Ecology: Ecosystems and Biodiversity

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Abstract Using ecosystems as examples, this chapter engages with the emergence of understanding life by producing and assembling modules of knowledge, and finally linking them to create a holistic picture of the entire system. Ecosystems as theoretical units of arbitrary size are understood to consist of abiotic and biotic components on the one hand and of the interactions of the components on the other. The latter is extraordinarily complex but generates functionality in the system as a basis of its properties and services. Functionality can be further partitioned into processes, such as flow of energy and matter, resulting from food chains or webs. Functional diversity is considered as a composite variable that includes all significant physiological information as processes and/or traits, weighted by their abundances in a community whose composition has been filtered by environmental conditions. Two types of ecological experiments can be used to unravel the significance of the interactions of species in a functional community: The analytical approach by intentional disturbance, i.e., a change of an external condition, or the synthetic approach by using artificial species compositions in an otherwise natural environment. Both approaches allow the characterization of functional modules in an ecosystem. Due to the complexity of even simple appearing modules like biomass production, models are required for a comprehensive insight. The more so linking modules to achieve a higher level of integration is unthinkable without comprehensive synthesis models. Examples are presented for each step in the emerging knowledge about, and understanding of ecosystems.

Introduction—Another Focus

This chapter is not dedicated to the emergence of ecosystems and their progressive development by the arrival of new species, like the stepwise assembly of the vegetation on uncovered glacier moraines after the ablation of the ice (Chapin III et al.

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1994) or by the planting of a selected pioneer flora on restoration areas in former lignite mining areas (Baasch et al. 2012). It rather engages with a second aspect of the complex "understanding life", the emergence of understanding by creating, assembling and linking of modules of knowledge, a process, often termed synthesis. Ecosystems are prime examples in that respect due to their composition of abiotic features and biotic components on the one hand and the mutual interactions of these components on the other, which effect the ecosystem's functionality contributing to the system's continuance and stability. Putting both into a whole, an ecosystem is (much) more than the sum of its (abiotic and biotic) components. In most, and in particular the terrestric ecosystems, the biotic components are exceedingly numerous and a complete list is virtually beyond imagination, especially with regard to microbial life. Nevertheless, investigating an ecosystem has to start with the identification of the components, mostly the species, or if the individuals are not tangible, e.g., soil organisms, at least their DNA-sequential data, termed operational taxonomic units (OTUs). Usually, there is some additional knowledge on the species together with the name, e.g., about habitat and growth conditions, pollinators, seed dispersers and so on which is very useful information for the next emerging level of an ecosystem study.

The Next Level. Functionality in an Ecosystem, Flow of Matter and Energy

Focusing on the ecosystem, the players can be labeled by ecosystem functions which result from their metabolic and developmental activities. All organisms which by photo- or chemosynthesis produce biomass from CO_2, water and inorganic nutrients belong to the category of the producers which by their own growth and reproduction serve as foodstuff for the large group of consumers, starting with the herbivores as the basic group of a pyramid containing several so-called trophic levels (primary, secondary, tertiary consumers…). The (pseudo)steady state of the ecosystem is ultimately maintained by the heterogeneous group of the destruents or decomposers, animals, fungi, microorganisms which chop, degrade and mineralize the dead organic matter in the ecosystem, forming a parallel, top-down pyramid, the decomposers' food chain (Schuldt et al. 2017). Components of both food chains interact, effecting community and ecosystem-level processes and properties (Wardle et al. 2004). Pathogens and parasites may be considered as consumers at various levels of the consumer pyramid. Associating a species—as individual or population—with one of these functional classes is relatively easy. Identifying their position in the consumers' or destruents' pyramids is, however, often difficult, as the so-called linear food chains are in reality food webs, especially in the kingdom of the invertebrates and microbes. Likewise, omnivorous animals may not maintain a fixed position in a food chain or web.

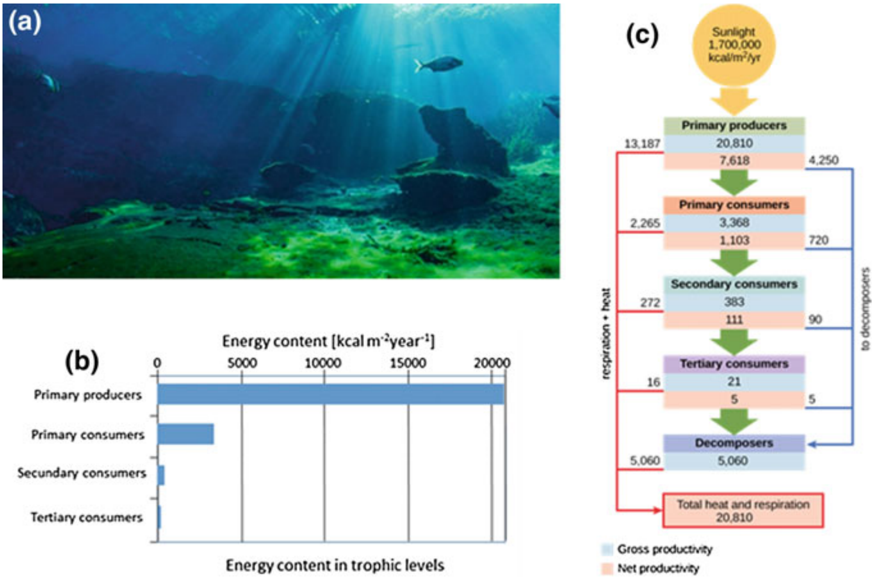

Fig. 1 The Silver Springs aquatic ecosystem: **a** view Silver Springs State Park (http://www.silversprings.com/), **b** energy content of trophic levels in a Silver Springs ecosystem, Florida, is shown. The available energy decreases from level to level, supporting fewer organisms at the subsequent level. **c** A conceptual model of the flow of energy through a spring ecosystem in Silver Springs, Florida. Notice that the energy decreases with each increase in trophic level. *Source* (**b**) and (**c**) Biology Libre texts Library, Chapter 46 Ecology of Ecosystems, Creative Commons Attribution-Noncommercial-Share Alike 3.0 United States License

The connections between the individual species (mostly as populations) might be apprehended by the flow of matter or energy associated with matter: Eating and being eaten. The classical example is that presented by H. T. Odum for the Silver Springs in Florida in 1957, an aquatic ecosystem of a manageable size, with more or less clearly defined functional groups. The energy content of each level as calculated from the amount of biomass shows that almost 90% are lost upon transition from one level to net higher level in the food chain through biological processes such as respiration, food search and mating activities. As a consequence, the pyramid of trophic levels ends when the amount of energy remaining in the food chain is insufficient for another higher level. In contrast to the energy which is finally lost as heat, nutrients are recycled by the action of the destruents.

The relatively simple Silver Spring system, structured by energy flow and trophic levels provides the design for a quantitative analysis of the interaction of processes constituting an ecosystem; in this case, feeding connections are considered (Fig. 1). However, these webs also include indirect and non-trophic relationships (Scherber et al. 2010; Kéfi et al. 2012) that necessarily remain undetected by analyses of feeding interactions, but play important roles in structuring ecosystems (Rzanny et al. 2013).

Dimensions of Ecosystems

Another important question is about the size and delimitation of the investigated ecosystem, which per se is not fixed, but depends on the purpose of research. If the structure of the food chains and the energy flow between the trophic levels are of interest, an ecosystem may be as small as a flower head of a thistle with seed predators and their parasites and parasitoids (Zwölfer 1987). On the other side, a forest, a region and even earth can be treated as ecosystem, depending on the scientific problem to be addressed. For laboratory investigations, micro- and mesocosm-systems are frequently used. Both are artificial ecosystems maintained under controlled external conditions like temperature, illumination and moisture. Microcosms are simplified miniature ecosystems, e.g., litterbags buried in the soil, which are used to simulate the performance of natural ecosystems, e.g., litter decomposition, under selected close-to nature or artificial conditions. Mesocosms are pieces of a natural ecosystem, e.g., a water column in the sea, separated for experimental purposes from the surrounding water (Fig. 2). Such mesocosms are used, e.g., for investigating the effects of the acidification of the ocean water by the increase of the atmospheric and dissolved CO_2 (Zark et al. 2017).

Fig. 2 **a** A series of **K**iel **O**ff-**S**hore **M**esocosms for **O**cean **S**imulations (KOSMOS) in the Northern Baltic Sea. The mesocosms were successfully employed in long-term experiments in different climate zones, from the high Arctic to the subtropics. Experimental perturbations include the addition of inorganic nutrients or organic compounds, CO_2 enrichment, manipulation of mixed layer depth, simulation of deep-water upwelling, species exclusion and addition of invasive species. **b** A mesocosm, consisting of a floatation frame and a flexible bag 2 m in diameter and 20 m in length. After deployment, the bag unfolds by weights pulling down its lower end to depth, thereby enclosing an undisturbed water column 55 m^3. The bag is then closed at the bottom by a full-diameter sediment trap (Riebesell et al. (2013). https://www.geomar.de/en/research/fb2/fb2-bi/infrastructure/kosmos-kiel-off-shore-mesocosms-for-oceanographic-studies). With permission by Gerd Hoffmann-Wieck

Functionality and the Use of Traits

In the following approaches in ecosystem research are addressed, which consider especially those aspects that render an ecosystem more than the sum of its components, namely the interactions, part of which has already been described above as flux of energy or matter. However, there are many more interactions, in particular the abiotic-biotic interactions and those biotic interactions which in addition to matter flow have other important functions in an ecosystem, e.g., mutualistical useful or detrimental relations. These are also subsumed under the term functionality in the ecosystem. Functional diversity is considered as a composite variable that includes all significant physiological information as processes and/or traits, weighted by their abundances in the community. The measured traits, e.g., transpiration also allow upscaling from the leaf to the plant and to the plot level. Trait-based approaches can thus be used to describe the relationship between community performance and ecosystem functioning on a higher level. The diversity of functional traits in natural communities depends on assembly processes driven by environmental filtering, such as competitive exclusion or facilitation, as well as on the size of the regional species pool (Keddy 1992; Diaz et al. 1998). Natural or anthropogenic changes of the environment can alter the strength and mesh size of the filters and thus the conditions of the assembly process. Rising temperatures for instance could cause an altitudinal upwards shift of the vegetation belts concomitant with a change in the competitive strength of the placeholder and the newcomer species. Mountain summits exhibiting characters of an island are considered as highly sensitive to climate change. Plant communities of the alpine and nival zones are adapted to lower temperatures and with respect to global warming their migration ability to colonize higher regions is geomorphologically limited. A worldwide monitoring web **Global Observation Research Initiative in Alpine Environments (GLORIA)** for the comparative study of climate change impacts on mountain biodiversity, encompassing 115 active target regions worldwide is being established since the year 2000 (http://www.gloria.ac.at:80/?a=9; Pauli et al. 2012). For the European mountains, a decline of cold-adapted and an increase of warm-adapted plant species in the summit regions have been documented between 2001 and 2008 showing an upwards shift of the thermoclines ("thermophilization") as the major environmental filters (Gottfried et al. 2012).

Due to the genetic and trait variability in the populations, many interactions can only be represented by models which must allow for the variability of the responses to the triggering abiotic or biotic factors. Many models are "only" partial models for a selected type of interaction or response, e.g., the response of the plant's photosynthetic carbon acquisition to environmental factors or of a plant—animal interaction resulting in pollination or seed dispersal. Proper modeling requires knowledge about the underlying principle or mechanism of the selected interaction, as well as of its quantitative range. To that end, analytical studies are necessary either in a mechanistical or a statistical approach like the response and effect framework (Lavorel and Garnier 2002) or via ecological experiments. Finally, partial models are the modules which must be put together in the synthesis step to arrive at a higher level of ecosystem understanding.

Ecological Experiments: Analytical Approach

Ecological experiments are intentionally planned disturbances of the original ecosystem, thus differing from the mesocosms (Fig. 2), which are by some provision separated from the natural ecosystem. In the emergence of ecosystem understanding, ecological experiments are used to elucidate mechanisms operating in an ecosystem and to produce the basis for models and predictions. A vast multitude of scientific problems can be tackled by such field experiments, finances commonly limiting their spatial and temporal dimensions. The most well-known ecological experiments are the FACE-experiments (**Free Air Carbon dioxide Enrichment** experiments) where the CO_2 concentration in the free air is artificially enhanced (Fig. 3) (Ainsworth and Long 2005).

This is not the place to discuss the results of the various FACE-experiments in forests, grass- and cropland; however, one message is clear: If CO_2 is no longer limiting productivity, another environmental factor becomes limiting, in many cases nitrogen or phosphate. However, on the forest ecosystem level the so-called progressive nitrogen limitation hypothesis modified the simple explanation by Liebig's law of the decreasing effect of CO_2-enriched air on tree growth. It assumes that plant growth in elevated CO_2 sequesters nitrogen in wood or soil organic matter, resulting in reduced N availability and the observed negative feedback on growth (Norby and Zak 2011). For ecosystem research, other results than productivity may be interesting as well, e.g. the reduction of transpiration (Ainsworth and Rogers 2007) or the stimulating effect on ectotrophic but not on endotrophic mycorrhiza (Garcia et al. 2008).

Other frequently installed ecological experiments are the rain-out shelter experiments simulating drought accompanying global warming by climate change (Beier et al. 2012), which are, however neither easy to perform in a natural habitat (e.g., a forest) nor are the results easy to explain (Vogel et al. 2013), as the microclimate conditions under the shelter differ in more than the moisture aspect from the open situation. Provided a sufficiently long experimental time-span of several years, interesting effects, not only on ecosystem processes like litter degradation have been found, but also, e.g., on the different genetic adaptability of plant species (populations via selection, Ravenscroft et al. 2015) or soil animals (Bataillon et al. 2016). Such response effects of ecosystem components to a climate change in turn may have an effect on their interactions with other components, e.g., herbivores.

Fig. 3 Aerial view of the Aspen FACE experiment (after 2010 Northern Forest Ecosystem Experiment) showing the control facilities (middle left row), and the 12 atmospheric treatment rings (air, CO_2, ozone) for four treatments with three replicates each. Each 30 m-ring consists of vertical vent-pipes which disperse carbon dioxide, ozone or normal air alone or in combination into the center of the ring. *Photo* www.aspenface.mtu.edu, by courtesy of Janet Pikkarainen

Other diligently planned treatments of natural ecosystems, in particular tropical forests, investigate the effects of global change, e.g., the rise of the temperature in the "TRACE"-experiment in Costa Rica with infrared radiators and soil heaters. It should have started in 2016, but due to drought was postponed. Another interesting ecological experiment, the so-called NUMEX experiment (**Nutrient Manipulation Experiment**) in the tropical mountain rainforest of the South Ecuadorian Andes, simulates the atmospheric input of plant nutrients from fires in the Amazon or dust from the Sahara by the almost permanent easterly winds. Moderate fertilization of the mountain forest with nitrogen, phosphate and calcium resulted in a differentiated response of trees, some of which showed growth inhibition, others growth stimulation (Homeier et al. 2012, 2013; Werner et al. 2013). N and P additions resulted also in an altered soil microbial biomass and a reduced fine root biomass, but no generalizable effect on the rate of fine root colonization by arbuscular mycorrhizal fungi was detected. Partly contrasting responses of tree species (stem growth and litter production) suggest future changes in species composition of these forests by atmospheric nutrient inputs in the long term.

Such ecological experiments investigate responses to artificially set environmental changes of real ecosystems and their components and thus follow a top-down approach, addressing also the question of ecosystem stability and resistance.

Ecological Experiments: Synthetic Approach

More fundamental questions about the role of biological diversity for the functioning of ecosystems require another approach, namely by synthesis of biodiversity, in other words a bottom-up strategy. Two big and long-term experiments follow this approach, the Jena Experiment in Germany (16 years) and the Cedar Creek experiment in the USA (35 years), both using grassland ecosystems. Preset parameters are the numbers (1, 2, 4, 8, 16, 32, 60) of perennial grasses or herbs or other functional non-woody species (e.g., leguminous herbs) cultivated on a unit plot. The Jena Experiment, e.g., comprises more than 80 unit plots (Fig. 4).

No animals or microorganisms are added to the plots as these organisms are expected to enter the developing vegetation in a natural way. On the other hand, the soil is not sterilized before planting or sowing. Care is not taken to avoid extreme events such as drought or flooding; however, weeding is the major and costly task, as the natural seed-rain is permanently challenging the protocol of the experiments. Since not all components of the different quasi-steady state ecosystems arrive already during the first year, the full assembly of the ecosystem components even in a grassland takes several years. Moreover special treatments, e.g., fertilization or mowing can help to unveil basic relationships. Without going into details, a few typical results shall demonstrate the kind of questions addressed by such bottom-up approach:

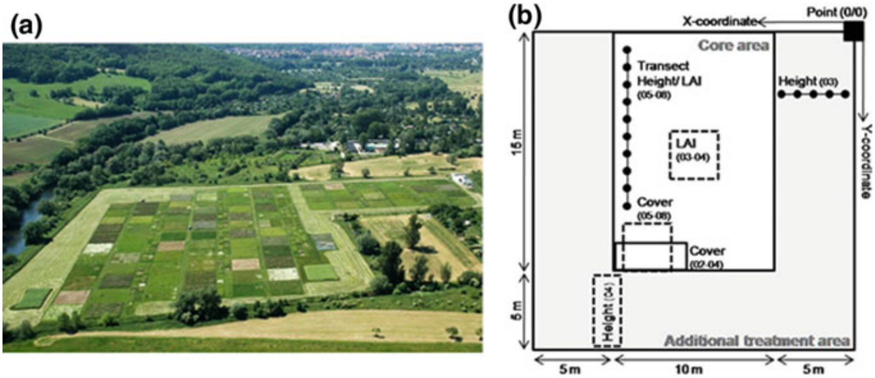

Fig. 4 The Jena experiment **a** Panoramic view over the entire facility in the river plain of the Saale near Jena (background). **b** Structure of one of the 20 × 20 m plots with a core area surrounded on three sides by lateral areas for experiments in the same vegetation as on the core area. LAI, leaf area index. *Source* (**a**) The Jena Experiment, by courtesy of N. Eisenhauer; (**b**) Weisser et al. (2017), by courtesy of the author

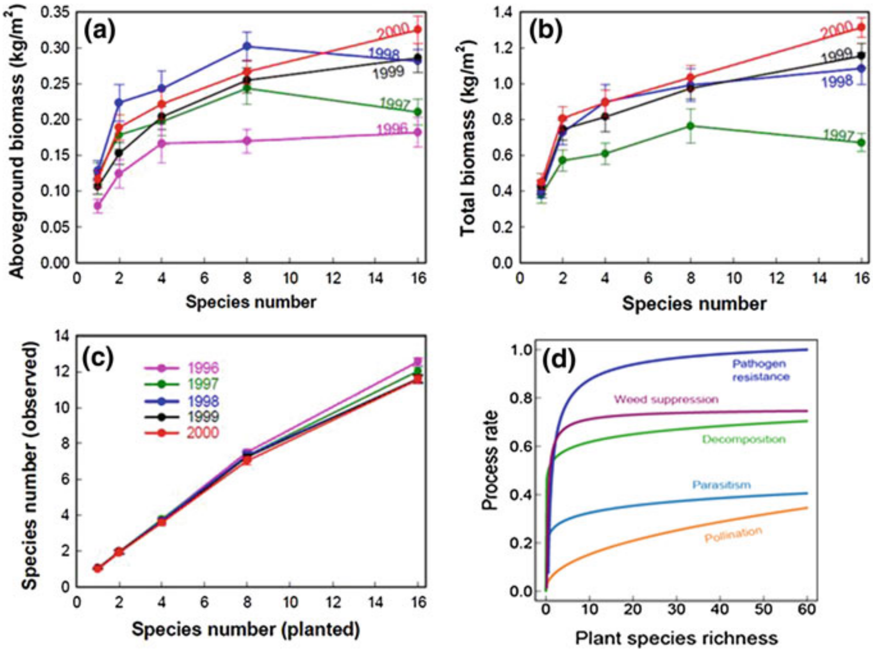

Fig. 5 The Jena experiment. **a**, **b** Effects of the number of plant species on the aboveground and total plant biomass in the sequence of the years. **c** Preservation of the original species composition over the years by annual weeding campaigns. **d** Effects of the plant diversity on various ecosystem processes based on biotic interactions. From Weisser et al. (2017), by courtesy of the author

- Plant diversity shows a persistent positive impact on ecosystem functioning, stability, and productivity (Fig. 5; Roscher et al. 2005; Proulx et al. 2010; Weisser et al. 2017). Increasing plant diversity from one to 16 species per plot had a similar positive effect on biomass production than standard agronomic fertilizing (Weigelt et al. 2009).
- Species diversity and carbon storage rates in the soil are positively correlated (Eisenhauer et al. 2010).
- Multitrophic interactions in highly diverse plant communities concur with more complex above- and below ground animal networks: Diversity creates diversity, the effect of species diversity being stronger than of species abundance (Scherber et al. 2010; Ebeling et al. 2011).
- Due to a high microbial activity, highly diverse plant communities show a closer nitrogen cycling (Oelmann et al. 2011), attenuating the leaching of N from agricultural soils into the groundwater and thus reducing the need of fertilization (Oelmann et al. 2007).
- About 45% of the examined ecosystem processes were found to correlate with the plant diversity value (Allan et al. 2013).

- Plasticity of most plant traits, both above- and below ground, depends on plant diversity in a complex way. Therefore, a caveat turns out for using plain database traits for associating plant traits with particular functions in an ecosystem.

Grassland and crop fields are ecosystems that are relatively open to experimental management and whose responses to interferences usually show up in short to moderate time spans.

A similar systematically structured experiment, however with subtropical woody plant species, termed biodiversity–ecosystem functioning (**BEF**) experiment, was established in 2009/2010 in the mountain area of Jiangxi Province, China. The goal is to assess the "role of tree and shrub diversity for production, erosion control, element cycling, interactions with other trophic levels and strata (herb layer, soil macrofauna, herbivores, decomposers, mycorrhiza, soil microorganisms), and species conservation in Chinese subtropical Forest ecosystems". About 200,000 saplings (50 species each of trees and shrubs, 50 species of each evergreen and deciduous plant life-forms were planted on 100 ha of previously cleared forest area. In a parallel observational approach, 27 comparative study plots were set up in existing forests in an adjacent National Nature Reserve. It is expected that the species and functional richness of shrubs and trees will lead to increased productivity, which may in turn lead to increases in other ecosystem variables.

The Highest Level: Ecological Models

Processes taking place in an ecosystem can be analyzed by suitable measurements and experiments, however, upscaling in space and time requires models which capture the processes under varying external conditions. Nevertheless, a model is in principle a reductionistic approach, as usually not all variables can be included that are effective in nature. Nevertheless, a model can show the real effect of a process, e.g., on biomass production, whereas understanding the mechanisms and reactions driving the process is another dimension or category. To illustrate it by analogy: Understanding the control of stomatal conductance by the interplay of several biophysical and biochemical partial reactions constitutes the process; in contrast, quantifying the rate or the amount of transpired water at any moment or over a longer time period can only be accomplished by a model. To stay with the analogy: Plant ecophysiologists are interested in stomatal conductance, ecologists in transpiration. Because any kind of process taking place in an ecosystem can be modeled, given sufficient analytical data, countless models (conceptual, analytical and simulation models) have been developed and published. In this essay, only numerical simulation models will be considered. The so-called land surface models (LSM) linking soil-vegetation-atmosphere processes and the vegetation (plant communities) are usually considered as an assembly of only a few (global) Plant Functional Types (PFT; Bonan et al. 2002; Sakschewski et al. 2016).

In order to create and parameterize the model, it is not necessary to know any detail of the involved processes. To simplify the models, proxies can be used which have proven to portray particular processes and their interdependences in a realistic way. For instance in a model of photosynthetic carbon acquisition, instead of the maximal carboxylation activity the nitrogen content of RubisCO as share of the leaf's total nitrogen content can be used (Oleson et al. 2013), allowing to transfer the measurement from a tree to the lab. Models, however, have to be forced by the most effective drivers, in many cases by climate or weather, data of which can be collected continuously.

A relatively simple example shall illustrate the architecture and use of a Land Surface Model (LSM): In the tropical Andes, as in many other tropical high mountains, anthropogenic pastures are often invaded and finally ruined by a highly competitive weed, the bracken fern (*Pteridium* spp.). Competition of the widely used tropical pasture grass *Setaria sphacelata* (a C4 plant) with the C3 plant bracken fern was modeled using photosynthetic biomass production as proxy for growth (Silva et al. 2012). The architecture of the model followed the two-big leaf approach (Dai et al. 2004), which is a derivative of the Common or Community Land Models (CLM, Lawrence and Fisher 2013), however, differentiating between the portions of sunlit and shaded leaves on a plot. The model involves five modules, as shown in Fig. 6 and is parameterized by 20 physiological and ecological parameters, e.g., the light- and CO_2-responses of photosynthetic net carbon uptake and stomatal conductance. Recording microclimate and radiation continuously over a year at an elevation of 2100 m a.s.l, growth of both plant species could be realistically modeled for that year 2008, showing better growth of the grass at dry and warm weather whereas the fern grew better under wet and cool conditions. Over the entire year growth of both species was nearly balanced with a slight advantage of the grass (Fig. 7). The advantage of that model is that it provides also data on the belowground biomass. Thus for the year 2008, the total biomass production (dry matter) of *Setaria* was calculated as 58.8 Mg ha^{-1} a^{-1} and for bracken 55.5 Mg ha^{-1} a^{-1} (Beck et al. 2013).

The architecture of the model shows biophysical and biochemical parameters as the heart of the modules, but biological parameters such as the plants' capacity of (macro)nutrient extraction from the soil or the sensitivity for pathogen attack is completely missing. Especially, bracken is highly susceptible to infection by a fungus (*Cryptomycella pteridis* (Kalchbr.) Hohn) which kills the leaves within a few months (Roos et al. 2011). More modules are necessary to adjust the model better to the natural situation (see below).

While the development of a mature "forest" requires more than a few decades, partial modules can be addressed in shorter time, such as the influence of the plant species composition and age of the forest on the soil fungal community composition (Wu et al. 2013). Such modules can later on be integrated in a comprehensive land surface model.

Models need truthing by ground observations for assessing their correctness and accuracy. For models estimating the state of the vegetation, truthing by remote sensing has proven as a useful approach, if the absorbance, transmittance and reflection characteristics of the vegetation are known from flied spectroscopy (Bendix et al. 2010).

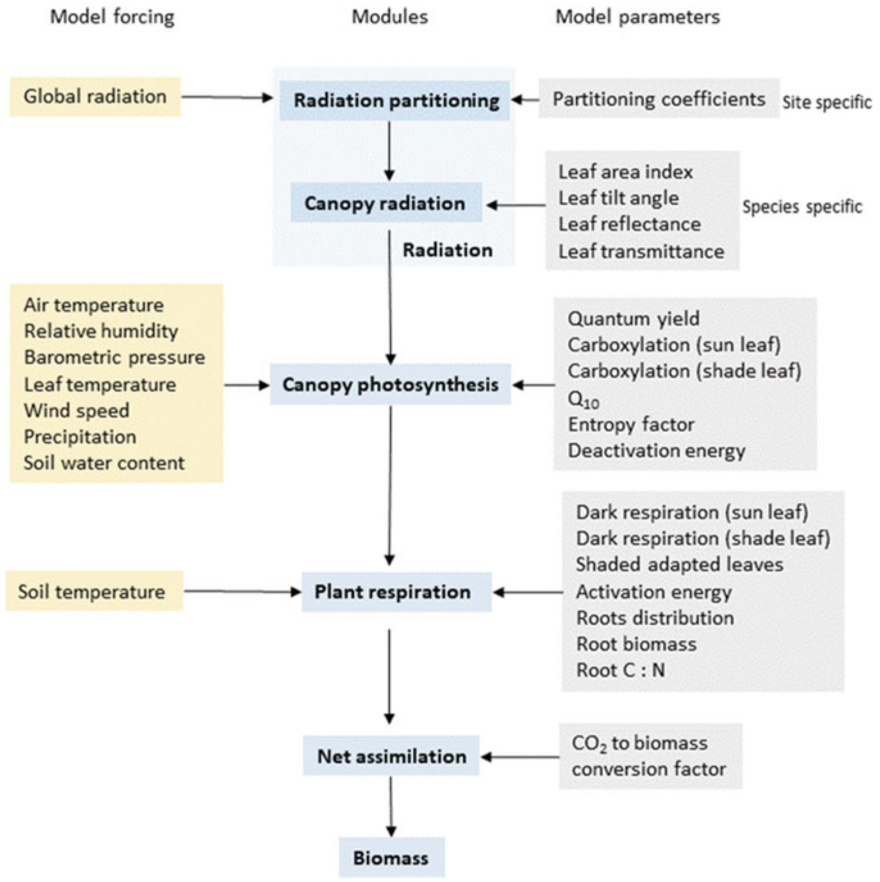

Fig. 6 Architecture of the southern bracken competition model (Silva et al. 2012, modified)

With those data of *Setaria* and bracken the increase of the dominance of bracken with increasing elevation could be demonstrated which agrees with the results of the model when forced with the altitudinal decreasing temperatures (Curatola et al. 2013; Göttlicher et al. 2009). Therefore, at least the most critical parameters have been used in the model.

Community Land Models (CLMs), as the basis for Land Surface Models (LSMs) undergo a continuous evolution by refining the involved modules and adding new modules. The latest CLM version 4.5 by Oleson and Lawrence et al. (2013) simulates in 24 Chapters (420 pages) landscape elements and processes, conveying an impression of the inexhaustibility of the approach. A few examples are shown:

- Surface characterization including land type heterogeneity and ecosystem structure,
- Absorption, reflection, and transmittance of solar radiation,

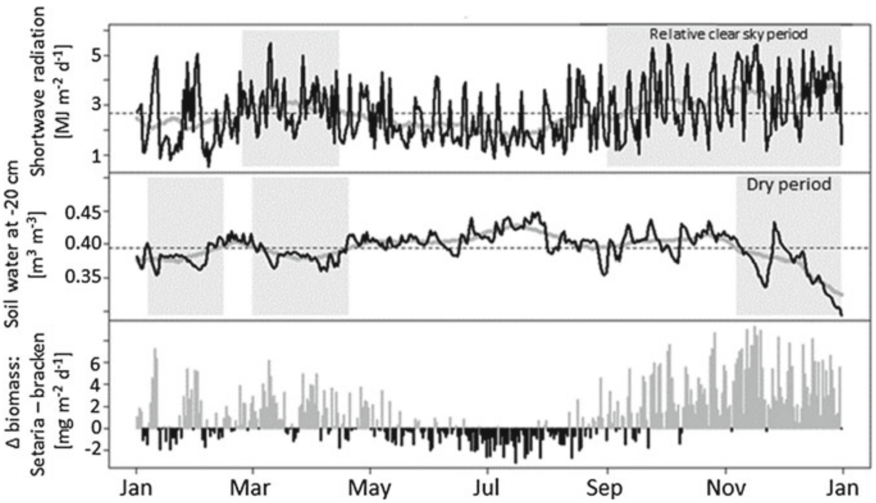

Fig. 7 Daily accumulated solar radiation, soil water content at 20 cm depth and difference between the biomass production (dry matter) of the two competing species *Setaria sphacelata* and bracken fern. The bold gray lines in the upper two panels represent means of 30 days determined with a moving window which were used for weather characterization. The dashed lines show the annual means. The gray bars in the lower panel show when and to which extent *Setaria* produces more biomass than bracken, the black bars indicate better growth of bracken. From Beck et al. (2013), slightly modified

- Momentum, sensible heat (ground and canopy), and latent heat (ground evaporation, canopy evaporation, transpiration) fluxes,
- Canopy hydrology (interception, throughfall and drip),
- Soil hydrology (surface runoff, infiltration, redistribution of water within the column, sub-surface drainage, groundwater),
- Stomatal physiology and photosynthesis,
- Urban energy balance and climate,
- Vegetation carbon and nitrogen allocation and respiration,
- Vegetation phenology,
- Soil and litter carbon decomposition,
- Plant mortality,
- Dynamic global vegetation distribution,
- Carbon isotope fractionation.

The modules and partial models work with fixed parameters, e.g., only 24 types of vegetation units are differentiated; however, many of them share the same parameters or coefficients and the spectrum of the units is rather coarse, e.g., there is only one type of tropical broadleaf evergreen forests and one type of tropical deciduous forests. As a consequence, the global PFTs fail in specific environments so that a regionalization with more specific PFTs is required (Wullschleger et al. 2014). Moreover, the traits used for PFT parameterization frequently show a high variability or

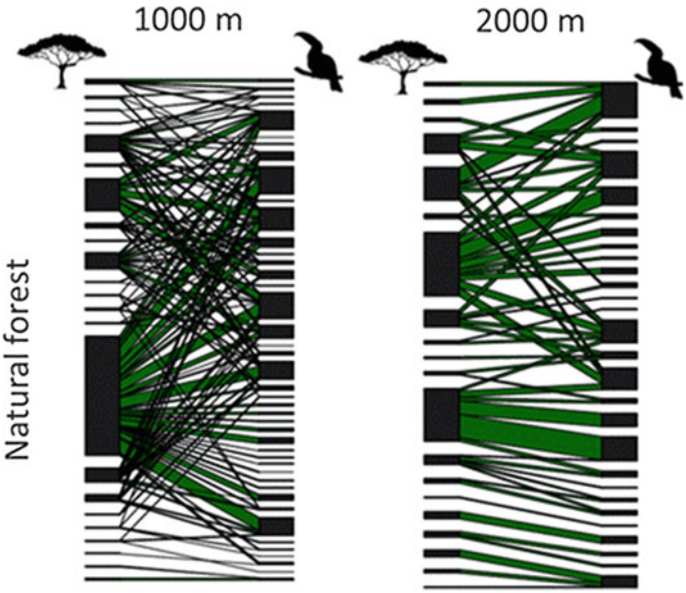

Fig. 8 Plant-frugivore interaction networks at two elevations (1000, 2000 m above sea level) in the natural mountain rain forest of the Podocarpus National Park (South Ecuador). Plant species are shown on the left side, frugivorous bird species on the right side of each plot. Each line between a plant and a bird indicates a visit during which the bird consumes fruits of the plant. The thicker the line, the more feeding events have been recorded of the two mutualistic partners. From Neuschulz (2016. Figure by M. Quitián). By courtesy of Eike L. Neuschulz

dynamics, thus, the inclusion of trait variability in LSMs is indispensable (Kattge et al. 2011; Sakschewski et al. 2016). Finally, biotic interactions, such as seed dispersal and plant regeneration, are usually oversimplified in the models and relevant biotic interactions responsible for the indirect internal feedback loops such as herbivory or pathogen attack are hardly implemented (Bonan 2008). Thus, even these very detailed current Land Surface Models have several flaws and need refinement.

To provide an idea, how manifold and complex even principally easy interactions can be, such as seed dispersal by birds, quantitative observations in an evergreen tropical mountain rain forest are shown in Fig. 8.

Those interactions, bearing per se many biologically interesting aspects, can be used as proxies for forest regeneration by the pattern of the seeds dispersed by the birds.

The challenge is, how to include this function in the modules listed above, e.g., vegetation phenology, vegetation carbon and nitrogen allocation and respiration, and plant mortality. This becomes even more complicated, if the dynamics of ecosystem traits have to be overlaid by biological interaction modules, like the change of the mycorrhizal interactions during the growth of a forest (Haug et al. 2010).

Conclusion

Learning to understand nature in its relation to space is by considering an ecosystem, its components and their interactions. Addressing the “nature of vegetation”, Tansley (1935) for the first time suggested to comprehend nature as a living “Quasi-Organism” which he termed “Ecosystem”. Nevertheless, due to the enormous complexity of ecosystems serious investigations must first concentrate on individual elements or modules which finally must be properly combined by a procedure termed synthesis. Whereas the investigation of individual modules in most cases already requires modeling the integration of the modules into a whole is unthinkable without a comprehensive model.

Emergent understanding of ecosystems by investigating its abiotic and biotic components, their functionality and their interactions as modules has been presented here by a few examples. Considering the case of the Land Surface Models, understanding has arrived at a level where simulations produce near-to-reality results, as revealed by truthing examinations. At that state, cautious predictions about the reactions of the ecosystem to changes in the environment, e.g., by climate change appear possible. However, it should be kept in mind that extrapolation is always risky as services and stability of an ecosystem are different traits. Services might be properly described using only a few modules of a system, while stability may depend on many more components and their interactions; and that is the reason why more complex ecosystems are considered more stable but not necessarily more effective. The question is whether focusing only on the principles, e.g., the dependence of C3- and C4-photosynthesis on the temperature would come up with similar results as the model explained above, in other words whether a similar result could be obtained with a simpler approach. The example of the competition between bracken and the pasture grass *Setaria* shows that under “normal” conditions components of the microclimate and of the soil might be sufficient for realistic modeling results, however, that more modules will be required if unusual events take place.

Proven models can not only be used for forecasts, but can also serve to propose an improvement of human land use (Knoke et al. 2014), in particular also with respect to global change.

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