungi” (Treseder et al. 2004).

The hyphal life span is reported to be 5–7 days (Godbold 2005), less than 1 week, although a subset can live for more than 1 month (Staddon et al. 2003). For rhizomorphs, this may be even longer. A discussion about the turnover rate of ERH is made in Godbold et al. (2006), mentioning that the turnover time may be longer than 30 days depending on the methodological details of the estimation. For comparison, turnover rates of leaves are about once per year and those of fine roots about three times per year (Godbold et al. 2006 and citations within). The turnover rate of organic matter derived from dead hyphae is much longer than the life of the hyphae because of recalcitrant substances like chitin. Due to the high turnover rate, “the mycorrhizal external mycelium was the dominant pathway, 62%, through which carbon entered the soil organic matter pool, exceeding the input via leaf litter and fine root turnover” (Godbold et al. 2006). Coutts and Nicoll (1990) report several months of life for rhizomorphs. In another study, rhizomorphs lived an average of 11 months in control plots, indicating that many individual rhizomorphs survive at least part of a nongrowing season (Treseder et al. 2005). Mushrooms (sporocarps) are short-lived, with an age of 1–2 weeks, and are formed by labile carbon derived from the ERH mycelium (Treseder et al. 2004). Based on the above information, we conclude that parts of EMF would fall, based on the biomass turnover criteria, into two dynamic classes: one with fast turnover rates (hyphae and sporocarps) and one with smaller turnover rates (ectomycorrhizae and rhizomorphs).

## ST Location of EM Fungi

Locating an EMF individual in soil is a difficult task, taking into consideration its distribution between the interface with the plant, soil, and sporocarps (Pickles et al. 2009). There is an obvious difference between the location of aboveground sporocarps and belowground structures. For the belowground parts of the fungi, there is solid knowledge supporting the idea to differentiate between soil horizons, as documented below.

*Vertical location* A niche separation of EM species in coarse woody debris and mineral soil was reported by Tedersoo et al. (2003). The web of ERH not only colonized mineral soil, but was also abundant in litter and decaying wood (Buée et al. 2009). ERHs were differently distributed in logs, stumps, forest floors, and mineral soil (Goodman and Trofymov 1998). The vertical, gradual differentiation of EMF community structure with depth has been documented (Landeweert et al. 2003; Calvaruso et al. 2007; Courty et al. 2008). Dickie et al. (2002) also report the vertical niche differentiation of ERH in soil. In a detailed study, Gebhardt et al. (2009) analyzed only a 3 cm organic layer and cut it into 1 cm slices. Even at this resolution, they identified two organic sublayers with different EMF communities (only four species in common). The vertical patchiness of EMFs is related to the distribution of substrates (Genney et al. 2006) and soil horizon properties (Rosling et al. 2003; Baier et al. 2006). This vertical partitioning can be interpreted more generally as niche portioning based on soil chemistry: nitrogen (ammonium) content, base saturation, carbon age, and soil moisture (Peay et al. 2008). Specialization of ERH parts of EMF may also occur with respect to organic matter content, leaf litter type, and litter source (Rillig 2004). Vertical niche partitioning is thought to be one way by which the high species diversity of mycorrhizal fungi can be maintained at small spatial scale (Wolfe et al. 2009). The EMF role changes with depth, not only because some EMF prefer organic or mineral soil layers but also because the number of root tips and mycorrhized root tips (EV for EMFs) vary with depth (Scattolin et al. 2008).

From this information, we infer that the aboveground sporocarps should be included in a separate dynamic module, and the belowground root tips and ERHs should be split vertically at least into two dynamic modules as a function of the organic matter content of the soil layer.

*Horizontal location* The available information concerning the horizontal distribution of EMF refers to individuals (genets), populations, and communities. Additional information is provided indirectly by niche differentiation as a function of host species and by the possibility of connecting several hosts. Such information can be coupled with the hosts location in ST in order to locate the host-specific EMF.

At the individual level, a cluster of root tips colonized by the same species is likely to be colonized by the same genet (Godbold 2005). EMF with saprophytic abilities colonize (by their ERH) the litter layer and discrete patches of organic nutrients (Graham and Miller 2005). Genet size patterns may be different as a function of the site, and large genets may have smaller scale structures because of

fragmentation and intense colonization of microsites (Lilleskov et al. 2004). Another problem in investigating the spatial structure of EMFs can also be the cryptic nature of some genera like *Cenococcum geophyllum* (Pickles et al. 2009). This genus was found to be distributed ubiquitously at a local tree plot scale, but patchily at microscale (within the  $5 \times 5$  m, Matsuda et al. 2009), and with a large genetic diversity even within a single soil core (Douhan and Rizzo 2005). Clearly, genetic tools have to be applied for characterizing the ST location of such species (see Sect. 12.5, research directions). In a study of the genet distribution of sporocarps and ectomycorrhizae of *Suillus* species, Hirose et al. (2004) found in a  $20 \times 24$  m plot four genets from sporocarps, which coincided with those identified for EMFs; the spatial distribution of EMFs of each genet were wider than those of sporocarps, the area occupied by each genet differed considerably within the plot.

Species are likely to differ in spatial colonization patterns because of different internal genet structure and rates of vegetative expansion (Lilleskov et al. 2004). These authors report that dominant EMF taxa showed patchiness at a scale of less than 3 m, with a range from 0 to more than 17 m. Minimal and maximal distances between cores for stand level EMF characterization are proposed to be 0.25 and 300 m (Lilleskov et al. 2004). Metapopulations of EMFs with epigeous fruiting bodies are genetically homogeneous over large distances (1 km), while those with hypogeous fruiting bodies tend to differentiate genetically at much smaller scales (Wolfe et al. 2009).

Griffiths et al. (1996) use two scales for the investigation of EMF: sampling within a stand of  $2 \times 10$  m (to see the effects of forest floor attributes, understory vegetation, and other species of fungi) and a sampling of stands located in the forest (to see the effect of succession gradients). They found no correlation with the forest floor, but proximity between EMF mats, distance from the closest tree, and density of living trees in a stand had an impact. At scales of  $<4$  m, there is a high community similarity, while at scales of  $<20$  cm, the community is temporally dynamic, suggesting a high degree of species turnover probably due to root senescence (Wolfe et al. 2009). “Late stage fungi” can be found on roots closest to the trunk of the tree and “early stage fungi” on roots farthest from the base of the tree (Wolfe et al. 2009, see also Table 12.1), which was interpreted as a succession in ectomycorrhizal development. These patterns may be indicative of niche differentiation by host tree species and the influence of the neighboring tree of the same or of different species on the host tree community, as documented below.

The structure of an ectomycorrhizal community depends on the host trees and host range of the fungi (reviewed by Bruns et al. 2002a; Buée et al. 2009). Sympatric oak species had different EMF community structures (Morris et al. 2008), partly explainable by extractable phosphorus, but mainly attributable to the tree species. Host specificity is a niche dimension in itself (Peay et al. 2008). “Selection pressure for host specificity may not relate as much to interspecific interactions between trees in later stages of succession but rather to adaptations to marginal habitats (post disturbance) by the plant and its fungal symbionts” (Horton et al. 2005). Neighboring tree species identity shaped the EM community structure of the host, and the effects were specific to host–neighbor combination (Hubert and

Gehring 2008); tree species may serve as reservoirs of EM inoculation to one another. At the ecotone of a forest, there was an advancing front of EMFs by dispersal on barren soil, followed by trees, the invasiveness of a tree species being regulated by the spatial pattern of fungal inoculum in the soil (Thiet and Boerner 2007). Oak seedlings were less infected by EM fungi in a forest dominated by a different tree species than in oak forests, with consequences to the productivity (lower dry biomass, Lewis et al. 2008).

Another mechanism supporting the patterns is generated mainly by long range exploration fungi connecting trees and trees with mycoheterotrophic species. An implicit idea from Horton and Bruns (2001) is that this networking by fungi can be made not only by long distance exploration types but also by short distance types when the roots of the trees spatially overlap. Orchid EMF can simultaneously form ectomycorrhiza with forest trees (mycoheterotrophy, Bidartondo et al. 2004). The EMF can interconnect roots of the same or different species (Simard and Durall 2004). The same idea is also supported by Horton and Bruns (2001): dissimilar plants are associated with many of the same EMF on a small enough spatial scale to share those fungi. The observed structure at the tree and intertree levels may be different also because the observation of low abundance fungi as hyphae or tips is not possible. For instance, Koide et al. (2005) observed in a community some species as root tip, but not as hyphae, and vice versa. As long as we are interested in the function of EMF at an ecosystem level on short and average term, these methodological limits are acceptable.

Based on the above elements (which in the case of intertree location also include elements related to the functional niche), one has to separate the fungi species into potentially six dynamic modules in the two dimensional space:

- At tree level (about 4 m around the tree) and at plot level (group of trees and mycoheterotrophic plants occupying a surface of 400–900 m<sup>2</sup>)
- Three types of functionally differentiated plots (a) with trees of the same species, (b) with trees of different species, and (c) intertree-mycoheterotrophic plant level
- Tree level dynamic modules in function of their position inside the forest: those at the ecotones between different vegetation patches should be placed in separate strata

*Location in time* Some EMF populations build up mostly in winter and others in summer periods (Courty et al. 2008; Buée et al. 2009 and the references within). Koide et al. (2007) found an even more complex temporal partitioning of niches: three groups of EMF separated in time over 13 months with respect to their hyphae in the bulk soil (ERH) and two groups of EMF separated at the same time with respect to their parts associated to roots. EMF sporocarps may have a specific location in time. For instance, Nara (2008) reports on the seasonality of sporocarp formation in a volcanic desert on Mount Fuji, Japan.

Related to the location in time, some authors use the notion of “ectomycorrhiza turn-over,” referring not to the biomass turnover but to the community change over time. Izzo et al. (2005), for instance, conclude that “annual occurrence of the

dominant ectomycorrhizal species was constant at larger spatial scales but varied more across years at a fine spatial scale. Turnover of ectomycorrhizal species between years was observed frequently at scales  $<20$  cm.” Such information cannot be used for delineating the location in time of the communities unless some periodicity of community structure at the multi-year level is observed (and then the homomorphic model of the study system should be constructed with a multi-year characteristic timescale).

Based on the existing information, it seems that in some cases, several dynamic modules separated in time could be differentiated for each FDM separated in space. However, it is too early to generalize this. The decision in a real situation should be made after at least 2 years of monitoring the structure of an EMF community.

### Resources for Ectomycorrhizal Fungi and Their Space-Time Location

In general terms, fungi are considered to be organisms that strongly influence the microscopic and the macroscopic world (Peay et al. 2008) and a good model for experimenting with the coupling between processes of different scales and connecting soil microbes with animal populations via the direct effects on plants (Smith et al. 2010). The EVs with positive value for EMF are soil abiotic mineral and organic parts, litter, plants, and bacteria.

Many basidiomycetes EMF have retained some of their saprophytic abilities, and thus have the potential to access organic sources of nitrogen and phosphorus and to degrade the lignocellulose fraction of dead plant material (Graham and Miller 2005). A key service provided to fungi by plants is the carbon transfer to the fungus in the fine roots (Dell 2002), with the extra carbon accumulating at the edge of the hyphal mat. Fungi also redistribute water from moist layers to upper dry layers (“hydraulic lift”), which is beneficial to soil microorganisms and increases the availability of nutrients to plants (Liste and White 2008). In addition, bacteria, archaea, phages, saprophytic fungi, and soil fauna may interact with EMF (Buée et al. 2009).

Biological factors influencing the structure of soil microbial communities (Buée et al. 2009) are: plant developmental stage, plant species, and plant cultivar (genetic diversity). Mycorrhizae affect the functional diversity of rhizosphere bacteria, fungi, and other microbes (Buée et al. 2009 and the references within). In turn, EMF can be supported by rhizosphere bacteria, a phenomenon that lead to the concept of “mycorrhization helper bacteria,” reviewed in detail by Tarkka and Frey-Klett (2008). The distribution of “mycorrhization helper bacteria” followed the vertical EMF stratification both at tree level and between trees (Calvaruso et al. 2007).

A service provided to EMFs by other fungivorous organisms is spore dispersal. A variety of organisms have been shown to move viable spores of mycorrhizal fungi at scales from cms to kms (Wolfe et al. 2009). This is an important aspect because the scale of selection operating on EMF with direct consequences on genetic divergence (and in time speciation) is related to the maximal dispersal

capability of the fungi. Direct evidence of EMF spore dispersal by mobile animals was produced and reviewed by many authors (e.g., Johnson 1996; Carrey and Harrington 2001). In an excellent study, Lilleskov and Bruns (2005) found that EMF spore densities were high in the guts of arthropod fungivores (mites, springtails, millipedes, beetles, fly larvae) but present also in arthropod and vertebrate predators (centipedes and salamanders). A low percent of the spores had intact nuclei in predators, but most of the spores in the fungivores had intact nuclei and seemed viable.

### Organisms Using Resources and Services Provided by EMF

Organisms using EMF can be interpreted in many cases as EVs with negative value. In the particular case of trees and fungivorous animals, there is a reciprocal use ( $++$  interspecific relationships).

The key organisms benefiting from EMF are trees. EMF assist forest trees in exploiting the soil, in uptaking nutrients by solubilizing soil minerals with organic acids (Buée et al. 2009) and in mobilizing organic forms of nutrients by enzymatic activities (Courty et al. 2005). The variation in EMF perceived by the host plant may be of a discrete (presence – absence of EMF) rather than continuous nature (variation in identity or abundance of EMF) (Karst et al. 2008). The ability of EMF to capture and transport nutrients is believed to be strongly related to the exploration ability and function of ERH. The relevant contribution to nutrient uptake is estimated by the proportion of root tips colonized (Graham and Miller 2005). However, root colonization may not be a good predictor for nutrients uptake (Graham 2008). Instead of this, measurement of lower level mechanisms for nutrient uptake being needed is preferred; but it is difficult to scale up the information thus obtained to the field. Secondary services are also provided. EMF species differ in the ability to capture nutrients, uptake water, protect against pathogens, and increase tolerance to heavy metals (Godbold 2005), unfavorable pH, or salinity (Dell 2002).

EMF can transfer carbon and nutrients between host plants or to mycoheterotrophic plants (Bidartondo et al. 2004; Buée et al. 2009; Leake and Cameron 2010) and can facilitate interplant transfer of carbon, nitrogen, phosphorus, and water, eventually following source-sink gradients between plants (Simard and Durall 2004). Mycoheterotrophic and mixotrophic plants are dependent on the transfer of carbon by EMF networks, which in turn depend on their host photosynthetic plants (review in Selosse et al. 2006). Hyphal connections can also maintain physiological continuity between ramets of plants (Hutchings and Bradbury 1986) or between a tree and seedlings (Simard et al. 1997).

EMF provide an energy supply to the detrital food web as a result of the large hyphae turnover, benefiting saprophytic microbes and other soil organisms (Dell 2002). The EMF mycelium constitutes the largest part of the biomass of most EMF species (Godbold 2005). The hyphal mantle mycelium and extraradical hyphae can have a biomass of 500–700 kg/ha (Godbold 2005). The EMF mycelium supports

the activity of free living decomposers (Buée et al. 2009). EMF also provide food by mycophagy of the sporocarps (Dell 2002; details in Sect. 12.4.1.1.3 under the service of spore dispersal).

EMF provide indirect services to many organisms related to the structure of the soil (increasing the formation of soil aggregates) and to the cycling of nutrients (replenishment of the available nutrients pool, Dell 2002). Rillig and Mammey (2006) review how mycorrhizal fungi can influence soil aggregation at various scales. Many services provided by EMF SPU's might occur by this mechanism, but their understanding and quantification is still a matter of further research. EMF can also indirectly affect plants. In a review, Koricheva et al. (2009) analyze indirect effects of mycorrhizal fungi on insect herbivores. They describe significant effects on all aspects of insect herbivores performance, including consumption, growth rate, mass, fecundity, survival, and density. The scale of this influence is dependent on space and time distribution of the insects.

It is clearly documented that soil invertebrates disrupt the carbon flow through mycorrhizal networks by feeding on hyphae (e.g., collembola, – Hiol Hiol et al. 2004, oribatid mites – Schneider et al. 2005). But, taking into consideration the high turnover rate of ERH and its very complex network (Lamour et al. 2007), the negative influence of this consumption on the connections between plants suggested by several authors is questionable (Moore et al. 1985; Johnson et al. 2005). However, predation at the rhizosphere level may have an aboveground effect on plant primary production if such interspecific interactions have an important influence on the overall pattern occurring at the root FDMs level (Moore et al. 2003). Earthworms (Szlavec et al. 2009) may also disrupt the mycelia through soil mixing and burrowing, and changes in nutrient availability by altering litter quality and quantity occur, resulting in a shift in the composition of the fungal community. Humans also use EMF, but we do not discuss this here because the mechanisms supporting the use of EMF are not biological alone (see Sect. 12.4.3). In light of the literature reviewed here, the functional niches occupied by the EMF seem to be no more diverse than those already identified in Sect. 12.4.1.1.2 based on the species of the host plants and the number of hosts. Before looking at the structure of the resulting homomorphic model (Sect. 12.4.1.1.6), we will briefly mention the external control factors influencing the EMF system.

### External Control Factors

External factors should not be confused with the parameters describing them. The parameters resulting from the effect of the factors can be measured at all scales (e.g., concentrations of toxic metals), including within the EMF developmental system, but the action of the factor (pollution with metals by dry deposition) is from outside the system. From a scale larger than their DSs, EM fungi are affected by fire, increase of CO<sub>2</sub> in air, warming, drought, nitrogen deposition, deposition of toxic substances, and management practices. There can be direct effects or/ indirect effects of one factor (e.g., by plants). The effect of coupled external control factors

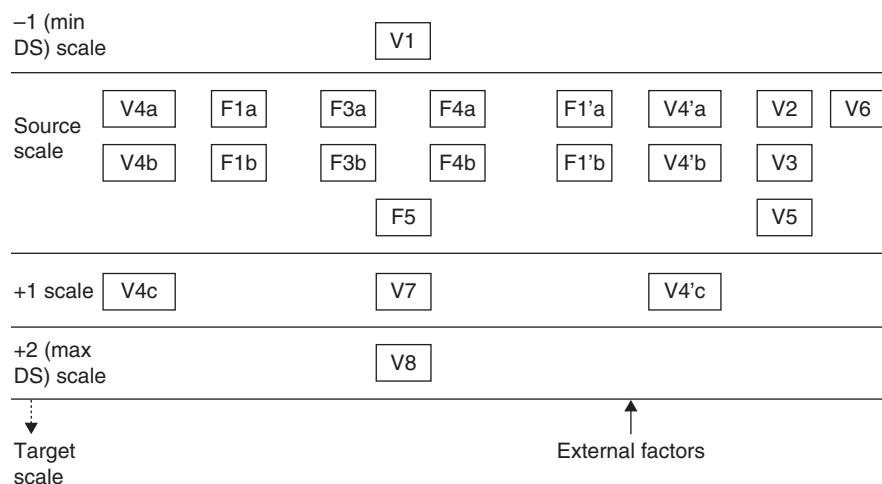


may be different than the separately considered effects. More information on the references supporting this statement and about the effects of these factors is provided in Sect. 12.4.2 under the heading of disturbance mechanisms, because the external control factors are investigated in fungal research only in the context of their effects.

### The Homomorphic Model for Up-Scaling

The homomorphic model of the community of fungi DSs is presented in Fig. 12.4. Some of these FDMs could be split into several ones separated in time with seasonal periodicity (see Sect. 12.4.1.1.2).

The extraradical FDMs, located between trees, and the sporocarps' FDMs do not include only the EM fungi but also other fungi if present in the same ST location, The root FDMs, as well, may not only be limited to the EM fungi present in the rhizosphere but could also include other fungi (eventually mycorrhizal) along the mutualism–parasitism continuum (Schulz and Boyle 2005), if present in the same



**Fig. 12.4** Maximal homomorphic model of a community of EM fungi DSs (relationships not represented for reason of visibility; a connectivity matrix can be easily constructed using the information presented in the text). The scale refers to scale in space, not in time. The physical part is not represented. The part of the model within the source scale (within a stratum) is the homomorphic model for up-scaling under the constraints from FDMs of different scales and external factors. *Legend:* the ET is noted with F (from fungi), the EVs with V (from value); F1a,b = fungi parts (root tips in the case of EMF) in two vertical layers at the roots of tree 1, F1'a,b = fungi parts in two vertical layers at the roots of tree 1', F3a,b = hyphae in the extraradical mycelium in two vertical layers, F4a,b = rhizomorphs in the extraradical mycelium in two vertical layers, F5 = sporocarps, V1 = bacteria, V2 = mineral P and N, V3 = organic P and N, V4 = trees (a,b = roots by layer, c = aboveground parts), V5 = mycoheterotrophic plants, V6 = soil microinvertebrates, V7 = fungivorous invertebrates, V8 = fungivorous mammals

ST location. To the extent that interspecific interactions within the fungi species of a FDM are important, they should be taken into consideration when assessing the roles of an individual EMF species, or the EMF community as a whole by each FDM.

We need four (apparent) hierarchical levels for understanding the ecological functioning of EMF communities, and one more level eventually for management purposes, if the target scale (of management) is larger than the maximal DS scale (given by the size of fungivorous mammal populations). One more scale should be added if one looks also for speciation processes (Sect. 12.4.1.2.2). There is a convergence with the opinion of other authors about the number of needed scales but not about exactly what those scales are. Wolfe et al. (2009), for instance, “believe four scales are most relevant for the discussion of spatial pattern and process of mycorrhizal population and communities (1) across landscapes, (2) within plant communities/ecosystems, (3) within an individual host root system, and (4) within an individual mycelium.”

### 12.4.1.2 Functional Issues

#### Stratification

According to the review of the literature, the basic unit for stratification of the target system in the case of EM fungi is a 400–900 m<sup>2</sup> tree plot. However, as we have shown in Sect. 12.4.1.1.2, several classes of tree plots should be differentiated as a function of the position in the center or at the ecotone of the target system and as a function of the structure of the vegetation. Other criteria might include management practices. As the differences between the soil horizons of the EMF community can be modified by liming, in addition to the tree host species (Rineau and Garbaye 2009), it means that one should stratify the target system both as a function of the vegetation structure and of (at least in part) the management measures applied. In general, the principle for stratification should be that one stratum type corresponds only to one type of homomorphic model of the EMF community, as reflected both by the fungi per se and by their symbiotic hosts.

#### Scale-Specific Mechanisms of EMF Productivity

We have touched on these mechanisms in the previous part because researchers rarely look only at structural issues without approaching the functional aspects as well. Here, we attempt to systematize the information from the scales and systems synthesized in Fig. 12.4. Most of the knowledge concerning the productivity mechanisms of EMF is in a verbal, nonmathematical form.

*Organism and population level* Function at the organism level is supported by metabolic processes and ecophysiological processes (in the classic sense). The scarcity of literature concerning the function of an individual fungi in an

ecological context is probably due not only to experimental difficulties but also to a lack of concentrated effort on a model species. Fungi seem to not yet be in the focus of systems biologists. We have not insisted on the exploration of this type of literature. In a singular study, Ritter et al. (1989) analyzed in detail cytological aspects of the stages of ectomycorrhizal vitality. Smith et al. (2010) characterized plant-inducible phosphorus transporters in fungi and mycorrhiza-inducible transporters in plants. Lewis et al. (1994) studied the effect of CO<sub>2</sub> on an individual plant–fungi system; the pattern of results with the same control factor was found to show interspecific variation between EMF species. A new approach for the study of in vitro transport of amino acids in hyphae is proposed by Watkinson et al. (2005). Bonneville et al. (2009) report a first direct observation of the effect of a soil fungus on the surface of a mineral. A recent review (Rosling 2009) summarizes the current knowledge on fungal weathering as affected by experimental setup and conditions (pure or symbiotic growth, nitrogen source, the means of detecting weathering activity and the species examined).

The extra productivity (compared to the individual level) emerging at the population level is in principle related to the intraspecific mechanisms. We have not found literature about such interactions, and this is probably due to the methodological difficulties in delineating such individuals.

*Tree and plot level* We refer here to the fungal FDMs at tree and intertree levels, within each stratum. Each such FDM should correspond, in our opinion, to a community in the classical sense (it is the system within which alpha diversity should be measured). The extra productivity at this level is due to interspecific interactions; however, the literature does not always make clear what kind of diversity is discussed with respect to its effects.

A review of the EMF community ecology was done by Dahlberg (2001). Data aggregation at different scales may lead to different control variables for the community composition; soil parameters at subplot level, but plant community at plot level (Fitzsimons et al. 2008). We interpret this as being within FDM diversity at subplot level and between FDM diversity at plot level. Some EM species were found significantly more frequently as mycelia than as root tips, while others were less dominant as mycelia than as root tips (Kjoller 2006). We can interpret this as being a consequence of the exploration type in the FDMs structure. Kranabetter et al. (2009) found significant changes in an EMF community along a 25 km productivity gradient (to nitrogen rich sites). EMF species abundance in relation to site productivity included parabolic, negative, linear, and exponential curves. A functional diversity of EMFs was observed, with the specialization of EMF communities contributing to the successful soil exploitation by a single tree host species. The phenotypic plasticity of the tree species was much enhanced as a result of the interaction with the EMF. The diversity described by Kranabetter et al. (2009) seems to be of at least gamma type (aggregates of communities).

The detailed heterogeneity of abiotic parameters at the FDM level might influence the functioning of the community. A detailed review of the space-time heterogeneity of key abiotic parameters at rhizosphere level was done by Hinsinger et al. (2009). They point out that the integration of such models into root growth and

root architecture models for up-scaling of rhizosphere processes is still a matter of future research, but no knowledge of fungal distribution at this fine scale (to be related to the abiotic parameters) is referred to.

The interaction of EMF with lower scale EVs increases their productivity. The coinoculation of EMF with bacteria increased mineral weathering, plant uptake of soluble forms of K and Mg, and tree biomass, as compared to simple EMF inoculation, while the bacteria alone had no effect (Koele et al. 2009). The relationship between two plants at the same time may increase the productivity too. Intertree EM linkages can reduce plant competition for resources, promote forest recovery, and influence the pattern of plant succession (Amaranthus and Perry 1994). Seedlings were hydraulically linked by the mycorrhizal network to large trees in a study by Warren et al. (2008).

Some generalizations accepted for AMF could also hold for EMF. The species composition and richness of AMF was found to be an important contributor to plant species composition and productivity, with an effect mainly on subdominant plant species, and with different plant species benefiting from different AMF taxa (van der Heijden et al. 1998). The external driving factors affect both AMF and EMF. For instance, Godbold et al. (1997) found changes in the relative proportion of EMF to AMF as a result of elevated CO<sub>2</sub> concentrations. Consequently, the roles of EMF and AMF in the functioning of the vegetation communities, especially in the up-scaling context, should probably be approached in an integrated manner. It is clear that the FDMs should be seen as based on fungi species, not just separately on EM, AM, or saprophytic fungi, especially in the case of the FDMs associated with the external mycelium.

*Ecosystem level* We refer here to systems of FDMs from the plot scale up to the “ecosystem” scale, to the control of EMF productivity by feedback from the host plants, and to indirect effects by changing the soil structure. The scale approached here is that between the stratum and the target scale envisaged in the up-scaling procedure. The intermediate scales to be tackled will depend on the organisms retained as relevant from the point of view of direct and indirect interactions with the EMF.

In an excellent review of mycorrhizal–plant–insect interactions, Gehring and Bennett (2009) summarize the proven effects of mycorrhizal plants as follows: negative on root herbivores, positive on pollinators, negative, neutral, or positive on herbivores, and positive or negative on herbivore enemies. Each such group is characterized by specific scales, and the decision whether or not to include these interactions in the overall homomorphic model for up-scaling should be done as a function of the feedback effects of these groups (as influenced by EMFs) on the primary productivity of the ecosystem and on the dynamic of carbon in the forest floor.

Other complex effects come from the action of external driving factors on several types of organisms of different scales. In many systems exposed to elevated CO<sub>2</sub>, mycorrhizal fungi sequester increased amounts of carbon in living, dead, and residual hyphal biomass in the soil (Treseder and Allen 2000). When this is coupled with nitrogen deposition, an increased turnover rate of hyphal biomass can occur. The two processes are associated with a shift in the EMF community’s composition as a result of physiological interspecific differences.

The facilitative effects of mycorrhizal fungal networks depend on the seedling species identity, mycorrhizal identity, plant species combination, and study system, but seedlings associated with EMF benefited in the majority of reported cases (van der Heijden and Horton 2009). Southworth et al. (2005) applied the network theory to mycorrhizal networks from a phytocentric and fungicentric perspective and concluded that all individual plants are more or less equal in linking fungi, but from a mycocentric perspective the network is scale free (Barabasi and Albert 1999; Barabasi and Bonabeau 2003), meaning that certain species of fungi act as hubs with frequent connections to the other elements of the network.

Productivity may be increased also by changing over time the structure of the soil. While AMF produce large quantities of glycoproteins in soil ( $1.45 \times 10^6$  g/ha, 3.2% of the total soil carbon in the 0–10 cm soil layer, Lovelock et al. 2004), EMF are characterized mainly by the production of extracellular enzymes responsible for the mobilization of organic carbon and associated nutrients (Maijala et al. 1991; Courty et al. 2005). Both mycorrhizal fungi types also produce effectors responsible for colonization (Martin and Nehls 2009). The influence of AMF's ERH on soil structure might be of even greater importance to the carbon stock than the influence of hyphal standing crops (Miller and Kling 2000), and this statement can hold as well for EMF. This is because, in both cases, there are feedback responses between the soil and canopy mediated by fungi and supported by mechanisms linked to nutrient acquisition and the allocation of the tree's assimilated carbon by mycorrhiza or indirectly by litter fall.

EMF may facilitate the dispersal of plants and thus increase the productivity of the target system. In an interesting article, Thiet and Boerner (2007) studied the EMF's role at the ecotones of a forest. The invasion of a pine species on an unforested area was dependent on the previous dispersals of EMF either as spores by animals or wind, or as hyphae from the ecotonal trees. The latter mechanism proved in this case to be the most important for pine seedlings, underlying the need for a stratified analysis of EMF's role in the central and peripheral parts of the forest.

At the ecosystem scale is supported also the stability of the fungal community, by dispersal between plot scale areas. With regard to the stability issue (and assuming that diversity is directly related to functional stability), in a study of tree islands ranging from  $<10$  to  $>10,000$  m<sup>2</sup> (Peay et al. 2007), the species area slope was similar to slopes for macroorganisms, suggesting that microbes are not ubiquitous even in suitable habitats (if small); the trade-off between dispersal and competition played an important role in structuring EMF assemblages.

*Speciation of EMF* We refer here to systems larger than ecosystems, at the scale of which speciation of EMF occur. This scale has not been discussed or included in Fig. 12.4 because the up-scaling is usually only needed for management over a short time, without taking into account speciation. Underlining of the importance of evolutionary processes is needed, both for diversity conservation and for the interpretation of the apparent redundancy of species within the FDMs. The large number of rare EMF species (as indicated by non saturated rarefaction curves) indicates a functional redundancy in the relatively short term, but this apparent

redundancy in fact supports the stability of the ecological system in the average term and the potential for EMF's evolution in the long term.

High treeless ridgelines are effective barriers to EMF gene flow even at distances less than 65 km, whereas populations (according to Amend et al. 2010, but probably metapopulations) located within watersheds are structured at greater distances (125 km). So the scale at which speciation takes place is much larger than the ecosystem scale and is the maximal one indicated by Wolfe et al. (2009) to be included in the study of EMF. It is documented that the structure of the landscape influences the evolutionary outcome. For instance, Read and Perez-Moreno (2003) point out that selection has favored EMF systems with well-developed saprophytic capabilities in those ecosystems characterized by retention of nitrogen and phosphorus as organic complexes in the soil.

To sum up the information presented in Sect. 12.4.1.2.2, different productivity mechanisms involving EMF are distributed across many scales. The information is scarce at individual level, apparently absent at population level, richer at community and ecosystem levels, and scarce again at large landscape levels. The production takes place at all levels, but with maximal intensity and stability in time at the large landscape scale.

## 12.5 Disturbance and Succession of Ectomycorrhizal Systems

The change in the relative importance of fungi and bacteria in forest soils with succession seems to remain uninvestigated, but in many secondary succession grassland chronosequence studies, the soil microbial community tends to shift towards a less bacterial and more fungal-dominated food web (Maharning et al. 2009). Hypothetically, this may occur in forests too. A discussion of fungal succession is much more complicated, however, because it envisages processes at very different scales. Iordache et al. (2009b) presented and critiqued the early and late stage species approach for the succession of EMFs and then introduced an ecosystem approach to fungal succession in an improved framework based on Pahl-Vostl's TDM concept. We refer the reader to Iordache et al. (2009b) for aspects relating to succession. In this present text, we develop the analytical framework sketched there and apply it to the more general up-scaling problem of EMF functioning. Another subject discussed in the paper is EMF disturbance due to heavy metals, for which a data processing and interpretation framework was proposed. This picture is complemented here by a short review of disturbance factors relevant to EMF.

Cudlin et al. (2007) review the effects of acidic deposition, nitrogen deposition, increased ozone levels, elevated CO<sub>2</sub>, and drought on fine roots and EMF. EMF colonization was not a suitable parameter for assessing the effects of these driving factors, but fine root length and biomass could be useful. This does not mean that the FDMs of EMF have not been affected because they are not delineated in space at the fine root level but at the plant root/rhizosphere level. The disturbance factors

usually act at a large scale, but the mycorrhizal response is at an FDM scale and depends on the species composition of the EM community and the relationships of ectomycorrhizal FDMs with other types of FDMs (the structure of the FDM network at stratum scale).

Acid rain reduced the number, length, and biomass of lateral tree roots and the percent and number of EMF (Esher et al. 1992). Some EMF confer drought tolerance to their host (via influencing the plant's osmoregulation), while others confer drought avoidance (by hyphal transport via EMHs, Mudge et al. 1987). The experimental warming of root-associated fungal communities in an arctic region increased the density of different genotypes but did not affect the biodiversity within the time frame of the experiment (Fujimura et al. 2008). Burning either decreases or increases the colonization of EMF. The increase is attributed to the reduction of substances that inhibit germination (Cairney and Bastias 2007), and the decrease occurs mostly in the organic layer, not in the mineral soil. Peay et al. (2009) provide a comparison of disturbance factors by scale. With regard to fire, they conclude that spore heat resistance plays an important role in the disturbance-mediated assemblage shift of EMF. Fire disturbance favors competitively inferior species, keeping diversity of EMF at landscape scale. Nilsson and Wallander (2003) report a negative influence of nitrogen fertilization on the external mycelium of EMF, not directly by the soil nitrogen concentrations but rather by the nitrogen status of the trees.

The effect of enhanced CO<sub>2</sub> concentrations mediated by EM communities takes place through the modification of carbon inputs from plant to soil, with consequences on the biomass, infectivity, and species composition of the symbionts (Diaz 1996). Godbold and Berntson (1997) reported changes in EMF community structure as a result of elevated CO<sub>2</sub>. A review by Staddon et al. (2002) about temperature and CO<sub>2</sub> effects on EM fungi concluded that they should involve the study at the individual-plant level, multiple species level, and community level. An interesting finding about the effect of CO<sub>2</sub> is that of Pritchard et al. (2008): "CO<sub>2</sub> enrichment increased mycorrhizal root tip production in deep soil, but did not influence it in shallow soil;" also "the rhizomorph turnover was accelerated in shallow soil, but effects on survivorship in deep soil varied according to diameter." These FDM-specific effects open the way to a line of research on how external control parameters especially influence some of the FDMs from the structure of the homomorphic model. For now, the experiments for assessing the effect of CO<sub>2</sub> have been performed mostly at small plot level (10<sup>-2</sup> m<sup>2</sup>) with fewer at "field" level (10<sup>2</sup> m<sup>2</sup>) and especially with monoculture (Staddon et al. 2002).

Miller and Lodge (1997) review the fungal response to disturbances in agriculture and forestry. By disturbance they mean the physical and chemical phenomena that disrupt communities and ecosystems. Fungi are concluded to be control points in management practices (tillage and crop rotation, nutrient additions, air pollution, site preparation, woody debris, opening the canopy, and moisture fluctuations). Jones et al. (2003) review in detail the dynamics of ectomycorrhizal communities after clear-cut logging, identifying the amount and type of inoculum, and the changes in the soil abiotic and biotic environment as the major groups of factors controlling the succession without discussion of diversity indexes as aggregated

indicators of ecosystem state. Studies of another forest management practice, gap opening, show a significant reduction in EMF diversity indices and a change in EMF and fine root dynamics compared to closed stands (Grebenc et al. 2009) but with some fungi preferring the new conditions.

Colpaert (2008) reviews the effects of metal on fungi and their adaptation. He concludes that there is true tolerance of EMF to metals. Investigations of EMF species at the community level have revealed wide inter- and intraspecific variations in sensitivity to metals (Hartley et al. 1997). The EMF community in a soil contaminated with metals was rich (not with just a few specialist fungi as expected) but did not vary with the soil horizon, season, or plot location in the forest (Krpata et al. 2008). This suggests an interesting hypothesis that the FDM structure of EMF communities is simplified as a result of toxic pressure compared to uncontaminated areas. Different metals controlled in a specific way the EMF community, the results of a multimetal stress being complex at forest levels and reflecting the distribution of metals at tree scale (Gherghel 2009). Alleviation of metal toxicity in plants through EMF has been demonstrated (review by Jentschke and Godbold 2000), but the mechanism remains unclear. Possibilities include immobilization in fungi, exudation of metal chelating substances in the soil, or nutritional and hormonal effects in plants mediated by fungi. EMF and associated bacteria protect pine seedlings against bioavailable forms of Cd, but there are differences in the level of protection provided by different fungi species (Kozdrój et al. 2007). Bioaccumulation factors for Zn and Cd in fruiting bodies of EMF decreased with increasing soil concentration, showing that in such a case fungi did not act by accumulation as an effective barrier against metal uptake by the symbiotic tree (Krpata et al. 2009).

### ***12.5.1 Role of EMF in the Functioning of the Natural Capital***

Through some of its EV, the fungal DS reaches the smaller scale directly relevant for the management of the natural capital (hectares to square kms, here by convention the ecosystem scale). Griffiths et al. (1996) propose an even larger system for analyzing the role of EM SPUs, namely the watershed. This is similar to the scale of EMF speciation. Fungi and their ecosystem services might be in jeopardy if habitat (tree patch) size is a strong determinant of fungal richness, as it seems to be (Peay et al. 2007, 2008).

As an example of the explicit connection between basic and applied ecology in our target domain, Dighton (2003) analyzes the role of fungi in the production of ecosystem services, including mycorrhizal fungi and their relationships with arthropods, as well as the consequences of human action on the relevant mechanisms. Recently, Jackson et al. (2008) also reviewed the effects of root processes (including the dependence on mycorrhization for nutrient acquisition) on ecosystem services. The value of EMF to people is related to local consumption and trade of sporocarps, to their use in medicine, biomonitoring and bioremediation, to their esthetic value, and to the services provided by EM SPUs to other biological



compartments supporting the ecosystem function – implicitly the production of other biological resources and services directly relevant to the people (Dell 2002). Hall et al. (2003) reviews the literature about edible ectomycorrhizal mushrooms.

The EMF SPU are perceived as useful mainly through their support of the resources and services associated with forest ecosystems. Management practices that create intense disturbance and loss of organic matter decrease the ability of plants to form EMF linkages, but management practices that retain living trees and shrubs and the input of organic matter facilitate EMF linkages (Amaranthus and Perry 1994). Helpful forestry management practices targeted to EMF can be taken at various scales: small ones (retaining refuge plants, mature trees) and larger ones (retaining old-growth forest, avoiding high intensity broadcast burn, and retaining the edge to area ratio of harvested areas within certain limits) (Wiensczyk et al. 2002).

Heneghan et al. (2008) review the use of soil ecological knowledge for restoration. From their perspective, when the goal is loosely defined (no specific recovery trajectory envisaged), less precise knowledge can be useful (for instance, the concept of “soil quality” is acceptable in this context for management issues), but when a complex outcome is desired, exact knowledge is needed (we would say, down to the SPU’s level). Another point in their analysis (and of others, e.g., Neagoe et al. 2009) is that a restoration project should be seen as a scientific experiment and valued as such by the scientist.

In prescribed burning, unburned patches act as an inoculation source. The return to the preburn state of the EMF community takes place in about 15 years (Cairney and Bastias 2007). The role of fungi in ecosystem restoration after fire (Claridge et al. 2009) is related to the stabilization of the soil in the absence of plants (by some species of fungi), to nutrient acquisition from minerals, and to mycorrhizal function once the plants start to recover (other species of fungi). It can be said that the fungi are strongly involved in the secondary succession and restoration management after such a disturbance is in fact an attempt to control the secondary succession (Neagoe et al. 2009; Iordache et al. 2009b). Change in soil structure is an important process during succession and, as we have noticed in Sect. 12.4.1.1.4, the EM SPU provide important services by influencing the soil structure.

The use of mycorrhizal fungi can also be targeted to restoration goals related to the control of toxic substances, metals, or hydrocarbons (Robertson et al. 2007; Ghergel 2009). Filamentous fungi and their enzymatic system were found to be a “potent tool to decrease the levels of contaminants in soils by degradation and stabilization” (review by Mougín et al. 2009). Measures taken in the frame of restoration projects, such as liming, strongly affect the EMF community (in this case by pH increase, Kjoller and Clemmensen 2009). The decline of the services valued by humans is, of course, related not to mycorrhizal fungi alone. For instance, Gilliam (2006) identifies six types of mechanisms supporting the deterioration of the herbaceous layer by nitrogen deposition (Fig. 4 in Gilliam 2006): interspecific competition, herbivory, mechanisms related to mycorrhizal infection, pathogenic fungal infection, species invasion, and exotic earthworm activity.

We conclude that understanding the effects of EMF-mediated deterioration at a large scale needs integration in the up-scaling model of all other mechanisms

observable at intermediate scales related to SPUs of EMF. The integration of other ecological mechanisms, depending on the service and resources identified, will be needed as well for a full understanding and effective specific goal-directed management of that natural capital.

### **12.5.2 Mathematical Modeling**

On the mathematical modeling side, Johnson et al. (2006) provide an excellent review of seven types of mycorrhizal models (that include mycorrhizal parameters in their structure), varying in their scale of resolution and dynamics and discuss approaches for integrating these models with each other and with general models of terrestrial ecosystems. They use the classical hierarchy (individual, populations, communities, and ecosystems). At individual and population levels, there are biomass allocation (functional equilibrium) models, economic biological market models, and integrative agent-based models. At the community scale, there are community feedback models, and co-evolutionary mosaic models. At the ecosystem scale, there are food web models and pedogenesis models. In the concluding part, Johnson et al. (2006) mention that “mycorrhizal effects on resource availability and biomass allocation patterns have not been included in these models, partly because of insufficient information but also because of scaling differences [...] mycorrhizal effects on soil properties, disease resistance, and trophic cascades are not emphasized to the same extent in current models,” and “encourage future efforts to develop methods for measuring mycorrhizal structure and function at relevant spatial and organizational scales.”

If one looks into each category of models for relevance of the mathematical formalism to EMF, the picture is not encouraging. Functional equilibrium models are exemplified by a conceptual model dedicated to AM fungi, and the primary source cited does not include mathematical relationships between the mycorrhizal biomass and the carbon and nutrient resources. Economic models and food-web models referred also to AM fungi. Agent-based models and pedogenesis models referred both to AM and EMF; community feedback models and co-evolutionary mosaic models referred to mycorrhizal fungi in general.

It seems that the state of mathematical models needed for up-scaling the EMF ecological processes from the stratum scale to the target scale is not yet appropriate, and that developing such models is an important research direction.

## **12.6 Research Directions**

The proposed framework for conceptualizing the DS’s functioning across scales is convergent with recent proposals for coupling traditionally small scale targeted ecophysiology to the functioning of ecosystems under the umbrella of a “macro-physiology” (Gaston et al. 2009).

For the up-scaling of EM fungi functions, we must (adapted from Lilleskov et al. 2004) identify individuals in tips, soil (as hyphae), and sporocarps, discern patch change over time, identify endogenous factors (intraspecific such as clonal expansion or high spore rain and interspecific interactions structured by a FDM approach), identify exogenous factors (patterns of resource availability, disturbance history, and current external driving factors), then on the resulting dynamic architecture add the functional information inside each FDM and between FDMs, and finally aggregate it from the original to the target scale. Doing this is still precluded by many gaps, both at structural and at functional levels. A structured analytical approach to the problem (like the one proposed here) might accelerate the knowledge development in the area.

Coupling observations at the molecular scale (plant–fungus gene expression, TE level, and internal EVs), interfacial scale (TE–external EV level, to quantify ion uptake by plants), experiments at pot scales (individual fungi–plant or FDM level), lysimeter scales (FDM level), and plot scales (system of FDMs level) with long term field ecosystem studies is crucial for obtaining the knowledge needed for integrating (up-scaling) lower level processes into the management (remediation, restoration, control of secondary succession) of the natural capital at ecosystem and landscape scales (Neagoe et al. 2005; Graham and Miller 2005; Meixner et al. 2006; Neagoe et al. 2009). Hinsinger et al. (2009) underline the need for the integration of ST models of abiotic parameters in the rhizosphere into root growth and root architecture models for up-scaling of rhizosphere processes. Graham (2008) states that “experimental design should either integrate multiple mechanisms of the landscape scale and include such measures as mycorrhizal influences on net primary production, evapotranspiration and nutrient cycling, or integrate measures of [...] fungal diversity into assessment of ecosystem function.” We believe that an FDM approach allows for the structured investigation of functional diversity and complementarities between EMF species within FDMs (for example, some fungi may be effective in scavenging organic nitrogen, and others more effective in phosphorus uptake and transport – Buée et al. 2009), and the functional complementarities between different types of FDMs. Pool-flux classical ecosystem type research can be associated with a FDM based homomorphic model, and theoretical research on the characteristics of the fungal networks are also compatible with this framework.

A major limitation to scaling the mycorrhizal symbioses to higher organizational levels is knowledge about the fungal biomass in the characteristic FDMs. The ERH biomass can be assessed by total hyphal length (Graham and Miller 2005), using biochemical markers (chitin, ergosterol, or a specific fatty acid) or by competitive PCR (Godbold 2005). The background biomass of saprophytic fungi should also be determined. Satomura et al. (2006) present direct methods to quantify the fungal content in EM fine roots. One needs long term field studies in order to appropriately assess the biomass production (Staddon et al. 2002).

The available methods for investigating the distribution of functional parameters across scales summarized by Wolfe et al. (2009) include rotated cores (for nutrient uptake and decomposition), molecular approaches for expression of functional

genes, and the use of natural gradients. To these, one can add extracellular enzymes profiles (e.g., microplate assays developed by Courty et al. 2005) and the assay developed by Rineau et al. (2008) for comparing iron chelation, free iron uptake, and oxalate production of freshly sampled EMs. Graham (2008) mentions additional methods for AMF, including in situ root observation windows, mesh dividers, bags and isotopic tracers, and signature fatty acids, the third of which can be applied to EMFs as well (Buée et al. 2009). A tool-box for mycorrhizal research at the ecosystem scale is also provided by Rillig (2004).

Scaling-up from sequence data to a whole plant and its functions requires a genomic-based approach and a systems approach to study the information flow (Graham and Miller 2005). There is also a need to understand the genetic basis of tolerance to metals in ECM symbiosis (Hartley et al. 1997). An important review of the molecular tools in EM ecology is made by Horton and Bruns (2001). An overview of the molecular techniques available for the analysis of fungal communities was done by Peay et al. (2008). The use of genomics for EMF ecological insights is essential (Martin and Nehls 2009). Tools allowing for the production of extensive data sets needed for models in order to couple the characterization of EMF with indicators of their functional rates have also started to be available. Vargas and Allen (2008), for instance, use CO<sub>2</sub> microsensors for characterizing respiration in an EM root system. The use of new sensor technologies is of great promise for the generation of both small scale intensive data sets (with structural and function significance – Allen et al. 2007; Hasselquist et al. 2009) and large scale ones (indicators of ecosystem functions or external control factors – Porter et al. 2005, 2009; Rundel et al. 2009).

Specific research directions/questions are:

- Describing the formal structure of the DS population's models and deriving from them the Price equation, if possible. Formulating a decoupling theory for the apparent ecological hierarchical levels based on the scale specificity of the types of abiotic and biological processes (Iordache et al. 2011).
- Exploring the potential of new theoretical tools (Barabasi and Albert 1999; Barabasi and Bonabeau 2003) for the conceptualization of fungal networks (and of the emergence function relevant for EMF). A theoretical network approach to the EMF – plant systems (and more generally MF-plant systems) at stratum level and interstratum level is proposed by Southworth et al. (2005). A cost benefit approach to the individual members of a mycorrhizal network is suggested van der Heijden and Horton (2009).
- Study of taxa area relationships for EMF taxa based on functional genes (gene area relationships, Zhou et al. 2008).
- Linking proteomics and ecological processes with a focus on soil enzymes as mediators of decomposition, dissolved organic carbon production, and nitrogen and phosphorus mineralization (Allison et al. 2007).
- To what extent the driver/passenger hypotheses formulated for AMF (Hart et al. 2001; fungi drive the plant community or are just a by-product of changes in the plant community) could be relevant also to EMF?

- How the external control factors influence especially some of the FDMs from the structure of the homomorphic model (fire for the top FDMs and CO<sub>2</sub> for the deep FDMs).
- Is the gene flow affected in landscapes fragmented by contamination with metals? Is the FDM structure of EMF communities simplified as a result of toxic substances pressure?
- Is there an optimal form of natural capital's modularization maximizing the value produced by SPUs associated to EMF?

## 12.7 Conclusions

We have developed an analytical framework for up-scaling ecological processes and applied it to EMF. One has to construct four “hierarchical” levels in order to understand the ecological role of EMF in the ecological productivity of ecosystems, and one more if interested in evolutionary processes (gene flow, speciation). The modularization scales for understanding the role of EMF are those specific to bacteria, to fungi (FDM occupying surface of tenths of m<sup>2</sup>, and tree plot of 400–900 m<sup>2</sup>), to epigeous fungivorous invertebrates, and to fungivorous mammals, and, for speciation, to small catchments of several hundreds of km<sup>2</sup>. The analysis showed that the source scale for up-scaling has to be a plot of 400–900 m<sup>2</sup>. This plot has an associated homomorphic model with a maximum number of nine FDM for the structural and functional modeling of EMF communities. Only one modeling step is needed for up-scaling from the source scale (plot) to the ecosystem scale, but the model's construction involves the previous construction of several up-scaling and down-scaling models in order to quantify the effects on smaller and larger scale organisms on fungi.

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